

Referential aspects in the vocal repertoire of bonobos (*Pan paniscus*)

by

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Abstract

The complexities of animal communication continue to be investigated. However, the potential for referential communication in nonhuman great apes' vocal repertoire has only been studied in chimpanzees' (*Pan troglodytes*) food vocalizations. The current study aimed to examine whether bonobos' (*Pan paniscus*) food vocalizations contained referential aspects. Vocalizations were collected from one bonobo while feeding on one of six different food types. These vocalizations could be significantly distinguished based on food type when using a four-variable model containing low frequency, delta time, average power, and energy. They also could be reclassified into the correct food type based on these variables on a consistent basis, and most food groups were significantly distinguishable from each other. Consequently, this participant's food vocalizations suggest that bonobo food vocalizations contain information based on food type. However, this does not ensure referential vocalizations. Importantly, this study did not examine whether listeners used this information or if these food vocalizations were intentionally elicited. This study raised many important questions regarding the study of referents in nonhuman primates. First, it demonstrated the complexity of examining referents in a nonhuman species. This included aspects related to initial assumptions, such as whether or not one is starting from a standpoint that great ape and human communication is continuous. Equally difficult is setting up or finding a situation in which you can expect a one-to-one correspondence between a stimulus or setting and one specific referent. Finally, even with a sound methodology, the question of what statistical requirements should be required in order to prove a case for nonhuman referential communication remains unclear. All of these considerations have large impacts the interpretation of referential communication and must be scrutinized deeply before any conclusion regarding nonhuman great ape vocal referential capability can be made.

Chapter One: Introduction

1.1 Background & Significance

Although the difference between language and animal communication has been a hotly debated topic, with the exception of a few key studies (Slocombe & Zuberbühler, 2006; Slocombe & Zuberbühler, 2005; Taglialatela et al., 2003; Marler et al., 1986a; Marler et al., 1986b; Seyfarth et al., 1980a; Seyfarth et al., 1980b) most research has not addressed the question of referential communication in animals directly. This has led to an established dichotomy between language and animal communication. Human language generally has been placed on a pedestal while animal communication is thought of as less cognitively-based and more emotion-based (Seyfarth & Cheney, 2003; Ploog, 1981; Jürgens, 1979a; Jürgens, 1979b; Marler, 1977; Smith, 1977).

Anthropologists are by definition interested in the evolution of the human (*Homo sapiens*) lineage (King, 2002). However, when it comes to language, a dichotomy between human language and animal communication, reflecting a lack of evolutionary connection, has predominantly been assumed. Considering the sister relationship between the *Homo* and *Pan* genera (Goodman et al., 2001), there has been relatively little investigation into referential communication in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*).

A referent is defined by the Merriam-Webster Dictionary as “one (any item, object, symbol, vocalization, etc.) that can be thought of, regarded as, or classified within a general category or group.” A referent requires a consistent one-to-one relationship between an item, object, or concept and its corresponding word. They are meant to intentionally convey specific information. The ability to use referential communication is considered one of the dividing features between humans and other animals (Deacon, 1997). Although it has been

studied in other primates, the capacity for vocal referential communication among nonhuman great apes has been explored in relatively few studies (Gibbons, 2007; Slocombe & Zuberbühler, 2006; Slocombe & Zuberbühler, 2005; Hallberg et al., 2003; Taglialatela et al., 2003; Hallberg, 2000). Although there has been research on non-vocal referential capabilities in great apes utilizing symbols, tokens, or sign language (Savage-Rumbaugh et al., 1986; Rumbaugh, 1977; Premack, 1971; Gardner & Gardner 1969), these studies have limited their conclusions to great ape capacities and have not expanded inquiries to include whether great apes naturally utilize referential capabilities in their normal vocal repertoire. Even fewer studies have investigated the capacity for referential communication in the vocal repertoire of great apes (Gibbons, 2007; Slocombe & Zuberbühler, 2006; Slocombe & Zuberbühler, 2005; Hallberg et al., 2003; Taglialatela et al., 2003; Hallberg, 2000).

This study aims to investigate the vocal referential capabilities in bonobos. Kanzi, the study subject, has participated in a wide variety of experiments focusing on referential capabilities in both the vocal and non-vocal realm. Kanzi was the first nonhuman great ape to demonstrate acquisition of a symbol system with no explicit training (Savage-Rumbaugh et al., 1986). While humans attempted to teach his mother, Matata, abstract symbols, Kanzi spontaneously began to demonstrate an understanding of these symbols (Savage-Rumbaugh et al., 1986). He conclusively demonstrated that he was able to use these symbols in a referential manner to communicate (Savage-Rumbaugh, 1990). Furthermore, Kanzi utilizes a conversational manner of communication including turn-taking and grammar (Greenfield & Savage-Rumbaugh, 1991). In addition, he appears to have modulated his vocal levels during communicative interactions with humans (Taglialatela et al., 2003). Taglialatela and colleagues (2003) further revealed that Kanzi produces acoustically distinct sounds in four

discrete semantic contexts (banana, grape, juice, and yes) when communicating with humans. Therefore, the subject of this study has demonstrated the ability to use referential communication in both a non-vocal realm and in a vocal realm when communicating with humans. Further investigation is needed to determine whether Kanzi uses referential communication in other contexts as well.

1.2 Objectives & Hypotheses

The aim of the current study is two-fold. I will expand the number of great ape subjects in which the potential for referential communication in food calling has been explored and, more specifically, explore food calls in a second great ape species, bonobos.

The objectives of this study are:

- 1) to produce a general catalog of an individual bonobo's food peeps,
- 2) to perform a general comparison of bonobo food peeps based on food type, and
- 3) to determine if bonobos have any aspect of referential communication in their food calls.

Because *Pan* is the closest living genus to humans (Goodman et al., 2001), we would expect to find continuity in both biology and behavior between humans and bonobos. Despite the perceived dichotomy between language and animal communication, apes have demonstrated structural continuity for language-related brain structures (*Pan troglodytes* & *Gorilla gorilla*: Sherwood et al., 2003; *Pan troglodytes*: Gannon et al., 1998). Therefore, I hypothesize that bonobos will demonstrate referential capabilities in their natural vocal repertoire due to the close relationship between *Homo* and *Pan* and the extreme reliance on referents in human languages.

1.3 Human Language & Animal Vocal Communication Systems

Language is one of the hallmarks of humans, yet we still know very little about where this ability originated and how it evolved into the variable and complex languages present today (Christiansen & Kirby, 2003). Traditionally seen as one of the characteristics dividing humans from other animals, there are many unique features of human language not seen in other animal groups (Arcadi, 2005). Some define language as “a system for representing and communicating complex conceptual structures, irrespective of modality” (Fitch, 2000: 258). However, this leaves much to the imagination and allows subjectivity based on how one defines a complex conceptual structure. It is usually acknowledged that in order to understand language we need to know what it is and how it developed (Christiansen & Kirby, 2003). Therefore, researchers have looked to animal communication for similarities and as possible precursors to human language.

Speech is the primary way that human language is constructed, with sign language being the other (Fitch, 2000). Speech can be defined as the particular vocal medium humans use to convey meaning (Fitch, 2000). Morphological adaptations associated with human speech might explain some of the differences between human language and animal communication. The larynx in mammals typically helps to produce sounds (Hauser & Fitch, 2003). Mammals have paired vocal cords that vibrate when air flows through the glottis (Hauser & Fitch, 2003). During human ontogeny the larynx descends further in the throat than in great apes (Nishimura et al., 2006; Nishimura, 2005; Nishimura et al., 2003). This allows for more mobility of the tongue in humans than is seen in great apes, resulting in the latter’s inability to produce vowels and many of the vocalizations humans can make.

Many unique characteristics of human language relate to two features: a vast number of meaningful utterances and the anatomical changes associated with the production and processing of speech (Arcadi, 2005). Human language is syntactic (Nowak et al., 2000). This results in the ability to create an enormous number of meaningful utterances. Each language has its own set of phonemes, which are discrete units of sound or production (Arcadi, 2005). Humans can combine the discrete phonemes into a vast number of combinations to create meaningful units or words (Arcadi, 2005). This allows humans the ability to talk about a large variety of items in a wide variety of contexts including past and future events, which most, if not all, natural animal communication systems lack (Hauser & Fitch, 2003).

Rather than possessing an infinite number of vocal combinations, nonhuman animals are usually categorized as having a graded vocal system. Some maintain they can only call about occurrences happening in present time and elicited by emotional arousal (Parr et al., 2005; Seyfarth & Cheney, 2003; Ploog, 1981; Jürgens, 1979a; Jürgens, 1979b; Marler, 1977; Smith, 1977). Animal communication has generally been perceived as under strong genetic control, requiring little to no higher cortical processing (Parr et al., 2005; Seyfarth & Cheney, 2003; Ploog, 1981; Jürgens, 1979a; Jürgens, 1979b; Marler, 1977; Smith, 1977). Many researchers view the gap between humans and animals as insurmountable. However, as some recent studies have indicated, this division may not necessarily be as wide as we once thought. As scientists continue to study animal communication, the disparity between animal communication and human language has lessened (Seyfarth & Cheney, 2003). These studies have demonstrated the stereotypical view of animal communication as involuntary, emotional outcries and human language as complex higher order thinking is not accurate. Realistically, both humans and nonhumans demonstrate emotional and higher cortical

processing when communicating (Seyfarth & Cheney, 2003; Jürgens, 1998; Gamba et al., 1995). This paradigm shift has caused some researchers to scrutinize animal communication for the possibility of discrete vocal categories rather than a graded communication system.

Despite the perceived discontinuity between human language and animal communication, there remains related neurological anatomy among great apes and humans. The differentiation in human morphology results in an increased control over the nervous system (Fitch, 2000). Therefore, human language is able to require better control over the movement of the tongue, lips, and mouth. In humans, language production has been associated with Broca's area (Sherwood et al., 2003). This area is usually asymmetrical within the brain. In 95% of humans, the left hemisphere is dominant for language (Sherwood et al., 2003). On the other hand, it was thought that animal communication was primarily controlled by the hypothalamus and limbic system, rather than the neocortical region (Gamba et al., 1995). This tied into the idea that animal vocalizations were primarily caused by emotional displays.

Recent work has demonstrated the possibility that higher cortical processing does play some role in nonhuman primate calls. Gamba, Miki, and Sasaki (1995) were able to demonstrate neocortex control in vocalizations among Japanese monkeys (*Macaca fuscata*). Furthermore, Sherwood and colleagues (2003) were able to determine that there did appear to be a homologous Broca's area in chimpanzees and gorillas (*Gorilla gorilla*). This portion of the brain is noted as Brodmann's area 44 and also appears to exhibit humanlike asymmetry (Sherwood et al., 2003; Gannon, et al., 1998). Gannon and colleagues (1998) demonstrated that 17 of the 18 chimpanzees they investigated also showed a left hemisphere asymmetry homologous to Broca's area in humans. Similarly, Petkov et al. (2008) demonstrated that

primates process vocalizations similar to humans. These authors located a specific high-level auditory region in macaque monkeys (*Macaca mulatta*), which processes species-typical calls and vocal identification of conspecifics (Petkov et al., 2008). This region is similar to a region of the human brain that specifically processes human vocalizations rather than general sounds.

Additionally, the behavioral context surrounding animal calls indicates that animal communication systems are not purely emotional outcries. Audience effect has been studied in many species (Wich & Sterck, 2003; Cheney & Seyfarth, 1990; Marler & Mitani, 1988; Gyger et al., 1986; Cheney & Seyfarth, 1985). Audience effect refers to the likelihood that an individual will vocalize based on the social context surrounding them, such as the presence of conspecifics (Wich & Sterck, 2003). Numerous studies have indicated that bird calls are influenced by audience effect (Marler & Mitani, 1988; Gyger et al., 1986; Marler et al., 1986b). Nonhuman primates have also demonstrated control over their communication systems based on audience effect (Wich & Sterck, 2003; Cheney & Seyfarth, 1990; Cheney & Seyfarth, 1985). Male Thomas langurs (*Presbytis thomasi*), for example, are known to produce loud calls in response to a tiger (*Panthera tigris*) predator. However, solitary males generally do not produce a loud call when encountering a tiger, but males in mixed-sex groups do produce loud calls (Wich & Sterck, 2003).

Nonetheless there remains an emotional component to animal communication (Hauser, 1993; Morton, 1977). Morton (1977) predicted that in bird and mammal communication, aggressive calls would be relatively low in frequency and have a harsh quality while fearful or nonaggressive calls would be more tonal and high-frequency. This does hold true in nonhuman primates (Hauser, 1993), which has been cited as evidence for

the hypothesis that animal communication is based primarily on emotion rather than logical thought. However, the same trend has also been demonstrated in humans (Seyfarth & Cheney, 2003; Jürgens, 1998). This could indicate that animal and human communication systems developed via similar pressures, both of which have an emotional aspect.

Some researchers emphasize human language's uniqueness regarding the importance of learning. Learning is a major component for human child language acquisition (Gómez & Gerken, 2000). It is only through the learning process that semantic context and grammatical rules are acquired, yet birds are also especially known for the intensive learning process involved in the acquisition of their songs (Snowdon & Elowson, 1992). Nevertheless, it is generally thought that learning plays only a small role, if any, in the acquisition of calls in nonhuman primates (Seyfarth & Cheney, 2003).

Despite the characterization of language as being differentiated by intensive learning, there are examples from the laboratory of vocalization learning among nonhuman primates. These range from cross-fostering experiments to dialect learning and differentiation of calls through reinforcement (Crockford et al., 2004; Hihara et al., 2003). Hihara and colleagues (2003) provided evidence for the spontaneous learning of coo-calls among Japanese monkeys. In this study, monkeys were given tools in order to get food. Spontaneously, the monkeys differentiated a coo-call for food and a coo-call specifically for the tool to get food (Hihara et al., 2003). The spontaneous differentiation of calls for specific items by nonhuman primates and the few instances of vocal learning help shed some light on the complexity of primate communication and, specifically, the possibility of referential communication.

In human language words are considered referential. Referents are an essential part of human speech (Deacon, 1997). They are context specific and also initiate responses that are

context-independent (Di Bitetti, 2003). In language, certain words stand for particular items and can conjure an image of that item in the mind of the listener (context-specific). Additionally, regardless of what contexts surround the word, it still retains the same meaning (context-independent). They are meant to intentionally convey specific information.

There has been a recent trend in primatology to focus on potential referents in nonhuman primates (Slocombe & Zuberbühler, 2005; Gill & Sealy, 2004; Di Bitetti, 2003; Seyfarth & Cheney, 2003; Tagliabata et al., 2003; Fischer & Hammerschmidt, 2001; Owren & Rendall, 2001; Zuberbühler, 2000; Evans & Evans, 1999). This trend has been controversial. Potential referential signals have been seen in capuchin monkeys (*Cebus apella*), vervet monkeys (*Cercopithecus aethiops*), and chimpanzees among others (Slocombe & Zuberbühler, 2006; Di Bitetti, 2003; Seyfarth et al., 1980a; Seyfarth et al., 1980b). This concept helps to draw human and nonhuman primate communication systems closer together and makes it possible to envision the evolution of language as a process rather than as a quantum leap between humans and apes. Even if referents are not prevalent in every animal communication system, their development in some, especially closely related nonhuman primates, could provide a focal point for all referents within language to develop.

In summary, human language is thought to differ both morphologically and behaviorally from any other form of animal communication we know of today. This is exemplified through the use of syntax and grammar in every human language. This hypothesized change in communication during our evolutionary history was also accompanied by morphological changes, which perhaps led to neurological changes in the brain. Finally, human language could not be possible if humans did not retain the ability to

learn language and imitate the many sounds and gestures they have heard. All of these factors together have led to the unique utilization of speech in humans.

Despite the complexity of human language, it may not be as unique as once thought. It does share similar emotional aspects with “typical” animal communication systems. Also, human language and animal communication appear to share some neurological characteristics along with the potential for learning and development of referential communication. However, human language still differs from animal communication in its total reliance on these factors while animal communication systems demonstrate these aspects as exceptions rather than the rule. The similarities and discontinuities between human language and animal communication systems can help to shed light on the possible evolutionary path of the development of human language.

1.4 Evolutionary Process

Primatologists, as well as anthropologists, not only examine primates for their own accord, but via the comparative method in order to better understand the evolutionary path leading to primates, apes, and particularly the genus *Homo*. The study of the evolution of linguistic abilities in our lineage is a highly controversial topic (Marler et al., 1992). Researchers have debated over questions ranging from what comprises language, whether it is present in great apes, when and how it evolved, and how one can utilize the fossil record to pinpoint when it evolved (Christiansen & Kirby, 2003; Hauser et al., 2002).

1.4.1 Gestural Origin of Language

One theory of language origins suggests that language developed from gestural communication rather than vocalizations (Corballis, 2003a). It was noted long ago that nonhuman primates are efficient at using gestures to communicate (Vauclair, 2004).

Additionally, it has been noted that nonhuman primates, even our closest relatives, the chimpanzees, have a dramatically limited vocal communication system compared to human speech (Corballis, 2003a). Due to the perceived lack of voluntary control in chimpanzees' limited vocalizations and the dyadic relationship gestures provide, it is thought that gestures preceded the origin of human language (Corballis, 2003b). The basic concept behind this is that the bipedal nature of hominids freed their hands for communication (Corballis, 2003a). Therefore, the increased freedom of hands allowed for expansion on the successful gestural communication already used among quadrupedal apes.

Proponents of the gestural origin of language have looked to neurological components of language in order to demonstrate a link between language and gestures. Broca's area is considered responsible for the production of speech in humans. It has been demonstrated by proponents of the gestural origin of language that the homologous area in monkeys is actually responsible for manual activity (Corballis, 2003b). Therefore, this suggests that language developed in this area, being gestural in origin. Selective pressures then resulted in a change to a vocal form of communication. However, since language was already fixed to be processed in Broca's area, it shifted to maintain control of the vocal linguistic realm. Furthermore, Broca's area is in the left hemisphere of the brain. Humans as a species are primarily right-handed. Some hypothesize this to be a consequence of vocal language (Corballis, 2003a). Broca's area was initially associated with gestures, but as language shifted to a vocal realm, Broca's area also shifted its responsibility to vocal rather than gestural control. As Broca's area began to take on its new role with vocal language, it became more asymmetrical, left hemisphere dominant (Corballis, 2003a). The remaining link

between gestures, hand use, and speech created a right-hand dominance among humans (Corballis, 2003a).

Further evidence for a linguistic link to gestural communication and right hand bias is provided by chimpanzees. Chimpanzees have been shown to use manual gestures in communication (Hopkins & Cantero, 2003). They appear to use manual gestures rather than vocalizations to gain the attention of humans (Hostetter et al., 2001). Observations of their handedness when communicating with humans indicate a right-handed bias (Hopkins & Cantero, 2003). This further supports the possibility that right-handedness could be tied to language and Broca's area in humans.

Using the gestural theory of language, it is hypothesized that there was eventually selective forces for a gradual shift towards vocal communication. One possibility for this shift includes the use of more sophisticated technology, which required the hands, so vocalizations began to take its place (Corballis, 2003a). Also, perhaps as groups became more sedentary, carrying food and offspring became more vital to their life, leaving the hands occupied (Corballis, 2003a).

The gestural theory of the origins of language examines nonhuman primates and maintains their vocal communication is too limited to develop into human language. Instead gestures provide the best possible link. This link also led to handedness in humans. Gestures became a primary form of communication once bipedalism and a move to terrestriality freed the hands. Eventually the sophistication of tool manufacture and requirement of the hands for carrying resulted in the incorporation of vocalizations. Vocalizations began to take over, and speech in language was developed.

1.4.2 Speech Origin of Language

A second main theory of language evolution maintains that language developed from vocalizations similar to those seen in nonhuman primates. This theory criticizes the gestural origin of language as being highly unlikely (Dunbar, 2003). The gestural origin requires hominids to lose an efficient vocal communication system to use gestures. This advanced form of gestural communication must then be abandoned with a return to vocal communication. This is not parsimonious, and it appears more likely that the vocal communication system would simply be expanded and modified to create human language (Dunbar, 2003). Furthermore, there would have to be a strong selective force for the development of speech in language, and the gestural theory lacks any proof of a force powerful enough (Dunbar, 2003).

MacNeilage (1998) advocates the theory that language evolved through speech and vocalizations. He suggests one of the differences between animal communication systems and human language is that the latter uses “a continual rhythmic alternation between open and closed mouth on the sound production processes” (MacNeilage, 1998: 499). MacNeilage (1998) also suggests that bipedalism allowed a change in vocal anatomy to a two-tubed vocal tract, which gave the tongue more room to move. This resulted in an increase in acoustic potential for hominids (MacNeilage, 1998). MacNeilage (1998) proposes this change in communication, to involve the rhythmic opening and closing, was shared with and developed from ingestion. Chewing, licking, and sucking all require a rhythmic opening and closing of the mouth that appear to reflect speech in humans (MacNeilage, 1998).

Apes show a rhythmic opening and closing of the mouth in social situations. In particular, the lip smack (Goodall, 1986), which is used in social circumstances, is very

similar to speech patterns in humans. It is also used in one-to-one social interactions involving eye contact and possibly turn-taking (MacNeilage, 1998). Additionally, chimpanzees produce a particular bilabial fricative, the raspberry, in captivity seemingly to gain the attention of humans in a captive setting (Hopkins et al., 2007; Leavens & Hopkins, 1998). Perhaps lipsmacks and raspberries accompanied by a vocalization were one of the first communications in speech. As support of this theory, MacNeilage looks at speech ontogeny in human infants. This suggests that infants begin to use the rhythmic opening and closing of the mouth (~ 5 months of age) prior to babbling vocalizations (~ 7 months), supporting the opening and closing ingestion function occurs before vocalizations synchronize with it (MacNeilage, 1998).

The theory of a vocal origin of human language is supported by evidence stemming from the study of Broca's area as well. The portion of the brain that contains Broca's area is the main locus for the control of ingestive properties in mammals (MacNeilage, 1998). This supports the concept that Broca's area was originally responsible for ingestion but was modified as vocalizations began to use ingestive properties to create speech. Additionally, MacNeilage (1998) points out that left hemisphere dominance in vocal communication is seen in other animals, as is right-handedness in higher primates. Therefore, this does not provide special support for the gestural origin of language.

The evolution of language via speech suggests a multi-stage process from vocalizations to language (Dunbar, 2003). Perhaps, the initial form would be much like that found in other nonhuman primates and would act as social calls either to keep contact with the group, convey information over long distances, or in a more intimate interaction such as grooming (Dunbar, 2003). Next, a more developed form would result, perhaps with many or

all vocalizations being referents but still lacking grammatical structure. After this, there would be a move towards grammatical structure and the use of vocalizations to contain a wide variety of information vital to group living and socialization. Finally, fully developed language would emerge with abstract symbolic information included and also the ability to speak about future and past occurrences.

1.4.3 When Did Language Evolve?

Paleoanthropologists have looked to fossils in order to suggest when language began to evolve and what species in our past had language rather than a communication system. Primarily, this research has focused on the hyoid bone (as an indicator of larynx position), brain size, neurocranium endocasts, and basicranial flexion as potential correlates to the development of language in past hominid species (Davidson, 1991). Problems arise because there is no one-to-one correlation between any one of these traits and language. Therefore, researchers are left arguing about not only what features are present in paleospecies, but also what the interpretation of these traits indicates.

To further hamper pinpointing the origin of language, the different origin theories of language (e.g. gestural vs. speech origins) have different implications for what anatomical features suggest linguistic capabilities. Proponents of the gestural origin for language focus specifically on endocasts of the neurocranium and relative brain size as the main indicators of linguistic ability (Corballis, 2003b). Speech became sort of an ‘after thought,’ resulting after gestural language had already developed (Corballis, 2003b). Paleontologists supporting the speech origin theory believe, not only that an increase in relative brain size and endocasts demonstrating prefrontal expansion and development of Broca’s area are necessary prerequisites, but also that the hyoid, basicranial angle, and hypoglossal canal size must also

show linguistic ability in order for the full form of language to be present in the hominid fossil record. Proponents of both origin theories argue about the steps and sequence leading to the development of language. Some researchers assert that symbolic communication developed before brain expansion and laryngeal descent (e.g. Deacon, 1997), which evolved into language. Others believe brain expansion came first but argue whether language developed before or after laryngeal modifications (e.g. Chomsky, 1986). Therefore, the study of language evolution using the paleontological record, along with pinpointing who exactly has language is a very difficult process.

References

- Arcadi AC. 2005. Language evolution: what do chimpanzees have to say? *Current Biology* 15:R884-R886.
- Cheney DL, Seyfarth RM. 1985. Vervet monkey alarm calls: manipulation through shared information? *Behaviour* 93:150-166.
- Cheney DL, Seyfarth RM. 1990. *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: University of Chicago Press.
- Chomsky N. 1986. *Knowledge of Language: Its Nature Origin, and Use*. New York: Praeger Publishers.
- Christiansen MH, Kirby S. 2003. Language evolution: consensus and controversies. *Trends in Cognitive Sciences* 7:300-307.
- Corballis M. 2003a. From hand to mouth: gesture, speech, and the evolution of right-handedness. *Behavioral and Brain Sciences* 26:199-260.
- Corballis M. 2003b. From hand to mouth: the gestural origins of language. In: Christiansen MH, Kirby S, editors. *Language Evolution*. New York: Oxford University Press. p 201-218.
- Crockford C, Herbinger I, Vigilant L, Boesch C. 2004. Wild chimpanzees produce group-specific calls: a case for vocal learning. *Ethology* 110:221-243.
- Davidson I. 1991. The archaeology of language origins - a review. *Antiquity* 65:39-48.
- Deacon TW. 1997. *Symbolic Species: the Co-Evolution of Language and the Brain*. New York: W.W. Norton & Co.
- Di Bitetti MS. 2003. Food-associated calls of tufted capuchin monkeys (*Cebus apella nigrinus*) are functionally referential signals. *Behaviour* 140:565-592.

- Dunbar R. 2003. The origin and subsequent evolution of language. In: Christiansen MH, Kirby S, editors. *Language Evolution*. New York: Oxford University Press. p 219-234.
- Evans CS, Evans L. 1999. Chicken food calls are functionally referential. *Animal Behaviour* 58:307-319.
- Fischer J, Hammerschmidt K. 2001. Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition* 4:29-35.
- Fitch TW. 2000. The evolution of speech: a comparative review. *Trends in Cognitive Sciences* 4:258-267.
- Gannon PJ, Holloway RL, Broadfield DC, Braun AR. 1998. Asymmetry of chimpanzee planum temporale: humanlike pattern of Wernicke's brain language area homolog. *Science* 279:220-222.
- Gardner RA, Gardner BT. 1969. Teaching sign language to a chimpanzee. *Science* 165:664-672.
- Gemba H, Miki N, Sasaki K. 1995. Cortical field potentials preceding vocalization and influences of cerebellar hemispherectomy upon them in monkeys. *Brain Research* 697:143-151.
- Gibbons CM. 2007. *The referentiality of vocal signaling: behavioral and acoustic analysis of food barks*. Columbus: Ohio State University.
- Gill SA, Sealy SG. 2004. Functional reference in an alarm signal given during next defence: set calls of yellow warblers denote brood-parasitic brown-headed cowbirds. *Behavioral Ecology & Sociobiology* 56:71-80.

- Gómez RL, Gerken L. 2000. Infant artificial language learning and language acquisition. *Trends in Cognitive Sciences* 4:178-186.
- Goodman M, Czelusniak J, Page S, Meireles C. 2001. Where DNA sequences place *Homo sapiens* in a phylogenetic classification of primates. In: Tobias PV, Raath MA, J. M-C, Doyle GA, editors. *Humanity from African Naissance to Coming Millennia: Firenze University Press/Witwatersrand University Press*. p 279-290.
- Greenfield PM, Savage-Rumbaugh ES. 1991. Imitation, grammatical development, and the invention of protogrammar by an ape. In: Krasnegor NA, Rumbaugh DM, editors. *Biological and Behavioral Determinants of Language Development*. New York: Lawrence Erlbaum Associates. p 235-258.
- Gyger M, Karakashian S, Marler P. 1986. Avian alarm calling: is there an audience effect? *Animal Behaviour* 34:1570-1572.
- Hallberg KI. 2000. *Specificity of chimpanzee food barks: reference to food type and quality*. Columbus: Ohio State University.
- Hallberg KI, Nelson DA, Boysen ST. 2003. Representational vocal signaling in the chimpanzee. In: de Waal FBM, Tyack PL, editors. *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*. Cambridge, MA: Harvard University Press. p 317-322.
- Hauser MD. 1993. The evolution of nonhuman primate vocalizations: effects of phylogeny, body weight, and social context. *American Naturalist* 142:528-542.
- Hauser MD, Chomsky N, Fitch TW. 2002. The faculty of language: What is it, who has it, and how did it evolve? *Science* 298:1569-1579.

- Hauser MD, Fitch WT. 2003. What are the uniquely human components of the language faculty? In: Christiansen MH, Kirby S, editors. *Language Evolution*. New York: Oxford University Press. p 158-181.
- Hihara S, Yamada H, Iriki A, Okanoya K. 2003. Spontaneous vocal differentiation of coo-calls for tools and food in Japanese monkeys. *Neuroscience Research* 45:383-389.
- Hopkins WD, Cantero M. 2003. From hand to mouth in the evolution of language: the influence of vocal behavior on lateralized hand use in manual gestures by chimpanzees (*Pan troglodytes*). *Developmental Science* 6:55-61.
- Hopkins WD, Taglialatela JP, Leavens D. 2007. Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Animal Behaviour* 73:281-286.
- Hostetter A, Cantero M, Hopkins WD. 2001. Differential use of vocal and gestural communication in response to attentional state of a human experimenter. *Journal of Comparative Psychology* 115:337-343.
- Jürgens U. 1979a. Neural control of vocalization in nonhuman primates. In: Raleigh MJ, editor. *Neurobiology of Social Communication in Primates*. New York: Academic Press. p 11-44.
- Jürgens U. 1979b. Vocalization as an emotional indicator. A neuroethological study in the squirrel monkey. *Behaviour* 69:88-117.
- Jürgens U. 1998. Common features in the vocal expression of emotion in human and non-human primates. In: Santi S, Guaitella J, Cave C, Konopczynski G, editors. *Oralite et Gestualite*. Paris: L' Harmattan. p 153-158.
- King B. 2002. *Biological Anthropology: An Evolutionary Perspective*. New York: Teaching Company Limited Partnership.

- Leavens D, Hopkins WD. 1998. Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology* 34(5):813-822.
- MacNeilage PF. 1998. The frame/content theory of evolution of speech production. *Behavioral and Brain Sciences* 21:499-546.
- Marler P. 1977. Primate vocalizations: affective or symbolic? In: Bourne G, editor. *Progress in Ape Research*. New York: Academic Press. p 85-96.
- Marler P, Dufty A, Pickert R. 1986a. Vocal communication in the domestic chicken: I. does a sender communicate information about the quality of a food referent to a receiver. *Animal Behaviour* 34:188-193.
- Marler P, Dufty A, Pickert R. 1986b. Vocal communication in the domestic chicken: II. is a sender sensitive to the presence and nature of a receiver. *Animal Behaviour* 34:194-198.
- Marler P, Evans CS, Hauser MD. 1992. Animal signals: motivational, referential, or both? In: Papousek H, Jurgens U, Papousek M, editors. *Nonverbal Vocal Communication: Comparative and Developmental Approaches*. Cambridge: Cambridge University Press. p 66-86.
- Marler P, Mitani J. 1988. Vocal communication in primates and birds: parallels and contrasts. In: Todt D, Goedeeking P, Symmes D, editors. *Primate Vocal Communication*. Berlin: Springer-Verlag. p 3-14.
- Morton ES. 1977. On the occurrence and significance of motivation-structural rules in some birds and mammal sounds. *American Naturalist* 111:855-869.

- Nishimura T. 2005. Developmental changes in the shape of the supralaryngeal vocal tract in chimpanzees. *American Journal of Physical Anthropologist* 126:193-204.
- Nishimura T, Mikami A, Suzuki J, Matsuzawa T. 2003. Descent of the larynx in chimpanzee infants. *Proceedings of the National Academy of Sciences* 100:6930-6933.
- Nishimura T, Mikami A, Suzuki J, Matsuzawa T. 2006. Descent of the hyoid in chimpanzees: evolution of face flattening and speech. *Journal of Human Evolution* 51:244-254.
- Nowak MA, Plotkin JB, Jansen VAA. 2000. The evolution of syntactic communication. *Nature* 404:495-498.
- Owren MJ, Rendall D. 2001. Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology* 10:58-71.
- Parr LA, Waller BM, Fugate J. 2005. Emotional communication in primates: implications for neurobiology. *Current Opinion in Neurobiology* 15:716-720.
- Petkov CI, Kayser C, Steudel T, Whittingstall K, Augath M, Logothetis NK. 2008. A voice region in the monkey brain. *Nature Neuroscience* 11:367-374.
- Ploog D. 1981. Neurobiology of primate audio-vocal behavior. *Brain Research Review* 3:35-61.
- Premack D. 1971. Language in chimpanzees? *Science* 172:808-822.
- Rumbaugh DM. 1977. *Language Learning by a Chimpanzee: the Lana Project*. New York: Academic Press.
- Savage-Rumbaugh ES. 1990. Language acquisition in a nonhuman species: implications for the innateness debate. *Developmental Psychobiology* 23:599-620.

- Savage-Rumbaugh ES, McDonald K, Sevcik RA, Hopkins WD, Rubert E. 1986. Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General* 115:211-235.
- Seyfarth RM, Cheney DL. 2003. Signalers and receivers in animal communication. *Annual Review of Psychology* 54:145-173.
- Seyfarth RM, Cheney DL, Marler P. 1980a. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* 210:801-803.
- Seyfarth RM, Cheney DL, Marler P. 1980b. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour* 28:1070-1094.
- Sherwood CC, Broadfield DC, Holloway RL, Gannon PJ, Hof PR. 2003. Variability of Broca's area homologue in African great apes: implications for language evolution. *Anatomical Record* 271A:276-285.
- Slocombe KE, Zuberbühler K. 2005. Functionally referential communication in a chimpanzee. *Current Biology* 15:1779-1784.
- Slocombe KE, Zuberbühler K. 2006. Food-associated calls in chimpanzees: responses to food types or food preferences? *Animal Behaviour* 72:989-999.
- Smith WJ. 1977. *The Behavior of Communicating: an Ethological Approach*. Cambridge, MA: Harvard University Press.
- Snowdon CT, Elowson MA. 1992. Ontogeny of primate vocal communication. *Human Origins* 1:279-290.
- Tagliapietra JP, Savage-Rumbaugh S, Baker LA. 2003. Vocal production by a language-competent *Pan paniscus*. *International Journal of Primatology* 24:1-17.

- Vauclair J. 2004. Lateralization of communicative signals in nonhuman primates and the hypothesis of the gestural origin of language. *Interaction Studies* 5:365-386.
- Wich SA, Sterck EHM. 2003. Possible audience effect in Thomas langurs (Primates; *Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology* 60:155-159.
- Zuberbühler K. 2000. Referential labeling in Diana monkeys. *Animal Behaviour* 59:917-927.

Chapter Two: Functionally Referential & Referential Communication

Functional referents are animal calls that are both context-specific for the signaler and context-independent for the receiver. Particularly conclusive studies regarding referential communication have been done on vervet monkeys, Diana monkeys (*Cercopithecus diana*), tufted capuchin monkeys, chimpanzees, chickens (*Gallus domesticus*), and yellow warblers (*Dendroica petechia*). However, this concept suggests that these calls do not contain encoded information and can create more confusion rather than clarification of animal communication systems. Rather, the close evolutionary relationship between humans and living nonhuman great apes and homologous neurological systems warrants the examination of referents in great ape vocal repertoire. Continued investigation into referential communication will have the opportunity to expand the field of animal communication even further.

2.1 Development of the Functional Referent Concept

In the 1980s scholars began to reexamine the complexity of animal communication systems. These new studies included a novel outlook on animal communication systems. It became apparent that animal communication systems were more complex than we once thought (Marler, 1985; Seyfarth et al., 1980a; Seyfarth et al., 1980b). In the 1990s, in response to this recognition of the concept that animal communication systems were more complex than emotional outcries, the concept of ‘functional referent’ was coined (Macedonia & Evans, 1993; Marler et al., 1992).

In human language, referential signals provide information about external objects to the signaler (Smith, 1991; Smith, 1977). Many human words are referents. These words consistently stand for a single object and allow the listener to have an image of that object in their mind, even if the object is not in view. For example, if an individual stated ‘the dog was

running,' dog would be a referent. A listener would be able to conjure a general image of a dog in his/her mind without seeing the particular dog the speaker is referring to. The term 'functional referent' was adopted because researchers were unable to determine if animals are conjuring an image of the object in their mind when they hear a vocalization and whether the vocalization was intended to communicate information even though they are behaving as if they do (Macedonia & Evans, 1993; Marler et al., 1992). Therefore, the terms 'functional referent' goes no further than identifying scenarios in which referential communication may be present but makes no claim on whether it is truly referential.

Functional referents in animal communication systems must meet two criteria (Macedonia & Evans, 1993; Marler et al., 1992). First, when the signaler uses a functionally referential call, the call should be context-specific. That means a specific call is given for a specific item or external condition (e.g. vervet alarm calls for specific predators). These conditions define the referent of the call. The second condition is that the receiver of the call should respond similarly to the call, which is context-independent (e.g. consistently respond differently to different vervet alarm calls). Receivers should understand the vocalization and respond accordingly without having firsthand knowledge of where the referent is. They should demonstrate the adequate behavioral response regardless of the context (e.g. demonstrate the specific predator avoidance behavior associated with that predator). The possibility of functional referents in animal communication suggests, rather than purely emotionally-based, these call systems may be more sophisticated than some researchers suggest. Furthermore, they require individuals to learn the meaning and appropriate context in which to give these calls.

2.2 Functional Referents in Birds

Birds are especially known for the intensive learning process involved in their acquisition of songs (Snowdon & Elowson, 1992). They have complex vocalizations and songs, which makes them likely candidates for functionally referential communication. Food vocalizations in chickens became the second conclusive study on referents after vervet monkey alarm calling.

Male domestic chickens produce food calls. Acoustical characteristics differentiated these food calls based upon preference (Marler et al., 1986a). Males also tend to give these calls in the presence of females. A playback experiment demonstrated that females are more likely to approach a male that is giving these food calls and also more likely to approach if the call signals a highly preferred food item (Marler et al., 1986a). Furthermore, females are more likely to begin searching the ground for food upon hearing a male's food call (Evans & Evans, 1999).

Food calls given by males fulfill both requirements for functional referents. In addition, the study was expanded to test whether males account for the audience effect (Marler et al., 1986b). Males did perceive the audience effect. When females were present compared to no audience, the males called more often. Additionally, if other males were present compared to no audience, the signaler was even less likely to food call. This indicates not only that food calls have referential information but also that the signaler uses this in meaningful ways.

Yellow warblers produce a predator-specific alarm call (Gill & Sealy, 2003). These birds encounter many dangers at their nest site including conspecific intruders, non-threatening invaders, avian and mammalian nest predators, and aerial predators such as

hawks (Gill & Sealy, 2004). When encountering any of these dangers, they use a variety of alarm calls including ‘chips’ and ‘warbles.’ However, the birds also have a very unique predator. Yellow warblers are common hosts to the brood-parasitic brown-headed cowbirds (*Molothrus ater*). Cowbirds will lay their eggs in the warbler’s nests, resulting in the cowbird chick being raised by the warbler, usually with negative consequences for its own offspring (Lorenzana & Sealy, 1999; Ortega, 1998).

Yellow warblers have a specific alarm call, the ‘seet’ call, for brown-headed cowbirds (Gill & Sealy, 2003). A playback experiment, along with predator models, was used to examine the context of the ‘seet’ call in relation to cowbirds. Yellow warblers give this call regardless of urgency, indicating it is specific to brown-headed cowbirds and not just to predator risk (Gill & Sealy, 2004). These ‘seet’ calls are rarely given in areas where warblers are allopatric with the predator. Additionally, recipients produce a very specific behavioral response indicating context-independence. Upon hearing these calls or seeing the cowbird model females would immediately fly back to the nest and sit very tight on it so as to protect its nest from brood parasitism. This contrasts the behavioral response to other predators in which males will also respond and predator deterrence involves luring a predator away from the nest (Gill & Sealy, 2004).

2.3 Functional Referents in Non-Primate Mammals

Many non-primate mammals’ vocal repertoires have been tied to the level of urgency rather than actual referential information (*Suricata suricatta*: Manser, 2001; Manser et al., 2001; *Parotomys brantsii*: Le Roux et al., 2001; *Marmota flaviventris*: Blumstein & Armitage, 1997; Blumstein & Arnold, 1995; *Spermophilus beecheyi*: Robinson, 1981; Owings & Virginia, 1978). However, some mammals appear to demonstrate referential

aspects in their vocal repertoire as well. Gunnison's prairie dogs have demonstrated the potential for referential communication. They give alarm calls for approaching predators, and these calls encode information about the predator (Slobodchikoff, 1991).

Gunnison's prairie dogs have had humans as predators for a substantial period of time. Therefore, they give alarm calls to any human approaching their colony (Slobodchikoff, 1991). This study examined whether their alarm calls differentiated individual predators. Having various people approach the prairie dogs' homes dressed in different clothing demonstrated that prairie dogs did differentiate their alarm calls. Their alarm calls differentiated primarily based on color and shape. This could be beneficial to their deterrence behaviors over time. However, this study did not focus on the perception of alarm calls by the receiver. Therefore, only context-specificity has been demonstrated. A separate experiment would have to be developed in order to determine whether the prairie dogs can perceive these differences and respond accordingly.

Bottlenosed dolphins' (*Tursiops truncatus*) appear to exhibit referent behavior as well. Bottlenosed dolphins are known for complex communication that includes individually specific whistles (Caldwell & Caldwell, 1968; Caldwell & Caldwell, 1965). These signature whistles are not only individually specific but also appear to be the result of vocal learning (Sayigh et al., 1995). However, a study investigating the question of vocal reference has not yet been conducted (Reiss et al., 1997). As with the prairie dogs, further investigation could clarify whether or not these calls fulfill the criterion necessary for functional reference.

2.4 Functional Referents in Nonhuman Primates

2.4.1 Prosimians

Very few species of prosimians demonstrate any indication of functionally referential signals in their vocal repertoire. The only species that currently indicates possible functional referents in their vocal repertoire is the ringtailed lemur (*Lemur catta*). Ringtailed lemurs appear to use anti-predator calls similar to vervet monkeys, with distinctions between aerial and terrestrial predators (Pereira & Macedonia, 1991). Continued exploration into calls of prosimians may reveal future functional referents. However, if the general concept stating referents require some sort of higher cortical processing is true, we might expect to find less referential communication in prosimians due to their more primitive nature in comparison to other nonhuman primates.

2.4.2 New World Monkeys

Certain species of New World tamarins and capuchin monkeys have demonstrated functionally referential aspects to their call systems. Tufted capuchins provide another conclusive example of functionally referential signals (Di Bitetti, 2005; Di Bitetti, 2003). These food-associated calls are called 'grgrs' and whistle series. Using observation and preliminary recordings of vocalizations, Di Bitetti (2003) determined that the 'grgr' and whistle series were given at higher rates when feeding at a highly productive area and exclusively in a feeding context. This study is slightly different from other studies with free-ranging groups because they used provisioning of bananas to elicit food vocalizations and as a comparison to other fruit sources. This method was also used in the playback portion of the experiment and can draw criticisms due to the possible effect this provisioning may have had on their behavior. Nonetheless the tufted capuchins would look towards the speakers and

would also move towards the speaker more frequently when it was playing a food-associated call in comparison to the control calls (Di Bitetti, 2003). This study concluded by confirming that the ‘grgr’ and whistle series are context-specific and that receivers can differentiate between these calls during playback experiments. Furthermore, Di Bitetti (2005) demonstrated that tufted capuchins will use these functionally referential food calls to withhold information about the presence of food to other conspecifics during times of food scarcity or when only small amounts of food were discovered. These two studies help to evaluate some of the complexities within tufted capuchins’ vocal repertoire.

Several other New World monkey species have demonstrated potential functionally referential communication although these species provide less conclusive evidence than tufted capuchins. First, cotton-top tamarins (*Saguinus oedipus*) were examined. These tamarins show a correlation between the rate of food-calling and their food preference (Elowson et al., 1991). This allows individuals to gather information about food sources even if they are not in a direct line of sight. Several other captive New World monkey species have demonstrated similar results (*Leontopithecus rosalia*: Benz, 1993; *Saimiri sciureus sciureus*: Barclay & Maurus, 1992). These studies require further investigation before conclusions can be made regarding their use of functionally referential signals.

2.4.3 Old World Monkeys

The first study focusing on referential complexity in animal communication systems was done on nonhuman primates. In 1980, vervet monkeys’ alarm calls were examined regarding their possible semantic content (Seyfarth et al., 1980a; Seyfarth et al., 1980b). Vervet monkeys encounter a variety of predators in their natural environment, which require different anti-predator strategies (Seyfarth et al., 1980a; Seyfarth et al., 1980b). These

predators include large raptors, large cats, and also snakes. Seyfarth and colleagues investigated the alarm calls of vervets associated with these different predators. Using playback experiments and acoustical analysis, they determined that these monkeys give acoustically distinct alarm calls for specific predator types, and vervets also have unique behavioral responses to these calls. Their alarm calls can be divided into three distinct categories: terrestrial predator alarms, avian predators, and snakes (Seyfarth et al., 1980a; Seyfarth et al., 1980b). When the vervet monkeys hear a leopard alarm call, they quickly climb into the nearest tree, apparently to avoid the ambush predation style of leopards. When hearing an avian alarm call, they look up and then run into dense brush to avoid the bird's attack from above. Finally, when vervets hear a snake alarm call, they stand bipedally and look down at the ground in their immediate vicinity since the best avoidance is presumably increased vigilance. This study of vervet monkey predator alarm calls was the first to determine that nonhuman primate calls may be more complex than involuntary emotional outcries. With this insight, numerous studies were subsequently undertaken.

Further study of nonhuman primate vocalizations revealed that vervet monkeys were not the only Old World monkeys to demonstrate functional referents in their vocal repertoire. Zuberbühler (2000) specifically looked at acoustically distinct alarm calls in Diana monkeys and sought to determine whether these calls varied according to the predator's distance, elevation, or category. Diana monkeys also appeared to categorize predators, with distinct calls for terrestrial and aerial predators (Zuberbühler, 2000). Again, this suggests the possibility of different behavioral strategies for these predators. Similarly, barbary macaques (*Macaca sylvanus*) give a shrill bark to disturbances in their surroundings (Fischer & Hammerschmidt, 2001). Analysis suggests they give an acoustically distinct shrill bark for

dogs versus nocturnal disturbances (Fischer, 1998). However, these calls are not as clear-cut as the alarm vocalizations in Diana and vervet monkeys. Although the calls are distinct, there is not as definite a relationship between their behavioral responses (Fischer & Hammerschmidt, 2001). Therefore, the second criterion of context-independence in the receiver is not fulfilled.

Vocalizations in baboons and macaques have also been examined for the appearance of functional referents. Chacma baboons (*Papio hamadryas ursinus*) appear to give acoustically distinct grunts in two contexts (Rendall et al., 1999). These grunts are fairly quiet and given either 1) at the start of a determined move across an open area or 2) during social approaches, especially approaches to a female with a young infant (Rendall et al., 1999). Finally, rhesus macaques appear to use agonistic screams as functional referents (Gouzoules et al., 1984). Rhesus macaques have five acoustically distinct agonistic screams (Gouzoules et al., 1984). These monkeys form complex alliances where females are more likely to aid closely related relatives (Kaplan, 1978; Kaplan, 1977). It appeared distinct screams are given by infants in different contexts in order to elicit certain modes of help (Gouzoules et al., 1984). When a noisy scream was given, mothers responded the strongest because this appeared to indicate physical contact such as biting and they were given to high-ranking individuals. The pulsed screams were the weakest in eliciting responses because they were given solely to related individuals and not necessarily to high-ranking relatives. Receivers appear to respond differentially to these calls and determine whether or not they will act on the signalers behalf.

2.4.4 *Great Apes*

Phylogenetically, great apes are the closest living relatives of humans (Goodman et al., 2001). As such, they provide an appropriate model for examining the process of language evolution. Specifically, functional referents can help to provide insight into the origins of language. However, very few studies have been conducted on functional referents in great ape communication. This is partially due to the difficulty in conducting these studies on wild great apes. Those studies that have been done have focused on captive apes.

The only great ape species to be examined for functional referents to date is the common chimpanzee. Food calls have been the primary focus of these studies. Several studies did not use the typical playback experiment prevalent in previous studies but instead had subjects in an experimental setup listen to food grunts and then choose a picture on a computer touch-screen (Gibbons, 2007; Hallberg, 2000; Hallberg et al., 1999). These studies suggested that chimpanzee food barks did contain referential information (Gibbons, 2007; Hallberg et al., 2003; Hallberg, 2000; Hallberg et al., 1999). The chimpanzees were able to discriminate between food barks and could choose the corresponding food picture. Also, they were able to differentiate between food categories. They were able to choose pictures based on their categorical preference: low, medium, or high. This provides at least some evidence that chimpanzees exhibit functional referents in their vocal repertoire.

A recent study conducted on chimpanzees in captivity required the subjects to pick between real food items in certain locations (Slocombe & Zuberbühler, 2006; Slocombe & Zuberbühler, 2005). In this experiment, chimpanzees were habituated to a feeding system in which two artificial trees were set up in opposite ends of the enclosure. Food was put into PVC pipes and dropped from the artificial trees simultaneously. One tree contained apples

and the other bread. PVC pipes would drop from both trees simultaneously but only one tree would be baited so that only bread or only apples was available at any given time. Once the chimpanzees were habituated to this process, the playback experiment began. A food grunt was played as the subject walked out and was able to examine the trees. The idea was that if the chimpanzee could discriminate between the food grunts, the subject would go to the correct tree (e.g. move to the apple tree if an apple food grunt was played and vice versa). The subject tested who always moved into the outdoor yard first did demonstrate a distinction between the two food grunts. Results suggest that chimpanzees were able to discriminate between food grunts based on food type or food preference. A food preference hierarchy (high-medium-low) was determined for nine food items. Vocalizations for these nine items were recorded and analyzed for acoustic structure. Discriminate function analysis indicated that food grunts were different based on the food item present. However, among those nine items, the largest difference was between highly preferred food items. Slocombe and Zuberbühler (2006) hypothesized that the acoustic differences between food grunts were based primarily on the overall preference. For those food items of very high preference, acoustical differences were more common whereas with lower preference food items there was less motivation to differentiate between food items, so there was only one call for the entire category. These calls appear to demonstrate both context-specificity and context-independence in captive groups of chimpanzees. However, one main unknown feature of these food referents is whether the calls truly are context-specific or whether they are more general, indicating a food preference hierarchy rather than a specific food item. Further studies will hopefully help to clarify this question by expanding the field to free-ranging populations and to other species of great apes.

Bonobo communication, to date, has not been examined for functional referents. However, general analysis of their vocal repertoire has been categorized. De Waal (1988) created a catalog of bonobo calls compared to that of chimpanzees. He created 12 distinct vocal categories. Three of these categories can consistently apply to feeding situations. High hooting can be used during feeding anticipation and feeding time. This call is defined as a high-pitched long-distance whooping call and is more highly correlated with communication between parties out of sight of each other (De Waal, 1988). It is generally associated with a highly excited state. The “wieew” bark is also associated with feeding anticipation. This is “a single, very loud bark in which one can hear the voice rise and fall” (De Waal, 1988: 205). When used in a feeding context, it can serve to draw the group’s attention to new developments (De Waal, 1988).

Finally, the food peep occurs primarily while bonobos are feeding or foraging. Food peeps are one of the bonobos most common calls (De Waal, 1988). These calls are short, clear, and tonal. De Waal also notes that food peeps “are used to draw attention to and ‘comment’ on objects, food, and events in environment” (1988: 211). Furthermore, de Waal (1988) notes that these food peeps are highly variable and may potentially demonstrate meaningful differences to the bonobos. Therefore, food peeps can provide a potential link to examining referential communication in bonobos.

Some investigation into food peeps revealed that the food peep is the vocalization frequently used when discovering a hidden food source, and food peeps occurred more often when no feeding competition was possible (Van Krunkelsven, 1996). There appeared to be no sex differentiation associated with rate of calling. Van Krunkelsven (1996) hypothesized that males can use food peeps in order to attract potential mates while females may vocalize

in order to attract coalition partners. Therefore, with the high occurrence and variation within food peeps, this call will be the focus of this study. Further investigation into the variation of these calls provided by this study will allow the opportunity to examine referents within the bonobo vocal repertoire.

2.5 Critiques of Functional Referents

Several cases examining functional referents stand out as providing the most conclusive evidence of this phenomenon. These include vervet monkeys, Diana monkeys, tufted capuchin monkeys, chimpanzees, chickens, and yellow warblers. These studies have provided definitive evidence to fulfill all of the requirements for identifying functional referents and are generally regarded as methodological archetypes for examining functional referents.

Not all researchers accept the validity of functional referents in animal communication system (Zuberbühler, 2003). Critics of the concept say that researchers have accepted linguistic terminology for calls without any biological evidence to advocate its use (Owren & Rendall, 2001; Owren & Rendall, 1997). These critics maintain that functional referents are only a metaphor for what we see in humans and what we see in animals. This term also implies that it is unclear whether animals are intentionally eliciting these 'functionally referential' vocalizations. Furthermore, inherent in this lack of intentionality is the implication that animals exhibiting these characteristics are by some means producing vocalizations that are not truly referential despite behaving as if they do. It is thought that we cannot determine whether this information is encoded through higher processing or if individuals are conjuring images of referents when they hear a call. Cheney and Seyfarth (2007) propose investigation into the cognitive links behind language as a better means of

examining the evolution of language in humans. Instead, the term ‘functional referent’ opens the possibility that a referent signal simply results from an infant’s repeated exposure to these calls and witnessing conspecifics behavioral responses to these signals (Owren & Rendall, 2001; Owren & Rendall, 1997). Consistent relationships between these vocalizations and a particular context allow individuals to respond as if the signals contain information without the acoustics in the call actually containing any information in itself.

Some scholars argue further that the concept of functional referents draws away from other forms of analysis (Cheney & Seyfarth, 2007; Owren & Rendall, 2001). First, functional referents do not allow researchers to investigate both the signaler and receiver separately. Rather, they are combined into a single cooperative unit. In reality signalers may have different intentions than receivers, and signalers may be communicating unintentionally or trying to deceive receivers (*Macaca mulatta*: de Waal, 1986; *Pan troglodytes*: de Waal, 1986; *Cercopithecus aethiops*: Cheney & Seyfarth, 1985). Second, categorization of signals as either referential or emotional is a misrepresentation of reality (Cheney & Seyfarth, 2007). The ability for a call to convey specific information does not examine whether that call is affective or not (Cheney & Seyfarth, 2007). Calls can carry precise information while still maintaining an emotional component.

Critics also suggest that functional referents are too complex to characterize non-human animals and imply too much higher order thinking, especially if they are found in animals such as prairie dogs (*Cynomys gunnisoni*) (Zuberbühler, 2003). Owren and Rendall “propose adopting the more basic stance that the function of sound production is to influence others, no matter how that effect is achieved” (2001: 60). This model suggests that individuals use calls to affect the emotional responses of receivers (Zuberbühler, 2003).

Responses to these calls can be made by the acoustic structure of the signal itself or through learning the interactions that are typically associated with that call (Owren & Rendall, 2001).

Advances in the study of neurological processing between animals and humans suggest at least some higher order thinking (Sherwood et al., 2003; Gemba et al., 1995). Therefore, researchers should be wary of being too anthropocentric and denying nonhumans of particular abilities before examining whether they are actually present. It may be correct to apply linguistic terminology to the study of primate communication. However, the difficulty comes in the term ‘functional referent,’ which implies a vocalization behaving as a referent but somehow still lacking an essential aspect that creates human referents. Because of the close genetic relationship between great apes and humans, along with evidence of homologous neurological structure, the examination of referents, rather than functional referents, is warranted. Following an evolutionary perspective, the presence of referents in great apes’ vocal repertoire is expected and a necessary area to examine. Despite critical views regarding functional referents, it continues to be an area intensively investigated in all nonhuman animals.

2.6 Development of Referential Communication Studies with Great Apes

Beginning in the 1940s, Keith and Cathy Hayes ignited the first serious interest in great apes’ linguistic abilities (Hayes, 1951). The Hayes raised a chimpanzee, named Vicki in their home. Their goal throughout her upbringing was to investigate whether they could teach Vicki to speak English (Hayes, 1951). With limited success, she was able to mouth some words such as “mama,” “papa,” and “cup” (Hayes, 1951). However, the Hayes realized the difficulty Vicki seemed to have with attempting to say these words. This was later understood to result from the differing chimpanzee vocal anatomy, which prohibits them

from articulating the wide range of consonants and vowels found throughout human languages.

Although, Hayes (1951) noted that Vicki was able to pronounce a limited number of words, she did not always utilize these words in the correct context. Because she was not able to utilize these words in the correct context, it was generally accepted, even by the Hayes, that Vicki did not demonstrate a true knowledge or utilization of referential communication (Hayes, 1951). However, the Hayes' work with Vicki was not in vain. This study brought the potential differences in vocal anatomy between chimpanzees and humans to the attention of researchers. Also, the Hayes' research with teaching a chimpanzee language resulted in more researchers attempting to discover exactly how developed great apes' linguistic capabilities were.

As research interest in the topic of great ape linguistic ability increased, scientists quickly discovered the complexities involved with examining referential capabilities of another species. The first question after Vicki revealed the limited vocal capabilities of chimpanzees was which method would be best to examine referents (e.g. vocal, gestural, artificial symbols). Researchers tried various methods to teach reference, but then another issue arose: how exactly do you identify referential capabilities, and how do you ensure cueing and/or training are not producing artificial results? The Hayes' work with Vicki led researchers down an arduous road of discovery about humans as well as nonhuman great apes.

After the Hayes' work with Vicki, researchers' interest was piqued, resulting in numerous studies looking at great apes' referential capabilities. Allen and Beatrice Gardner were the next to take up the quest to examine *Pan's* referential capability. The Gardners

taught American Sign Language to a female chimpanzee named Washoe (Gardner & Gardner, 1969). They chose American Sign Language because by this time it was known that chimpanzee vocal anatomy and behavior was different from humans (Gardner & Gardner, 1969). Additionally, it was known the chimpanzees naturally communicate via gestural communication, so perhaps American Sign Language would simply be an expansion of a natural ability (Yerkes, 1943).

In order to examine referential capabilities of Washoe, the Gardners had three requirements for her. They thought in order for an approximation of language to be present, Washoe needed not only to be able to request food items and materials but also to answer questions and ask questions of the researchers (Gardner & Gardner, 1969). Washoe was able to learn over 30 words in the first 22 months of her life, and the Gardners considered this a successful example of referential communication by a nonhuman species (Gardner & Gardner, 1969).

Not all researchers accepted Washoe's abilities as indicative of referential communication, nor do all researchers accept American Sign Language as the best approach for examining referential abilities (Savage-Rumbaugh et al., 1980; Rumbaugh, 1977; Premack, 1971). Because *Pan* hand anatomy is different from human hand anatomy opponents of the work with Washoe suggest that a different method not requiring the use of vocals nor the use of gestures should be utilized (Savage-Rumbaugh et al., 1980; Premack & Premack, 1972). Because chimpanzees are knuckle-walkers, their hands have limited mobility in comparison to humans (Marzke & Wullstein, 1996). Therefore, some researchers believe that American Sign Language is difficult for apes and also results in ambiguity of signs (Braake & Savage-Rumbaugh, 1995).

Opponents claim that Washoe is not demonstrating true referential communication (Savage-Rumbaugh et al., 1980; Premack, 1971). Rather, she is usually imitating what she has seen researchers do in the past in similar contexts and utilizing those signs which are commonly correct in multiple contexts, resulting in a string of signs until she gets the desired result she is looking for from humans (Savage-Rumbaugh et al., 1980). The final result of the Vicki and Washoe research was a tremendous number of studies on referential capabilities of great apes, including some of the well known beginning cases such as: Sarah (Premack & Premack, 1972; Premack, 1971), Lana (Rumbaugh, 1977), Sherman and Austin (Savage-Rumbaugh, 1981), Koko (Patterson, 1979), and Kanzi (Savage-Rumbaugh et al., 1986).

2.7 Referential Communication with Kanzi

The laboratory investigation into referential communication in nonhumans has led researchers to an ongoing argument over the correct methodology and the proper determination of what results conclusively demonstrate referential communication. Sue Savage-Rumbaugh and colleagues hoped to end the debate surrounding referential communication by creating sound studies with rigorous methodologies (Savage-Rumbaugh et al., 1980). Kanzi, the participant of this study, was the first nonhuman great ape to demonstrate acquisition of a symbol system with no explicit training (Savage-Rumbaugh et al., 1986). Researchers were attempting to teach Kanzi's mother, Matata, how to use symbols without success while Kanzi was being reared (Savage-Rumbaugh et al., 1986). Despite his mother's inability to use the lexigram symbols, Kanzi was learning and eventually researchers were astounded to discover he knew several of these symbols with no explicit training (Savage-Rumbaugh et al., 1986).

Kanzi conclusively demonstrated that he was able to use these symbols in a referential manner to communicate (Savage-Rumbaugh, 1990). Furthermore, Kanzi utilizes a conversational manner of communication with humans including turn-taking and grammar (Greenfield & Savage-Rumbaugh, 1991). Researchers not only utilized lexigrams to communicate with Kanzi, they also used normal spoken English when interacting or near Kanzi (Savage-Rumbaugh et al., 1993). This led researchers to believe that Kanzi could use lexigrams but also could understand spoken English in a referential manner (Savage-Rumbaugh et al., 1993). A double blind study utilizing novel English sentences demonstrated that Kanzi was proficient both with lexigrams and also with understanding spoken English, including semantic and grammatical structure (Savage-Rumbaugh et al., 1993).

Kanzi has demonstrated a referential capacity in both a laboratory setting utilizing lexigrams and a natural vocal setting. He appears to have modulated his vocal levels during communicative interactions (Taglialatela et al., 2003). Kanzi continues to demonstrate a conversational interaction with humans in the vocal realm, along with the use of lexigrams, leading to turn-taking between responses and requests (Savage-Rumbaugh et al., 2004; Taglialatela et al., 2003). Previously, it had been demonstrated that along with the species typical vocal repertoire, Kanzi produced four additional vocalizations used exclusively during human interactions (Hopkins & Savage-Rumbaugh, 1991).

Taglialatela et al. (2003) sought to determine the semantic context associated with Kanzi's vocalization. They analyzed four vocalization groups (banana, grape, juice, and yes). The results indicated that these four different semantic contexts were acoustically different from each other. Using multinomial logistic regression, Taglialatela et al. (2003) were able to accurately predict the semantic context in which Kanzi produced a vocalization based on its

acoustic structure. The acoustic structure of vocalizations was consistently distinct in each context. Therefore, in Kanzi's case, context-specificity has been determined for several food items already when interacting with humans.

Vocal analysis demonstrated that Kanzi was able to alter his vocal output, on both temporal and spectral levels, while interacting with humans (Taglialatela et al., 2003). Analysis of vocalizations associated with these turn-taking interactions revealed that Kanzi produces acoustically distinct sounds in discrete semantic contexts (Taglialatela et al., 2003). Therefore, examination of food vocalizations and communication within this particular group of bonobos provides a unique opportunity to examine differentiation of vocalizations both within language-competent and non-language bonobos.

References

- Barclay D, Maurus M. 1992. Interdependency between structural components in squirrel monkey calls: function and sequential context. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors. Topics in Primatology. Tokyo: University of Tokyo Press. p 211-224.
- Benz JJ. 1993. Food-elicited vocalizations in golden lion tamarins: design features for representational communication. *Animal Behaviour* 45:443-455.
- Blumstein DT, Armitage KB. 1997. Alarm calling in yellow-bellied marmots: I. the meaning of situationally variable alarm calls. *Animal Behaviour* 53:143-171.
- Blumstein DT, Arnold W. 1995. Situational specificity in Alpine-marmot alarm communication. *Ethology* 100:1-13.
- Brakke KE, Savage-Rumbaugh ES. 1995. The development of language skills in bonobo and chimpanzee - I. Comprehension. *Language & Communication* 15:121-148.
- Caldwell MC, Caldwell DK. 1965. Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature* 207:434-435.
- Caldwell MC, Caldwell DK. 1968. Vocalization of naive captive dolphins in small groups. *Science* 159:1121-1123.
- Cheney DL, Seyfarth RM. 1985. Vervet monkey alarm calls: manipulation through shared information? *Behaviour* 93:150-166.
- Cheney DL, Seyfarth RM. 2007. Baboon Metaphysics: the Evolution of a Social Mind. Chicago: University of Chicago Press.

- De Waal FBM. 1986. Deception in the natural communication of chimpanzees. In: Mitchell RW, Thompson NS, editors. *Deception: Perspectives on Human and Nonhuman Deceit*. Albany: SUNY Press.
- de Waal FBM. 1988. The communicative repertoire of bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behaviour* 106:183-251.
- Di Bitetti MS. 2003. Food-associated calls of tufted capuchin monkeys (*Cebus apella nigrinus*) are functionally referential signals. *Behaviour* 140:565-592.
- Di Bitetti MS. 2005. Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigrinus*. *Animal Behaviour* 69:911-919.
- Elowson MA, Tannenbaum PL, Snowdon CT. 1991. Food-associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour* 42:931-937.
- Evans CS, Evans L. 1999. Chicken food calls are functionally referential. *Animal Behaviour* 58:307-319.
- Fischer J. 1998. Barbary macaques categorize shrill barks into two call types. *Animal Behaviour* 55:799-807.
- Fischer J, Hammerschmidt K. 2001. Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition* 4:29-35.
- Gardner RA, Gardner BT. 1969. Teaching sign language to a chimpanzee. *Science* 165:664-672.
- Gemba H, Miki N, Sasaki K. 1995. Cortical field potentials preceding vocalization and influences of cerebellar hemispherectomy upon them in monkeys. *Brain Research* 697:143-151.

- Gibbons CM. 2007. The referentiality of vocal signaling: behavioral and acoustic analysis of food barks. Columbus: Ohio State University.
- Gill SA, Sealy SG. 2003. Tests of two functions of alarm calls given by yellow warblers during nest defence. *Canadian Journal of Zoology* 81:1685-1690.
- Gill SA, Sealy SG. 2004. Functional reference in an alarm signal given during nest defence: set calls of yellow warblers denote brood-parasitic brown-headed cowbirds. *Behavioral Ecology & Sociobiology* 56:71-80.
- Goodman M, Czelusniak J, Page S, Meireles C. 2001. Where DNA sequences place *Homo sapiens* in a phylogenetic classification of primates. In: Tobias PV, Raath MA, J. M-C, Doyle GA, editors. *Humanity from African Naissance to Coming Millennia*: Firenze University Press/Witwatersrand University Press. p 279-290.
- Gouzoules S, Gouzoules H, Marler P. 1984. Rhesus monkey (*Macaca mulatta*) screams: representational signaling in the recruitment of agonistic aid. *Animal Behaviour* 32:182-193.
- Greenfield PM, Savage-Rumbaugh ES. 1991. Imitation, grammatical development, and the invention of protogrammar by an ape. In: Krasnegor NA, Rumbaugh DM, editors. *Biological and Behavioral Determinants of Language Development*. New York: Lawrence Erlbaum Associates. p 235-258.
- Hallberg KI. 2000. Specificity of chimpanzee food barks: reference to food type and quality. Columbus: Ohio State University.
- Hallberg KI, Boysen ST, Mukobi K. Chimpanzee food barks as referential signals: evidence from a laboratory playback experiment; 1999. p 59.

- Hallberg KI, Nelson DA, Boysen ST. 2003. Representational vocal signaling in the chimpanzee. In: de Waal FBM, Tyack PL, editors. *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*. Cambridge, MA: Harvard University Press. p 317-322.
- Hayes C. 1951. *The Ape in Our House*. New York: Harper.
- Hopkins WD, Savage-Rumbaugh S. 1991. Vocal communication as a function of differential rearing experiences in *Pan paniscus*: a preliminary report. *International Journal of Primatology* 12:559-583.
- Kaplan JR. 1977. Patterns of fight interference in free-ranging rhesus monkeys. *American Journal of Physical Anthropology* 47:279-288.
- Kaplan JR. 1978. Fight interference and altruism in rhesus monkeys. *American Journal of Physical Anthropology* 49:241-250.
- Le Roux A, Jackson TP, Cherry ML. 2001. Does Brants' whistling rat (*Parotomys brantsii*) use an urgency-based alarm system in reaction to aerial and terrestrial predators? *Behaviour* 138:757-773.
- Lorenzana JC, Sealy SG. 1999. A meta-analysis of the impact of parasitism by the brown-headed cowbird on its hosts. *Studies in Avian Biology* 18:241-253.
- Macedonia JM, Evans CS. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology* 93:177-197.
- Manser MB. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London* 268B:2315-2324.

- Manser MB, Bell MB, Fletcher LB. 2001. The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London* 268B:2485-2491.
- Marler P. 1985. Representational vocal signals of primates. *Fortschritte der Zoologie* 31:211-221.
- Marler P, Dufty A, Pickert R. 1986a. Vocal communication in the domestic chicken: I. does a sender communicate information about the quality of a food referent to a receiver. *Animal Behaviour* 34:188-193.
- Marler P, Dufty A, Pickert R. 1986b. Vocal communication in the domestic chicken: II. is a sender sensitive to the presence and nature of a receiver. *Animal Behaviour* 34:194-198.
- Marler P, Evans CS, Hauser MD. 1992. Animal signals: motivational, referential, or both? In: Papousek H, Jurgens U, Papousek M, editors. *Nonverbal Vocal Communication: Comparative and Developmental Approaches*. Cambridge: Cambridge University Press. p 66-86.
- Marzke MW, Wullstein KL. 1996. Chimpanzee and human grips: a new classification with a focus on evolutionary morphology. *International Journal of Primatology* 17:117-139.
- Ortega CP. 1998. *Cowbirds and Other Brood Parasites*. Tucson: University of Arizona Press.
- Owings DH, Virginia RA. 1978. Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Zeitschrift für Tierpsychologie* 46:58-70.
- Owren MJ, Rendall D. 1997. An affect-conditioning model of nonhuman primate signaling. In: Beecher MD, Owings DH, Thompson NS, editors. *Perspectives in Ethology*. New York: Plenum Press. p 299-346.

- Owren MJ, Rendall D. 2001. Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology* 10:58-71.
- Patterson F. 1979. *Linguistic Capabilities of a Lowland Gorilla*. Palo Alto: Stanford University.
- Pereira ME, Macedonia JM. 1991. Ringtailed lemur anti-predator calls denote predator class, not response urgency. *Animal Behaviour* 41:543-544.
- Premack AJ, Premack D. 1972. Teaching language to an ape. *Scientific American* 227:92-99.
- Premack D. 1971. Language in chimpanzees? *Science* 172:808-822.
- Reiss D, McCowan B, Marino L. 1997. Communicative and other cognitive characteristics of bottlenose dolphins. *Trends in Cognitive Sciences* 1(4):140-145.
- Rendall D, Seyfarth RM, Cheney DL, Owren MJ. 1999. The meaning and function of grunt variants in baboons. *Animal Behaviour* 57:583-592.
- Robinson SR. 1981. Alarm communication in Belding's ground squirrels. *Zeitschrift für Tierpsychologie* 56:150-168.
- Rumbaugh DM. 1977. *Language Learning by a Chimpanzee: the Lana Project*. New York: Academic Press.
- Savage-Rumbaugh ES. 1981. Can apes use symbols to represent their world. *Annals of the New York Academy of Sciences* 364:35-59.
- Savage-Rumbaugh ES. 1990. Language acquisition in a nonhuman species: implications for the innateness debate. *Developmental Psychobiology* 23:599-620.

- Savage-Rumbaugh ES, McDonald K, Sevcik RA, Hopkins WD, Rubert E. 1986. Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General* 115:211-235.
- Savage-Rumbaugh ES, Rumbaugh DM, Boysen S. 1980. Do apes use language? *American Scientist* 68:49-61.
- Savage-Rumbaugh S, Fields WM, Spircu T. 2004. The emergence of knapping and vocal expression embedded in a *Pan/Homo* culture. *Biology & Philosophy* 19:541-575.
- Savage-Rumbaugh SE, Murphy J, Sevcik RA, Brakke KE, Williams SL, Rumbaugh DM. 1993. Language comprehension in ape and child. *Monographs of the Society for Research & Child Development* 58:1-256.
- Sayigh LS, Tyack PL, Wells RS, Scott MD, Irvine AB. 1995. Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology & Sociobiology* 36(3):171-177.
- Seyfarth RM, Cheney DL, Marler P. 1980a. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* 210:801-803.
- Seyfarth RM, Cheney DL, Marler P. 1980b. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour* 28:1070-1094.
- Sherwood CC, Broadfield DC, Holloway RL, Gannon PJ, Hof PR. 2003. Variability of Broca's area homologue in African great apes: implications for language evolution. *Anatomical Record* 271A:276-285.

- Slobodchikoff CN, Kiriazis J, Fischer C, Creef E. 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. *Animal Behaviour* 42:713-719.
- Slocombe KE, Zuberbühler K. 2005. Functionally referential communication in a chimpanzee. *Current Biology* 15:1779-1784.
- Slocombe KE, Zuberbühler K. 2006. Food-associated calls in chimpanzees: responses to food types or food preferences? *Animal Behaviour* 72:989-999.
- Smith WJ. 1977. *The Behavior of Communicating: an Ethological Approach*. Cambridge, MA: Harvard University Press.
- Smith WJ. 1991. Animal communication and the study of cognition. In: Ristau C, editor. *Cognitive Ethology: The Minds of Other Animals*. Hillsdale, New Jersey: Lawrence Erlbaum Associates, Publishers. p 209-230.
- Snowdon CT, Elowson MA. 1992. Ontogeny of primate vocal communication. *Human Origins* 1:279-290.
- Tagliabue JP, Savage-Rumbaugh S, Baker LA. 2003. Vocal production by a language-competent *Pan paniscus*. *International Journal of Primatology* 24:1-17.
- Van Krunkelsven E, Dupain J, Van Elsacker L, Verheyen RF. 1996. Food calling by captive bonobos (*Pan paniscus*): an experiment. *International Journal of Primatology* 17:207-217.
- Yerkes RM. 1943. *Chimpanzees*. New Haven: Yale University Press.
- Zuberbühler K. 2000. Referential labeling in Diana monkeys. *Animal Behaviour* 59:917-927.

Zuberbühler K. 2003. Referential signaling in non-human primates: cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior* 33:265-307.

Chapter Three: Methods

3.1 Hypotheses

Because *Pan* is the closest living genus to humans (*Homo sapiens*) (Goodman et al., 2001) we would expect to find some continuity between the biology and behavior of humans and bonobos. With special regard to language, apes have shown structural continuity for certain brain structures (Petkov et al., 2008; Sherwood et al., 2003; Gannon et al., 1998; Gamba et al., 1995). Furthermore, results of several experimental tests suggest aspects of referential communication characterize the vocal repertoire of the common chimpanzee (Gibbons, 2007; Slocombe & Zuberbühler, 2005; Hallberg, 2000), a sister taxa to bonobos. Therefore, I expect aspects of referential communication to characterize the vocal repertoire of bonobos as well.

The objectives of this study include:

- 1) to produce a general catalog of an individual bonobo's food peeps,
- 2) to perform a general comparison of bonobo food peeps based on food type, and
- 3) to determine if bonobos have any aspect of referential communication in their food calls.

3.2 Study Site

Great Ape Trust of Iowa is a scientific research facility dedicated to understanding the origins and future of culture, language, tools, and intelligence through noninvasive interdisciplinary study¹. It is located on a 240 acre campus in southeast Des Moines. The seven bonobos who make this home are housed in a 10,000 square foot enclosure. The indoor enclosure consists of seventeen dividable rooms along with an exit to two outdoor rooms.

¹ <http://www.greatapetrust.org/about/index.php>

The family is housed in various groups throughout their enclosure ranging from all seven individuals together to several groups of one to several individuals. These groups are determined by the caretakers on a daily basis.

3.3 Study Subject & Materials

The bonobo participant, Kanzi, is a 27 year old male housed as part of a family unit at Great Ape Trust of Iowa. The family consists of seven bonobos: three adults (Matata, Panbanisha, and Kanzi) and four adolescents (Elikya, Nyota, Maisha, and Nathan) (Table 3.1). There are four males and three females ranging in age from approximately eight to 38 years of age. The bonobo participant for this study has taken part in vocalization research in the past and is considered language-competent (Savage-Rumbaugh et al., 1993). Kanzi was raised in a *Pan-Homo* culture, with the English language playing an important role in his daily life. A *Pan-Homo* culture occurs when infants are co-reared by both humans and their own *Pan* species resulting in integration of very different care-giving, communication patterns, and enculturation of both *Homo* and *Pan* aspects into their daily lifestyles (Savage-Rumbaugh et al., 2005). His understanding of spoken English has been demonstrated (Savage-Rumbaugh et al., 1993).

Table 3.1 Demographics of the bonobo community housed at Great Ape Trust of Iowa.

Individual	Age	Sex	Rearing Style	Raised By
Matata	~39	Female	Non-language	Wild-caught
Kanzi	28	Male	Language	Matata
Panbanisha	23	Female	Language	Matata
Elikya	11	Female	Non-language	Matata
Nyota	11	Male	Language	Panbanisha
Maisha	8	Male	Non-language	Matata
Nathan	8	Male	Language	Panbanisha

Several main material items were used for this study. Six food items were made available for the vocalization recording. These six food items included: peanuts, green onions, mushrooms, blueberries, diet coke, and banana. All vocalizations were recorded with a directional Senheiser microphone (ME66 w/ K-6 power supply) and a TasCam (HD-P2) digital recorder.

3.4 Data Collection

I recorded the participant's food vocalizations. Food peeps were recorded from the individual as he was feeding exclusively on one type of food, preferably in his outdoor enclosure for clearer recordings. Recording distances varied depending on the location of the individual but did not exceed 10 meters and were usually within one to two meters.

One session consisted of each food item being presented. Each food item was placed in a brown paper bag and brought to the area of the enclosure the participant was housed in. I controlled the recorder while a caretaker presented one bag at a time to the individual. I recorded all vocalizations made. When the individual finished the food item in the paper bag, the caretaker presented the next bag. The session ended when all food items had been presented. A minimum criterion of at least ten clear food vocalizations was recorded for the participant with each food item.

3.5 Raven Program

Vocalizations were analyzed using the program Raven. The Raven program is typically used for examining animal vocalizations². This program, contrary to programs used for human speech, ignores formants instead looking primarily at frequency, time, power, and energy as indicators of vocalizations. Furthermore, Raven analyzes each sound as a distinct

² www.birds.cornell.edu/brp/raven/Raven.html

vocalization to be measured. I examined nine distinct features and seven distinct calculations from those measurements (Table 3.2). The features utilized within the Raven Program include: low frequency, high frequency, maximum frequency, delta time, energy, average power, and maximum power. Initial frequency and terminal frequency were measured by taking the maximum frequency in the first and last 0.03 seconds of the vocalization.

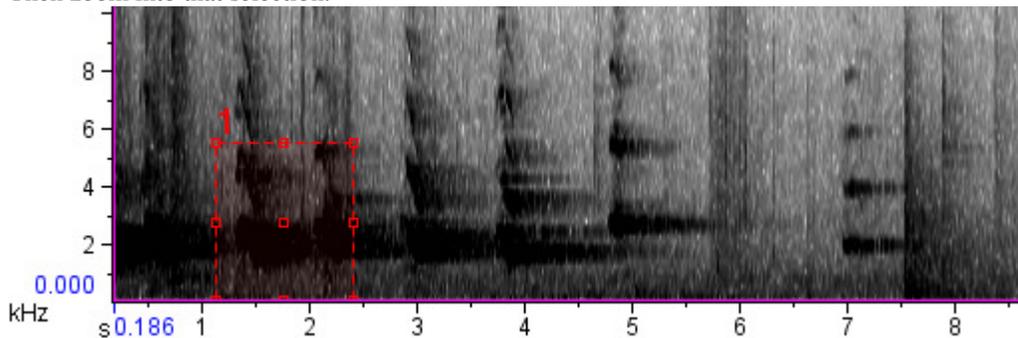
Table 3.2 Vocalization measurements analyzed in Raven, adopted partially from Tagliatela et al., 2003.

Acoustic Variables	Description
Onset	Initial frequency of vocalization (kHz)
Peak	Highest frequency of vocalization (kHz)
Endpoint	Terminal frequency of vocalization (kHz)
Minimum	Lowest frequency of vocalization (kHz)
Duration	Endpoint Time minus onset time (ms)
(Onset+Peak+Endpoint)/3	Sum of initial, high, and terminal frequency divided by three (kHz)
Range Frequency	Difference between high and low frequency (kHz)
Delta Frequency	Difference between initial and terminal frequency (kHz)
Peak – Minimum Range	Maximum frequency minus minimum frequency (kHz)
Peak – Endpoint Range	High frequency minus terminal frequency (kHz)
Onset – Peak Range	High frequency minus initial frequency (kHz)
Slope	Onset freq (kHz) – endpoint freq (kHz)/duration (ms)
Energy	Total energy of the vocalization (dB)
Maximum Frequency	Frequency at which maximum power occurs (kHz)
Maximum Power	Highest power of vocalization (dB)
Average Power	Power averaged across entire vocalization (dB)

Figure 3.1 demonstrates the measuring technique used in the Raven Program. Vocalizations tend not to provide a precise cut-off for measurement. Therefore, I tried to be as consistent as possible when measuring vocalizations. Figure 3.1 depicts a sample of vocalizations recorded. In order to measure the vocalization, I would place a box, the measurement tool, clearly around the borders of the lowest graded section of a single vocalization. Once the box was clearly around these borders, I zoomed to that selection, where I more specifically adjusted the box around the border of the vocalization. As an endpoint criterion for all vocalizations, I placed the right border of the box where the vocalization first begins to fade. This criterion was established because it provided a

relatively simple, consistent measurement for all vocalizations and also appeared to be the end of a vocalization when listened to at a slow speed. To help ensure this criterion was met, after I finished all data collection, I reviewed all vocalizations ensuring I used consistent measurement techniques.

Part A. This is an example of a segment of a recording session with Kanzi on 14 May 2008 while feeding on mushrooms. In the process of measuring a vocalization, I would first make a large box around one vocalization. Then zoom into that selection.



Part B. Once zoomed close to the vocalization, I would make a more precise box around the vocalization, which I would later use for my analysis.

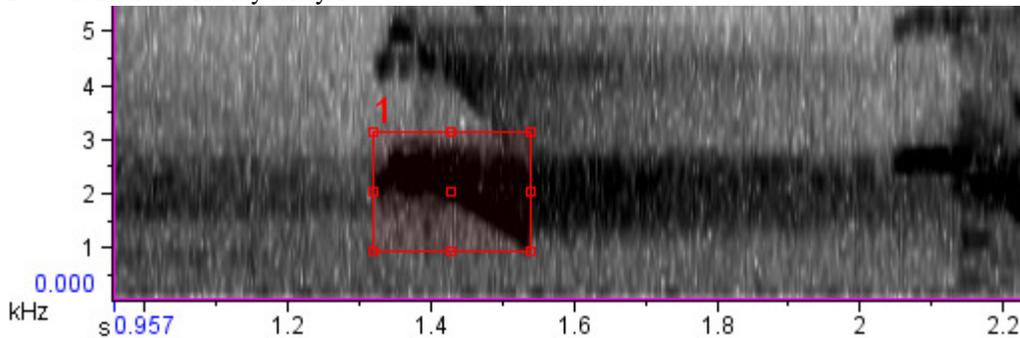


Figure 3.1 Spectrogram of a recording session magnified to show the measurement used for one particular vocalization.

3.6 Data Analysis

Once all of the vocalizations were recorded, several features were examined:

- Acoustic features present in food peeps,
- Features differentiating specific calls, and
- Whether vocalizations can be categorized using features into correct food type.

There is no consensus within the field of primate vocalizations on which acoustic analysis provides the best description of the variation within vocalizations. There tends to be three different analyses used to examine acoustic features in primate vocalizations. First, multinomial regression (e.g. Taglialatela et al., 2003) can be used to examine acoustic features. This analysis tends to give a more detailed analysis of acoustic variation (pers. comm. M. Shelley, statistician). However, this can provide more detail than is needed and is difficult to interpret. Furthermore, multiple regression analysis is intended for continuous variables and is not an adequate method to investigate distinct vocalizations for food categories. The other two acoustic analyses include principal component analysis (e.g. Mitani et al., 1996) and discriminant function analysis (e.g. Slocombe & Zuberbühler, 2005). These two forms are sometimes used in conjunction with each other (Oyakawa et al., 2007).

I converted recorded vocalizations into spectrograms and drew the appropriate measurements. All analysis was conducted in the SAS 9.1 program. Before more complex analysis was conducted, a oneway analysis of variance was conducted comparing each variable measured to food type. This determined which acoustic features tend to be relevant distinguishers of food type within food peeps. Then more intensive analysis was conducted. Stepwise discriminant procedure was utilized in order to provide insight into multinomial regression and also a starting point for the development of models. A stepwise procedure involves entering or removing variables based on the amount of information they can explain. Due to criticism that stepwise procedures capitalize on chance and should not be heavily relied on (pers. comm. M. Shelley), initial investigation into models was conducted without the stepwise procedure. Additionally, the stepwise procedure was run in a variety of patterns and starting points to create a number of models on which further analyses could be

conducted. The stepwise procedure allowed investigation into the variable significance and R^2 value for each model.

After a model was created, the variables were then entered into a discriminant function analysis (DFA). This analysis was used to identify the differences in vocalizations between contexts (specific food items) (Fischer et al., 2001). It identified how well a set of acoustic variables differentiated between food types. Acoustic variables were combined into one or more discriminant functions, resulting in $N-1$ discriminant functions where N is the number of groups (e.g. the number of food items). After these discriminant functions were created, DFA provided a reclassification procedure that assigned a call to an appropriate group or the other group. The reclassification procedure compared the classified vocalizations to the contexts in which the vocalizations were actually elicited to develop a percentage of correct classification. Also, a two-way analysis of variance assessed whether the differences between these discriminant functions were significant. If differences between food items are significant, this would support the hypothesis that bonobo food peeps are context-specific.

Additionally, a canonical discriminant analysis was conducted for each model. The canonical discriminant analysis has not been utilized in analyzing nonhuman primate vocalizations. However, it can offer another level of investigation. The canonical discriminant analysis creates canonical variables, which are linear combinations of the model's variables that provide the maximal separation between food types. This analysis is also able to calculate the squared distance between the different food types. Significant distances between two food types suggest that vocalizations given for these two different foods are significantly distinguishable from one another. Therefore, this analysis can offer

particular insight into whether food type vocalizations are clearly distinguishable from other food types or based more generally on food preference.

Finally, a principal component analysis (PCA) and varimax rotation factor analysis was used to summarize the acoustic variables present in food peeps. PCA calculated the associations between variables and determined which acoustic variables were accounting for the most variation in food peeps (Rendall et al., 1998).

References

- Fischer J, Hammerschmidt K, Cheney DL, Seyfarth RM. 2001. Acoustic features of female chacma baboon barks. *Ethology* 107:33-54.
- Gannon PJ, Holloway RL, Broadfield DC, Braun AR. 1998. Asymmetry of chimpanzee planum temporale: humanlike pattern of Wernicke's brain language area homolog. *Science* 279:220-222.
- Gemba H, Miki N, Sasaki K. 1995. Cortical field potentials preceding vocalization and influences of cerebellar hemispherectomy upon them in monkeys. *Brain Research* 697:143-151.
- Goodman M, Czelusniak J, Page S, Meireles C. 2001. Where DNA sequences place *Homo sapiens* in a phylogenetic classification of primates. In: Tobias PV, Raath MA, J. M-C, Doyle GA, editors. *Humanity from African Naissance to Coming Millennia: Firenze University Press/Witwatersrand University Press*. p 279-290.
- Mitani JC, Gros-Louis J, Macedonia JM. 1996. Selection for acoustic individuality within the vocal repertoire of wild chimpanzees. *International Journal of Primatology* 17:569-583.
- Oyakawa C, Koda H, Sugiura H. 2007. Acoustic features contributing to the individuality of wild agile gibbon (*Hylobates agilis agilis*) songs. *American Journal of Primatology* 69:777-790.
- Petkov CI, Kayser C, Steudel T, Whittingstall K, Augath M, Logothetis NK. 2008. A voice region in the monkey brain. *Nature Neuroscience* 11:367-374.

- Rendall D, Owren MJ, Rodman PS. 1998. The role of vocal tract filtering in identity and cueing in rhesus monkey (*Macaca mulatta*) vocalizations. *Journal of the Acoustic Society of America* 103:602-614.
- Savage-Rumbaugh S, Segerdahl P, Fields WM. 2005. Individual differences in language competencies in apes resulting from unique rearing conditions imposed by different first epistemologies. In: Namy LL, editor. *Symbol Use and Symbolic Representation: Developmental and Comparative Perspectives*. New York: Routledge. p 199-220.
- Savage-Rumbaugh SE, Murphy J, Sevcik RA, Brakke KE, Williams SL, Rumbaugh DM. 1993. Language comprehension in ape and child. *Monographs of the Society for Research & Child Development* 58:1-256.
- Sherwood CC, Broadfield DC, Holloway RL, Gannon PJ, Hof PR. 2003. Variability of Broca's area homologue in African great apes: implications for language evolution. *Anatomical Record* 271A:276-285.
- Slocombe KE, Zuberbuhler K. 2005. Functionally referential communication in a chimpanzee. *Current Biology* 15:1779-1784.
- Tagliabue JP, Savage-Rumbaugh S, Baker LA. 2003. Vocal production by a language-competent *Pan paniscus*. *International Journal of Primatology* 24:1-17.

Chapter Four: Results

4.1 Data Collected

Data were collected for a period of thirty days from 30 April to 28 May 2008. A total of 378 vocalizations were recorded. Attempts were made to balance the number of vocalizations per each food item. However, the number of vocalizations was ultimately controlled by the amount of time and attention the participant decided to spend with particular food items. The food items diet coke and peanuts were vocalized over the most (Table 4.1). Green onions had the least amount of vocalizations with only sixteen vocalizations recorded. All of the vocalizations for green onions were recorded in one data session.

Table 4.1 Number of vocalizations recorded for each food type utilizing the full data set.

Food Type	Number of Vocalizations
Banana	32
Blueberry	78
Diet Coke	91
Green Onion	16
Mushroom	63
Peanut	98
Total	378

Using all of these vocalizations, a oneway analysis of each variable by food type was constructed. The majority of the 16 variables are significantly related to food type (Table 4.2). Only maximum frequency ($F=1.2534$, $p\text{-value}=0.2836$), high-initial frequency ($F=0.5967$, $p\text{-value}=0.7025$), terminal frequency ($F=1.0428$, $p\text{-value}=0.3921$), and low frequency ($F=1.9656$, $p\text{-value}=0.0830$) are not significantly related. The remaining 12 variables significantly differ based on food type.

Also, the full data set was examined for any outliers. Out of the 378 vocalizations, 25 contained outliers for at least one of the variables (Table 4.3). Eighteen of the outliers were for peanut and diet coke. These two food items may have the most outliers because some vocalizations were given while simultaneously feeding (e.g. vocalizing with diet coke in the mouth). Since the large discrepancy could be indicative of a relevant difference or preference between food type, rather than eliminate outlying vocalizations, all outliers were moved to three standard deviations away from the mean through a process of winsorizing the data.

Table 4.2 Results of oneway analysis on food type for each variable using the full data set (* indicates significant difference based on food type).

Variable	R ² Value	F-Statistic	P-Value
Low Frequency	0.025739	1.9656	0.0830
High Frequency	0.0429	3.348	0.0058*
Delta Time	0.16126	14.3045	<0.0001*
Initial Frequency	0.0395	3.0597	0.0101*
Terminal Frequency	0.013822	1.0428	0.3921
Frequency Mean	0.032236	2.4783	0.0317*
Frequency Range	0.069108	5.5234	<0.0001*
Initial-Terminal Frequency	0.048185	3.7664	0.0024*
High-Initial Frequency	0.007957	0.5967	0.7025
High-Terminal Frequency	0.049388	3.8654	0.002*
Slope	0.033634	2.5895	0.0255*
Energy	0.067645	5.3979	<0.0001*
Maximum Frequency	0.016568	1.2534	0.2836
Maximum Power	0.076864	6.1948	<0.0001*
Average Power	0.084832	6.8966	<0.0001*
(Initial+High+Terminal)/3	0.032236	2.4783	0.0317*

A second set of data was also used to analyze vocalizations. Since in one recording session upwards of 30 vocalizations could be recorded for one food item, I wanted to take into account possible outside influences affecting later vocalizations. As time continued to pass from the initial viewing of a food item, it was more probable that his vocalizations could have changed meaning due to different stimuli or motivation becoming a dominant force. Therefore, I created a subset of data using only the first four vocalizations emitted upon first

observing a food item. A breakdown of the total number of vocalizations for the limited data set can be seen in Table 4.4. Green onion was eliminated as a food item in this data set. He only vocalized for green onions during one recording session, so this was too small of a sample size to include in the population of vocalizations. In situations where he vocalized less than four times in one session, the entire set of vocalizations was used.

Table 4.3 Outliers from the full data set.

Food Type	Variable
Peanut	Delta Time
Peanut	Slope
Peanut	Maximum Frequency
Peanut	High-Initial Frequency
Peanut	High-Initial Frequency
Peanut	Delta Frequency
Peanut	High-Terminal Frequency
Blueberry	Delta Time
Blueberry	Delta Time
Blueberry	High-Initial Frequency
Blueberry	High-Initial Frequency
Diet Coke	High-Terminal Frequency; Delta Frequency
Diet Coke	High-Terminal Frequency; Slope; Delta Frequency
Diet Coke	High-Initial Frequency
Diet Coke	High-Terminal Frequency
Diet Coke	Delta Frequency
Diet Coke	Low Frequency; Terminal Frequency
Diet Coke	Maximum Power; Average Power; Energy
Diet Coke	Average Power
Diet Coke	Average Power
Diet Coke	Average Power
Diet Coke	Initial Frequency; Delta Frequency; Slope; Average Power
Mushroom	High-Initial Frequency
Mushroom	High-Terminal Frequency
Banana	Slope

Table 4.4 Number of vocalizations recorded for each food item utilizing the limited data set.

Food Type	Number of Vocalizations
Banana	18
Blueberry	27
Diet Coke	23
Mushroom	26
Peanut	26
Total	120

Using the limited data set, a oneway analysis of each variable by food type was constructed. Of the 16 variables in the limited data set, only seven are significantly related to food type (Table 4.5). These include: low frequency (F=5.4206, p=0.0005), high frequency (F=2.6904, p=0.0346), terminal frequency (F=3.3270, p=0.0128), frequency mean (F=2.9020, p=0.0249), high-terminal frequency (F=2.8705, p=0.0261), maximum frequency (F=2.7482, p=0.0316), and (initial+high+terminal frequency)/3 (F=2.902, p=0.0249). The limited data set was also examined for any outliers. Out of the 120 vocalizations, six contained outliers for at least one of the variables (Table 4.6). All outliers were winsorized. Before conducting further statistical tests, models were created using both the data set with outliers unchanged and the data set with winsorized outliers. The conclusion of discriminant function procedures didn't change dramatically. Therefore, it was determined that these outliers must not have a significant impact on the data set. Models presented in the results used winsorized data sets unless stated otherwise.

Table 4.5 Results of oneway analysis on food type for each variable using the limited data set (* indicates significant difference based on food type).

Variable	R ² Value	F-statistic	p-value
Low Frequency	0.158634	5.4206	0.0005*
High Frequency	0.085571	2.6904	0.0346*
Delta Time	0.50844	1.5401	0.1952
Initial Frequency	0.078048	2.4338	0.0513
Terminal Frequency	0.10372	3.3270	0.0128*
Frequency Mean	0.091685	2.9020	0.0249*
Frequency Range	0.064476	1.9814	0.1020
Initial-Terminal Frequency	0.067969	2.0966	0.0857
High-Initial Frequency	0.0031387	0.9316	0.4483
High-Terminal Frequency	0.09078	2.8705	0.0261*
Slope	0.056758	1.7300	0.1481
Energy	0.005968	0.1726	0.9520
Maximum Frequency	0.087251	2.7482	0.0316*
Maximum Power	0.00614	0.1776	0.9495
Average Power	0.022528	0.6626	0.6192
(Initial+High+Terminal)/3	0.091685	2.902	0.0249*

Table 4.6 Outliers from the limited data set.

Food Type	Variable
Diet Coke	Delta Frequency, High-Terminal Frequency, Slope
Diet Coke	Delta Frequency, High-Terminal Frequency, Slope
Mushroom	High-Initial Frequency
Peanut	Delta Time
Peanut	High-Initial Frequency
Peanut	Delta Frequency

4.2 Full Data Set Models

4.2.1 Modell

A variety of models were created using SAS 9.1 to see how well vocalizations could be categorized according to food type. Models were created by testing variable combinations and also using different forms and starting points for a stepwise procedure. Over 60 models were initially created. All models demonstrated a significant difference in vocalizations according to food types. Only six models will be discussed here. Five of these models were determined to be among the candidates for the best variables differentiating food types. The remaining model included all of the variables initially measured in the Raven program and is included as a general indication of the variable relationship to food type.

Prior to winsorizing the data set, a stepwise discriminant procedure was conducted. The procedure is outlined in Table 4.7. This procedure developed a six-variable model containing low frequency, delta time, energy, maximum frequency, average power, and $(\text{initial}+\text{high}+\text{terminal})/3$. This six-variable model was then entered utilizing the winsorized full data set. This six-variable model has a total R^2 equal to 0.3136. Most variables add significantly to the model (Table 4.8). However, average power does not add significantly ($F=2.13$, $p=0.0617$). Therefore, it is not a candidate for the best model.

This model was entered into a discriminant procedure to see how well it did at classifying vocalizations into food type using these six variables. The model developed to

explain food type with these variables demonstrated a significant difference between food types (Chi-Square=457.264324, p-value<0.0001). This was further substantiated by Wilk's Lambda test (F=7.14, p-value<0.0001), Pillai's Trace test (F=6.81, p-value<0.0001), Hotelling-Lawley Trace test (F=7.31, p-value<0.0001), and Roy's Greatest Root test (F=18.09, p-value<0.0001).

Table 4.7 Stepwise procedure to producing six-variable Model 1.

Order	Step	Partial R ²	F-Statistic	P-Value
1	Entered delta time	0.1613	14.30	<0.0001
2	Entered average power	0.1008	8.32	<0.0001
3	Entered range frequency	0.1118	9.32	<0.0001
4	Entered low frequency	0.0342	2.61	0.0246
5	Entered maximum frequency	0.0406	3.11	0.0091
6	Entered (initial+high+terminal)/3	0.0376	2.87	0.0149
7	Removed range frequency	0.0197	1.47	0.1982
8	Entered energy	0.0323	2.45	0.0333

Table 4.8 Variable significance for Model 1 utilizing the winsorized full data set.

Variable	Partial R ²	F-Statistic	P-Value
Low Frequency	0.0488	3.77	0.0024
Delta Time	0.0945	7.66	<0.0001
Energy	0.0323	2.45	0.0333
Maximum Frequency	0.0687	5.42	<0.0001
Average Power	0.0282	2.13	0.0617
(Initial+High+Terminal)/3	0.0411	3.14	0.0086

After the relationship between food type and these six variables was established, the vocalizations were re-entered into the model to see if the predicted food type matched the actual food type when the vocalization was emitted. Table 4.9 shows the percentage classified into the various food types. Generally, a correct classified percentage of at least 50% is considered good, and a classification of at least 80% is ideal (pers. comm. M. Shelley, statistician). Blueberry (57.69%) and peanut (59.18%) were classified well, and green onion (100%) was classified perfectly. This suggests that blueberry, peanut, and green onion were fairly discrete categories based on the six-variable model. Banana, diet coke, and mushroom

were not as discrete and tended to be misclassified. Diet coke and mushroom were most often misclassified as peanut.

Table 4.9 Percentage of vocalizations reclassified into correct food type for full data Model 1.

	Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	15.63	28.13	6.25	12.50	25.00	12.50
Blueberry	1.28	57.69	11.54	6.41	5.13	17.95
Diet Coke	1.10	13.19	45.05	10.99	3.30	26.37
Green Onion	0.00	0.00	0.00	100.00	0.00	0.00
Mushroom	4.76	12.70	9.52	14.29	20.63	38.10
Peanut	3.06	13.27	6.12	8.16	10.20	59.18

In addition to the discriminant function analysis, a canonical discriminant analysis was conducted. Canonical variables were created to explain the differentiation of food groups using the variables presented in this model. Four canonical variables can explain a significant amount of variation in food types (Table 4.10). The four canonical variables can explain a total of 99.75% of the food type variation.

Table 4.10 Description of created canonical variables and significance for full data Model 1.

	Canonical Corr.	Eigenvalue	Proportion Explained	Cumulative	F-Statistic	P-Value
Canonical Variable 1	0.475754	0.2926	0.4878	0.4878	7.14	<0.0001
Canonical Variable 2	0.397645	0.1878	0.3132	0.8010	5.53	<0.0001
Canonical Variable 3	0.286064	0.0891	0.1486	0.9496	3.62	<0.0001
Canonical Variable 4	0.167743	0.0290	0.0483	0.9979	1.85	0.0864
Canonical Variable 5	0.035824	0.0013	0.0021	1.0000	0.24	0.7880

The squared distances between food groups were determined using these four canonical variables (Table 4.11). Not all of the groups are distinct from one another. In particular, there is not a significant difference between mushroom and green onion ($F=0.8372$, $p=0.1071$). Finally, a principal component factor analysis with a varimax rotation was conducted. The principal component analysis determined there were two factors

applicable to Model 1 (Figure 4.1). The varimax orthogonal rotated factor pattern (Table 4.12) demonstrates that Factor 1 groups maximum frequency, (initial+high+terminal frequency)/3, and low frequency together explaining the most variation, while Factor 2 groups average power, energy, and delta time together explaining the greatest amount of variation in food type (Figure 4.2).

Table 4.11 Squared distance between food groups and associated F-statistics and p-values for full data Model 1.

		Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.8702	2.0429	1.4250	1.4967	1.7580
	F-Statistic	0.0000	3.2469	7.9525	2.4993	5.2225	6.9732
	P-Value	1.0000	0.0040	<0.0001	0.0221	<0.0001	<0.0001
Blueberry	Squared Distance	0.8702	0.0000	1.5443	3.4043	2.0330	1.8502
	F-Statistic	3.2469	0.0000	10.6645	7.4318	11.6499	13.2127
	P-Value	0.0040	1.0000	<0.0001	<0.0001	<0.0001	<0.0001
Diet Coke	Squared Distance	2.0429	1.5443	0.0000	2.3897	1.4678	1.0784
	F-Statistic	7.9525	10.6645	0.0000	5.3467	8.9847	8.3665
	P-Value	<0.0001	<0.0001	1.0000	<0.0001	<0.0001	<0.0001
Green Onion	Squared Distance	1.4250	3.4043	2.3897	0.0000	0.8372	1.6632
	F-Statistic	2.4993	7.4318	5.3467	0.0000	1.7565	3.7615
	P-Value	0.0221	<0.0001	<0.0001	1.0000	0.1071	0.0012
Mushroom	Squared Distance	1.4967	2.0330	1.4678	0.8372	0.0000	0.4287
	F-Statistic	5.2225	11.6499	8.9847	1.7565	0.0000	2.7302
	P-Value	<0.0001	<0.0001	<0.0001	0.1071	1.0000	0.0140
Peanut	Squared Distance	1.7580	1.8502	1.0784	1.6632	0.4287	0.0000
	F-Statistic	6.9732	13.2127	8.3665	3.7615	2.7302	0.0000
	P-Value	<0.0001	<0.0001	<0.0001	0.0012	0.0140	1.0000

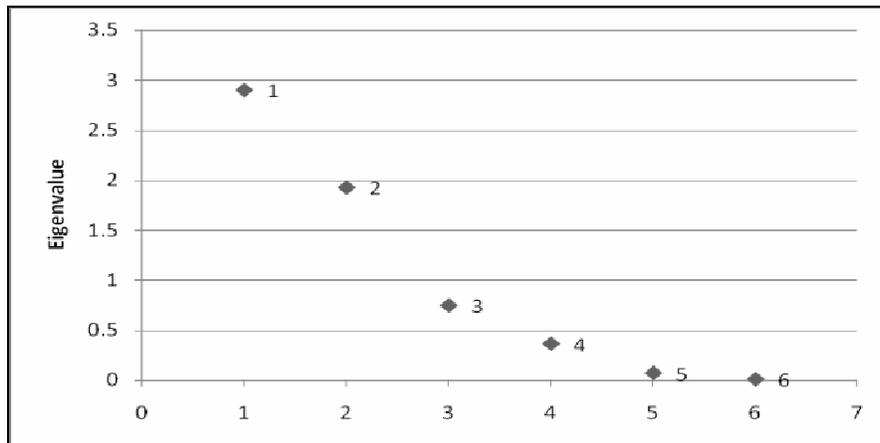


Figure 4.1 Graph of factors based on eigenvalues for the various factors created for full data Model 1. Values greater than one are viable factors (mineigen criterion).

Table 4.12 Rotated factor pattern for factors retained by the mineigen criterion for full data Model 1.

	Factor 1	Factor 2
Delta Time	0.21581	0.59291
Average Power	-0.03024	0.93526
Low Frequency	0.86352	-0.13275
Maximum Frequency	0.91302	0.23735
Energy	0.06690	0.98913
(Initial+High+Terminal)/3	0.92562	0.22918

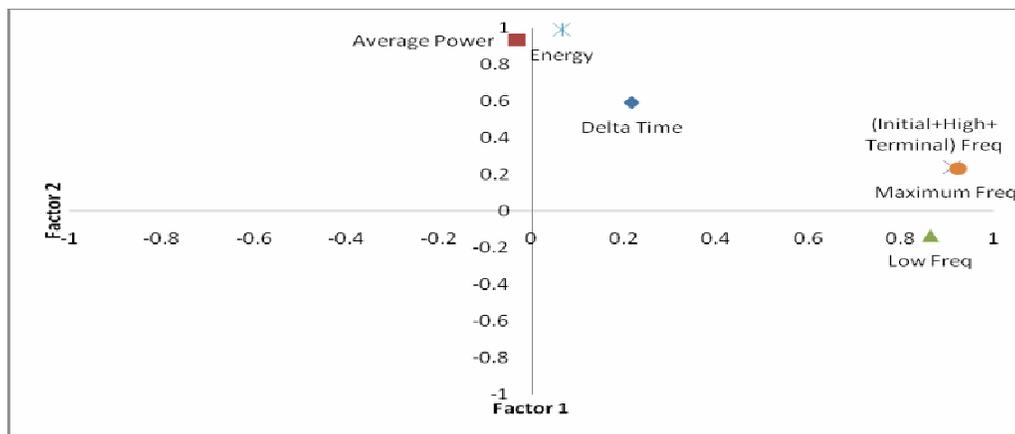


Figure 4.2 Plot of variable pattern for Factor 1 versus Factor 2 in full data Model 1.

4.2.2 Model 2

Once the data was winsorized, a stepwise discriminant procedure was run again to see if a different model was chosen. This procedure (Table 4.13) did choose a different model containing low frequency, delta time, initial frequency, slope, energy, maximum frequency,

and average power. This seven-variable model has a total R^2 equal to 0.4645. Each variable adds significantly to the model (Table 4.14). Therefore, it is a candidate for the best model.

Table 4.13 Stepwise procedure to producing seven-variable Model 2.

Order	Step	Partial R^2	F-Statistic	P-Value
1	Entered delta time	0.1613	14.30	<0.0001
2	Entered average power	0.1008	8.26	<0.0001
3	Entered range frequency	0.1129	9.42	<0.0001
4	Entered low frequency	0.0351	2.69	0.0211
5	Entered maximum frequency	0.0425	3.27	0.0067
6	Entered energy	0.0383	2.92	0.0134
7	Removed range frequency	0.0166	1.24	0.2915
8	Entered initial frequency	0.0449	3.45	0.0047
9	Entered slope	0.0315	2.38	0.0384

Table 4.14 Model 2's variable significance created by stepwise procedure with full data.

Variable	Partial R^2	F-Statistic	P-Value
Low Frequency	0.0607	4.73	0.0003
Delta Time	0.1250	10.46	<0.0001
Initial Frequency	0.0530	4.10	0.0012
Slope	0.0315	2.38	0.0384
Energy	0.0588	4.57	0.0005
Maximum Frequency	0.0847	6.77	<0.0001
Average Power	0.0508	3.92	0.0018

After the stepwise model was created, a discriminant function analysis was conducted utilizing the winsorized full data set. The model developed to explain food type with these variables demonstrated a significant difference in variables at predicting food type (Chi-Square=506.859835, $p<0.0001$; Wilk's Lambda test $F=6.54$, $p<0.0001$; Pillai's Trace test $F=6.25$, $p<0.0001$; Hotelling-Lawley Trace test $F=6.71$, $p<0.0001$; Roy's Greatest Root test $F=16.41$, $p<0.0001$). When reclassifying food type, blueberry (66.67%) and peanut (53.06%) were classified well while green onion (93.75%) was classified almost perfectly (Table 4.15). Banana, diet coke, and mushroom were not as discrete and tended to be misclassified. Diet coke and mushroom were most often misclassified as peanut. This is similar to the results for Model 1.

Table 4.15 Percentage of vocalizations reclassified into correct food type with full data Model 2.

	Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	31.25	25.00	3.13	21.88	9.38	9.38
Blueberry	2.56	66.67	6.41	3.85	5.13	15.38
Diet Coke	1.10	19.78	43.96	9.89	3.30	21.98
Green Onion	0.00	0.00	0.00	93.75	6.25	0.00
Mushroom	4.76	15.87	4.76	6.35	31.75	36.51
Peanut	2.04	17.35	10.20	8.16	9.18	53.06

The canonical discriminant analysis demonstrated that four canonical variables can explain a significant amount of variation in food types (Table 4.16). The four canonical variables can explain a total of 99.75% of the variation in food type. The squared distances between food groups demonstrate that not all of the groups are distinct from one another (Table 4.17). In particular, there is not a significant difference between mushroom and green onion ($F=1.5501$, $p=0.1492$).

Table 4.16 Description of created canonical variables and significance for full data Model 2.

	Canonical Corr.	Eigenvalue	Proportion Explained	Cumulative	F-Statistic	P-Value
Canonical Variable 1	0.486754	0.3105	0.4823	0.4823	6.54	<0.0001
Canonical Variable 2	0.400933	0.1915	0.2975	0.799	4.99	<0.0001
Canonical Variable 3	0.298460	0.0978	0.1519	0.9318	3.43	<0.0001
Canonical Variable 4	0.201407	0.0423	0.0657	0.9975	2.01	0.0432
Canonical Variable 5	0.040332	0.0016	0.0025	1.0000	0.20	0.8957

The principal component analysis determined there were three factors applicable to Model 2 (Figure 4.3). The varimax orthogonal rotated factor pattern (Table 4.18) shows Factor 1 grouping maximum frequency, initial frequency, and low frequency together explaining the most variation. Factor 2 groups average power, energy, and potentially delta

time together, and Factor 3 groups slope by itself explaining the greatest amount of variation in food type (Figure 4.4 & Figure 4.5).

Table 4.17 Squared distance between food groups for full data Model 2 and associated F-statistics and p-values.

		Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.9068	2.2045	1.5786	1.7638	1.8234
	F-Statistic	0.0000	2.8921	7.3356	2.3668	5.2609	6.1824
	P-Value	1.0000	0.0059	<0.0001	0.0224	<0.0001	<0.0001
Blueberry	Squared Distance	0.9068	0.0000	1.6181	3.4768	2.2157	1.9727
	F-Statistic	2.8921	0.0000	9.5519	6.4879	10.8534	12.0422
	P-Value	0.0059	1.0000	<0.0001	<0.0001	<0.0001	<0.0001
Diet Coke	Squared Distance	2.2045	1.6181	0.0000	2.3746	1.4789	1.2218
	F-Statistic	7.3356	9.5519	0.0000	4.5415	7.7380	8.1030
	P-Value	<0.0001	<0.0001	1.0000	<0.0001	<0.0001	<0.0001
Green Onion	Squared Distance	1.5786	3.4768	2.3746	0.0000	0.86433	1.7726
	F-Statistic	2.3668	6.4879	4.5415	0.0000	1.5501	3.4268
	P-Value	0.0224	<0.0001	<0.0001	1.0000	0.1492	0.0015
Mushroom	Squared Distance	1.7638	2.2157	1.4789	0.86433	0.0000	0.56364
	F-Statistic	5.2609	10.8534	7.7380	1.5501	0.0000	3.03796
	P-Value	<0.0001	<0.0001	<0.0001	0.1492	1.0000	0.0041
Peanut	Squared Distance	1.8234	1.9727	1.2218	1.7726	0.56364	0.0000
	F-Statistic	6.1824	12.0422	8.1030	3.4268	3.03796	0.0000
	P-Value	<0.0001	<0.0001	<0.0001	0.0015	0.0041	1.0000

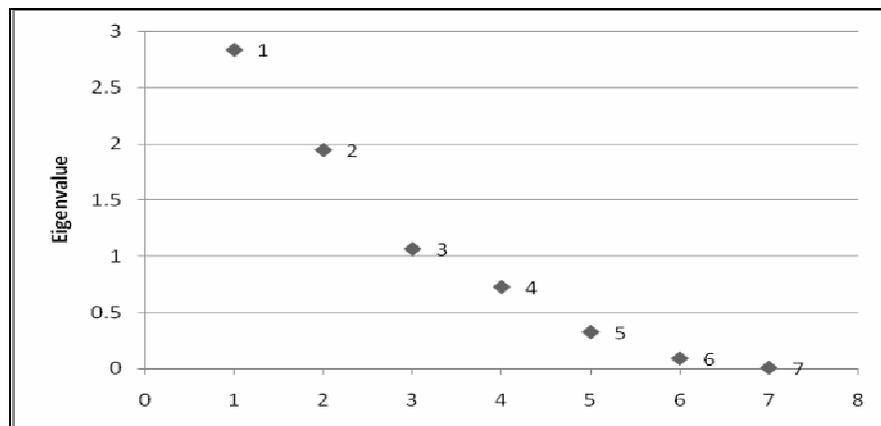
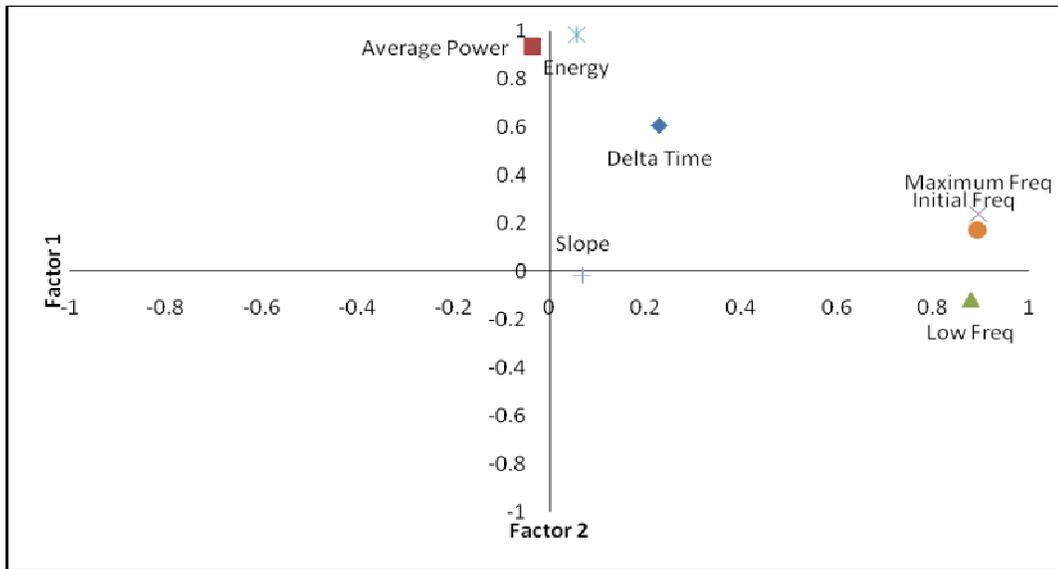
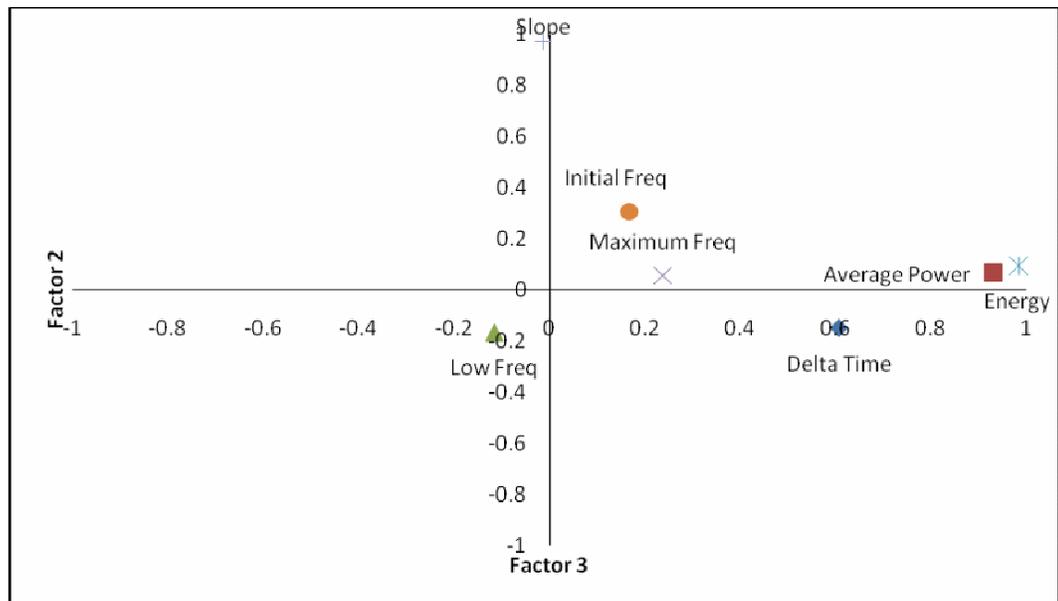


Figure 4.3 Graph of factors based on eigenvalues for full data Model 2. Values greater than one are viable factors (mineigen criterion).

Table 4.18 Rotated factor pattern for factors retained by the mineigen criterion with full data Model 2.

	Factor 1	Factor 2	Factor 3
Delta Time	0.22813	0.60781	-0.15070
Average Power	-0.03586	0.93240	0.06392
Low Frequency	0.87914	-0.11483	-0.16816
Maximum Frequency	0.89566	0.23902	0.05703
Energy	0.05612	0.98513	0.09302
Initial Frequency	0.89426	0.16934	0.30808
Slope	0.06929	-0.01443	0.96993

**Figure 4.4** Plot of factor pattern for Factor 1 versus Factor 2 with full data Model 2.**Figure 4.5** Plot of factor pattern for Factor 2 versus Factor 3 with full data Model 2.

4.2.3 Model 3

Of the 16 variables used to measure vocalizations, nine of them were measured within the Raven Program while seven were based off calculations of other variables. Therefore, a model was created to see how well the nine variables measured within Raven did at predicting food type. This nine-variable model has a total R^2 equal to 0.3513. High frequency ($F=0.85$, $p=0.5121$), terminal frequency ($F=1.34$, $p=0.2451$), and maximum power ($F=1.45$, $p=0.2051$) do not add significantly to the model (Table 4.19). Therefore, it is not a candidate for the best model.

Table 4.19 Full data Model 3's variable significance.

Variable	Partial R^2	F-Statistic	P-Value
Low Frequency	0.0633	4.92	0.0002
High Frequency	0.0116	0.85	0.5121
Delta Time	0.0808	6.40	<0.0001
Initial Frequency	0.0324	2.44	0.0342
Terminal Frequency	0.0181	1.34	0.2451
Energy	0.0329	2.48	0.0318
Maximum Frequency	0.0548	4.22	0.0010
Maximum Power	0.0195	1.45	0.2051
Average Power	0.0379	2.87	0.0148

Despite all of the variables not adding significantly, the Wilk's Lambda test ($F=5.19$, $p<0.0001$) and Pillai's Trace test ($F=4.98$, $p<0.0001$) demonstrate that the model is useful. Therefore, a discriminant function procedure was conducted utilizing this nine-variable model with the full winsorized data set. The model developed to explain food type with these variables demonstrated a significant difference in variables at predicting food type (Chi-Square=696.156909, $p<0.0001$; Wilk's Lambda test $F=5.19$, $p<0.0001$; Pillai's Trace test $F=4.98$, $p<0.0001$; Hotelling-Lawley Trace test $F=5.35$, $p<0.0001$; Roy's Greatest Root test $F=12.78$, $p<0.0001$). Banana (56.25%), blueberry (57.69%), and peanut (60.20%) were all classified with accuracy (Table 4.20). Again green onion (100%) was classified with perfect

accuracy. Blueberry and mushroom both tended to be misclassified as peanut the majority of the time. Despite not all variables adding significantly, Model 3 shows a better accuracy at predicting the correct food type.

Table 4.20 Percentage of vocalizations correctly reclassified into food type utilizing full data Model 3.

	Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	56.25	12.50	0.00	18.75	6.25	6.25
Blueberry	7.69	57.69	7.69	2.56	6.41	17.95
Diet Coke	9.89	15.38	43.96	6.59	3.30	20.88
Green Onion	0.00	0.00	0.00	100.00	0.00	0.00
Mushroom	7.94	9.52	4.76	7.94	34.92	34.92
Peanut	6.12	11.22	6.12	7.14	9.18	60.20

Three canonical variables can explain a significant amount of variation in food types (Table 4.21). The three canonical variables can explain a total of 93.45% of the variation in food type. The squared distances between food groups were determined using these three canonical variables (Table 4.22). Not all of the groups are distinct from one another. In particular, there is not a significant difference between mushroom and green onion ($F=1.5501$, $p=0.1492$). Because there is still no significant difference between mushroom and green onion and not all variables add significant information, the high reclassification could be due to over-fitting the model. Therefore, Model 3 is not in the running for the ‘best’ model.

Table 4.21 Description of canonical variables and corresponding significance for full data Model 3.

	Canonical Corr.	Eigenvalue	Proportion Explained	Cumulative	F-Statistic	P-Value
Canonical Variable 1	0.488017	0.3126	0.4713	0.4713	5.19	<0.0001
Canonical Variable 2	0.416253	0.2096	0.3159	0.7872	3.90	<0.0001
Canonical Variable 3	0.298362	0.0977	0.1473	0.9345	2.43	0.0003
Canonical Variable 4	0.178164	0.0328	0.0494	0.9839	1.32	0.1988
Canonical Variable 5	0.102698	0.0107	0.0161	1.0000	0.78	0.5613

Table 4.22 Squared distance between food types and associated F-statistics and p-values utilizing full Model 3.

		Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.9102	2.2008	1.73271	1.6361	1.8270
	F-Statistic	0.0000	2.2455	5.6648	2.0094	3.7748	4.7918
	P-Value	1.0000	0.0188	<0.0001	0.0373	0.0001	<0.0001
Blueberry	Squared Distance	0.9102	0.0000	1.8193	3.5894	2.2294	1.9846
	F-Statistic	2.2455	0.0000	8.3074	5.1812	8.4472	9.3713
	P-Value	0.0188	1.0000	<0.0001	<0.0001	<0.0001	<0.0001
Diet Coke	Squared Distance	2.2008	1.8193	0.0000	2.8055	1.5601	1.2433
	F-Statistic	5.6648	8.3074	0.0000	4.1505	6.3145	6.3782
	P-Value	<0.0001	<0.0001	1.0000	<0.0001	<0.0001	<0.0001
Green Onion	Squared Distance	1.73271	3.5894	2.8055	0.0000	1.0368	1.9460
	F-Statistic	2.0094	5.1812	4.1505	0.0000	1.4383	2.9101
	P-Value	0.0373	<0.0001	<0.0001	1.0000	0.1699	0.0024
Mushroom	Squared Distance	1.6361	2.2294	1.5601	1.0368	0.0000	0.4780
	F-Statistic	3.7748	8.4472	6.3145	1.4383	0.0000	1.9927
	P-Value	0.0001	<0.0001	<0.0001	0.1699	1.0000	0.0392
Peanut	Squared Distance	1.8270	1.9846	1.2433	1.9460	0.4780	0.0000
	F-Statistic	4.7918	9.3713	6.3782	2.9101	1.9927	0.0000
	P-Value	<0.0001	<0.0001	<0.0001	0.0024	0.0392	1.0000

4.2.4 Model 4

When utilizing the limited data set another stepwise discriminant procedure was conducted to see which model was chosen. This procedure (outlined in Table 4.44) developed a different model containing only three variables: low frequency, high-terminal frequency, and delta time. The same model was chosen whether the stepwise looked at adjusted or non-adjusted outliers with the limited data set. Because this was the model chosen for the limited data set, it was also necessary to test the results using the full data set. This three-variable model utilizing the full winsorized data set has an R^2 equal to 0.2664.

Each variable added significantly to the model (Table 4.23). Therefore, it is a candidate for the best model. However, since its R^2 value is lower than that for Model 1 and Model 2, it is not the best model for predicting food type.

Table 4.23 Model 4's variable significance using the full data set.

Variable	Partial R^2	F-Statistic	P-Value
Low Frequency	0.0300	2.29	0.0452
High-Terminal Frequency	0.0639	5.05	0.0002
Delta Time	0.1725	15.43	<0.0001

A discriminant function procedure demonstrated a significant difference in variables at predicting food type (Chi-Square=154.238574, $p < 0.0001$; Wilk's Lambda test $F = 6.98$, $p < 0.0001$; Pillai's Trace test $F = 6.65$, $p < 0.0001$; Hotelling-Lawley Trace test $F = 7.28$, $p < 0.0001$; Roy's Greatest Root test $F = 18.30$, $p < 0.0001$). This model did very poorly at correctly reclassifying food type (Table 4.24). Only peanut (67.35%) made it above the 50% quantile. Also, most vocalizations were commonly misclassified as peanuts.

Table 4.24 Percentage of vocalizations correctly reclassified into food type utilizing full data Model 4.

	Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	0.00	40.63	6.25	25.00	0.00	28.13
Blueberry	0.00	46.15	11.54	2.56	0.00	39.74
Diet Coke	0.00	13.19	25.27	8.79	7.69	45.05
Green Onion	0.00	0.00	6.25	37.50	6.25	50.00
Mushroom	0.00	4.76	14.29	12.70	19.05	49.21
Peanut	0.00	8.16	8.16	10.20	6.12	67.35

A canonical discriminant analysis determined there were two statistically significant canonical variables (Canonical 1: 0.8309 proportion explained variation, $F = 6.98$, $p < 0.0001$; Canonical 2: 0.1037 proportion of variation, $F = 2.32$, $p = 0.0184$). The two canonical variables can explain a total of 93.46% of the variation in food type. The squared distances between food groups were determined using these two canonical variables (Table 4.25). Several of the groups are indistinguishable from one another. There is not a significant difference between

mushroom and green onion ($F=1.7971$, $p=0.1473$), blueberry and banana ($F=2.2169$, $p=0.0858$), diet coke and green onion ($F=1.6843$, $p=0.1699$), diet coke and peanut ($F=0.4271$, $p=0.7337$), and green onion and peanut ($F=2.4501$, $p=0.0633$). Therefore, this model did poorly in explained variation, reclassification of food type, and in distance between food groups, so it will not be considered for the ‘best’ model.

Table 4.25 Squared distance between food groups and associated F-statistics and p-values for full data Model 4.

		Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.2947	0.6510	1.3883	1.1256	0.6357
	F-Statistic	0.0000	2.2169	5.1095	4.9095	7.9195	5.0838
	P-Value	1.0000	0.0858	0.0018	0.0023	<0.0001	0.0018
Blueberry	Squared Distance	0.2947	0.0000	1.2639	2.5991	1.6966	1.0832
	F-Statistic	2.2169	0.0000	17.5990	11.4405	19.6039	15.5970
	P-Value	0.0858	1.0000	<0.0001	<0.0001	<0.0001	<0.0001
Diet Coke	Squared Distance	0.6510	1.2639	0.0000	0.3733	0.2900	0.0273
	F-Statistic	5.1095	17.5990	0.0000	1.6843	3.5745	0.4271
	P-Value	0.0018	<0.0001	1.0000	0.1699	0.0142	0.7337
Green Onion	Squared Distance	1.3883	2.5991	0.3733	0.0000	0.4248	0.5370
	F-Statistic	4.9095	11.4405	1.6843	0.0000	1.7971	2.4501
	P-Value	0.0023	<0.0001	0.1699	1.0000	0.1473	0.0633
Mushroom	Squared Distance	1.1256	1.6966	0.2900	0.4248	0.0000	0.2386
	F-Statistic	7.9195	19.6039	3.5745	1.7971	0.0000	3.0330
	P-Value	<0.0001	<0.0001	0.0142	0.1473	1.0000	0.0293
Peanut	Squared Distance	0.6357	1.0832	0.0273	0.5370	0.2386	0.0000
	F-Statistic	5.0838	15.5970	0.4271	2.4501	3.0330	0.0000
	P-Value	0.0018	<0.0001	0.7337	0.0633	0.0293	1.0000

4.2.5 Model 5

Because Model 4 did so poorly when looking at the full data set, it was entered as a starting point in the stepwise discriminant procedure with the full data set to see how the

model could be improved upon. The stepwise procedure (Table 4.26) developed a six-variable model containing low frequency, high-terminal frequency, delta time, maximum frequency, maximum power, and average frequency. This six-variable model has an R^2 equal to 0.5860. All variables added significantly to the model (Table 4.27). Because all variables add significantly and the R^2 value is greater than the previous four models, Model 5 is in the running for the best model at explaining food type.

Table 4.26 Stepwise procedure to producing six-variable Model 5.

Order	Step	Partial R^2	F-Statistic	P-Value
1	Begin with low frequency, high-terminal frequency, delta time			
2	Entered maximum power	0.1114	9.25	<0.0001
3	Entered average frequency	0.0857	6.89	<0.0001
4	Entered maximum frequency	0.0611	4.77	0.0003

Table 4.27 Model 5's variable significance using the full data set.

Variable	Partial R^2	F-Statistic	P-Value
Low Frequency	0.0923	7.46	<0.0001
High-Terminal Frequency	0.0296	2.24	0.0500
Delta Time	0.1837	16.52	<0.0001
Maximum Frequency	0.0611	4.77	0.0003
Maximum Power	0.1415	12.09	<0.0001
Average Frequency	0.0778	6.19	<0.0001

A discriminant function procedure determined this model demonstrated a significant difference in variables at predicting food type (Chi-Square=467.206137, $p<0.0001$; Wilk's Lambda test $F=7.08$, $p<0.0001$; Pillai's Trace test $F=6.73$, $p<0.0001$; Hotelling-Lawley Trace test ($F=7.28$, $p<0.0001$; Roy's Greatest Root test $F=18.29$, $p<0.0001$). This model did much better at predicting the correct food type than Model 4 (Table 4.28). Blueberry (62.82%) and peanut (54.08%) were reclassified with a high degree of accuracy, and green onion (81.25%) was extremely high. Mushroom and diet coke again were most often misclassified as peanut.

The canonical discriminant analysis determined three canonical variables accounts for a significant proportion of the variation in food types (Table 4.29), explaining a total of 95.54% of the variation in food type. Not all of the groups are distinct from one another when looking at squared distances between food groups (Table 4.30). There remains no significant difference between mushroom and green onion ($F=1.6502$, $p=0.1323$).

Table 4.28 Percentage of vocalizations correctly reclassified into food type utilizing full data Model 5.

	Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	25.00	25.00	6.25	21.88	12.50	9.38
Blueberry	1.28	62.82	10.26	5.13	2.56	17.95
Diet Coke	5.49	16.48	40.66	8.79	3.30	25.27
Green Onion	12.50	0.00	0.00	81.25	6.25	0.00
Mushroom	9.52	14.29	6.35	15.87	23.81	30.16
Peanut	6.12	15.31	6.12	9.18	9.18	54.08

Table 4.29 Description of canonical variables and corresponding significance for full data Model 5.

	Canonical Corr.	Eigenvalue	Proportion Explained	Cumulative	F-Statistic	P-Value
Canonical Variable 1	0.477804	0.2958	0.4952	0.4952	7.08	<0.0001
Canonical Variable 2	0.408311	0.2001	0.3349	0.8301	5.40	<0.0001
Canonical Variable 3	0.263901	0.0749	0.1253	0.9554	3.09	0.0003
Canonical Variable 4	0.159590	0.0261	0.0437	0.9992	1.63	0.1354
Canonical Variable 5	0.022202	0.0005	0.0008	1.0000	0.09	0.9126

The principal component analysis determined there were three factors applicable to Model 5 (Figure 4.6). The varimax orthogonal rotated factor pattern (Table 4.31) demonstrates that Factor 1 groups maximum frequency, average frequency, and low frequency together explaining the most variation, Factor 2 groups maximum power and delta time together, and Factor 3 groups high-terminal frequency by itself explaining the greatest amount of variation in food type (Figure 4.7 & Figure 4.8)

Table 4.30 Squared distance between food groups and associated F-statistics and p-values for full data Model 5.

		Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.6822	2.1673	1.5382	1.3687	1.5226
	F-Statistic	0.0000	2.5451	8.4370	2.6979	4.7757	6.0392
	P-Value	1.0000	0.0199	<0.0001	0.0142	0.0001	<0.0001
Blueberry	Squared Distance	0.6822	0.0000	1.6737	3.5156	2.2102	1.8288
	F-Statistic	2.5451	0.0000	11.5583	7.6747	12.0439	13.0598
	P-Value	0.0199	1.0000	<0.0001	<0.0001	<0.0001	<0.0001
Diet Coke	Squared Distance	2.1673	1.6737	0.0000	2.6653	1.3675	1.0090
	F-Statistic	8.4370	11.5583	0.0000	5.9634	8.3708	7.8281
	P-Value	<0.0001	<0.0001	1.0000	<0.0001	<0.0001	<0.0001
Green Onion	Squared Distance	1.5382	3.5156	2.6653	0.0000	0.7865	1.6761
	F-Statistic	2.6979	7.6747	5.9634	0.0000	1.6502	3.7905
	P-Value	0.0142	<0.0001	<0.0001	1.0000	0.1323	0.0011
Mushroom	Squared Distance	1.3687	2.2102	1.3675	0.7865	0.0000	0.4785
	F-Statistic	4.7757	12.0439	8.3708	1.6502	0.0000	3.0168
	P-Value	0.0001	<0.0001	<0.0001	0.1323	1.0000	0.0068
Peanut	Squared Distance	1.5226	1.8288	1.0090	1.6761	0.4780	0.0000
	F-Statistic	6.0392	13.0598	7.8281	3.7905	1.9927	0.0000
	P-Value	<0.0001	<0.0001	<0.0001	0.0011	0.0392	1.0000

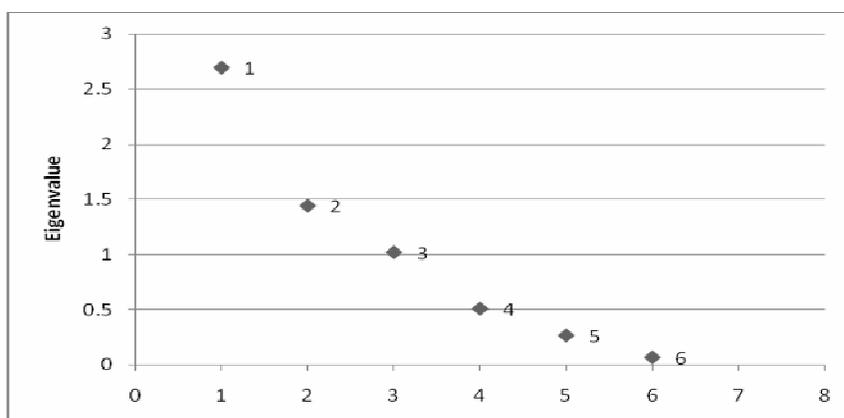
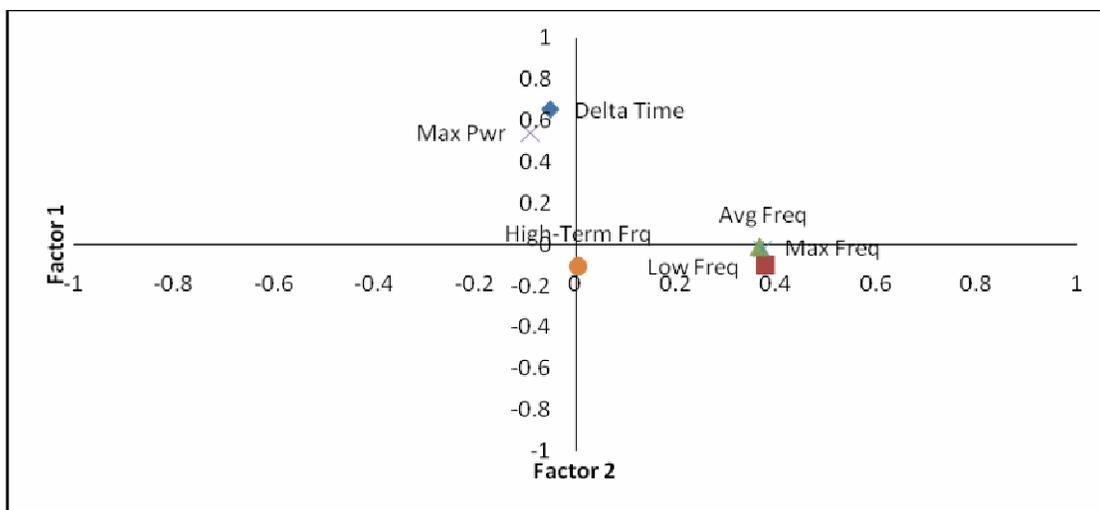
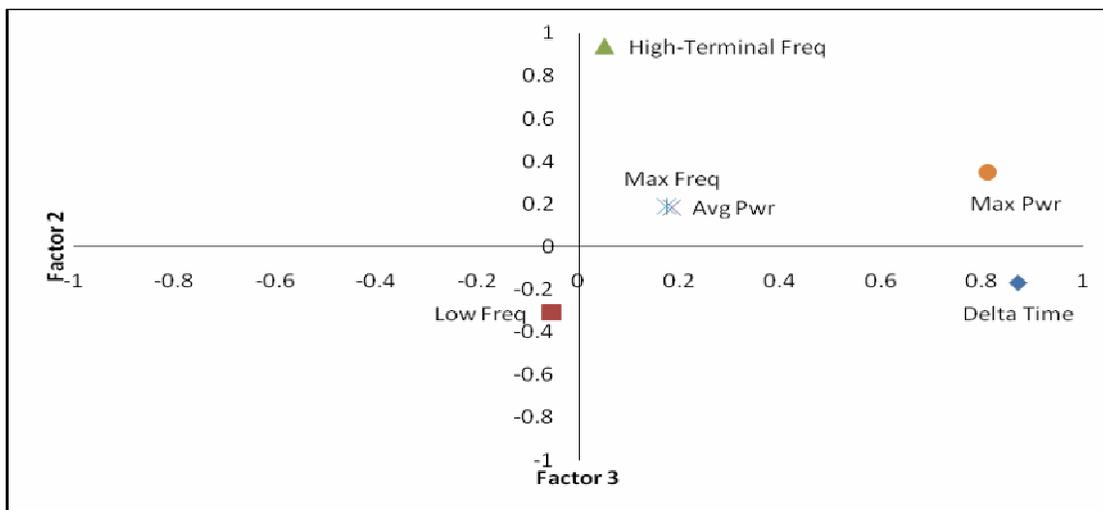
**Figure 4.6** Graph of factors based on eigenvalues for full data Model 5. Values greater than one are viable factors (mineigen criterion).

Table 4.31 Rotated factor pattern of full data Model 5 for factors retained by the mineigen criterion.

	Factor 1	Factor 2	Factor 3
Delta Time	0.14949	0.87032	-0.17004
Low Frequency	0.85724	-0.05121	-0.31215
High-Terminal Frequency	0.05332	0.05201	0.93766
Maximum Frequency	0.91992	0.18476	0.18059
Average Frequency	0.93287	0.17653	0.18439
Maximum Power	0.05711	0.81038	0.34633

**Figure 4.7** Plot of factor pattern for Factor 1 versus Factor 2 with full data Model 5.**Figure 4.8** Plot of factor pattern for Factor 2 versus Factor 3 with full data Model 5.

4.2.6 Model 6

Because Model 1 and Model 2 had several non-significant variables when utilizing the limited data set, it was entered as a starting point in the stepwise discriminant procedure

with the limited data set to see how the model could be improved upon. The stepwise procedure (Table 4.53) developed a four-variable model containing low frequency, delta time, average power, and energy. When conducted with the full data set, this four-variable model has an R^2 equal to 0.4535. All variables added statistically significant information at predicting food type (Table 4.32). Despite all variables adding statistically significant information, the R^2 is lower than that in Model 5. Therefore, it is not the best model when utilizing the winsorized full data set, but it still has the possibility of being a very good model.

Table 4.32 Model 6's variable significance using the full data set.

Variable	Partial R^2	F-Statistic	P-Value
Low Frequency	0.0403	3.10	0.0094
Delta Time	0.1926	17.60	<0.0001
Average Power	0.1115	9.26	<0.0001
Energy	0.1091	9.04	<0.0001

The discriminant function model developed to explain food type with these variables demonstrated a significant difference in variables at predicting food type (Chi-Square=273.883306, $p<0.0001$; Wilk's Lambda test $F=8.65.08$, $p<0.0001$; Pillai's Trace test $F=8.32$, $p<0.0001$; Hotelling-Lawley Trace test $F=8.81$, $p<0.0001$; Roy's Greatest Root test $F=19.68$, $p<0.0001$). This model did slightly worse at predicting the correct food type than Model 5 (Table 4.33). Green onion (68.75%) and peanut (69.39%) were reclassified with a high degree of accuracy. Banana was most often misclassified as blueberry. Blueberry, diet coke, and mushroom were most often misclassified as peanut.

Three canonical variables can explain a significant proportion of the variation in food types (Table 4.34), explaining a total of 97.19% of the variation in food type. The squared

distances between food groups suggest every food type is significantly different than all other food types (Table 4.35). This is the first and only model utilizing the full data set to have all food types at significant distances from one another.

Table 4.33 Percentage of vocalizations reclassified correctly into food type utilizing full data Model 6.

	Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	6.25	34.38	6.25	25.00	15.63	12.50
Blueberry	1.28	43.59	11.54	1.28	3.85	38.46
Diet Coke	1.10	13.19	34.07	9.89	3.30	38.46
Green Onion	0.00	0.00	0.00	68.75	12.50	18.75
Mushroom	3.17	6.35	9.52	11.11	22.22	47.62
Peanut	1.02	6.12	8.16	5.10	10.20	69.39

Table 4.34 Description of canonical variables and corresponding significance for full data Model 6.

	Canonical Corr.	Eigenvalue	Proportion Explained	Cumulative	F-Statistic	P-Value
Canonical Variable 1	0.457476	0.2647	0.5527	0.5527	8.65	<0.0001
Canonical Variable 2	0.353727	0.1430	0.2986	0.8513	6.51	<0.0001
Canonical Variable 3	0.233625	0.0577	0.1206	0.9719	4.37	0.0002
Canonical Variable 4	0.115243	0.0135	0.0281	1.0000	2.50	0.0832

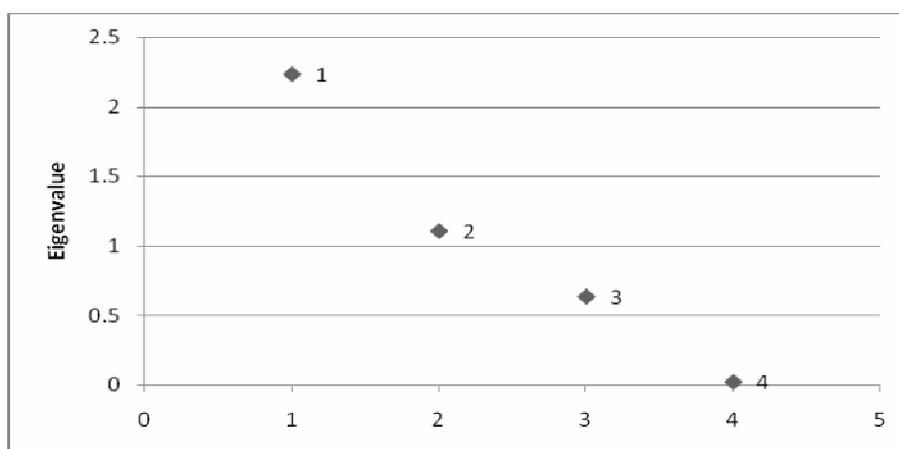


Figure 4.9 Graph of factors based on eigenvalues created for full data Model 6. Values greater than one are viable factors (mingeigen criterion).

The principal component analysis determined there were two factors applicable to Model 6 (Figure 4.9). The varimax orthogonal rotated factor pattern (Table 4.36)

demonstrates that Factor 1 groups energy, average power, and potentially delta time explaining the most variation and grouped together and Factor 2 groups low frequency by itself explaining the greatest amount of variation in food type (Figure 4.10).

Table 4.35 Squared distance between food groups and associated F-statistics and p-values for full data Model 6.

		Banana	Blueberry	Diet Coke	Green Onion	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.8418	1.8083	1.3998	1.4448	1.5362
	F-Statistic	0.0000	4.7369	10.6163	3.7028	7.6030	9.1898
	P-Value	1.0000	0.0010	<0.0001	0.0057	<0.0001	<0.0001
Blueberry	Squared Distance	0.8418	0.0000	1.3304	3.3653	1.9110	1.4412
	F-Statistic	4.7369	0.0000	13.8568	11.0799	16.5161	15.5217
	P-Value	0.0010	1.0000	<0.0001	<0.0001	<0.0001	<0.0001
Diet Coke	Squared Distance	1.8083	1.3304	0.0000	2.0014	0.9681	0.4924
	F-Statistic	10.6163	13.8568	0.0000	6.7537	8.9373	5.7611
	P-Value	<0.0001	<0.0001	1.0000	<0.0001	<0.0001	0.0002
Green Onion	Squared Distance	1.3998	3.3653	2.0014	0.0000	0.8080	1.3729
	F-Statistic	3.7028	11.0799	6.7537	0.0000	2.5565	4.6828
	P-Value	0.0057	<0.0001	<0.0001	1.0000	0.0385	0.0011
Mushroom	Squared Distance	1.4448	1.9110	0.9681	0.8080	0.0000	0.2677
	F-Statistic	7.6030	16.5161	8.9373	2.5565	0.0000	2.5461
	P-Value	<0.0001	<0.0001	<0.0001	0.0385	1.0000	0.0392
Peanut	Squared Distance	1.5362	1.4412	0.4924	1.3729	0.2677	0.0000
	F-Statistic	9.1898	15.5217	5.7611	4.6828	2.5461	0.0000
	P-Value	<0.0001	<0.0001	0.0002	0.0011	0.0392	1.0000

Table 4.36 Rotated factor pattern for factors retained by the mineigen criterion with full data Model 6.

	Factor 1	Factor 2
Delta Time	0.60447	0.50615
Low Frequency	-0.11112	0.91866
Energy	0.98678	-0.01974
Average Power	0.93681	-0.10972

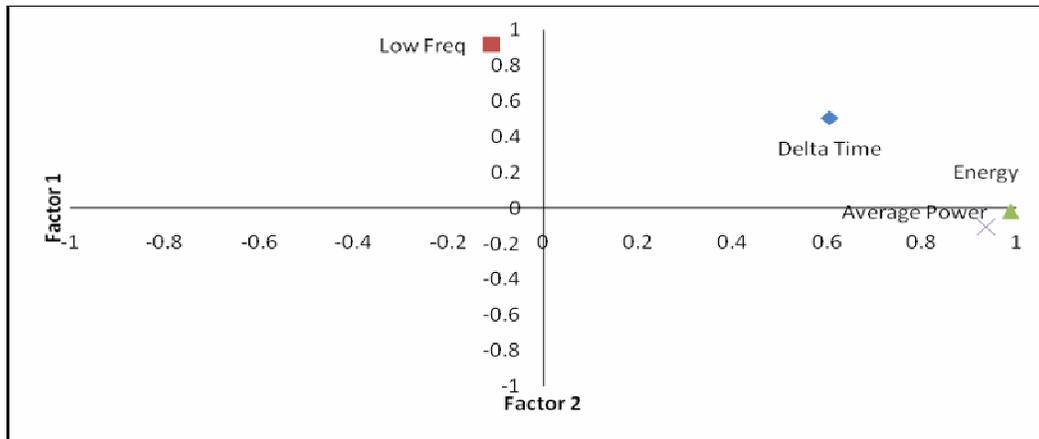


Figure 4.10 Plot of factor pattern for Factor 1 versus Factor 2 with full data Model 6.

4.3 Limited Data Set Models

4.3.1 Model 1

Model 1 was created from the full data set using a stepwise discriminant function before the outliers were winsorized (procedure outlined in Table 4.7). Model 1 contains delta time, average power, low frequency, maximum frequency, (initial+high+terminal)/3, and energy. With the limited winsorized data set, this six-variable model has an R^2 equal to 0.5330. However, maximum frequency and (initial+high+terminal)/3 do not add significantly to the model (Table 4.37). Because all variables do not add significantly this is not a candidate for the best model when using the limited data set.

Table 4.37 Model 1's variable significance using the limited data set.

Variable	Partial R^2	F-Statistic	P-Value
Delta Time	0.1309	4.14	0.0036
Low Frequency	0.1234	3.87	0.0056
Average Power	0.0903	2.73	0.0327
Maximum Frequency	0.0648	1.91	0.1146
(Initial+High+Terminal)/3	0.0461	1.33	0.2639
Energy	0.0775	2.31	0.0623

Despite all of the variables not adding significantly, the Wilk's Lambda test ($F=2.65$, $p<0.0001$) and Pillai's Trace test ($F=2.5$, $p<0.0001$) demonstrate that the model is useful.

Therefore, a discriminant function procedure was conducted with the limited winsorized data set. This model demonstrated a significant difference in variables at predicting food type (Chi-Square=159.449504, $p<0.0001$; Wilk's Lambda test $F=2.66$, $p<0.0001$; Pillai's Trace test $F=2.60$, $p<0.0001$; Hotelling-Lawley Trace test $F=2.71$, $p<0.0001$; Roy's Greatest Root test $F=6.56$, $p<0.0001$). Despite not all of the variables adding significantly, this model was able to reclassify four of the five food types above the 50% quantile (Table 4.38). Peanut (38.46%) was the only food type that didn't reach the 50% criterion and was most often misclassified as mushroom.

There were two statistically significant canonical variables created (Canonical 1: 0.5838 proportion explained variation, $F=2.66$, $p<0.0001$; Canonical 2: 0.2269 proportion of variation, $F=1.83$, $p=0.0297$). The two canonical variables can explain a total of 81.07% of the variation in food type. When examining the squared distances between food groups, many of the groups are not distinct from one another (Table 4.39). There is not a significant difference between blueberry and banana ($F=1.2119$, $p=0.3056$), diet coke and banana ($F=1.8005$, $p=0.1055$), diet coke and peanut ($F=1.8569$, $p=0.0947$), and blueberry and peanut ($F=1.6293$, $p=0.1457$). This model did poorly in establishing significant distance between food groups and not all variables added significant information, so it is not a candidate for the 'best' model with the limited data.

Table 4.38 Percentage of vocalizations correctly reclassified into food type utilizing limited data Model 1.

	Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	72.22	0.00	11.11	16.67	0.00
Blueberry	14.81	66.67	7.41	7.41	3.70
Diet Coke	17.39	8.70	52.17	13.04	8.70
Mushroom	11.54	3.85	19.23	61.54	3.85
Peanut	11.54	3.85	11.54	34.62	38.46

Table 4.39 Squared distances between food groups and associated F-statistics and p-values for limited data Model 1.

		Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.7039	1.1185	2.3306	1.3122
	F-Statistic	0.0000	1.2119	1.8005	3.9519	2.2250
	P-Value	1.0000	0.3056	0.1055	0.0013	0.0459
Blueberry	Squared Distance	0.7039	0.0000	1.2473	1.4725	0.7716
	F-Statistic	1.2119	0.0000	2.4696	3.1093	1.6293
	P-Value	0.3056	1.0000	0.0280	0.0075	0.1457
Diet Coke	Squared Distance	1.1185	1.2473	0.0000	3.0371	0.9544
	F-Statistic	1.8005	2.4696	0.0000	5.9090	1.8569
	P-Value	0.1055	0.0280	1.0000	<0.0001	0.0947
Mushroom	Squared Distance	2.3306	1.4725	3.0371	0.0000	1.4684
	F-Statistic	3.9519	3.1093	5.9090	0.0000	3.0432
	P-Value	0.0013	0.0075	<0.0001	1.0000	0.0086
Peanut	Squared Distance	1.3122	0.7716	0.9544	1.4684	0.0000
	F-Statistic	2.2250	1.6293	1.8569	3.0432	0.0000
	P-Value	0.0459	0.1457	0.0947	0.0086	1.0000

4.3.2 Model 2

Model 2 was created from the full data set using a stepwise discriminant function after the outliers were winsorized (procedure outlined in Table 4.13). Model 2 contains delta time, average power, low frequency, maximum frequency, energy, initial frequency, and slope. When conducted with the limited data set, this seven-variable model has an R^2 equal to 0.6301. Maximum frequency, initial frequency, and slope do not add significantly to the model (Table 4.40). Because all variables do not add significantly this is not a candidate for the best model when using the limited data set.

Despite all of the variables not adding significantly, the Wilk's Lambda test ($F=2.43$, $p<0.0001$) and Pillai's Trace test ($F=2.38$, $p=0.0001$) demonstrate that the model is useful.

The discriminant function for Model 2 demonstrated a significant difference in variables at

predicting food type (Chi-Square=220.189703, $p < 0.0001$; Wilk's Lambda test $F=2.44$, $p < 0.0001$; Pillai's Trace test $F=2.39$, $p=0.0001$; Hotelling-Lawley Trace test $F=2.47$, $p=0.0001$; Roy's Greatest Root test $F=5.66$, $p < 0.0001$). Despite not all of the variables adding significantly, this model was able to reclassify all of the five food types above the 50% quantile (Table 4.41).

Table 4.40 Model 2's variable significance using the limited data set.

Variable	Partial R ²	F-Statistic	P-Value
Delta Time	0.1396	4.42	0.0024
Low Frequency	0.1335	4.20	0.0034
Average Power	0.1058	3.22	0.0153
Maximum Frequency	0.0669	1.95	0.1066
Energy	0.0906	2.72	0.0335
Initial Frequency	0.0505	1.45	0.2222
Slope	0.0432	1.23	0.3022

Table 4.41 Percentage of vocalizations correctly reclassified into food type utilizing limited data Model 2.

	Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	77.78	0.00	11.11	11.11	0.00
Blueberry	18.52	55.56	11.11	11.11	3.70
Diet Coke	8.70	8.70	69.57	8.70	4.35
Mushroom	7.69	3.85	19.23	65.38	3.85
Peanut	11.54	0.00	11.54	19.23	57.69

There were two statistically significant canonical variables created (Canonical 1: 0.5516 proportion explained variation, $F=2.44$, $p < 0.0001$; Canonical 2: 0.2358 proportion of variation, $F=1.75$, $p=0.0307$). The two canonical variables can explain a total of 78.73% of the variation in food type. The squared distances between food groups determined many of the groups are not distinct from one another (Table 4.42). Mushroom is the only group with significant distance between all other groups. Because the R² is so high but the distances between groups is not significant, the model overfits the data and is not a candidate for the best model.

Table 4.42 Squared distances between food groups and associated F-statistics and p-values for limited data Model 2.

		Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.7046	1.2429	2.3531	1.2679
	F-Statistic	0.0000	1.0304	1.6993	3.3889	1.8261
	P-Value	1.0000	0.4142	0.1166	0.0026	0.0893
Blueberry	Squared Distance	0.7046	0.0000	1.5766	1.5763	0.8647
	F-Statistic	1.0304	0.0000	2.6514	2.8270	1.5507
	P-Value	0.4142	1.0000	0.0143	0.0096	0.1579
Diet Coke	Squared Distance	1.2429	1.5766	0.0000	3.1155	1.1305
	F-Statistic	1.6993	2.6514	0.0000	5.1484	1.8681
	P-Value	0.1166	0.0143	1.0000	<0.0001	0.0817
Mushroom	Squared Distance	2.3531	1.5763	3.1155	0.0000	1.5721
	F-Statistic	3.3889	2.8270	5.1484	0.0000	2.7672
	P-Value	0.0026	0.0096	<0.0001	1.0000	0.0110
Peanut	Squared Distance	1.2679	0.8647	1.1305	1.5721	0.0000
	F-Statistic	1.8261	1.5507	1.8681	2.7672	0.0000
	P-Value	0.0893	0.1579	0.0817	0.0110	1.0000

4.3.3 Model 3

The model created to see how well the nine variables measured within Raven did at predicting food type has a total R^2 equal to 0.4104 when utilizing the winsorized limited data set. Eight of the nine variables do not add significantly to the model (Table 4.43). Only low frequency ($F=3.48$, $p\text{-value}=0.0103$) adds significant information to predicting food type. Because so many variables do not add significantly to the model, it is not a candidate for the best model.

Table 4.43 Limited data Model 3's variable significance.

Variable	Partial R ²	F-Statistic	P-Value
Delta Time	0.0675	1.94	0.1096
Low Frequency	0.1151	3.48	0.0103
High Frequency	0.0202	0.55	0.6989
Initial Frequency	0.0178	0.49	0.7462
Terminal Frequency	0.0358	0.99	0.4141
Energy	0.0258	0.71	0.5874
Maximum Frequency	0.0699	2.01	0.0982
Maximum Power	0.0102	0.28	0.8925
Average Power	0.0489	1.38	0.2471

4.3.4 Model 4

When utilizing the limited data set another stepwise discriminant procedure was conducted to see which model was chosen. This procedure (Table 4.44) developed a model containing only three variables: low frequency, high-terminal frequency, and delta time. The same model was chosen whether the stepwise looked at adjusted or non-adjusted outliers. This three-variable model utilizing the winsorized limited data set has an R² equal to 0.3666. Each variable added significantly to the model (Table 4.45). Since it is the only model thus far, using the limited data set, to have all variables add significant information, it is currently the best model in the limited data set.

Table 4.44 Stepwise procedure to producing three-variable Model 4.

Order	Step	Partial R ²	F-Statistic	P-Value
1	Entered low frequency	0.1586	5.42	0.0005
2	Entered high-terminal frequency	0.0832	2.59	0.0405
3	Entered delta time	0.0878	2.72	0.0332

Table 4.45 Model 4's variable significance using the limited data set.

Variable	Partial R ²	F-Statistic	P-Value
Low Frequency	0.0878	2.72	0.0332
High-Terminal Frequency	0.1847	6.40	0.0001
Delta Time	0.0941	2.93	0.0237

A discriminant function procedure was conducted utilizing this three-variable model with the limited data set adjusted for outliers. The model developed to explain food type with these variables demonstrated a significant difference in variables at predicting food type (Chi-Square=53.867864, $p=0.0004$; Wilk's Lambda test $F=3.60$, $p<0.0001$; Pillai's Trace test $F=3.51$, $p<0.0001$; Hotelling-Lawley Trace test $F=3.66$, $p<0.0001$; Roy's Greatest Root test $F=6.87$, $p<0.0001$). This model did very poorly at correctly predicting food type (Table 4.46). Only blueberry (74.07%) and mushroom (69.23%) made it above the 50% quantile. Banana, diet coke, and peanut were commonly misclassified as blueberry.

Table 4.46 Percentage of vocalizations reclassified into correct food type utilizing limited data Model 4.

	Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	5.56	55.56	5.56	27.78	5.56
Blueberry	0.00	74.07	7.41	14.81	3.70
Diet Coke	0.00	52.17	30.43	8.70	8.70
Mushroom	0.00	19.23	7.69	69.23	3.85
Peanut	7.69	46.15	19.23	23.08	3.85

There were two statistically significant canonical variables created (Canonical 1: 0.6094 proportion explained variation, $F=3.60$, $p<0.0001$; Canonical 2: 0.3826 proportion of variation, $F=2.81$, $p=0.0116$). The two canonical variables can explain a total of 99.21% of the variation in food type. The squared distances between food groups determined that banana and blueberry ($F=0.0687$, $p=0.9765$), banana and peanut ($F=1.2656$, $p=0.2896$), blueberry and peanut ($F=1.8025$, $p=0.1508$), and diet coke and peanut ($F=1.3910$, $p=0.2492$) do not have significant distances between them based on the two canonical variables (Table 4.47).

The principal component factor analysis identified only one factor applicable to Model 4 (Figure 4.11). Principal component demonstrates that Factor 1 groups low frequency

and delta time together explaining the most variation (Table 4.48). A varimax orthogonal rotated factor pattern was not possible with only one factor. Despite all variables adding significantly, this model did poor at establishing significant differences between groups and reclassifying correctly. Therefore, it is probably not an optimal model to utilize.

Table 4.47 Squared distances between food groups and associated F-statistics and p-values for limited data Model 4.

		Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.0194	1.1280	1.2493	0.3633
	F-Statistic	0.0000	0.0687	3.7307	4.3524	1.2656
	P-Value	1.0000	0.9765	0.0133	0.0061	0.2896
Blueberry	Squared Distance	0.0194	0.0000	1.2092	1.4231	0.4155
	F-Statistic	0.06873	0.0000	4.9191	6.1739	1.8025
	P-Value	0.9765	1.0000	0.0030	0.0006	0.1508
Diet Coke	Squared Distance	1.1280	1.2092	0.0000	2.1417	0.3480
	F-Statistic	3.7307	4.9191	0.0000	8.5609	1.3910
	P-Value	0.0133	0.0030	1.0000	<0.0001	0.2492
Mushroom	Squared Distance	1.2493	1.4231	2.1417	0.0000	0.9608
	F-Statistic	4.3524	6.1739	8.5609	0.0000	4.0910
	P-Value	0.0061	0.0006	<0.0001	1.0000	0.0085
Peanut	Squared Distance	0.3633	0.4155	0.3480	0.9608	0.0000
	F-Statistic	1.2656	1.8025	1.3910	4.0910	0.0000
	P-Value	0.2896	0.1508	0.2492	0.0085	1.0000

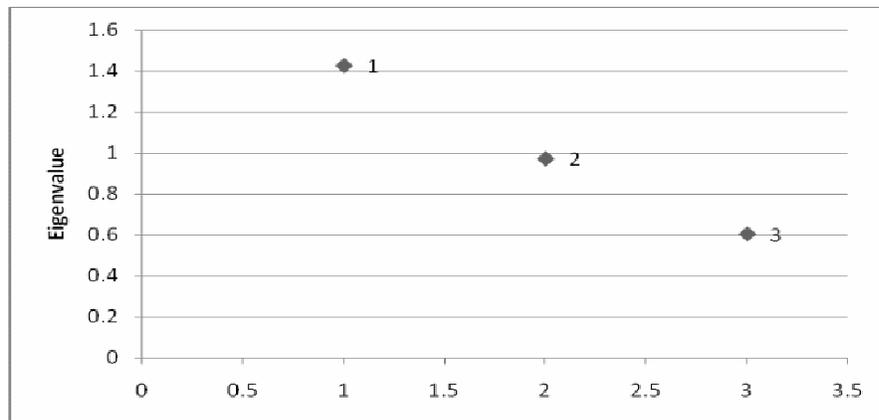


Figure 4.11 Graph of factors based on eigenvalues created for limited Model 4. Values greater than one are viable factors.

Table 4.48 Principal component factor pattern for retained factors for limited Model 4.

	Factor 1
Delta Time	0.71745
Low Frequency	0.82864
High-Terminal Frequency	-0.47319

4.3.5 Model 5

Because Model 4 did so poorly when considering the full data set, it was entered as a starting point in the stepwise discriminant procedure with the full data set to see how the model could be improved upon. The stepwise procedure (displayed in Table 4.26) developed a six-variable model containing low frequency, high-terminal frequency, delta time, maximum frequency, maximum power, and average frequency. When conducted with the limited data set, this six-variable model has an R^2 equal to 0.4432. Only low frequency ($F=2.82$, $p=0.0286$) and average frequency ($F=2.49$, $p=0.0471$) added significant information to the model (Table 4.49). Because not all of the variables added statistically significant information, this model is not a candidate for the best model when utilizing the limited data set.

Table 4.49 Model 5's variable significance using the limited data set.

Variable	Partial R^2	F-Statistic	P-Value
Delta Time	0.0700	2.07	0.0894
Low Frequency	0.0930	2.82	0.0286
High-Terminal Frequency	0.0741	2.20	0.0734
Maximum Frequency	0.0693	2.05	0.0924
Maximum Power	0.0537	1.56	0.1896
Average Frequency	0.0831	2.49	0.0471

A discriminant function procedure demonstrated a significant difference in variables at predicting food type (Chi-Square=181.129948, $p<0.0001$; Wilk's Lambda test $F=2.53$, $p=0.0001$; Pillai's Trace test $F=2.50$, $p=0.0001$; Hotelling-Lawley Trace test $F=2.53$,

$p=0.0002$; Roy's Greatest Root test $F=4.98$, $p=0.0001$). This model did better at predicting the correct food type than Model 4 (Table 4.50). Banana (72.22%), blueberry (55.56%) and mushroom (53.85%) were reclassified with a high degree of accuracy. Diet coke was most often misclassified as banana or blueberry while peanut was most often misclassified as banana or mushroom.

Table 4.50 Percentage of vocalizations correctly reclassified into food type utilizing limited data Model 5.

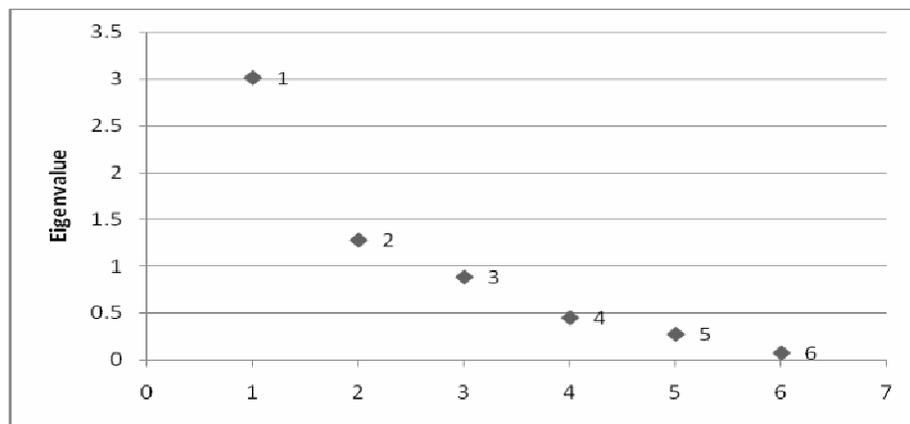
	Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	72.22	5.56	0.00	16.67	5.56
Blueberry	22.22	55.56	7.41	7.41	7.41
Diet Coke	21.74	21.74	34.78	17.39	4.35
Mushroom	15.38	7.69	7.69	53.85	15.38
Peanut	23.08	11.54	11.54	23.08	30.77

There were two statistically significant canonical variables created (Canonical 1: 0.4729 proportion explained variation, $F=2.53$, $p<0.0001$; Canonical 2: 0.3198 proportion of variation, $F=2.16$, $p=0.0078$). The two canonical variables can explain a total of 79.26% of the variation in food type. The squared distances between food groups revealed that banana and blueberry ($F=1.0470$, $p=0.3991$), blueberry and peanut ($F=2.1030$, $p=0.0585$), diet coke and banana ($F=2.0076$, $p=0.0706$), and diet coke and peanut ($F=1.6195$, $p=0.1484$) do not have significant distances between them based on the two canonical variables (Table 4.51).

The principal component analysis determined there were two factors applicable to Model 5 (Figure 4.12). The varimax orthogonal rotated factor pattern (Table 4.52) demonstrates that Factor 1 groups low frequency by itself to explain the most variation and, Factor 2 groups high-terminal frequency, maximum frequency, average frequency, and maximum power together (Figure 4.13). Delta time does not group with any other variables.

Table 4.51 Squared distances between food groups and associated F-statistics and p-values for limited data Model 5.

		Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.6081	1.2471	1.8864	1.3443
	F-Statistic	0.0000	1.0470	2.0076	3.1986	2.2795
	P-Value	1.0000	0.3991	0.0706	0.0062	0.0411
Blueberry	Squared Distance	0.6081	0.0000	1.4355	1.4673	0.9959
	F-Statistic	1.0470	0.0000	2.8424	3.0982	2.1030
	P-Value	0.3991	1.0000	0.0130	0.0077	0.0585
Diet Coke	Squared Distance	1.2471	1.4355	0.0000	2.3553	0.8324
	F-Statistic	2.0076	2.8424	0.0000	4.5824	1.6195
	P-Value	0.0706	0.0130	1.0000	0.0003	0.1484
Mushroom	Squared Distance	1.8864	1.4673	2.3553	0.0000	1.2702
	F-Statistic	3.1986	3.0982	4.5824	0.0000	2.6325
	P-Value	0.0062	0.0077	0.0003	1.0000	0.0201
Peanut	Squared Distance	1.3443	0.9959	0.8324	1.2702	0.0000
	F-Statistic	2.2795	2.1030	1.6195	2.6325	0.0000
	P-Value	0.0411	0.0585	0.1484	0.0201	1.0000

**Figure 4.12** Graph of factors based on eigenvalues created for limited data Model 5. Values greater than one are viable factors.**Table 4.52** Rotated factor pattern for factors retained by the mineigen criterion for limited data Model 5.

	Factor 1	Factor 2
Delta Time	0.60566	0.09760
High-Terminal Frequency	-0.37402	0.83924
Low Frequency	0.88035	0.00370
Maximum Frequency	0.60787	0.68485
Maximum Power	0.39737	0.66201
Average Frequency	0.66386	0.65048

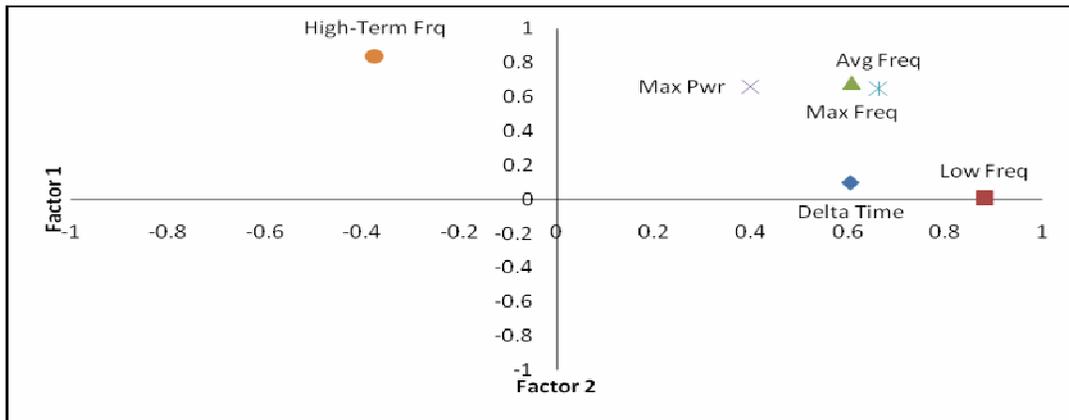


Figure 4.13 Plot of factor pattern for Factor 1 versus Factor 2 for limited data Model 5.

4.3.6 Model 6

Because Model 1 and Model 2 had several non-significant variables when utilizing the limited data set, it was entered as a starting point in the stepwise discriminant procedure with the limited data set to see how the model could be improved upon. The stepwise procedure (Table 4.53) developed a four-variable model containing low frequency, delta time, average power, and energy. When conducted with the limited winsorized data set, this four-variable model has an R^2 equal to 0.7052. All variables added significant information to the model (Table 4.54). Because all of the variables added statistically significant information and a larger R^2 than Model 4, this model is the best model when utilizing the limited data set.

Table 4.53 Stepwise procedure for producing four-variable Model 6.

Order	Step	Partial R^2	F-Statistic	P-Value
1	Begin with delta time, average power, low frequency, maximum frequency, (initial+high+terminal)/3, and energy			
2	Removed (initial+high+terminal)/3	0.0461	1.33	0.2639
3	Removed maximum frequency	0.0446	1.30	0.2758

Table 4.54 Model 6's variable significance using the limited data set.

Variable	Partial R ²	F-Statistic	P-Value
Delta Time	0.1794	6.12	0.0002
Low Frequency	0.2325	8.48	<0.0001
Average Power	0.1523	5.03	0.0009
Energy	0.1410	4.60	0.0018

The discriminant function model demonstrated a significant difference in variables at predicting food type (Chi-Square=90.155007, $p<0.0001$; Wilk's Lambda test $F=3.34$, $p<0.0001$; Pillai's Trace test $F=3.17$, $p<0.0001$; Hotelling-Lawley Trace test $F=3.44$, $p<0.0001$; Roy's Greatest Root test $F=9.75$, $p<0.0001$). This model did better at predicting the correct food type than Model 4 (Table 4.55). Banana (50.00%), diet coke (60.87%) and mushroom (65.38%) were reclassified with a high degree of accuracy. Blueberry was most often misclassified as mushroom, and peanut was most often misclassified as diet coke.

Table 4.55 Percentage of vocalizations correctly reclassified into food type utilizing limited data Model 6.

	Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	50.00	5.56	16.67	27.78	0.00
Blueberry	7.41	48.15	14.81	22.22	7.41
Diet Coke	4.35	13.04	60.87	8.70	13.04
Mushroom	0.00	3.85	15.38	65.38	15.38
Peanut	7.69	15.38	30.77	26.92	19.23

There were two statistically significant canonical variables created (Canonical 1: 0.6837 proportion explained variation, $F=3.34$, $p<0.0001$; Canonical 2: 0.2249 proportion of variation, $F=1.95$, $p=0.0458$). The two canonical variables can explain a total of 90.86% of the variation in food type. Based on the two canonical variables, there is not statistically significant distance between banana and blueberry ($F=1.4914$, $p=0.2096$), peanut and banana ($F=2.1809$, $p=0.0757$), peanut and blueberry ($F=0.7920$, $p=0.5328$), and peanut and diet coke ($F=1.7714$, $p=0.1396$) (Table 4.56).

The principal component analysis determined there was one factor applicable to Model 6 (Figure 4.14). The principal component factor pattern (Table 4.57) demonstrates that Factor 1 groups energy and average power explain the most variation and group together with delta time and low frequency also grouped together explaining less variation. A varimax orthogonal rotation is not possible with only one factor. Because all of the variables add significantly, the R^2 is high, reclassification was reasonable, and squared distances were fairly distinct, this model is the candidate for ‘best’ model when utilizing the winsorized limited data set.

Table 4.56 Squared distances between food groups and associated F-statistics and p-values for limited data Model 6.

		Banana	Blueberry	Diet Coke	Mushroom	Peanut
Banana	Squared Distance	0.0000	0.5672	1.0522	2.3114	0.8421
	F-Statistic	0.0000	1.4914	2.5868	5.9860	2.1809
	P-Value	1.0000	0.2096	0.0407	0.0002	0.0757
Blueberry	Squared Distance	0.5672	0.0000	1.2219	1.2499	0.2456
	F-Statistic	1.4914	0.0000	3.6949	4.0309	0.7920
	P-Value	0.2096	1.0000	0.0073	0.0043	0.5328
Diet Coke	Squared Distance	1.0522	1.2219	0.0000	2.9278	0.5961
	F-Statistic	2.5868	3.6949	0.0000	8.6997	1.7714
	P-Value	0.0407	0.0073	1.0000	<0.0001	0.1396
Mushroom	Squared Distance	2.3114	1.2499	2.9278	0.0000	1.1015
	F-Statistic	5.9860	4.0309	8.6997	0.0000	3.4866
	P-Value	0.0002	0.0043	<0.0001	1.0000	0.0101
Peanut	Squared Distance	0.8421	0.2456	0.5961	1.1015	0.0000
	F-Statistic	2.1809	0.7920	1.7714	3.4866	0.0000
	P-Value	0.0757	0.5328	0.1396	0.0101	1.0000

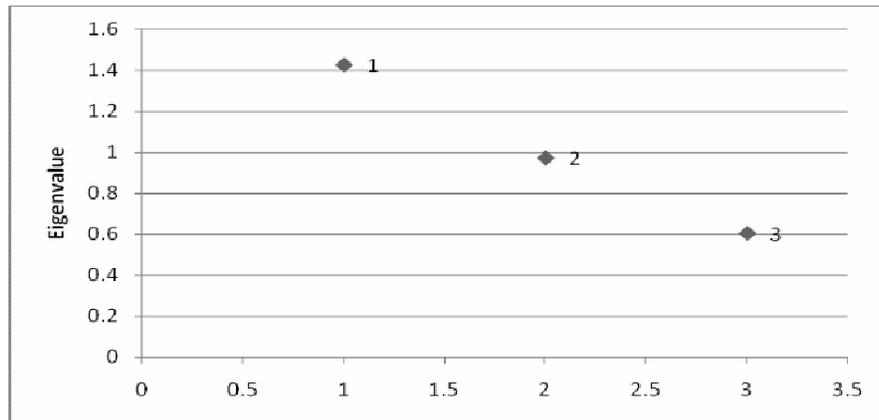


Figure 4.14 Graph of factors based on eigenvalues created for limited Model 6. Values greater than one are viable factors.

Table 4.57 Principal component pattern for factors retained by the mineigen criterion with limited Model 6.

	Factor 1
Delta Time	0.64928
Average Power	0.87705
Low Frequency	0.49888
Energy	0.94272

4.4 Model Summary

Six models were run with both the full winsorized data set and the limited winsorized data set. Each model produced different results depending on which data set was utilized. The decision becomes two-fold: which model is best for each data set and which model is best for both the limited and full data set. Because at least one variable is not significant, many of the models are eliminated as a candidate for the ‘best’ model (Table 4.58). Only Model 4 and Model 6 can be considered for the ‘best’ model when utilizing the limited data set. Of these models, Model 6 has a higher R^2 value, reclassifies more food types above the 50% criterion, and has an equal number of food pairs without significant distances between them. Therefore, when utilizing the limited data set, Model 6 is considered the ‘best’ model.

Among the models utilizing the full data set, Model 2, Model 4, Model 5, and Model 6 have all variables adding significantly to the model and are candidates for the ‘best’ model.

Model 4 has a low R^2 value, only reclassifies one food type above 50% and does not have significant distance between 5 different food pairings. Therefore, Model 4 is out of the running for the 'best' model. Model 2 and Model 5 reclassify equivalent numbers of food type and have equal number of food pairs without significant distances. Since Model 5 has a higher R^2 value than Model 2, Model 2 can be eliminated as the 'best' model when utilizing the full data set. Model 5 has a larger number of food pairs without significant distances between them compared to Model 6. However, Model 5 has a larger R^2 value and reclassifies a larger number of food types correctly. Therefore, when looking only at the full data set, Model 5 is the 'best' model for predicting food type.

Finally, it needs to be determined which model is 'best' for both the full and limited data sets. Only Model 4 and Model 6 have all variables significant for both the full and limited data set. Model 4, for both the limited and full data sets, has a lower R^2 value and reclassifies fewer food types above 50%. For the full data set, Model 4 also distinguishes between fewer food pairs based on distance, and the limited data set distinguishes between an equal number as Model 6. Because Model 6 consistently has a higher R^2 , performs better at reclassification of food types, and has equivalent or fewer food pairs without significant distances between them, Model 6 is the 'best' model for both the limited and full data sets.

Table 4.58 Summary of all models' characteristics relating to finding the candidate for best model.

	All variables significant?	R²	# food types reclassified correctly	# food pairs without sig. distances
Model 1 Limited Data	No	0.5330	4/5	4
Full Data	No	0.3136	3/6	1
Model 2 Limited Data	No	0.6301	5/5	5
Full Data	Yes	0.4645	3/6	1
Model 3 Limited Data	No	0.4104	n/a	n/a
Full Data	No	0.3513	4/6	1
Model 4 Limited Data	Yes	0.3666	2/5	4
Full Data	Yes	0.2664	1/6	5
Model 5 Limited Data	No	0.4432	3/5	4
Full Data	Yes	0.5860	3/6	1
Model 6 Limited Data	Yes	0.7052	3/5	4
Full Data	Yes	0.4535	2/6	0

Chapter Five: Discussion

5.1 Introduction

The current study provides some support for referents in the vocal repertoire of bonobos. Because every model demonstrated a strong significant difference between vocalizations based on food types and because the best model showed significant distances between all food groups, the question of whether there were different vocalizations for different food items is affirmed. Despite the statistical significance, however, researchers should not be quick to label these vocalizations as referential. Since an 80% criterion of correct reclassification of vocalizations into food types was rarely met, perhaps the relationship between vocalizations and their corresponding food types is too weak. Additionally, due to the context in which food peeps are elicited, researchers should investigate further the notion that these vocalizations are intentionally meant to convey information to conspecifics or that listeners are necessarily responding to this information.

The issue of distinguishing what degree of statistical significance is required and the context surrounding food vocalizations raises other important questions regarding the study of referents in nonhuman primates. First, this study demonstrated the complexity of examining referents in a nonhuman species. When trying to discover a referent in a communication system researchers do not fully understand, a vital concern is the methodology chosen for examination (Zuberbühler, 2003; Marler et al., 1992). This includes aspects related to initial assumptions, such as whether one is starting from a standpoint that great ape and human communication is continuous or not. Also, if human and nonhuman communication is continuous, does this necessarily mean that nonhuman communication systems function in similar manner as human communication (e.g. multiple phonemes

equating to a single word)? Equally difficult is setting up or finding a situation in which you can expect a one-to-one correspondence between a stimulus or setting and one specific referent. Finally, even with a sound methodology, the question then becomes what statistical requirements are required in order to provide a case for nonhuman referential communication. All of these can have significant impacts on the interpretation of referential communication and must be scrutinized deeply before any conclusion regarding nonhuman great ape referential capability can be made. The terminology and theory surrounding referential communication among nonhuman great apes has led to a murky area of study, which needs to be re-examined in order to establish sound theoretical and methodological background.

5.2 Statistical Significance – When is it Referential?

The current study demonstrated that bonobo vocalizations could be differentiated by food type. When using all 378 vocalizations and Model 6, approximately 45% of the variation in vocalizations could be attributed to food type. This value was substantially higher when using the limited data set, where approximately 70% of the variation in vocalizations could be attributed to food type. This model explained a substantial amount of variation based on food type, reclassified foods reasonably well, and demonstrated significant distances between vocalizations based on food groups. With such statistically significant results, it would seem reasonable to conclude that there is a difference between vocalizations based on food type. However, does statistical significance necessarily translate to referential communication?

In this particular case, the answer is no. The first order of business is establishing what is actually required to demonstrate that a vocalization is referential. Researchers have

developed different specifications for demonstrating referentiality. I have adopted the most conservative definition. First, the vocalization must be intentionally given. Second, the vocalization must contain information that can be decoded by a conspecific listener. Third, the vocalization must be intended to transmit information otherwise unknown to a conspecific. Finally, the listener of the vocalization must decode the vocalization and respond accordingly given this new information. This study cannot conclusively demonstrate referents in bonobos because it fails to address the final aspect of referential communication, the listener's perspective. Rather, the study exclusively focused on the vocalizer and, specifically, the information contained within the vocalization in order to determine if referential communication was even possible.

The content of and transmission of referential communication were most important to this study. Food vocalizations among bonobos and chimpanzees have generally been perceived as involuntary utterances, with a few studies indicating at least some degree of control (Hopkins et al., 2007; Hotstetter et al., 2001; Goodall, 1986). However, the importance and impact of this was not realized until after data collection was complete. Data collection helped to shed light on the potential for failure in meeting the requirement of voluntary control and intentionality to communicate. Collection of data made it exceedingly obvious that Kanzi was not necessarily attempting to engage in any sort of communicative interaction with others in the community, nor was the rest of the community attempting to engage him relative to his food vocalizations.

Due to these above mentioned shortcomings, the current study is limited to drawing conclusions related to the second caveat of referential communication: the vocalization must contain information. However, several important insights have been brought to light via

investigation into this caveat. First and foremost, this study did conclusively demonstrate that information contained within food vocalizations of bonobos does vary based on food type.

The next step is to determine if this information is strong enough to be considered referential.

In other words, is the evidence strong enough to suggest that each food type vocalization functions as its own word? To answer this, one must turn to the components present in human spoken words. Human words are comprised of phonemes. Additionally, human words are laden with emotions (Bachorowski & Owren, 1995) and individual variation.

Consequently, no two words will appear exactly the same on a spectrograph. Due to these various factors, a one hundred percent reclassification of vocalizations is ideal but not necessarily expected in order to demonstrate the ability of vocalizations to function as a word. Taking into account the potential emotional factor contained within vocalizations, along with individual variation, statistical significance to a $p < 0.0001$ and reclassification of vocalizations above to at least a 60% criterion but preferably an 80% criterion is ideal to demonstrate referential information in vocalizations. An 80% criterion still allows for individual variability while maintaining a high standard of correlation between categories.

Another factor that needs to be considered is which statistical analysis should be used in determining referential communication among nonhuman great apes. As demonstrated in this study, different analyses can provide different results. Although all analyses demonstrated a significant difference between food types for every model, the interpretation of results for the reclassification procedure in both the discriminant function analysis and the significant distances between food types in the canonical discriminant analysis differed even within models. For example, Model 2 with the limited data set demonstrated that all food types would be reclassified above 50%. However, five different pairings of food groups did

not demonstrate significant distances. Model 2 demonstrates an extreme example. The remaining models tended to follow a general trend where if the reclassification procedure performed poorly, there were a larger number of food pairs without significant distances. Despite this general trend, the potential for differences in the two forms of analysis demonstrates the importance of conducting multiple analyses on vocalizations. For studies examining referential vocalizations, both discriminant function analysis and canonical discriminant analysis should be used. Discriminant function analysis can provide much needed insight into how well a particular model would be able to predict the food type of particular vocalizations. This may have important implications regarding the listener's ability to decode information. However, canonical discriminant analysis also can provide insight into a different realm. Investigation into chimpanzee food grunts have demonstrated information contained within the vocalization but also suggest this information is partially tied to individual food preferences (Gibbons, 2007; Slocombe & Zuberbühler 2006; Hallberg, 2000). The canonical discriminant analysis can provide information regarding whether the lack of significant distances between specific food types tends to be associated with similar preference among food items.

This study demonstrated conclusively that referential information is contained within bonobo food vocalizations due to their significant distinction between food types, generally high reclassification of vocalizations, and the majority of food pairings with significant distances. However, in situations where this criterion is not met, there are two possibilities that should be investigated. First, it is possible that vocalizations do not contain specific information. Before that conclusion is drawn, the possibility that phonemes or several vocalizations provide specific information should be eliminated.

5.3 Initial Assumptions & Impact on Referential Studies

As this study demonstrated, deciding on an appropriate methodology is the most important detail of any study involving referential communication, and initial assumptions can make or break a methodology. Initial assumptions about a topic undoubtedly have an effect on the methodology chosen for a study (Sober, 1988). This aspect is pertinent to studies relating to referential capabilities in nonhuman great apes. Historically, investigators have assumed that animal communication is too limited to have led to the complexity of human language (Arcadi, 2005; Parr et al., 2005; Hauser & Fitch, 2003; Seyfarth & Cheney, 2003a; Seyfarth & Cheney, 2003b). Therefore, they assume that nonhuman great apes will be incapable of referential communication in their vocal repertoire. However, this assumption has several downfalls. First, it fails to follow the rule of parsimony generally obeyed by evolutionary anthropologists (Sober, 1988). With the heavy reliance on referents in human language, it seems particularly unwise to not follow the rule of parsimony. The assumption that the great ape vocal repertoire will not demonstrate referents seems highly unlikely, especially given the close evolutionary and behavioral relationship between *Homo* and *Pan* (Goodman et al., 2001; McGrew, 1992).

While the assumption that great ape vocal repertoire will not demonstrate referents violates the rule of parsimony in respect to phylogenetic similarity, researchers have additionally failed in general to acknowledge the impact this assumption can have on the approach to studying communication in animals. It is this impact that, historically, has certainly had the largest effect on conclusions related to animal communication (Seyfarth & Cheney, 2003b; Owings & Morton, 1998). The initial assumptions undertaken during these studies directly influence the interpretation of results. Historically, researchers have

maintained that animal communication is far less sophisticated than human language (Parr et al., 2005; Seyfarth & Cheney, 2003a; Seyfarth & Cheney, 2003b; Ploog, 1981; Marler, 1977; Smith, 1977). Due to this initial assumption in studies undertaken decades ago, a dichotomy of animal communication as emotional and human language as referential was adopted. Therefore, studies investigating animal communication were initially only interested in demonstrating the emotional aspect of vocalizations and have continued to adopt approaches that make it extremely difficult if not impossible to investigate complex communication among nonhumans or the interaction between emotion and semantics in nonhuman vocalizations (Seyfarth & Cheney, 2003b; Owings & Morton, 1998).

All studies examining referential capacities in nonhuman great apes should start with the assumption that referential abilities should be expected to some extent due to the close genetic and behavioral relationship between humans and nonhuman great apes. The current study assumed just that. However, as discovered in the planning stages, this is not the only assumption, nor even the most important assumption, affecting the methodology of referential studies in nonhumans. Many of the recent studies examining potential referential communication in nonhuman great apes have started with the initial idea that some degree of complex communication is likely among nonhuman animals, especially those closely related to humans (Cheney & Seyfarth, 2007; Zuberbühler, 2003; Marler et al., 1992; Marler, 1985). The most difficult decision to make regarding initial assumptions and subsequent methodology is what contexts would likely require referents and within those instances, what a referent would look like.

If approaching nonhuman communication with the assumption of evolutionary continuity between great apes and humans, the question then becomes where to look for

referents. The unique difficulty in investigating nonhuman communication is the attempt to decode a language or communication system for which there is no translator. Several key questions arise over methodology in such studies. First, researchers should determine where complex communication might be expected. The flaw of the current study, along with other great ape vocal referent studies, is the inability to examine vocalizations that have the highest likelihood of serving a referential function and the surrounding circumstances for referential communication.

Gibbons (2007), Slocombe and Zuberbühler (2005), and Hallberg (2000) all examined food grunts in the vocal repertoire of chimpanzees for referential aspects. All studies produced mixed results regarding the referential capacity of these apes. They concluded there was a degree of linkage between food type and vocalization but did not go so far as to label vocalizations referential, rather merely functionally referential. The current study continued this trend by investigating food peeps in bonobos. However, food calling is probably not the ideal place to begin examining vocal referential capabilities. The complexity of food calling in chimpanzees indicates a mixed background in terms of underlying influences. Initially, researchers suspected that these food vocalizations were under involuntary control (Goodall, 1986). This was anecdotally supported by Goodall (1986), who reported seeing a chimpanzee place two hands over his mouth when encountering a number of bananas, suggesting that he was trying to stifle what would normally be an involuntary reaction to seeing such a large quantity of desirable food. Nevertheless food grunts have been the only aspect of great ape vocal repertoire investigated in terms of referential communication. The current study also only investigated food peeps in the vocal repertoire of bonobos.

The reasoning behind the interest in food calling is not entirely unwarranted however. Food calling is a short vocalization in comparison to long-distance calls such as pant-hooting in chimpanzees, which can involve a long complex series of vocalizations (Goodall, 1986). Therefore, perceived differences between these vocalizations should be relatively simple to examine. Furthermore, differences should be at the level of specific acoustic features rather than the level of overlapping differences in acoustic features and ordering of vocalizations, which may be possible for longer more varied vocalizations. Specifically, long-distance vocalizations can involve a series of calls with the ordering of vocalizations and features potentially playing a vital role in meaning (Notman & Rendall, 2005). In addition, the cause of food vocalizations is relatively simple and directly observable. Food vocalizations are associated with eating, a directly observable action. Therefore, a researcher can investigate this situation clearly by recording food vocalizations along with the associated food items being consumed in the vicinity. This documentation allows investigators to easily test whether there are differences in vocalizations based on food type, abundance of food, and/or whether any of these differences are also tied to emotion.

Despite the apparent ease with which food calling can be examined for referents, I conclude that food calling is not the optimal choice in investigating vocalizations fulfilling all of the requirements for referential communication among nonhuman great apes. This ties into initial assumptions undertaken in any scientific study and, specifically, assumptions regarding evolutionary continuity between humans and nonhuman great apes. How one determines where to begin investigating usually involves some initial ideas about nonhuman great ape communication. In the case of food calling, the initial assumption involves investigating a situation that seems to have the potential for a one-to-one correspondence

(e.g. food item and specific vocalization). The function of food calling then would be to convey information to other individuals about what food item was present and being consumed. However, I maintain that the reasoning behind this assumption should be disregarded, and a new area of vocal communication should be investigated.

First, if food grunts in chimpanzees and food peeps in bonobos are not entirely under voluntary control, this is an inadequate area to begin research into referential communication. When a human uses a referent, the intention is to communicate a specific concept to another person that would otherwise not be known. If a human cries, screams, or groans, information is being conveyed to others. However, this information is not necessarily intentionally transmitted, nor is the information specific enough to be labeled a referent. Since there is expected continuity between human and nonhuman great ape communication patterns, nonhuman great apes, if capable of vocal referential communication, would be expected to exhibit referents in a situation where they are intending to communicate what would otherwise be unknown to a conspecific.

A referential ability would entail specific requirements on the vocalizer. First, the information would need to be intentionally conveyed (Seyfarth & Cheney, 2003b; Macedonia & Evans, 1993; Marler et al., 1992). Of course, this is not a widely accepted idea when examining food grunts and food peeps (Goodall, 1986). There have been some studies that suggest food grunts and food peeps are under voluntary control (Hopkins et al., 2007; Hotstetter et al., 2001), but the overall sentiment is still that *Pan* generally exhibits food calling involuntarily or at least not completely voluntarily (Goodall, 1986). In addition, the goal of a referent is to communicate an idea or concept that would otherwise be unknown between two communication partners (Seyfarth & Cheney, 2003b; Macedonia & Evans,

1993, Marler et al., 1992). It has not been demonstrated whether food calling among nonhuman great apes exhibits this characteristic. Food grunts and food peeps are characteristically relatively quiet vocalizations (Bermejo & Omedes, 1999; Goodall, 1986). Therefore they are audible for relatively short distances. Given the size of chimpanzee and bonobo home ranges, it is likely that these food calls are not meant to convey information to individuals at far distances within these ranges.

The purpose of food calling among nonhuman great apes has not been systematically studied. Therefore, it is not known whether unknown information is transmitted to a conspecific by such calls. It is possible that, due to the relatively close proximity of conspecifics within a feeding party or subgroup, there is less need for advertisement related to food type being consumed than would characterize between-party or subgroup communication. In addition, during situations of large fruiting trees or numerous fruiting trees in a small area, multiple individuals may vocalize, and it is possible that these vocalizations function to some degree in social cohesion (pers. comm. J. Pruetz). One possible hypothesis regarding food calling is that it functions as a form of social cohesion that is tied to excitement over specific food items. Therefore, referential information is contained due to the semantic relationship between emotional excitement and specific food items. Despite this, the function would not require the other components of referential information (e.g. intentionality and the transmission of unknown information). This would result in a vocalization that contained referential information but may not fulfill all of the requirements for a referent. However, it is also possible that despite the close proximity of conspecifics within a party, environmental factors create a lack of visibility between individuals, and information about food could be unknown to a conspecific within the same

party or subgroup. Because the function of food calling among nonhuman great apes has not been established, and it is possible the goal does not involve transmitting unknown information, another realm, with an established goal of transmitting unknown information (e.g. long distance vocalizations transmitting information between parties), should be investigated for referential communication.

If food calling does not contain all of the requirements necessary to be labeled a referent, where can one expect to find referential communication in the vocal repertoire of nonhuman great apes? The key lies in finding communicative interactions between conspecifics that involve intentionality and the ability of conveying information that would otherwise be unknown. Tagliatela et al. (2003) demonstrated that Kanzi did exhibit referential vocal capabilities in his interactions with humans. This study demonstrated that Kanzi usually partook in a conversational turn-taking with humans, and his modulated vocal utterances appeared to function much like that seen in human interactions (Tagliatela et al., 2003). However, the luxury in this situation is knowing exactly what was said on one side of the conversation. This condition is not possible in studies investigating referential capabilities of nonhuman great apes interacting with one another.

In order to determine where to look for referential communication, researchers need to establish which vocalizations would be most conducive to transmitting information to conspecifics. The vocal repertoire of nonhuman great apes can be divided into long-distance and short-distance vocalizations. Short-distance vocalizations are not necessarily precluded from containing referential information. However, it is much more difficult to establish what information would be communicated in these short-distance vocalizations. Short-distance vocalizations with the potential to communicate intentional information to conspecifics could

include the ‘whistle bark’ of bonobos (De Waal, 1988) and the homologous ‘bared-teeth bark’ of chimpanzees (De Waal & Van Hooff, 1981). These vocalizations are associated with agonistic interactions in an alliance context where the vocalizer is supporting one conspecific against another or where the vocalizer is recruiting aid from a conspecific during an agonistic interaction (De Waal, 1988). These vocalizations have the potential of carrying specific information differentiating a call emitted to gain aid versus a call emitted by an ally toward the victim along with potential information regarding the severity of the interaction (although this information would probably be readily available through visual cues as well). Also, alarm vocalizations such as the ‘wieew bark’ (De Waal, 1988) of bonobos and homologous ‘waa-bark’ (Goodall, 1986) of chimpanzees have the potential to demonstrate referential communication. These vocalizations are clearly audible to parties that are relatively close together but potentially out of sight and are associated with threats to the community. It would seem quite possible that these vocalizations would carry specific referential information regarding the threat (e.g. Diana monkeys: Zuberbühler, 2000; Barbary macaque: Fischer, 1998; Ring-tailed lemur: Pereira & Macedonia, 1991), urgency of the threat (e.g. Redfronted lemurs: Fichtel & Hammerschmidt, 2002), and/or specific plan of action (e.g. Vervet monkeys: Seyfarth et al., 1980a; Seyfarth et al., 1980b) in order to better convey messages to individuals out of a direct line of sight with the threat.

Long-distance vocalizations could contain information to communicate to unseen conspecifics, but the difficulty comes in determining what concrete information is being transmitted and how a one-to-one correspondence can be established. Among long-distance vocalizations, ‘high hooting’ in bonobos (De Waal, 1988) and the homologous ‘pant-hooting’ among chimpanzees (Goodall, 1986) have the potential to convey information over

long distances to conspecifics. Pant-hooting and high-hooting are generally associated with communication between parties that are out of sight (De Waal, 1988). Therefore, it would be an ideal context for individuals to convey information regarding food sources, party location, party direction, etc (Wrangham, 1977). The issue with these communications is that they involve a complex series of vocalizations, so they can be difficult to analyze for a one-to-one correlation between a stimulus and the vocalization (Notman & Rendall, 2005; Clark & Wrangham, 1993; Marler & Hobbett, 1975).

In addition to investigating relevant areas for referential communication, investigators need to take into consideration how the vocalizations will be analyzed. Typically researchers have assumed that each vocalization is a unit to be analyzed separately. Therefore, the meaningful unit is a single vocalization, not the patterning of several vocalizations. This has led investigators to measure vocalizations for each unit's individual characteristics and compare it to other single vocalizations. However, this is not how complex human language is analyzed. Human words are composed of phonemes, which appear as individual vocalizations in a spectrogram. Yet the human ear tells us that meaning comes in the grouping of several phonemes. There is no visible distinction between words on a spectrogram but meaning comes in the breaks between words that the human ear creates. Therefore, analysis of meaningful words actually involves the patterning of several vocalizations. No investigation has systematically examined nonhuman primate vocalizations to see whether patterning of vocalizations plays any role in potential referentiality. Because of this, investigators need to be aware that if one form of analysis (e.g. looking at vocalizations as single units) does not demonstrate referentiality, it does not necessarily

preclude another form of analysis (e.g. examining the patterning of vocalizations) from demonstrating potential referential communication.

In conclusion, the history of vocal referential studies in nonhuman great apes, including the current study, have left the issue of whether nonhuman great apes utilize referential communication in their vocal repertoire still open to debate (Seyfarth & Cheney, 2003b). However, what this study clearly has demonstrated is that the initial assumptions undertaken before beginning investigation into referents must be clearly determined from the onset and their impact on studies acknowledged. Particularly the importance of continuity between nonhuman great ape communication and human communication must be determined. Due to the close relationship between all great apes, genetic and otherwise, it seems necessary to approach referential communication from a standpoint of expected continuity. Buried within this assumption is the necessity to examine communication patterns that would seemingly carry intentional, otherwise unknown information to conspecifics. These vocalizations could include alliance vocalizations, alarm vocalizations, or long-distance vocalizations rather than the typical food calling investigated to date. Furthermore, careful attention to analysis and the assumptions on which it is housed also needs to be taken into account in the investigation of nonhuman primate communication.

5.4 Methodology of Referential Studies

The previous section determined that the initial assumptions of this study and all studies investigating referential communication among nonhuman great apes thus far have been flawed. With that in mind, the methodology of these studies is brought into question. Methodology necessarily varies based on whether referential studies are being conducted on a wild group of great apes or a captive group. For a wild group of great apes, it is more

difficult to establish referential communication, but this is not to say that it does not exist. Since there has been limited investigation into these abilities amongst wild great apes, the first obvious course of action is to produce a catalog of potentially referential vocalizations. Therefore, vocalization recording could focus on the high-hooting, wieew bark, and whistle bark of bonobos or the pant-hooting, waa-bark, and the bared-teeth bark of chimpanzees. Behavioral and environmental data must be taken at the time of these vocalizations as well. If investigating high-hooting or pant-hooting, data categories may include current direction of travel, first feeding location after vocalizing, and description of current environmental surroundings and that of first feeding location (characteristics such as general fruit availability, fruit abundance, presence/absence of watering hole – if that is a limiting factor, etc.). If investigating the wieew bark or waa-bark, data categories could include the perceived threat, if known, the distance of the threat, and the reaction to these vocalizations. Recordings of whistle barks or bared-teeth barks could involve recording whether the individual was attempting to gain support or giving support to a conspecific and the course of action that follows. Once a sufficient database of vocalizations in at least several different behavioral categories was produced, analysis could be done with each one of the categories in order to assess whether vocalizations could be discriminated from one another based on the various contexts and to determine whether vocalizations are differentiating based on one particular context type (e.g. alarm vocalizations based on perceived threat) or several contexts.

Studies involving captive nonhuman great apes can have significantly more control. A similar study involving cataloging vocalizations and contexts could be conducted, or a study with more experimental control could be undertaken. The current study involved presenting one food at a time to the subject and recording all vocalizations made once the

subject had the food item. The reasoning behind this was to establish a one-to-one correlation between a particular food item and all vocalizations given during that time. However, this ideal was not necessarily met. First, if a vocalization is meant to convey information and each vocalization is equivalent to a word (assumptions in their own right), it would seem illogical for the subject to repeat himself upwards of thirty times when the food was in front of himself. It is more likely that a) these vocalizations do not contain any information (which the results does not support), b) each vocalization is not the equivalent of a word, rather a number of vocalizations equate one word, or c) partially through the trial, the vocalizations change from describing what food item was being eaten to some other motivating factor such as what was wanted next or excitement level etc. Although deeper thought into initial assumptions suggests studying food peeps is not the route to discovering referential communication amongst nonhuman great apes, this study demonstrates the difficulty in determining a methodology that can assure the vocalizations given correspond to a particular referent.

Bared-teeth bark and whistle bark are not conducive to anything more than observational study. However, both pant-hooting/high-hooting and waa-bark/wieew-bark are conducive to experimental examination. As previous studies with other species have demonstrated, alarm vocalizations could be examined in an artificial setting with predator models displayed, predator vocalizations played in order to elicit alarm vocalizations, or alarm vocalizations played back in order to examine the listener's behavior (Thomas langurs: Wich & Sterck, 2003; Yellow Warbler: Gill & Sealy, 2004; Gill & Sealy, 2003; Brant's Whistling Rat: Le Roux et al., 2001; Diana monkeys: Zuberbühler, 2000; Yellow-bellied Marmots: Blumstein & Armitage, 1997; Gunnison's prairie dog: Slobodchikoff et al., 1991;

Ring-tailed lemur: Pereira & Macedonia, 1991; Vervet monkey: Seyfarth et al., 1980a; Seyfarth et al., 1980b). These models could vary by predator type and distance to the enclosure. However, predators typically do not vocalize while hunting and predator models are usually unrealistic depictions as well because they are not moving (Zuberbühler 2000; Boesch & Boesch, 1989). Nevertheless, nonhuman primates appear to respond to these models as if the predator is present and thus can provide increased stress for the group (Zuberbühler et al., 1997). Therefore, the best situation in which to examine referential communication among nonhuman great apes, which has never been studied in an experimental setting, involves investigation into long-distance vocalizations. These vocalizations probably would be the most difficult to examine for referents in the wild because of the variability between contexts. However, in captivity much more control can be allotted to investigate referents intricately.

Since long-distance vocalizations are intended for conspecifics out of sight, these vocalizations would seemingly serve the purpose of transmitting information to other members of the community. This has been substantiated by several studies examining the complexity of pant-hoots in chimpanzees. Clark and Wrangham (1993) determined that a particular phase of a pant-hoot, the letdown phase, tended to be associated with initial arrival at a fruiting tree. The letdown phase was not exclusive to first arrival at fruiting trees but was significantly associated with this context. This lends support to the idea that pant-hoots can serve a communicative function to group members, in this case inform others of a particular food source or at least arrival at that source. Uhlenbroek (1996) suggested there may be referential subtypes of pant-hoots related to travel, arrival, and feeding contexts. Therefore, these vocalizations are serving the purpose of communicating information otherwise

unknown. In addition, these vocalizations are probably intentionally communicating something to conspecifics, but the question is what information is being transmitted (Clark & Wrangham, 1993). As such, the chimpanzee pant-hoot and homologous bonobo high-hooting seemingly fulfill the circumstances in which information is communicated in a referential manner among humans. Finally, a study of this nature should approach with the assumption of continuity between humans and nonhuman great apes. Therefore, the expectation of continuity between species and the study of a context where referential communication among humans would be present sets up a clear opportunity to determine whether nonhuman great apes use referential communication in their vocal repertoire.

The methodology for an experimental investigation into pant-hooting or high-hooting needs to be very controlled in order to adjust for the various information that could potentially be transmitted during the vocal interactions. In order to record these long-distance vocalizations, a condition where communication was possible, necessitated, or at least advantageous would allow for a clear methodological start point to record potential communicative interactions. In a captive setting, an ape's life tends to be structured around food. Therefore, food-related vocalizations may still provide the key to examining vocal referential capabilities among nonhuman great apes. The current study attempted to establish a one-to-one correlation between food item and vocalizations. A similar correlation would need to be established in order to control what information would most likely be communicated. Since it is not entirely clear what the function of long-distance vocalizations are, it is possible these vocalizations are used for a variety of contexts including food, direction of travel, particular surprising events, activities, or any other information that would be relevant to an individual out of sight. Consequently, during a recording session, it would

have to be established that food is the only variable changing or about to change in the community's environment.

During this study, Kanzi did not seem to be establishing contact with other members of the group regarding his food. Rather his vocalizations were soft, individuals did not respond, and Kanzi did not attend to the situation for a response. The presence of food did not necessarily equate with a need or desire to communicate to the rest of the community. Therefore, a context in which it would be important to communicate a food's presence would need to be established. Chimpanzees in the wild would communicate a food source to other members of the community in order to notify them of an otherwise unknown food source. Individuals could then have the opportunity to move toward that site and eat. However, in the situation created by my study, an otherwise unknown food source was presented, but the individuals in the remainder of the group had no possibility of moving to that food source to eat. Therefore, there was no need to communicate that information to them. Consequently a methodology investigating the referential aspect of long-distance vocalizations will need to entail one of two possibilities. One would be to set up a situation where travel is possible within the community. This would mean that upon hearing a vocalization, individuals would have the opportunity to move toward the source, similar to that set up by Slocombe and Zuberbühler (2005). Secondly, a situation could be set up where one individual is aware of a food shortly before other individuals, and the purpose would be for the knowledgeable individual to pass on the information, so the unknowing individuals can be aware of what is coming, similar to that set up by Menzel (1988) but with more focus on vocalizations. These two situations would establish a specific context, which could be communicated to the group as a whole. Long-distance vocalizations collected during either of these two situations would

hypothetically exhibit acoustic differences dependent on context if vocal referential communication was actually being used by *Pan* in these scenarios.

Another important factor influencing methodology of referential study is the establishment of the analysis for vocalizations. Proper analysis of relevant vocalizations needs to be established beforehand. As mentioned, individuals studying animal communication systems are in a unique situation of attempting to decode a language or communication system without a translator. Typically, vocalizations have been analyzed as separate units. This assumes that if referents were present in nonhuman great ape vocal repertoire, each vocalization would be equivalent to a word. However, this may not necessarily be the case. Humans use phonemes to create words. In a spectrogram analysis, each phoneme would appear as a different vocalization and there would be no visible differentiation between words. It is currently not known whether nonhuman referential communication would appear as different phonemes, creating words, or each vocalization standing as its own word.

Due to the lack of clarity regarding the fundamentals of nonhuman great ape vocal communication, it is necessary to perform a spectrograph analysis in several ways. The Raven program is typically used for examining animal vocalizations³. This program, contrary to others used for human speech, ignores formants, instead looking primarily at frequency as an indicator of vocalizations. Raven analyzes each sound as a distinct vocalization to be measured, ignoring the potential for several vocalizations to stand in for one 'word.' Another form of spectrograph analysis utilizing the Praat program could be utilized. Praat is typically

³ www.birds.cornell.edu/brp/raven/Raven.html

used for human speech⁴, but has been used with animal vocalizations as well. This program allows for the analysis of elements, peak periodicity, amplitude, intensity, and pitch. Most importantly, differentiating Praat from Raven involves the ability to examine formants, an acoustic feature defining the human vowel system. However, the basis for examining this feature and the changes necessary for examining it in nonhumans has not yet been established. Finally, long-distance pant-hooting or high-hooting usually consists of a series of vocalizations. It has generally been thought that series of vocalizations, such as the numerous food grunts given when feeding, is really the same vocalization given multiple times. However, it is quite possible that it is the series of vocalizations that provides information to group members rather than a single vocalization in particular. A final analysis examining the crescendo and falling cycle among a series of pant-hoots or high-hoots should be conducted to determine if perhaps it is the cycling and patterning of vocalizations providing information to the community.

The final component of a methodological investigation into the referential capabilities of nonhuman great apes involves examining vocalizations from the listener's perspective. The current study did not examine any aspect of communication related to the listener's perspective. However, before referential communication can be established, studies must be conducted on this perspective within a communication bout. Referential communication involves not only intentional communication of otherwise unknown information but also that the listener perceives that information and responds or adjusts his/her behavior based on the information provided (Macedonia & Evans, 1993; Marler et al., 1992). Consequently, no

⁴ www.praat.org

study establishing referential communication among nonhuman great apes will be complete without examination from the listener's perspective.

Depending on which context discussed above was used to collect long-distance vocalizations, different methodologies surrounding the listener's perspective could be established. If recording vocalizations in a setting where individuals would have the opportunity to move toward the food source, a situation similar to that of Slocombe and Zuberbühler (2005) could be adopted. This involves establishing pre-determined food stations. When individuals are acquainted with the concept of specific food stations, the vocalizer could be positioned so as to see which food station/item will be offered and then communicate to the remainder of the community out of sight. Once the remainder of the group has the opportunity to investigate feeding stations for themselves, their behavior could be recorded to see if they differentially responded to the vocalizations with the knowledge of which food station would have food. Additionally, a modified form of this study could investigate whether vocalizations could give directional cues if rather than having feeding stations with different food items, feeding stations all provided the same food item but only one location would have the food.

If vocalizations were recorded where everyone would consequently receive the food item vocalized about, two different approaches could be used to investigate the listener's perspective. Several of the bonobos housed at Great Ape Trust of Iowa have demonstrated an understanding of spoken English along with the ability to use lexigrams (Savage-Rumbaugh et al., 1993; Savage-Rumbaugh, 1990). Consequently, after listening to the vocalizer, an individual experienced with the bonobos could simply ask one of the listeners to tell them what was said. The listener could utilize the lexigram board to translate and all uses of the

board could be documented and compared with what was actually being shown to the vocalizer. Another possibility is to give out the food to the entire group after hearing the vocalization without taking any behavioral data and test the listeners' understanding in a separate study. At a later point in time vocalizations could be played back in a match-to-sample paradigm such as that used by Gibbons (2007) and Hallberg (2000). Vocalizations could be played back and then pictures of different food items could be displayed. This would allow the testing of multiple individuals' ability to distinguish vocalizations based on the information conveyed. If individuals could consistently choose the photograph of the food item which was actually given for those vocalizations, this would suggest that vocalizers not only intentionally communicate unknown information but also that listener's perceive that information.

In conclusion, communicative vocalizations offer the best starting point to investigate vocal referential capabilities of nonhuman primates. The best chance for studies conducted on free-ranging great apes is to record vocalizations along with the behavioral and environmental contexts surrounding them. If a large enough catalog is collected, investigation into differences between these vocalizations can be examined. Studies among nonhuman captive great apes provide much more of an opportunity for an experimentally-controlled documentation of differences in vocalizations. Long-distance vocalizations allow the best experimental study into referential capabilities of nonhuman great apes. These vocalizations provide the groundwork for referents by being intentional and conveying otherwise unknown information to conspecifics. Food items still provide the necessary one-to-one correspondence for referential communication to be present. Consequently, methodology for the recording of vocalizations could involve either recording long-distance

vocalizations for an individual who is able to see food being delivered to a particular location or record long-distance vocalizations given by an individual for a food item, and then the vocalizer and the remainder of the community receive that food item to eat. Analysis of these vocalizations should entail a variety of methods including spectrograph analysis with Raven, spectrograph analysis with Praat, and analysis that examines the entire series of long distance vocalizations as one unit of peaks and valleys. Finally, in order for a communication to be truly interactive, the listener's perspective also needs to be taken into account. A study into the listener's perspective could create a differential response, such as that used by Slocombe and Zuberbühler (2005), utilize a match-to-sample paradigm, such as that used by Hallberg (2000) and Gibbons (2007), or in the special case of the bonobos housed at Great Ape Trust of Iowa, ask for a translation via the lexigram board recording all responses. By utilizing this methodology, researchers will finally be able to determine whether nonhuman great apes demonstrate vocal referents in their repertoire.

5.5 Terminology

Investigation into the methodology surrounding studies of referential communication in nonhuman primates has led to the realization that a change in terminology is needed. As mentioned before, many studies investigating nonhuman primate vocal repertoire are stemming from the standpoint that nonhumans do not utilize referential communication. Therefore, these studies have generally adopted the terminology 'functional referent' when investigating communication. In human language, referential signals provide information about external objects to the listener (Smith, 1991; Smith 1977). In order for an animal vocalization to be considered referential, it needs to be intentionally elicited and contain information that would otherwise be unknown and the listener needs to perceive and respond

to this new information. Because it is difficult to establish whether particular vocalizations are referential or lacking certain aspects, the term 'functional referent' has been more often used. Despite the difficulty in establishing vocalizations as referential, it is a necessary step. A clear distinction needs to be made between the presence or absence of referential communication in nonhuman primate species versus the presence or absence of complex communication, which may contain information but does not need to fulfill all requirements of referential communication.

The term 'functional referent' is not beneficial to the advancement of our understanding of nonhuman primate communication and its relationship to human language. It is quite possible that referential vocal communication is not present in nonhumans, including the great apes. However, the identification of functional referents can go no further than identifying scenarios in which vocalizations contain information. These studies suggest complex communication, but they are unable to substantiate or eliminate any claim of truly referential communication. In order to discover the groundwork essential for the development of language, investigation based solely on identifying the presence or absence of the requirements for referential communication is necessary. 'Functional referent' leaves us no closer to this understanding. If a study determines the presence of functional referents, it is still unable to elucidate the features of complexity that may be present or absent. A functional referent demonstrates only that a vocalization appears to be more complex than the typical emotional outburst. However, it does not distinguish whether the complexity results from emotional information contained in the vocalizations, results from non-emotional information contained in the vocalizations, results from the communication of otherwise unknown information, results from intentionality of the vocalizations for

communicative purposes, results from the listener's ability to perceive this information and respond accordingly, or some combination of all of these factors. Therefore, the abandonment of this term is necessary in order to allow for a quicker and more efficient investigation into the complexity of nonhuman communicative interactions.

Individuals interested in complex or referential communication among nonhumans are better off starting with the question of whether communication is referential or not. If investigation into the presence of referents is the initial question, studies into each component of referential communication is necessary. Despite the fact that many studies may demonstrate a lack of referential communication in nonhuman species, the investigation into referential communication will establish which, if any, and what combination of complex communicative features may be present in the species under investigation. Investigation into this line of thinking will lead more directly to the answer of whether communication in a given species is complex and if so, what exactly makes it complex as compared to functional referents, which merely conclude the presence or absence of complex communication.

5.6 Evolutionary Implications

The study of the evolution of linguistic abilities in our lineage is a highly controversial topic (Marler et al., 1992). With referents being a vital component in human language (Deacon, 1997), insight into this ability with nonhumans can provide valuable knowledge about the evolution of language within the *Homo* lineage. Referents in nonhuman vocal communication may not be present and are not a common occurrence or vital to a competent communicative system. Nonetheless, investigation into this area can provide a clearer distinction between various animal communication systems and human language, along with a clearer sight of what aspect of communication began the selection for language.

The difference between human language and animal communication has historically been perceived as insurmountable, rather than envisioning the distinction between these systems as a continuum of shades of gray. Since evolution would suggest a continuum of stages before language, investigation into the details surrounding nonhuman, especially nonhuman great ape, communication systems is warranted. Particularly, investigation into the specific requirements of referential communication can lend insight into what suite of characters is or is not present in nonhuman vocal communication. Contemporary investigations into functional referents have led scientists to the realization that nonhuman vocal communication systems are complex. However, they have failed to provide a deeper understanding of exactly what factors are or are not leading to this complexity.

Investigation into referential communication, specifically methodology allowing the testing of each requirement for referential communication, allows researchers to categorize a variety of species by their ability or lack thereof to create intentional vocalizations, transmit information through their vocalizations that would otherwise be unknown, and to respond to these vocalizations accordingly. As these systematic studies continue to be performed with a wide variety of species, a catalog of the characteristics of vocalizations for different species can be created. This can lend insight into what areas of complex communication are prevalent in nonhuman primates and other animal communication systems. Perhaps vocalizations of many nonhuman species do contain information and listeners respond to the information, but the vocalizations are not intentional, or perhaps vocalizations are intentional but the information carried in them is not specific enough to be labeled as referential. It is also possible that vocalizations in nonhuman primates will predominantly lack complexity, which may lend credence to a theory emphasizing the gestural origins of human language.

An understanding of the degree of complexity of communication in nonhuman primates will lead investigators towards the selective factor for the development of human language. Therefore, it is only through this systematic approach to examining referential communication that a deeper understanding of nonhuman primate vocal communication and its possible link to human language will develop.

5.7 Conclusion

5.7.1 Findings of this Study

The complexity of nonhuman primate vocal communication has continued to remain a debated topic in primatology (Cheney & Seyfarth, 2007; Seyfarth & Cheney, 2003a; Seyfarth & Cheney, 2003b; Zuberbühler, 2003). The current study, investigating referential aspects of the bonobo vocal repertoire, provides preliminary evidence that bonobo vocalizations contain such information. Specifically, vocalizations elicited by the bonobo participant of this study could be significantly distinguished in an analysis based on six different food types: banana, blueberry, diet coke, green onion, mushroom, and peanut. These vocalizations could also be re-classified into the correct food type on a fairly reliable basis, and distance between the food groups was statistically significant. This statistical significance demonstrated that vocalizations did contain information. Despite this finding, I was unable to state conclusively that bonobos utilize referential communication in their vocal repertoire.

In order for nonhuman great apes to demonstrate referential ability in their vocal repertoire, they must exhibit several distinctive features. First, the vocalizations need to be intentionally elicited for a communicative purpose (Seyfarth & Cheney, 2003b; Macedonia & Evans, 1993; Marler et al., 1992). Next, the vocalizations need to contain specific

information that would otherwise be unknown to a conspecific (Seyfarth & Cheney, 2003b; Macedonia & Evans, 1993; Marler et al., 1992). Equally important is the requirement that a conspecific perceive this information, utilize it, and incorporate or adjust their behavior as necessary (Macedonia & Evans, 1993; Marler et al., 1992). The current study did not seek to determine how listening conspecifics respond to vocalizations. Instead I focused on determining referential aspects of bonobo calls from the vocalizer's perspective. Food peeps were the primary focus of this study. However, many researchers suggest the bonobo food peep and homologous chimpanzee food grunt are involuntary vocalizations (De Waal, 1988; Goodall, 1986) with others suggesting a degree of intentionality (Hopkins et al., 2007; Hotstetter et al., 2001). The recordings analyzed during this study also suggested that these vocalizations are not necessarily meant to intentionally communicate with conspecifics. Kanzi, the bonobo participant, generally was separated from other bonobos by a considerable distance during recording sessions, yet his vocalizations were still soft. Conspecifics in the community rarely responded to the participant's food peeps during recording sessions, suggesting they either did not hear the vocalizations or did not respond in a communicative manner. Finally, Kanzi's own behavior indicated he was not attentive for conspecifics response. These observations coupled with previous studies indication of a lack of intentionality in the homologous chimpanzee food grunt suggest that food peeps in bonobos are not necessarily intentionally communicating information to conspecifics.

The second requirement of referential communication is for the vocalization to contain specific information that would otherwise be unknown to a conspecific (Seyfarth & Cheney, 2003b; Macedonia & Evans, 1993; Marler et al, 1992). This study determined that vocalizations could be significantly differentiated based on the six different food types by

examining low frequency, delta time, average power, and energy values. Vocalizations could also be re-classified into the correct food type reliably, and distances between food groups were significant. This suggests that these vocalizations do contain specific information regarding food type. However, a higher degree of accuracy at re-classification would give even further credence to this theory. Despite these food vocalizations containing specific information, food peeps do not necessarily provide the best example of communicating information that would otherwise be unknown to a conspecific. Food peeps are short-distance vocalizations (Bermejo & Omedes, 1999) and consequently are only perceived by conspecifics in the vicinity. However, the information regarding food type contained in these vocalizations may not be inherently unknown to conspecifics. Food peeps contain information regarding food type and are relatively soft. Therefore, conspecifics able to hear these vocalizations may already be aware of the presence of food, so the vocalization does not necessarily reveal any information otherwise unknown. In addition, the vocalization may function as a form of social cohesion for conspecifics. However, it is possible that the environment obscures visibility even at short distances, and information regarding food type may be unknown to close conspecifics. No systematic study has yet investigated the goal of these vocalizations. Therefore, it is possible that food peeps in bonobos are not necessarily intended to communicate unknown information with conspecifics in this particular context, yet the information contained within them is specific to food type due perhaps to food preferences and underlying emotion. Nonetheless, these vocalizations are not necessarily communicating an unknown to other conspecifics in the vicinity.

5.7.2 Future Directions of Study

Despite not conclusively determining the presence or absence of referents in the vocal repertoire of bonobos, this study demonstrated the importance the assumptions, methodology, and analysis has for all studies relating to referential communication in nonhumans and can serve as a guide to a better examination of referents in nonhumans. It has been thought that language is too complex to have its evolutionary roots in animal communication (Arcadi, 2005; Parr et al., 2005; Hauser & Fitch, 2003; Seyfarth & Cheney, 2003a; Seyfarth & Cheney, 2003b). However, this violates the general rule of parsimony (Sober, 1988). Acceptance of the discontinuity between human language and animal communication historically led researchers to investigate only the emotional aspect of nonhuman vocalizations (Seyfarth & Cheney, 2003b; Owings & Morton, 1998). More recently, investigators have accepted the notion that animal communication is complex and have started investigating accordingly (Cheney & Seyfarth, 2007; Zuberbühler, 2003; Marler et al., 1992; Marler, 1985). However, many studies, including the current one, also follow faulty reasoning by looking for complex communication in counterintuitive places (Gibbons, 2007; Di Bitetti, 2005; Slocombe & Zuberbühler, 2005; Di Bitetti, 2003; Hallberg, 2000; Evans & Evans, 1999; Benz, 1993; Elowson et al., 1991). Referents, prevalent in human language (Deacon, 1997), entail specific provisions in nonhumans: intentionality, specifying otherwise unknown information, and inducing responses to the information (Seyfarth & Cheney, 2003b; Macedonia & Evans, 1993; Marler et al., 1992). However, research into referential vocal communication in nonhuman great apes may doom their study to failure if their investigation into referents examines a vocalization lacking intentionality (Gibbons, 2007; Slocombe & Zuberbühler, 2005; Hallberg, 2000). Investigators need to examine

complex communication patterns that do not inherently prohibit the possibility of referential communication. Finally, investigators have adopted a form of analysis that examines each vocalization as a potentially meaningful unit. However, human language is composed of individual phonemes, and meaning is only created through the combination of several phonemes or vocalizations. Since researchers have rarely investigated the possibility of nonhuman communication gaining meaning through the patterning of vocalizations, several forms of analysis should be adopted when examining referents to allow the potential for several communicative paths.

Insight into the assumptions of where referential communication should be present, how it should be investigated, and how it should be analyzed led to the conclusion that a new methodology into the investigation of referential communication needs to be adopted. An appropriate methodology into nonhuman great ape referential vocal capacities should begin by examining a vocalization that has the potential to fulfill the requirements. Within *Pan*, the best candidate is the long-distance high-hooting of bonobos or pant-hooting of chimpanzees. Investigation in an experimental setting can establish an environment where there could be a one-to-one correspondence between a vocalization and the stimulus that may have elicited it. Vocalizations recorded during these sessions can be analyzed through several different techniques, including simple measurement of each vocalization and measures of vocalization patterns. Furthermore, these investigations should design a situation in which listeners' response to vocalizations can be recorded. These can be modified along the lines of the feeding stations created by Slocombe and Zuberbühler (2005), the match-to-sample created by Hallberg (2000) and Gibbons (2007) or, in the special case of the bonobos housed at Great Ape Trust of Iowa, the translation of vocalizations to lexigrams.

5.7.3 Theoretical Implications

This study demonstrated the current flaws in investigations of functional referents and referents in nonhuman vocal communication patterns. Functional referent studies acknowledge and allow investigation into whether vocalizations are complex or not. However, they do not distinguish what features lead to the complexity or lack of complexity in nonhuman communication systems. Animal communication systems may lack the use of any referential communication or may be exceedingly rare. Investigation into referential communication can provide meaningful information about nonhuman communication regardless. The identification of which complex features are found in nonhumans and the patterning of these features across species can lend tremendous insight into the evolution of language. A specific patterning of complex features in nonhumans may suggest the ordering of increased complexity in animal communication and, potentially, which feature of complexity ultimately selected for the evolution of the complex languages present in human society today. In conclusion, researchers must adopt an appropriate methodology and acknowledge the impact of assumptions undertaken in their study. If such an appropriate methodology is undertaken by numerous researchers investigating referential communication, insight into the patterning of specific complex features of vocal communication may be forthcoming. Consequently, researchers can continue to bridge the gap between human language and animal communication elucidating the continuum and evolutionary path of complex communication among both humans and nonhumans.

References

- Arcadi AC. 2005. Language evolution: what do chimpanzees have to say? *Current Biology* 15:R884-R886.
- Backorowski JA, Owren MJ. 1995. Vocal expression of emotion: acoustic properties of speech are associated with emotional intensity and context. *Psychological Science* 6:219-224.
- Benz JJ. 1993. Food-elicited vocalizations in golden lion tamarins: design features for representational communication. *Animal Behaviour* 45:443-455.
- Bermejo M, Omedes A. 1999. Preliminary vocal repertoire and vocal communication of wild bonobos (*Pan paniscus*) at Lilungu (Democratic Republic of Congo). *Folia Primatologica* 70:328-357.
- Blumstein DT, Armitage KB. 1997. Alarm calling in yellow-bellied marmots: I. the meaning of situationally variable alarm calls. *Animal Behaviour* 53:143-171.
- Boesch C, Boesch H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology* 78:547-573.
- Cheney DL, Seyfarth RM. 2007. *Baboon Metaphysics: the Evolution of a Social Mind*. Chicago: University of Chicago Press.
- Clark AC, Wrangham R. 1993. Acoustic analysis of wild chimpanzee pant hoots: Do Kibale forest chimpanzees have an acoustically distinct food arrival pant hoot? *American Journal of Primatology* 31:99-109.
- de Waal F, Van Hooff J. 1981. Side-directed communication and agonistic interactions in chimpanzees. *Behaviour* 77:164-198.

- de Waal FBM. 1988. The communicative repertoire of bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behaviour* 106:183-251.
- Deacon TW. 1997. *Symbolic Species: the Co-Evolution of Language and the Brain*. New York: W.W. Norton & Co.
- Di Bitetti MS. 2003. Food-associated calls of tufted capuchin monkeys (*Cebus apella nigrinus*) are functionally referential signals. *Behaviour* 140:565-592.
- Di Bitetti MS. 2005. Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigrinus*. *Animal Behaviour* 69:911-919.
- Elowson MA, Tannenbaum PL, Snowdon CT. 1991. Food-associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour* 42:931-937.
- Evans CS, Evans L. 1999. Chicken food calls are functionally referential. *Animal Behaviour* 58:307-319.
- Fichtel C, Hammerschmidt K. 2002. Responses of redfronted lemurs to experimentally modified alarm calls: Evidence for urgency-based changes in call structure. *Ethology* 108(9):763-778.
- Fischer J. 1998. Barbary macaques categorize shrill barks into two call types. *Animal Behaviour* 55:799-807.
- Gibbons CM. 2007. *The referentiality of vocal signaling: behavioral and acoustic analysis of food barks*. Columbus: Ohio State University.
- Gill SA, Sealy SG. 2003. Tests of two functions of alarm calls given by yellow warblers during nest defence. *Canadian Journal of Zoology* 81:1685-1690.

- Gill SA, Sealy SG. 2004. Functional reference in an alarm signal given during next defence: set calls of yellow warblers denote brood-parasitic brown-headed cowbirds. *Behavioral Ecology & Sociobiology* 56:71-80.
- Goodall J. 1986. *The Chimpanzees of Gombe*. London: Belknap Press.
- Goodman M, Czelusniak J, Page S, Meireles C. 2001. Where DNA sequences place *Homo sapiens* in a phylogenetic classification of primates. In: Tobias PV, Raath MA, J. M-C, Doyle GA, editors. *Humanity from African Naissance to Coming Millennia*: Firenze University Press/Witwatersrand University Press. p 279-290.
- Hallberg KI. 2000. *Specificity of chimpanzee food barks: reference to food type and quality*. Columbus: Ohio State University.
- Hauser MD, Fitch WT. 2003. What are the uniquely human components of the language faculty? In: Christiansen MH, Kirby S, editors. *Language Evolution*. New York: Oxford University Press. p 158-181.
- Hopkins WD, Tagliabue JP, Leavens D. 2007. Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Animal Behaviour* 73:281-286.
- Hostetter AB, Cantero M, Hopkins WD. 2001. Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional state of a human (*Homo sapiens*). *Journal of Comparative Psychology* 115:337-343.
- Le Roux A, Jackson TP, Cherry ML. 2001. Does Brants' whistling rat (*Parotomys brantsii*) use an urgency-based alarm system in reaction to aerial and terrestrial predators? *Behaviour* 138:757-773.
- Macedonia JM, Evans CS. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology* 93:177-197.

- Marler P. 1977. Primate vocalizations: affective or symbolic? In: Bourne G, editor. Progress in Ape Research. New York: Academic Press. p 85-96.
- Marler P. 1985. Representational vocal signals of primates. *Fortschritte der Zoologie* 31:211-221.
- Marler P, Evans CS, Hauser MD. 1992. Animal signals: motivational, referential, or both? In: Papousek H, Jurgens U, Papousek M, editors. *Nonverbal Vocal Communication: Comparative and Developmental Approaches*. Cambridge: Cambridge University Press. p 66-86.
- Marler P, Hobbett L. 1975. Individuality in long range vocalization of wild chimpanzees. *Zeitschrift fur Tierpsychologie* 38:97-109.
- McGrew WC. 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. New York: Cambridge University Press.
- Menzel EW. 1988. A group of young chimpanzees in a 1-acre field: leadership and communication. In: Byrne RW, Whiten A, editors. *Machiavellian Intelligence*. New York: Oxford University Press. p 155-159.
- Notman H, Rendall D. 2005. Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour* 70:177-190.
- Owings DH, Morton ES. 1998. *Animal Vocal Communication: A New Approach*. New York: Cambridge University Press.
- Parr LA, Waller BM, Fugate J. 2005. Emotional communication in primates: implications for neurobiology. *Current Opinion in Neurobiology* 15:716-720.
- Pereira ME, Macedonia JM. 1991. Ringtailed lemur anti-predator calls denote predator class, not response urgency. *Animal Behaviour* 41:543-544.

- Ploog D. 1981. Neurobiology of primate audio-vocal behavior. *Brain Research Review* 3:35-61.
- Savage-Rumbaugh ES. 1990. Language acquisition in a nonhuman species: implications for the innateness debate. *Developmental Psychobiology* 23:599-620.
- Savage-Rumbaugh SE, Murphy J, Sevcik RA, Brakke KE, Williams SL, Rumbaugh DM. 1993. Language comprehension in ape and child. *Monographs of the Society for Research & Child Development* 58:1-256.
- Seyfarth RM, Cheney DL. 2003a. Meaning and emotion in animal vocalizations. *Annals of the New York Academy of Sciences* 1000:32-55.
- Seyfarth RM, Cheney DL. 2003b. Signalers and receivers in animal communication. *Annual Review of Psychology* 54:145-173.
- Seyfarth RM, Cheney DL, Marler P. 1980a. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* 210:801-803.
- Seyfarth RM, Cheney DL, Marler P. 1980b. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour* 28:1070-1094.
- Slobodchikoff CN, Kiriazis J, Fischer C, Creef E. 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. *Animal Behaviour* 42:713-719.
- Slocombe KE, Zuberbühler K. 2005. Functionally referential communication in a chimpanzee. *Current Biology* 15:1779-1784.
- Smith WJ. 1977. *The Behavior of Communicating: an Ethological Approach*. Cambridge, MA: Harvard University Press.

- Smith WJ. 1991. Animal communication and the study of cognition. In: Ristau C, editor. *Cognitive Ethology: The Minds of Other Animals*. Hillsdale, New Jersey: Lawrence Erlbaum Associates, Publishers. p 209-230.
- Sober E. 1988. *Reconstructing the Past: Parsimony, Evolution, and Inference*. Cambridge: MIT Press.
- Taglialatela JP, Savage-Rumbaugh S, Baker LA. 2003. Vocal production by a language-competent *Pan paniscus*. *International Journal of Primatology* 24:1-17.
- Uhlenbroek C. 1996. *The structure and function of long-distance calls given by male chimpanzees in Gombe National Park*: University of Bristol.
- Wich SA, Sterck EHM. 2003. Possible audience effect in Thomas langurs (*Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology* 60:155-159.
- Wrangham R. 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor. *Primate Ecology*. New York: Academic Press. p 503-538.
- Zuberbühler K. 2000. Referential labeling in Diana monkeys. *Animal Behaviour* 59:917-927.
- Zuberbühler K. 2003. Referential signaling in non-human primates: cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior* 33:265-307.
- Zuberbühler K, Noe R, Seyfarth RM. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour* 53:589-604.