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# Vocal communication in chimpanzees (*Pan troglodytes*)

Katie Slocombe

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for the degree of Doctor of Philosophy

October 2005



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## **Abstract**

Animal vocalisations have the capacity to function as referential signals. In order for this to occur signallers must reliably produce acoustically distinct calls in response to specific events in the world. In such cases, listeners have the potential to draw inferences about the eliciting stimulus from listening to the signaller's calls. Functionally referential communication has been documented in some monkey species in contexts of predator avoidance, food discovery and agonistic encounters, but never in any ape species. I address this anomaly by asking whether chimpanzees produce and understand functionally referential calls as part of their natural communication.

I examined 'agonistic screams' and 'rough grunts', two common chimpanzee vocalisations, in a wild group in Budongo Forest, Uganda, and a captive group housed at Edinburgh Zoo, UK. My results showed that chimpanzees produced acoustically distinct screams depending on the role they played in a fight. Consistent differences were found in the call structure produced by victims and aggressors. In addition, the structure of victim screams varied consistently with the severity of aggression received. These screams may have provided listening chimpanzees with important social information about ongoing fights.

Chimpanzees produce 'rough grunts' when discovering food and I found that signallers varied the acoustic structure of these calls according to the kind of food encountered. In order to explore whether rough grunts were labelling food quality or type, I examined the patterns underlying rough grunt production. The acoustic structure of rough grunts varied principally with the chimpanzees' preferences for different foods. I then tested the responses of listeners to the different rough grunts variants with a naturalistic playback experiment. This revealed that the subject was able to extract meaningful information about the kind of food originally discovered by the caller. I concluded that rough grunts functioned as referential signals.

## **Chapter 1: Study of vocal communication**

### **Summary**

Understanding the meaning and appreciating the complexity of vocal communication in non-verbal species can appear to be an insurmountable challenge. One key strategy for the study of this demanding topic is the separation of signaller and receiver roles in communication. Different species of animal demonstrate greatly varying degrees of proficiency in signaller and receiver abilities, which are required for participation in complex vocal communication. Asymmetry between the capacities of signallers and receivers has been found in primates. Within the framework of the receiver-signaller dichotomy, the informational content of vocalisations is explored and the concept of functional reference is introduced. Definitions and criteria for identifying functionally referential calls are presented, before the relevance of functional reference for the understanding of the evolution of language is outlined.

## **Signallers and receivers**

Communication between individuals requires the participation of both the signaller and receiver. Different perceptual, motor and cognitive skills are required for these two roles. Signallers and receivers can also have quite different goals. This is illustrated by the behaviour of predators that use the social or alarm calls given by prey to aid their ability to locate and kill them (e.g. bats and frogs, Ryan et al., 1982). In many species, including the Tungara frog, *Physalaemus pustulosus*, and the domestic chicken, *Gallus gallus*, this has led to the dynamic selection of calls, which reduce the information available to unwanted eavesdropping receivers, whilst maximising the efficacy of the message for conspecific receivers (Ryan et al., 1982; Bayly and Evans, 2003). Although the evolutionary interests of signaller and receiver are often convergent and cooperative, considering the two communicating roles separately is the best approach for understanding the complexities of vocal communication (Macedonia and Evans, 1993; Seyfarth and Cheney, 2003).

To our knowledge, humans have the most complex vocal communication system of all animals. We can therefore look to human language as a model of complex vocal communication and a standard upon which to evaluate the vocal communication systems of other species. From a signaller's perspective the key elements that contribute to a complex vocal communication system such as ours are vocal learning, vocal plasticity and call usage. From a receiver's perspective the key elements are vocal comprehension through semantic and syntactic skills. A brief overview of the extent to which different species of animals have shown proficiency at these different elements of communication will provide a global picture of vocal communication skills in the animal kingdom and more specifically the primate world.

## **Signaller capacities**

### *Vocal learning*

The ability to imitate sequences of sounds and to modify their production through a process of vocal learning is key to the acquisition of human language. There is extensive evidence that numerous bird species from three different orders, the

songbirds, *Passiformes* (Kroodsma and Baylis, 1982), parrots, *Psittaciformes* (Todt, 1975) and hummingbirds, *Apodiformes*, (Baptista and Schuchmann, 1990) can imitate songs and in some cases novel sounds. In mammals the evidence is limited to a surprisingly small number of species. Although modification of the temporal patterning of a call through learning has been demonstrated in several species including the rhesus monkey, *Macaca mulatta* (Sutton et al. 1973) and the domestic cat, *Felis domesticus* (Molliver, 1963), learning to alter frequency parameters of a call is much more sparsely demonstrated (reviewed in Janik and Slater, 1997). It is this modification of frequency parameters through social learning, however, that is considered to be ‘true’ vocal learning (Janik and Slater, 1997) and this phenomenon is limited in mammals to a small number of species. Social vocal learning has been proposed for one African elephant, *Loxodonta africana*, which produced a chirp call that deviated from the natural repertoire of this species (Poole et al., 2005). The frequency parameters of this individual’s chirps matched those produced by companion Asian elephants, *Elephas maximus*. The frequency of pure tone echolocation calls produced by greater horseshoe bats, *Rhinolopus ferrumequinum*, appears to be determined by social learning mechanisms (Jones and Ransome, 1993). Captive harbour seals, *Phoca vitulina*, have been reported to imitate human speech (Ralls et al. 1985) and captive dolphins have been reported to modify their whistles through learning, both spontaneously (Reiss and McCowan, 1993) and as a result of training (Richards et al. 1984). Progressive changes in the complex songs of male humpback whales, *Megaptera novaeangliae*, are also best accounted for by a process of vocal imitation (reviewed in Janik and Slater, 1997).

In contrast, there is extremely limited comparable evidence for vocal learning of new frequency parameters in non-human primates. Some of the strongest available evidence comes from observations of convergence in the acoustic structure of trill calls in newly paired pygmy marmosets, *Callithrix pygmaea*. The socially mediated alteration of the frequency parameters in these calls remained stable over a three-year period (Snowdon and Elowson, 1999). In addition, female Campbell’s monkeys, *Cercopithecus campbelli*, seem to demonstrate socially mediated frequency changes in the production of ‘combined harmonic’ calls (LeMasson and Hausberger, 2004). Over a three-year period variants of this call type were observed to transform in frequency structure, and novel variants emerged. Individuals shared certain variants of

this call type and the pattern of vocal convergence varied with the stability of the social structure. Vocal convergence seemed most important during periods of social instability.

More controversial evidence for vocal learning comes from common chimpanzees, *Pan troglodytes*. The existence of local dialects in the long distance pant hoot vocalisation of distant communities of chimpanzees (Mitani et al., 1992) was initially cited as evidence for vocal learning. Differences in genetics, habitat acoustics and body size were, however, later offered as more parsimonious explanations for these observations (Mitani et al., 1999). Recent work has sought to avoid these potentially confounding factors, and evidence for communities converging on a group specific pant hoot vocalisations through vocal learning is now available for both captive groups (Marshall et al., 1999) and wild neighbouring communities of chimpanzees in the Taï Forest, Ivory Coast (Crockford et al., 2004). Flexible modification of pant hoot structure has also been demonstrated in wild chimpanzees during chorusing (Mitani and Brandt, 1994; Mitani and Gros-Louis, 1998). Males modify their pant hoot structures when chorusing to match elements of their partner's calling pattern, resulting in a strong correlation between association time and call similarity between pairs of males. Although this also supports the existence of vocal learning in this species, subtle, socially mediated changes in context could also be responsible for this effect.

### *Vocal plasticity*

The ability to generate acoustic variation and produce novel sounds is a key property of human vocal communication. However evidence for this is very sparse in the rest of the animal kingdom. This is partly due to the empirical problem of trying to isolate this type of vocal learning from other explanations. It is extremely difficult in the wild to exclude the possibility that any sound was not already in the repertoire and just infrequently used. Birds once again are the leaders in this field. Most passerines have a critical period in which they have great vocal plasticity (Marler and Peters, 1982), whilst some species of parrot (e.g. *Psittacus erithacus*) retain the ability to learn and imitate novel sounds over the lifetime. Seals and dolphins have both been shown to imitate novel sounds in captivity (Ralls et al. 1985; Richards et al. 1984), but the

evidence for non-human primates is both scant and controversial. Cross fostering experiments with Japanese macaques, *Macaca fuscata*, and rhesus macaques initially indicated that the fostered youngsters developed calls more typical of the adopted species (Masataka and Fujita, 1989). Whilst this indicated that monkeys do have a degree of vocal plasticity, these results were not fully replicated by Owren et al. (1992). In this study, although the cross-fostered Japanese macaques produced vocalisations which were similar to adoptive rhesus macaques in many frequency parameters, the vocalisations of these infants were judged to fall within the normal distribution of their own species. Perhaps one of the most tantalising cases of vocal plasticity in apes is proposed to have occurred in the enculturated bonobo, *Pan paniscus*, Kanzi. Tagliatela et al. (2003) suggest that Kanzi produced four distinct peep variants, to consistently label grape, juice, banana and yes. The authors argue that these peep variants were unique to Kanzi and they have been formed through a process of imitating the human words for these contexts. If true this generative production of novel call variants is significant; however, insufficient data are available on the peep variants naturally produced by a representative sample of bonobos to confidently conclude that Kanzi has modified the peep call into four novel variants.

### *Vocal usage*

The way in which signallers produce vocalisations influences the type and value of the information the call can provide receivers. If acoustically distinct calls are given reliably in response to a narrow range of stimuli, the calls can functionally reference those external events and objects. The term 'reference' and its derivations originate from linguistics. In linguistic terms, a referent is the set of entities in the world to which a word or expression refers (O'Grady et al., 1997). This term has been applied to animal communication in a comparable way; the referent of an animal call is determined by the set of stimuli that elicit the call and seem to be referenced by it. The size of the stimulus set to which calls and words refer can vary (e.g. bird, songbird, thrush) and this determines the 'referential specificity' of a call or word (Seyfarth and Cheney, 2003). If the call is only given to a very narrow range of stimuli, then the call can be described as having high referential specificity (Seyfarth and Cheney, 2003). If the association between the call and the eliciting stimulus is

highly predictive, the call can be described as having a high information value (Seyfarth and Cheney, 2003). Highly informative calls with high referential specificity can provide the listener with a reliable source of specific information about the external world. Calls such as these can only occur if the vocal behaviour of the signaller is highly predictive and context-specific.

The classic case of such signaller behaviour is to be found in the vervet monkey, *Cercopithecus aethiops*, alarm calling system. Struhsaker (1967) found that vervet monkeys, reliably gave acoustically different alarm calls to four of their main types of predators: large mammalian carnivores, (e.g. leopards, *Pantherus pardus*), raptors, (e.g. martial eagles, *Polemaetus bellicosus*), snakes, (e.g. pythons, *Python sebae*) and humans. Similarly high levels of predictability and context specificity have been found in the alarm calls of West African diana monkeys, *Cercopithecus diana* and Campbell's monkeys, *Cercopithecus campbelli* (Zuberbühler et al. 1997; Zuberbühler 2001), ringtailed lemurs, *Lemur catta* (Macedonia, 1990; Pereira and Macedonia, 1991), and suricates, *Suricata suricatta* (Manser, 2001). Acoustically distinct alarm calls with high informative value, but lower referential specificity are commonly elicited by aerial and ground dwelling predators in a number of species, including chickens, *Gallus domesticus*, (Gyger et al. 1987), Californian ground squirrels, *Spermophilus beecheyi* (Owings and Leger, 1980) and marmots, *Marmota marmota* (Lenti-Boero 1992). As aerial predators usually pose a more immediate threat than ground predators it is suggested that many of these alarm calling systems, including that of the ground squirrel, encode the urgency of response required rather than referencing the presence of an aerial or ground predator (Owings and Hennessey, 1984). An alarm system, which encodes several layers of information about the nature and behaviour of predators, has been discovered in the black-capped chickadee, *Poecile atricapillus* (Templeton et al., 2005). Firstly, this bird gives two different alarm calls; one to perched avian predators and one to aerial avian predators. Secondly, within the mobbing 'chick-a-dee' call, given to perched predators, subtle acoustic variation encodes the size and therefore the relative risk of each predator. Finally, one of the most complex vocal usage patterns known to date has been described in Gunnison's prairie dogs, *Cynomys gunnisoni*. It has been suggested that these species give acoustically distinct alarm calls to different predator types (Slobodchikoff, 1986) and also to individual predators within a predator class,

encoding information about their size and shape (Slobodchikoff et al. 1991; Ackers and Slobodchikoff, 1999).

## **Recipient capacities**

### *'Semantic' skills*

The term 'semantics' is a linguistic one and it is concerned with the meaning of words. Human language is semantic because words convey meaning through a set of agreed and fixed relationships between signs, referents and meanings (O'Grady, 1997). However, the nature of meaning is far from understood. Meaning has been seen in terms of the associations a word evokes (connotations), the entities to which it refers (referents/extensions) and the concepts it evokes or its 'sense' (intensions) (Harley, 2001). None of these terms provide a complete and satisfactory explanation of word meaning and models of how we represent and use word meanings are still being devised. The term semantics has been applied to animal communication (e.g. Seyfarth et al., 1980) and in this context the meaning of a call is inferred from the referents of the call alone. Currently, I would argue the other elements of meaning are very difficult to study in animals.

The ability to infer the referent and understand the meaning of another individual's vocalisations can be highly advantageous for animals. Extracting information about events from another's call allows receivers to respond in an appropriate manner in a given context. In the case of alarm calls this could increase survival chances, and in the case of social and food-related calls it could increase fitness levels. Evidence that animals have the ability to extract useful information about the world from the vocalisations of another individual comes predominantly from playback experiments; here calls are played back in the absence of the eliciting stimulus and thus the normal surrounding context. If responses to the playbacks mimic those given to the presence of the original eliciting stimulus, it is concluded that the listener has extracted and understood essential information about events in the world from the calls of another. Playbacks of alarm calls with wild vervet monkeys demonstrated that, in the absence of the real predator, recipients could gain sufficient information from the call alone to execute the appropriate predator avoidance behaviour (Seyfarth et al, 1980). Thus

monkeys habitually responded to snake alarm calls by standing bipedally and scanning the ground, and to eagle alarm calls by looking up and quickly descending from the tops of trees to thicker cover nearer the ground. Similar differential anti-predator responses have been elicited by playbacks of conspecific alarm calls in ring tailed lemurs (Macedonia, 1990), suricates (Manser et al., 2001), Californian ground squirrels (Leger and Owings, 1978) and chickens (Evans et al., 1994). Diana monkeys have been shown to attend to and understand the semantic content of both conspecific and Campbell's monkey alarm calls (Zuberbühler et al., 1999; Zuberbühler, 2000a). This demonstrates another advantageous strategy used by receivers: learning the meaning of other species' vocalisations. Diana monkeys have also shown adaptive sensitivity to the meaning and likely causes of chimpanzee screams (Zuberbühler, 2000b) and alarm calls of crested guinea fowl, *Guttera pucherani* (Zuberbühler, 2000c). Similarly, vervet monkeys attend to the semantic content of superb starling (*Lamprotornis superbus*) raptor alarm calls and despite the acoustic disparities, treat them as interchangeable with their own eagle alarm calls or actual eagle shrieks (Seyfarth and Cheney, 1990).

It is not merely in the contexts of predator avoidance that receivers extract information about the world from the vocal behaviour of others. For instance, rhesus monkeys, *Macaca mulatta*, have been shown to understand the socially potent information encoded in agonistic screams (Gouzoules et al., 1984) and it has been demonstrated that they understand the referents of food-related calls (Hauser, 1998).

### *Syntactic skills*

One principal constraint on the complexity of many animal communication systems is the relatively small number of calls a species can produce. The primary human solution to this problem is syntax, which enables us to "make infinite use of finite means" (von Humboldt, 1836). The term 'syntax' is a linguistic label for the system of rules and categories that underlie sentence formation in human language (O'Grady et al., 1997). Human syntax consists of rules that dictate the possible sequential and hierarchical combinations of words within sentences (O'Grady et al., 1997). Both the production and perception of these rules are fundamental to human linguistic competence. Although no other animal appears to possess syntax of this complexity,

the term has been applied to the study of animal communication. There is clear evidence that animals do possess some sequential ordering abilities and care has been taken to specify exactly what level of the linguistic term syntax is being applied to the study of animals. In this regard an important distinction has been made between 'phonological' syntax and 'lexical' syntax (Marler, 1977). Phonological syntax refers to rules that control the sequential ordering of small vocal units when combined into large units. Lexical syntax refers to changes in meaning caused by the combination of vocal units: it requires the signaller to combine of two or more elements and for the combination to have a different meaning to the constituent parts. It is also necessary that recipients recognise the change in meaning evoked by the combinatory rule (Nowak et al., 2000).

Songs produced by several species of birds are governed by a 'phonological' syntax, which dictates the way and order different elements of a song can be combined (e.g. Hailman and Ficken, 1987). The rules underlying the organisation and combination of primate calls are less clear, but there is evidence that primates construct compound calls from different call types (Robinson 1984) and that gibbon song construction is rule based (Mitani and Marler, 1989). The ability of receivers to extract simple phonological syntactical rules from their auditory input is confirmed by laboratory studies with cotton top tamarins, *Saguinus oedipus* (Hauser et al. 2001; Fitch and Hauser, 2004). Fitch and Hauser (2004) revealed that tamarins, like human infants, could discriminate certain violations in the syntactic structure of their auditory input. The tamarins were sensitive to the probability that certain elements would directly follow others in a sequence. In contrast, the tamarins were not sensitive to rules that dictated the order of non-adjacent items. Whether the failure of tamarins on this hierarchical processing task is representative of other non-human primates is currently being investigated (Fitch, personal communication). Evidence from Savage-Rumbaugh (1994) would indicate this is not the case. Kanzi, the bonobo, is reported to understand human syntax at a level where, when formally tested, his comprehension of sentences was equivalent to that of a two and a half year old human child. Crucially Kanzi demonstrated he understood embedded phrases, such as "Go get the carrot that's in the oven", indicating that he could process hierarchical syntactic structures (Savage-Rumbaugh et al., 1993).

Evidence for 'lexical' syntax is much harder to find, but it has been proposed that Diana monkeys demonstrate this type of syntactic processing when listening to alarm calls of Campbell's monkeys (Zuberbühler 2002). Campbell's monkeys give specific eagle and leopard alarm calls, but in addition they also give a less specific, alert alarm call sequence to a range of disturbances in the forest, such as trees falling. Diana monkeys do not respond vocally to these call sequences, which consist of two elements: a boom call followed by an alarm call, which resembles the leopard alarm. Diana monkeys respond vigorously to Campbell's leopard and eagle alarm calls, but when booms experimentally precede them, they ignore them. The boom calls seem to act as functional cues which modify the meaning of the subsequent alarm call. This modifying effect of the boom calls is specific to subsequent Campbell's alarm calls, showing the boom call does not merely have a direct inhibitory effect upon the Diana monkeys.

In summary, there is a startling asymmetry between the communicative complexity of receivers and signallers in the animal world, especially non-human primates (Seyfarth and Cheney, 2003). Whilst non-human primates show great proficiency with semantic skills and promise with syntactic skills, they are limited in the production mechanisms of vocal learning and plasticity. The premise that communication can be best understood when examined from these two distinct perspectives is a pervasive theme which underlies the research presented in this thesis.

### **Informational content of vocalisations**

Vocalisations can provide listeners with a vast array of information of different kinds. Many signals provide cues to various attributes of the sender, including the size, maturity, condition, sexual state and identity of the caller (e.g. Clutton-Brock and Albon, 1979). Signals can also provide information on the affective or motivational state of an animal (Morton, 1977) and their likely subsequent behaviour (Smith, 1977). Contrary to early theories of animal communication (e.g. Smith, 1977), as the review of vocal usage and semantic skills has illustrated, there is now strong evidence suggesting calls can provide reliable information about the circumstances of production, in terms of the eliciting event. Calls with such external referents have

been referred to by a host of names, including semantic (Seyfarth et al., 1980), referential (Macedonia and Evans, 1993) and representational (Cheney and Seyfarth, 1982). The application of these linguistic terms to animal communication has sparked controversy and objections. One of the principal contentious issues is the intentionality of the animal signallers: humans intentionally refer to external objects and events and children rely on cues of referential intent to learn the meaning of words (Bloom, 1997). A system without intention is, therefore, arguably different to the human one in a qualitative fashion. In addition, humans can refer to events distant in time or space with words, whereas animals seem tied to communicating about the present. In response to these criticisms the term ‘functionally referential’ was introduced (Macedonia and Evans, 1993; Evans, 1997). This is the term I will adopt and I will now provide the term with some key definitions and details of how these definitions can be operationalised in non-human animals.

Functionally referential communication describes the production of a signal from which receivers are able to extract information about the eliciting event. It is similar to linguistic reference in that the term focuses upon the set of external entities that the call refers to. It is different, however, in terms of assumptions made about the intentions of the caller and the process by which the referent of a signal is determined. In humans, the referents of words are understood and agreed upon by both signaller and receiver. In contrast animals may not know that sending a certain signal is the same as receiving one (Seyfarth and Cheney, 2003). The exact nature of a referent is also very difficult to determine in animals (Bloom, 2004), just as it can be for an observer of a foreign language (Quine, 1973). Humans are also assumed to intentionally refer to external entities by using words; no such assumptions are made in the study of functional reference. Evans (1997) summarises: “The term ‘functionally referential’ explicitly acknowledges that, although animals behave as though their signals provide information about external stimuli, and although this is consistent with the responses being mediated by mental representations, it does not compel such an interpretation.” (p. 118).

The study of functional reference in animals requires the combination of context-specific vocal usage in signallers and semantic skills in receivers. Thus, in order for a call to function in such a referential manner there are specific production and

perception criteria that need to be met. This means that studies focussing on signallers and receivers are equally important in furthering our understanding of functionally referential communication in animals.

### *Production criteria*

In order for a call to have the potential to function in a referential manner signallers have to produce acoustically distinct calls in response to a coherent category of stimuli (Evans, 1997). Just as our words are all acoustically discriminable, calls that serve as referential signals must be structurally distinct from other calls in the repertoire. In some species this means different call types are produced in different circumstances, in others with graded call repertoires this means quantitatively different calls are produced in different circumstances. The ‘stimulus-specificity’ criteria dictate that signallers must give calls in a predictable and reliable manner to a particular set of stimuli. These contingencies will allow listeners to make inferences about the likely nature of the eliciting stimulus. As outlined on pages 6-7, the strength of the association between the call and the eliciting stimulus set determines the ‘informational value’ of the call (Seyfarth and Cheney, 2003). The size of the stimulus set to which a call is given will determine the referential specificity of a call (Seyfarth and Cheney, 2003). Just as human words can have differing levels of specificity (animal, mammal, tiger), but remain referential, animal calls can function referentially, but with differing degrees of specificity depending on the breadth of the stimulus set which reliably elicits the call.

### *Perception criteria*

A functionally referential signal must permit the receiver to select the appropriate behavioural response in the absence of the eliciting stimulus and other normally available cues (Evans 1997). This is described as ‘context independence’ (Macedonia and Evans, 1993) and it is designed to test whether the call alone is sufficient for a receiver to infer meaningful information, about external events, from it. Observations of natural responses to calls are difficult to interpret, as it is usually impossible to exclude the possibility that the receiver was responding to either other sensory cues from the signaller or to the eliciting stimulus directly. Thus, as outlined earlier on page 8, the most powerful method to test this crucial criterion of functional reference

is playback experiments, where a call is played back in the absence of the normal eliciting stimuli. If receivers respond to playbacks as if the eliciting event was occurring, then it can be concluded that the calls are functioning to refer to the event. Although playback studies can show that certain contextual cues normally accompanying a call are not necessary for a receiver to respond appropriately, it is essential not to underestimate the role contextual information plays in naturally occurring communication. Leger (1993) highlights the importance of contextual cues in helping recipients make adaptive responses to calls. He defines context as a set of events, conditions and changeable recipient characteristics that modify the effect of a signal on a recipient's behaviour. Sources of contextual information therefore include the previous experience of the recipient, the earlier behaviour of the signaller, the behaviour of other recipients and the environmental conditions. Playbacks only remove the signaller-derived contextual cues from a communicative act. The value of just these cues in natural communication is indicated by the immediate orienting response most playbacks elicit from recipients; it seems their first reaction is to locate the signaller for additional cues to aid an adaptive response.

In addition to these established criteria, Hauser (2000) provides the following useful set of assumptions to consider when investigating functionally referential communication in primates: A call is the lowest level of functional unit and the sound-meaning pairs are stimulus bound; they do not refer to possible, previous or future events. Calls refer to whole objects, as young children's early words do (Markman, 1990), not parts of objects. Finally, referential signals should be regarded independently of the intentions of the caller.

### **Issues for the study of functional reference**

Despite the clear nature of these widely accepted criteria, there is still confusion over the issues of intentionality and mechanisms of perception and production in functionally referential communication. I will now address each of these issues in turn.

### *Mechanisms of Perception*

Receivers of functionally referential calls behave as if the calls refer to external events. The mechanisms underlying this ability to infer information from a call are currently debated and in animals they remain very difficult to assess. Some researchers argue that, like humans, animals map sounds on to mental representations in order to understand them (e.g. Zuberbühler et al. 1999), although the exact nature of the representations is almost impossible to investigate (e.g. denotive 'there's an eagle' or imperative 'run for cover'). Others suggest the acoustics of the sound have a direct physiological effect on the animal, which influences the responses the receiver consequently makes (Owren and Rendall, 1997). Although the debate about the nature of the mechanisms responsible for receiver interpretation and understanding of calls is a fascinating and important one, it is one that is not necessary for investigation of functionally referential calls. As Evans (1997) highlights, functionally referential communication does not compel any inferences to be made about the mental processes underlying call perception, thus one can identify a functionally referential call without making any assumptions about the nature of these psychological processes.

### *Mechanisms of production*

The mechanisms underlying call production have also caused considerable debate in relation to functionally referential communication. If the affective or motivational state of the caller is driving the production of calls it has been argued that the calls only convey the affective or motivational state of the caller to the receiver. Marler et al. (1992) proposed that animal calls could be placed on a continuum between reference and affect, with calls at the extremes providing highly referential information with little affective information, or highly affective information with little or no referential information. This conceptualisation has not aided the study of functional reference, however, because it gives credence to the notion that the mechanism driving production influences the capacity of a call to function referentially. Although the model was valuable in highlighting that a call can convey more than one type of information simultaneously, it strengthened the dichotomy that affective calls are not referential calls. This is simply not true. Highly referential calls could be caused entirely by a signaller's affective response to a specific stimulus, or they could be produced without substantial affective input (Seyfarth and Cheney,

2003). As long as calls meet the production criteria of stimulus-specificity and acoustic distinctiveness, the mechanisms by which they are produced are irrelevant. Seyfarth and Cheney (2003) state, “the mechanisms that cause a signaller to vocalize do not in any way constrain a listener’s ability to extract information from the call.” (p. 8) and it is the ability of the listener to extract information from a call which determines whether or not it functions referentially.

### *Intentionality*

Deliberations over the mechanisms driving call production in the signaller also raise the issue of intentionality in signallers. Humans communicate with the intention of informing, or indeed misinforming, others and for linguistics referential communication carries with it connotations of signaller intent. Functionally referential communication as explained in the previous paragraph, makes no assumptions about the mechanisms involved in call production, and this includes intentionality. Intentionality or lack thereof does not influence a call’s ability to inform, because receivers can extract information from a call without the signaller ever intending to provide it. Although many researchers support this stance (Hauser, 2000; Seyfarth and Cheney, 2003), ultimately researchers must strive to understand and combine work on intention and reference (e.g. Gyger and Marler, 1988).

Currently it seems that intentionality in the signaller is one of the principal chasms between human language and animal communication. Whilst human language is often receiver-oriented (centred around the receiver’s level of knowledge or beliefs), animal communication seems to be largely signaller-oriented. The mental state of the receiver in terms of their need for, or lack of, knowledge does not affect call production in a signaller-oriented system. For instance, chacma baboons, *Papio cynocephalus ursinus* produce contact barks when moving through low visibility habitat, which occur in temporal patterns that suggest the baboons are answering each other (Cheney et al., 1996). This would indicate that the baboons are calling with the intention of informing others about their location. However, playback studies found no evidence to support this hypothesis. In contrast, baboons only gave ‘replies’ to others’ contact barks when they themselves were separated from the group. Thus production of contact barks could be prompted by hearing another bark, but they were a direct reflection of the degree of separation of the caller from the group, not an intentional

announcement of current location to aid another. In addition, rhesus monkeys did not alter their calling behaviour as a function of the knowledge state of the recipient (Cheney and Seyfarth, 1990a). Captive adult females with knowledge of the presence of a predator or food did not attempt to use calls to impart this knowledge to ignorant offspring more than to knowledgeable offspring. Monkeys do not communicate with intent to modify the mental states of others because they do not seem to know that such mental states exist (Seyfarth and Cheney, 1993). Insufficient data are available on the use of vocalisations in apes to judge whether their seemingly superior level of social cognition (Hare et al., 2001; Tomasello et al., 2003) allows them to vocalise in a more receiver-centric fashion.

Despite the current lack of evidence for fully intentional signalling, animal vocalisations are no longer regarded as reflexive and involuntary. A number of species of primates (Caine et al., 1995; Cheney and Seyfarth, 1985; Mitani and Nishida, 1993), sciurid rodents (Blumstein et al., 1997) and birds (Marler et al., 1986; Sullivan, 1985) modulate their vocal behaviour as a function of the social context; demonstrating an 'audience effect'. Sensitivity to the presence and composition of a social audience shows that vocalisations can be produced with the intention of altering another animal's state; perhaps the first step towards fully intentional communication (Tomasello and Call, 1997).

### **Functional reference and the evolution of language**

Language is, without doubt, one of the most complex and intricate behaviours known to date, and is one of the few that clearly distinguishes humans from the rest of the living world. This view is illustrated by Pavlov (1927) who stated, "it is nothing other than words which has made us human". An evolutionary account for this unique and remarkable capacity is thus of enduring interest. Recent evidence suggests that our hominid ancestors did not have modern speech abilities until very recently (Enard et al. 2002) and archaeological records indicate representational artefacts, which require symbolic thought, only date back 50 000 years (Deacon, 1997). This evidence suggests that humans had a relatively short time period in which to evolve modern spoken language and the theories of language evolution must account for this limited evolutionary timescale. One powerful premise is that many of the underlying cognitive capacities involved in language processing are much older than language

itself, with their phylogenetic roots deep in the primate lineage (Hauser et al 2002). Thus, a promising empirical approach to understanding the origins of human behaviour, including language, has been to examine the capacities of extant primates, whose phylogenetic relationships to modern humans are known (McGrew, 1991; Fitch, 2000). By examining non-human primate communication, it is possible to test the hypothesis that human language built on abilities already present in the primate lineage before the advent of modern humans (Ghazanfar and Hauser, 1999). This comparative approach is vital for identifying the elements of language which appear to have evolved gradually from a common primate ancestor and those which have no clear evolutionary path and thus may be the 'novel' elements which caused human language to evolve into its current uniquely complex state (Evans and Marler, 1995; Hauser and Fitch, 2003; Fitch, in press). Chimpanzees are the closest living approximation to the common human-chimpanzee ancestor (McGrew, 1991) and as such are one of the most informative models for the comparative approach (Lieberman, 2000). Evidence for language-related abilities in lower order primates, mammals and birds could represent convergent evolution of such abilities and thus tell us little about the evolutionary path of our own communication system. Evidence of language-like capacities in apes, in contrast, strongly support the view that our last common ancestor possessed similar abilities.

The study of functional reference is fundamental to a comparative approach to language evolution. Humans possess an outstanding ability to extract and understand semantic information from spoken language and studying functional reference may reveal the evolutionary routes of this key linguistic ability in humans. Our understanding of functional reference is also fundamental to the investigation of the evolution of more complex linguistic capacities, such as syntax. Until we understand the meaning individual calls convey to recipients, it is impossible to study whether rule-governed combinations of calls convey different meanings than the individual constituent calls. In addition, until we comprehend the functional referents of calls it is almost impossible to tackle critical questions concerning the use of mental representations in receivers and intentionality in call production. The study of functional reference in non-human primates is therefore important for elucidating the evolutionary routes of human semantic abilities and to enable more complex questions to be posed about the evolution of other elements of language and cognition.

## **Chapter 2: Functionally referential communication**

### **Summary**

The previous chapter outlined the theoretical approaches and key definitions for the study of functional reference in the vocal communication of animals. This chapter will provide an overview of the current empirical evidence for functionally referential communication in the animal world. The review will primarily focus on non-human primates, but other species will be discussed if they show abilities surpassing those demonstrated by primates. The review will examine the production of functionally referential vocalisations in the contexts of predator encounters, food discovery and social interactions.

## **Predator encounters**

Alarm calls have proved an exemplary call type in which to study the ability of animals to communicate in a functionally referential manner (Macedonia and Evans, 1993). The eliciting stimulus for alarm calls is usually clearly identifiable and recipient responses are typically unambiguous and often predator-specific, especially if different predators use different hunting tactics (Macedonia and Evans, 1993). In addition, given the potentially important role alarm calls can play in maximising survival of offspring and other kin, there is significant selective pressure for the evolution of calling systems which give precise information about the nature of the predator, so the most adaptive response can be made.

The classic case of functionally referential communication is the vervet monkey alarm call system. As previously outlined on page 7, Struhsaker (1967) found that vervet monkeys gave acoustically different alarm calls to their main predators: eagles, leopards, snakes and humans. Three of these alarm calls evoked adaptive and unambiguous responses from recipients. Seyfarth et al. (1980) then conducted playback experiments with wild vervet monkeys and established that in the absence of the real predator, recipients could gain sufficient information from the call alone to execute the appropriate predator avoidance behaviour. They concluded that the alarm calls functioned to designate different classes of predator. Diana monkeys and Campbell's monkeys (Zuberbühler et al. 1997; Zuberbühler 2001) also give acoustically distinct alarm calls to leopards and crowned eagles. The playback of predator stimuli from different elevations and distances confirmed that regardless of the urgency to respond or the trajectory of an imminent attack, the Diana monkeys did not deviate from labelling the type of predator with their alarm calls (Zuberbühler, 2000d). Playback experiments based on a habituation-dishabituation paradigm, confirmed that recipients of these calls extracted information about the presence of a specific predator type from the calls (Zuberbühler, et al., 1999): despite the acoustic differences, Diana monkeys habituated across presentations of Diana monkey eagle alarm calls and eagle shrieks, indicating that they had equivalent meanings. Captive ringtailed lemurs have also been found to produce functionally referential alarm calls. Individuals of this species produce raptor and carnivore alarm calls, which elicit differential adaptive responses in recipients (Macedonia, 1990). Experimental

manipulation of response urgency (Raptor perched vs. swooping) failed to disrupt the consistent labelling of predator type in this species (Pereira and Macedonia, 1991). These results contrast with the alarm calls that are elicited by a wider set of stimuli and therefore have lower levels of referential specificity. Such alarm systems include those of ground-dwelling squirrels, which labels response urgency (Owings and Hennessy, 1984) and the chicken, which labels whether a predator is aerial or terrestrial (Evans et al. 1993).

Although primate alarm calls have been shown to have high levels of meaningful referential specificity, two species of non-primate animals have alarm calling systems that seem to convey even more specific and complex information. The study of suricate alarm calls was the first to demonstrate empirically that calls can meaningfully denote both predator class and response urgency (Manser et al., 2002). The social mongoose, *Suricata suricatta*, produces acoustically distinct calls in response to aerial and terrestrial predators, as well as a less specific recruitment call to snakes and deposits from predators or foreign suricates. In addition to providing information on predator type, suricate calls also encode the urgency of response in a predictable manner across all call types. The relative tonality or noisiness of all the call types varied reliably with the urgency of response; circumstances requiring a high urgency response elicited noisy calls compared with the tonal harmonic calls produced in low urgency situations (Manser, 2001). Playbacks of alarm calls have demonstrated that recipients were able to use the available information on predator type to adaptively modulate their responses; in addition they showed some sensitivity to the urgency of response information encoded in the alarm calls (Manser et al. 2001). Another potentially exciting element of this species' alarm calling behaviour concerns the recruitment alarm calls given to deposits from predators. This behaviour could represent the first evidence of animals using calls to label external entities that are currently absent and therefore distant in space and time. Whilst this is possible, a more parsimonious explanation proposes that the olfactory cues from the urine, faecal and hair deposits are an equally potent eliciting stimulus as the sight of the predator. Mental representations about the absent predator are not necessary to explain what could be a basic stimulus-response behaviour using the olfactory sensory modality.

The level of referential specificity proposed to be present in the alarm calls of Gunnison's prairie dogs, *Cynomys gunnisoni*, surpasses that of all other species. Prairie dogs produce acoustically distinct alarm calls to dogs, humans, hawks and coyotes (Slobodchikoff, 1986). Playbacks have shown their alarm calls elicit differential adaptive responses (Slobodchikoff, personal communication). This element of their communication is analogous to primate alarm calling systems, but it is proposed that within the human specific alarm call, subtle acoustic variation occurs which could function to refer to the characteristics of individual predators, including their colour and shape (Slobodchikoff et al., 1991). Experimental combinations of different sized human predators wearing t-shirts of different colours allowed researchers to conclude that the variation in the spectral features of the human specific alarm call varied consistently with the colour and shape of the human predator. Some may argue that these analyses are merely revealing statistical differences in call structure, not real perceptible differences, however an unpublished study indicates this is not the case (Slobodchikoff, personal communication). Slobodchikoff analysed calls given to similar-sized people in blue, green and yellow t-shirts. Alarm calls to predators in blue and yellow t-shirts were acoustically distinct, however alarm calls given to predators in green t-shirts were not significantly different from those given to humans in yellow t-shirts. A spectroscopy of the light array reflected from the green t-shirt revealed that a dichromatic colour system, such as that possessed by the prairie dogs, would not be able to distinguish the yellow t-shirt from the green t-shirt. This indicates that alarm calls only differ with phenomena the prairie dogs can perceive. It is therefore unlikely that the differences reported are purely statistical effects. The critical weakness in this research is the absence of any data to indicate that the extremely high referential specificity reported in the call production of this species is meaningful to recipients (e.g. playbacks). Until evidence to satisfy this perception criterion is met, the great potential for highly specific functional reference in the prairie dog alarm call system remains unconfirmed.

### **Food discovery**

Vocalisations which are elicited by food discovery have been well documented in a wide variety of species of birds (e.g. Elgar, 1986) and primates (e.g. Dittus, 1984). On a functional level most food-associated calls elicit approach responses from recipients,

meaning that producing food-associated calls can be costly to the signaller. The benefits accrued to signallers, to make producing these calls an evolutionarily stable strategy, include reduced predation risk from increased group size and attraction of potential mates or kin.

Food-associated calls can function to reference the presence of food, in a similar way to most alarm calls that reference the presence of an external danger. Such calls are high in informative value, but usually extremely low in referential specificity. Food-associated calls produced by free-ranging toque macaques, *Macaca sinica*, seem to reliably label the presence of large quantities of food, but there is no evidence that they have the potential to convey information about the type or quality of the food (Dittus, 1984). The acoustically distinct calls produced by toque macaques were elicited exclusively by abundant food sources in 98% of recorded cases, so the calls meet the perception criteria of functional reference (acoustic distinctiveness; stimulus specificity). Monkey listeners responded to these calls with rapid approach and their feeding bouts lasted significantly longer than comparable feeding bouts when calls were not produced. Although this observational evidence indicates the calls were meaningful to listeners, the case for regarding this call as a functionally referential one is weakened by the lack of playback experiments to test whether in the absence of other cues (e.g. olfactory, visual) the calls functioned to refer to the presence of plentiful food sources. Fortunately, more recent studies have used playback experiments to meet the perception criteria necessary to identify functionally referential calls. Tufted capuchin monkeys, *Cebus apella*, showed rapid and direct approaches to a speaker broadcasting food-associated calls compared to control stimuli (Di Bitetti, 2003). Similar findings were obtained for white-faced capuchins, *Cebus capucinus* (Di Bitetti, 2004), but as the author acknowledges these results remain ambiguous; although these monkeys respond to the presence of an abundant food source with direct and rapid approach, this response is also elicited by many other stimuli, therefore it is difficult to conclude that the responses of listeners are indicative of feeding. In contrast to these ambiguous responses, chickens provide clear evidence that male food-associated calls function to refer to the presence of food (Evans and Evans, 1999). Female chickens respond to male food calls with an anticipatory feeding stance; fixating downwards with the frontal binocular field. This

distinctive response was only observed in response to food calls, not to control alarm calls or contact calls.

It is proposed that several species of animal produce food-associated calls with greater degrees of referential specificity, than those that just reference the presence of food. Calls have the potential to provide information about the nature of the food source, as well as its presence. Several species of new world monkeys are able to vary the rate of food-associated call production as a function of the value or quantity of a food source. Golden lion tamarins, *Leontopithecus rosalia*, cotton-top tamarins and white-faced capuchins all produce food-associated calls at higher rates to highly preferred foods (Benz, 1992; Benz et al., 1993; Elowson et al., 1991; Roush and Snowdon, 2000; Gros-Louis, 2003). Whilst in these species the calls vary with preference, independently of quantity, red-bellied tamarins, *Saguinus labiatus*, produce calls at a higher rate to both large quantities and higher quality food (Caine et al., 1995). These calling systems have the potential to provide listeners with information about the relative value of a food source, but the absence of playback experiments to test this hypothesis leaves these results difficult to interpret. Further ambiguity is suggested by the finding that call rate in chickens, originally proposed to reference food preference, varies with hunger (Evans and Marler, 1994). This indicates recipients may obtain information on the internal state of the caller from the rate of these calls rather than the quality of the food.

Rhesus macaques are the only species in which functionally referential food calls, which provide information about the nature of a discovered food source, have been empirically demonstrated. This species produces five acoustically distinct types of food calls; warbles, harmonic arches and chirps to rare and highly desirable food and grunts and coos to low preference foods (Hauser and Marler, 1993). The grunts and coos elicited by food are acoustically distinct from grunt and coo variants produced in other social contexts. Whilst the type of call produced varied reliably with the quality of food discovered, call rate varied with the hunger levels of the signaller. A playback experiment using a traditional habituation-dishabituation technique illustrated that listeners attended to the meaning of the calls in terms of their referents, not to the different acoustic structures of the five calls (Hauser, 1998). This combination of

observational and experimental research indicates that these food-associated calls do function to reference the quality of a food source to recipients.

### **Social interactions**

In contrast to alarm and food-associated calls, there has been relatively little fruitful research conducted on the potential for purely social calls to function as referential signals. The most successful work has focussed on the calls produced during agonistic interactions. In evolutionary terms, there are clear indirect fitness benefits associated with responding appropriately to aggression directed at kin or allies, therefore signals which provide accurate information about the nature of an interaction could be highly adaptive. In contrast, in most social interactions, where rich visual contextual information from conspecifics is readily available and an unambiguous, immediate response is usually not necessary, the evolutionary advantage to functionally referential calls remains uncertain. In addition the empirical investigation of intra-party communication for evidence of functional reference is complicated by a number of factors (Rendall et al., 1999). Intra-party calls can be quiet and difficult to record and rarely elicit clear unambiguous responses. The perception criterion of functionally referential calls dictates that researchers must test the reactions of recipients in order to infer the functional referent of the call. In a context with relatively small fitness benefits for responding to the call, the recipient may perceive and understand the signal but not react in any discernible way. This could lead an observer to erroneously conclude the recipient had not understood the signal.

Despite the aforementioned difficulties a number of studies have found limited evidence for functional reference in the intra-party calls of old world monkeys. Differential responses in terms of direction, latency and duration of orientation to a playback speaker were elicited from vervet monkeys hearing grunts originally produced in four different contexts (Cheney and Seyfarth, 1982). Quantitatively different responses were given to grunts elicited by a monkey moving into an open area and the sight of a different troop of vervet monkeys, indicating that these grunts may function in a referential manner. Acoustic analysis confirmed that the grunts given in the four different contexts had limited acoustic differences and this indicates that the vervet monkeys may have been using the acoustic cues in the grunts to gain

information about external events. Similarly subtle behavioural responses were elicited from playbacks of grunt variants to wild yellow baboons, *Papio cynocephalus* (Rendall et al., 1999). Baboons produce grunts that have subtly different acoustic structures according to the circumstances of production. Specifically, 'move' grunts (produced when a group begins a co-ordinated move across an open area) are acoustically distinct from 'infant' grunts (produced principally by females approaching mothers with young infants) (Owren et al., 1997). Playbacks of both of these grunt variants in the naturally occurring contexts of moving and resting elicited responses that partially mirrored natural responses to the grunts (Rendall et al., 1999). 'Move' grunts elicited most reply grunts and the recipient looked towards the open ground. In contrast, 'infant' grunts elicited no reply grunts and the recipients looked towards the speaker. It seems that listeners were extracting information about external events, such as the onset of group movement, from the acoustic structure of a conspecific's grunts. It is important to note, however, that context also influenced these effects. Although different responses were observed to the playbacks of the two call types in the moving context, both call types elicited an orientation to the speaker response when played back in a resting context. It may be that in a resting context the likelihood of moving was perceived to be so low, the recipient oriented to the speaker in an attempt to gain additional information from the caller.

In addition to grunts, it is possible that copulation calls produced by female yellow baboons have the potential to function referentially. Copulation calls in this species are longer in duration and given in longer bouts when the mating male is of high rank (Semple et al., 2002). This could provide listening males with important information about the rank of their mating competitors, although playback experiments are needed to test this hypothesis.

Once hailed as one of the clearest pieces of evidence for functional reference in the sphere of social communication, the research on rhesus monkey agonistic screams has recently been subjected to extensive criticism. Gouzoules et al. (1984) identified five acoustically distinct types of screams that rhesus monkeys produced in agonistic interactions as a function of the severity of the attack and the nature of the opponent in terms of their relatedness and relative rank. Playbacks of four types of infant screams elicited differential responses in mothers in terms of latency and duration of

orientation to the speaker. The pattern of responses to the calls mirrored the natural responses of mothers to offspring engaged in agonistic interactions and indicated that the monkeys were able to extract important information about the ongoing interaction from the acoustic structure of the screams. Recent critiques of the methods used and results obtained in this study has led many to question the conclusion that rhesus monkey screams function as referential signals (Rendall et al., 1998; Le Prell et al., 2002; Owren et al., 2003; Owren and Rendall, 2003). Research into this species' agonistic screaming system is comprehensively discussed, along with the recent criticisms of this work, in Chapter 5, pages 80-83.

In conclusion, there is strong evidence for primate vocalisations functioning as referential signals in the contexts of predator encounter and food discovery. Due to both the less obvious evolutionary advantage associated with functionally referential social calls in other contexts and the methodological problems involved with the study of intra party calls the evidence for functional reference in the social realm is weaker and more controversial. One startling pattern that emerges across all the different call contexts considered is the total absence of evidence for naturally occurring functionally referential calls in any ape species. Although there is some observational evidence of context specific calls in chimpanzees, which is presented in the next chapter, there have been no ecologically valid playback experiments conducted to test if these calls function referentially from the listener's perspective. From an evolutionary perspective this is surprising both because apes are generally considered more cognitively advanced than monkeys and prosimians (Byrne, 1995) and apes are our closest living relatives.

### **Chapter 3: The study species: chimpanzees**

#### **Summary**

The previous chapter reviewed the evidence for functionally referential communication in a number of non-human primate species. One clear and surprising pattern that emerged was the lack of evidence for functional reference in any ape species. In order to address this anomaly the study species of this research is the chimpanzee, *Pan troglodytes*. This chapter aims to introduce the study species and to discuss key elements of their vocal and non-vocal behaviour.

The research presented in this thesis is based on data collected from two different populations. The first is the Sonso community of the chimpanzees of Budongo Forest, Uganda, and the second is the group housed at Edinburgh Zoo, UK. As the relevance of functionally referential signals to the evolution of human language is a theme running through this thesis, the description of the study species will concentrate on the naturally occurring social structure and ecology found in the wild chimpanzee population. To begin, I will present a brief overview of the ecology and social structure of wild chimpanzees. The focus of this chapter will then be the vocal communication of chimpanzees. The vocal repertoire will be outlined and illustrated before other aspects of vocal behaviour such as call perception and individual variation in call production will be discussed. Finally, a comprehensive review of the evidence for context specific calls and the potential for functional reference in the vocal behaviour of chimpanzees will be presented.

## **Social structure**

Chimpanzees form large, loosely bonded groups that have been called communities (Goodall, 1973). Communities can consist of between 20 to over 100 individuals (Nishida and Hiraiwa-Hasegawa, 1987) and within a community, chimpanzees share a common range, show mutual tolerance and commonly engage in affiliative interactions with one another. In contrast, if chimpanzees from different communities meet they react to each other with fear, hostility and potentially fatal aggression (Goodall, 1986). Within the community structure, chimpanzees live on a fission-fusion basis (Nishida, 1968; Goodall, 1986). This means chimpanzees form smaller temporary groups of individuals that demonstrate behavioural synchrony and spatial cohesion. These smaller groups are referred to as parties and the composition of these groups is fluid and constantly changing (Reynolds, 2005).

Males are philopatric, whereas females generally disperse (Nishida and Hiraiwa-Hasegawa, 1987). Males are more gregarious than non-oestrus females who spend most of their time in nursery parties or alone with their offspring (Goodall, 1986). It is proposed that females have core areas within the home range and that males patrol a large range incorporating the core areas of many females (Chapman and Wrangham, 1993). Males regularly patrol the borders of their home range and close encounters with neighbouring communities are often highly aggressive and occasionally lethal (Goodall et al., 1979). Within a community there is a clear dominance hierarchy amongst the males and considerable time is spent maintaining rank through grooming, dominance displays, agonistic interactions and alliance formations (Goodall, 1986). Females do differ in dominance, but they do not seem to strive constantly to obtain high status as the males do (Goodall, 1986; Nishida, 1989). Agonistic interactions within communities can result in serious injury and on occasions the outcome can be fatal (Fawcett and Muhumuza, 2000). In captive populations, both post-conflict reconciliation between opponents and consolation of victims by third parties have been commonly observed (de Waal and van Roosmalen, 1979), however these behaviours seem to be much rarer in wild populations (Arnold and Whiten, 2001).

## **Ecology**

Chimpanzees are primarily frugivores with the majority of their diet comprising of ripe fruit (McGrew et al., 1988; Wrangham et al. 1998; Tweheyo et al., 2004). They consume fruit from a vast number of species, but concentrate their feeding time on a few key species (Newton-Fisher, 1999; Tweheyo et al., 2004). In addition they commonly feed on young leaves and terrestrial herb vegetation (Wrangham et al. 1998). Meat in the form of captured monkeys, antelope and occasionally birds also supplements the diet of chimpanzees across Africa, although the regularity with which different communities hunt is highly variable. For instance, the chimpanzees of Tai Forest, Cote d'Ivoire, were observed to successfully hunt on 267 occasions in eleven years (Boesch and Boesch-Achermann, 2000), whilst the chimpanzees of Bossou, Guinea, were only observed to eat meat five times in eight years of observation (Sugiyama and Koman, 1987). Chimpanzees also use tools to obtain highly nutritious foods such as ants (Goodall, 1964; Nishida, 1973; McGrew, 1974), termites (McGrew et al., 1979; McGrew and Collins, 1985), honey (Nishida and Hiraiwa, 1982), and nut kernels (Sugiyama and Koman, 1979; Boesch and Boesch, 1984; Hannah and McGrew, 1987). The presence of these different tool using techniques varies highly across the long term study sites in Africa (Whiten et al. 1999; Whiten et al., 2001) and detailed investigations have revealed that not only environmental but also cultural factors determine the use of these different tool-oriented techniques to procure food (McGrew et al., 1997).

Chimpanzees habitually share meat (Boesch and Boesch-Ackerman, 2000) and this process has been interpreted as economic exchange: using meat to buy future coalitional support (Nishida & Hosaka, 1996; Mitani & Watts, 2001). Similar sharing of plant food is rare, and when it does occur, it is primarily between related individuals (McGrew, 1975; Goodall, 1986). Observations of food sharing between unrelated individuals, when individual procurement of food is possible and more efficient for the begging individual, highlights the possibility that food sharing functions as a socially significant event rather than just a purely nutritional exchange (Slocombe and Newton-Fisher, 2005).

Chimpanzees face serious predation threat from leopards (Boesch, 1991a) lions, *Panthera leo* (Tsukahara, 1993) and significantly humans. Aggressive behaviour has also been observed to be directed towards snakes (Goodall, 1986). The prevalence of these predators varies according to the habitat and location of each chimpanzee population, meaning predation pressures are highly variable across sites in Africa.

## **Vocal communication**

### *A graded vocal system*

Vocal systems can be placed on a continuum ranging from discretely organised to extensively graded (e.g. grading between call types and variation within call types). Rowell and Hinde (1962) first described the highly graded nature of the rhesus macaque vocal system and since then many species of primate including Japanese macaques (Green, 1975), red colobus monkeys, *Procolobus badius* (Marler 1970) and chimpanzees (Marler, 1976) have also been shown to have highly graded vocal repertoires. Within the chimpanzee repertoire the degree of grading which occurs between call types is variable, with waa barks being the most highly graded and laughter being the most discrete call type (Marler, 1976). Even within the more discrete call types such as laughter, there is still large variation within the call type, meaning that the chimpanzee repertoire shows extensive grading both between certain call types and within call types. Highly graded repertoires offer the potential for encoding large amounts of information, if the relationship between signal grading and circumstances of production is highly ordered (Marler, 1976). Such a system was revealed by Green (1975) with his detailed investigation into the coo vocalisations produced by Japanese macaques. Green (1975) identified seven acoustic variants within the coo call type and mapped these variants on to circumstances of production. Clear correlations were found between the coo variants and the contexts in which they were produced.

The critical factor which determines the degree and type of information a graded system can convey to recipients is the manner in which recipients perceive the continuum between certain call types. Human speech contains significant grading

between certain phonemes, however, we perceive the phonemes categorically. The classic illustration of this phenomenon is the human perception of the graded continuum between 'ba' and 'pa' (Abramson and Lisker, 1970). These two phonemes differ only in the length of the interval between the first release of air and the onset of laryngeal voicing. If presented with two exemplars from this continuum with a 10msec difference in the voicing interval, we would perceive them as the same or different, depending on whether the 10msec difference lay within a phoneme category or over the natural phonemic boundary (Liberman et al., 1961). In this regard, human speech has two vital lessons for the study of vocalisations; firstly, graded sounds can be perceived categorically and thus act discretely; secondly, the grading of sounds is not necessarily driven by emotion or motivation.

No direct research has been conducted to examine whether chimpanzees perceive their vocalisations as a continuum or categorically and this constrains our understanding of their vocal communication. The best we can currently do is extrapolate research on humans and other species of primate to estimate what chimpanzees are capable of. As reviewed above, humans perceive continuous speech sounds categorically. Similarly, Barbary macaques, *Macaca sylvanus*, demonstrate categorical perception of continuous variation in shrill barks (Fischer, 1998) and baboons perceive bark variants categorically (Fischer et al., 2001). In contrast to these studies, Le Prell (2002) suggests that rhesus monkeys cannot categorically perceive the continuum between arched and tonal screams. It seems that non-human primates have the ability to perceive continuous sounds categorically, although this does not necessarily apply to all sounds. It thus seems reasonable, until empirical research is available, to assume that chimpanzees could be perceiving at least some of the gradations between and within their call types in a categorical manner.

### *The repertoire*

Describing the graded vocal repertoire of a species is a significant challenge. In the absence of naturally occurring discontinuities in acoustic structure, investigators construct a list of characterisable sounds by, somewhat arbitrarily, selecting exemplars of vocalisations that are far removed from each other in physical form

(Green, 1975). Struhsaker (1967) suggested combining physical descriptions of the acoustic structure of the sound with behavioural data on circumstances of production and responses of others in order to differentiate more finely between discrete categories of calls in a graded continuum. In contrast, Marler (1965) highlights the dangers associated with this approach and suggests that consideration of signal function should be avoided until physical classification of signals is complete in order to avoid circular reasoning.

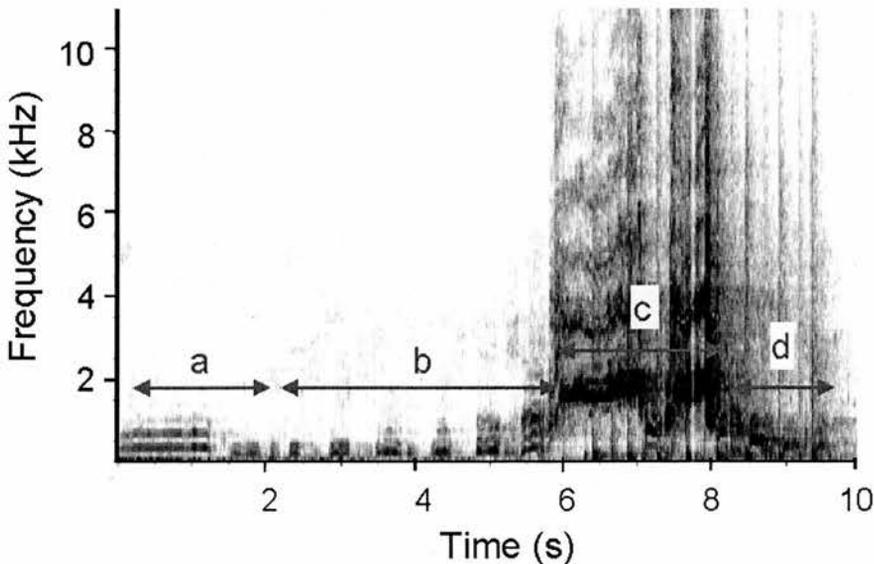
Reynolds (1965) provides one of the earliest accounts of the basic vocal repertoire of the chimpanzee. He proposed twelve basic call types. This was followed by the description of a more finely differentiated repertoire containing 24 putative call types (Goodall, 1968). The early accounts of the chimpanzee vocal repertoire relied heavily on the circumstances of production to define the calls, and in doing so a dangerous precedent of circular definitions of function was set (Marler, 1965). Reliance on a subjective description of the sound, the facial expression accompanying call production, the circumstances of production and the responses of others has continued (Goodall, 1986), despite the availability of acoustic analysis techniques which would allow a more objective classification system to be developed. Marler and Tenaza (1977) provide the only quantitative acoustic description of the chimpanzee repertoire, which they categorise into 13 broad call types. Although this work is the best objective mapping of the repertoire available, it is still constrained by the reliance on context rather than acoustics to classify calls. A detailed and comprehensive acoustic-based classification of the chimpanzee repertoire is still sorely needed, both in terms of aiding our understanding of their communication system and enabling field workers to confidently reference different call types, without the worry that the vocalisation they noted as a 'hoo' was really a 'hoo'.

In the tradition of Marler and Tenaza (1977), I will provide brief acoustic and contextual descriptions of the 13 call types they identified as well as the 'hoo' call proposed by Goodall (1986). In providing these descriptions I have drawn from my own knowledge of these calls and their usage, as well as the previous work of Goodall (1968; 1986) and Marler and Tenaza (1977). I will illustrate each call type with an example spectrogram and a description of the specific circumstances which elicited it, from my own observations of the chimpanzees in the Budongo Forest. Although the

categorisation of these call types is still constrained by the reliance on the context, it represents the most objective system available to date.

### *Pant Hoot*

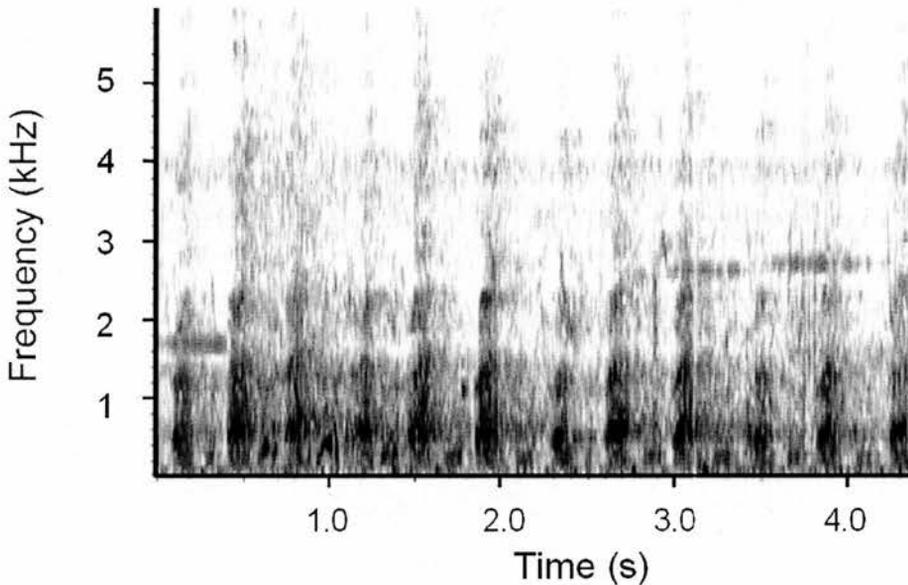
This composite vocalisation is the species typical long distance vocalisation, with calls carrying as far as 1km through the forest. The call is composed of four distinct phases: the introductory phase consisting of low frequency ‘hoo’ calls; the build up phase consisting of increasingly loud panting hoo calls, with energy in both the inhalation and exhalation; the climax phase, consisting of screams or roars; the let down phase, resembling the build up phase but with progressively decreasing energy. Individual calls will vary in the presence and absence of some of these elements; the introduction, let down and occasionally the climax are sometimes omitted (see Marler and Hobbett, 1975 for a full description). Pant hoots are produced predominantly by adult males, in a variety of contexts including display, travel, arrival at feeding sites, feeding and rest. The example pant hoot, provided by gamma male, Black, was produced during a display in which he charged and drummed on the buttress of a tree (Figure 3.1).



**Figure 3.1. A spectrogram of a pant hoot vocalisation given by adult male, Black, during a display.** The four phases of the pant hoot are illustrated:(a) = introduction; (b) = build up; (c) = climax; (d) = let down. The vertical lines in the let down phase represent drumming, where Black is striking a tree buttress with his feet. The darkness of the spectrogram image represents the amplitude of the acoustic energy in the call (Darker = more energy).

### *Pant grunt*

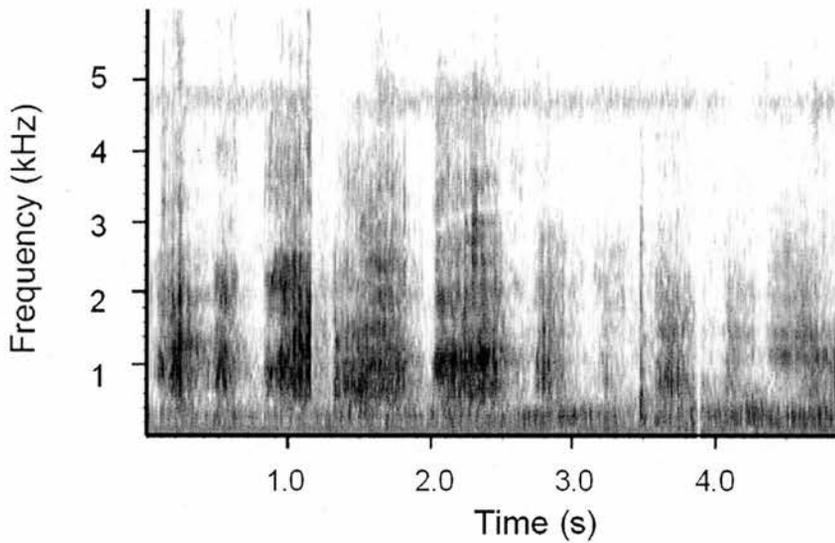
Pant grunts are noisy, low frequency grunts or barks, which are panted in a rapid rhythm so there is audible energy in both the inhalation and exhalation. Subordinate animals give these calls to dominant individuals usually as a greeting or a signal of subordination to an approaching aggressive chimpanzee. Adult female, Kalema, gave the example pant grunt as she approached Duane, the alpha male, who was resting on the ground (Figure 3.2).



**Figure 3.2.** A spectrogram of a pant grunt given by adult female, Kalema.

### *Laughter*

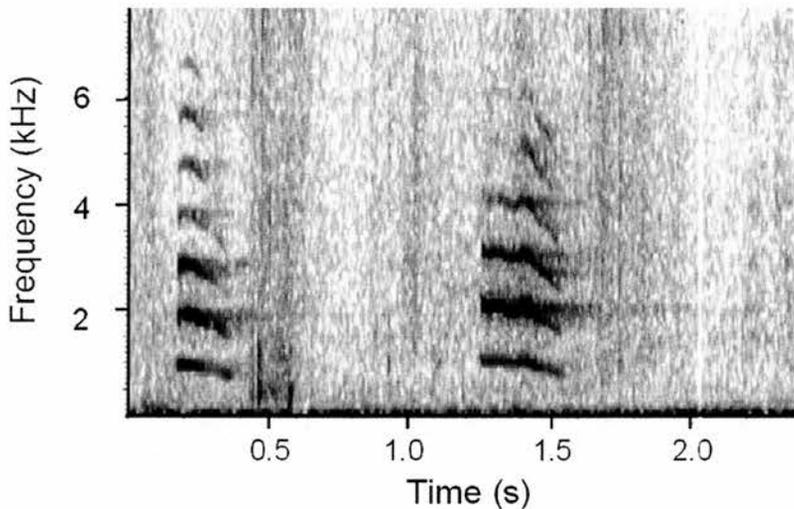
Laughter is the last of the three chimpanzee calls where acoustic energy is audibly present in both the inhalation and exhalation. This call consists of noisy, low frequency grunts and moans delivered in an irregular rhythm, which is reminiscent of hoarse, wheezing human laughter. This call is given in play contexts and particularly during play wrestling. The example laughter bout was given principally by juvenile female, Nora, whilst wrestling on the ground with juvenile female, Janet (Figure 3.3).



**Figure 3.3.** A spectrogram of a laughter from juvenile female, Nora.

*Squeak*

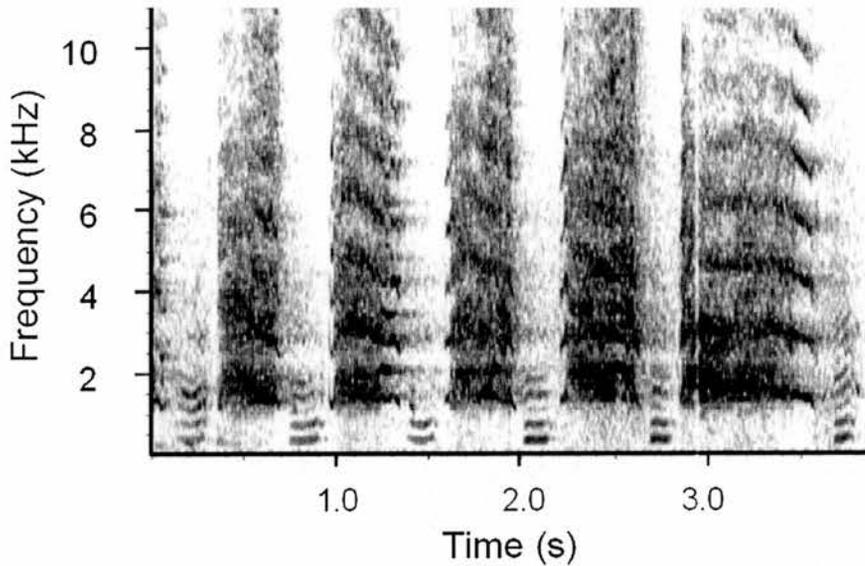
Squeaks are high-pitched, short, shrill calls often given in fast succession to form short bouts. Squeaks and screams often grade into one another and squeaks are usually elicited by mild threats of aggression, or after aggressive attacks. Females also produce squeaks during copulation. Adult female, Janie, gave the example squeaks, during the first 5 seconds of a copulation with adult male, Zefa (Figure 3.4).



**Figure 3.4.** A spectrogram of squeaks produced by adult female, Janie, during a copulation with adult male, Zefa.

### *Scream*

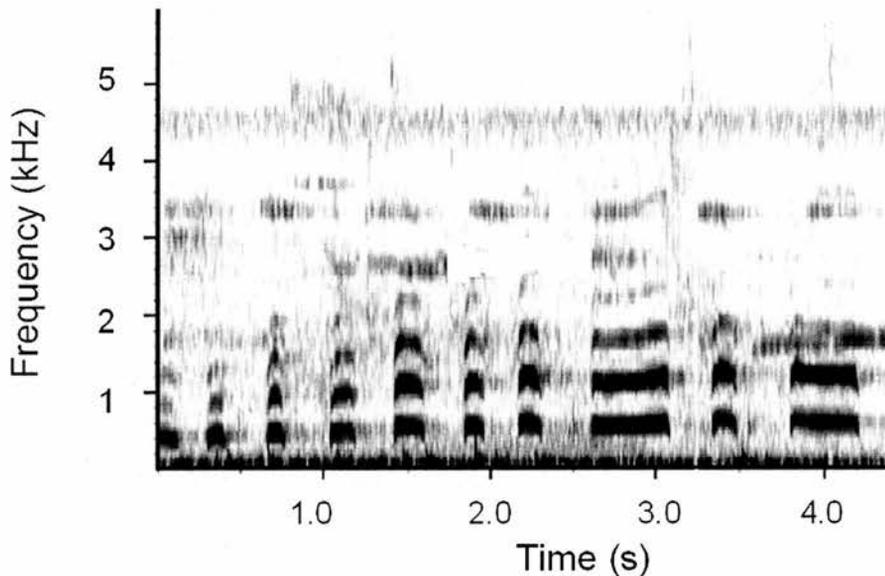
Screams are loud and harmonic vocalisations with varying degrees of tonality. These calls are given in a number of different circumstances; by victims and less commonly aggressors during agonistic interactions, by chimpanzees having tantrums and during periods of intense social excitement or feeding. Juvenile female, Janet, gives the example screaming bout during a tantrum caused by her mother's refusal to carry her (Figure 3.5).



**Figure 3.5.** A spectrogram of a screaming bout given by juvenile female, Janet, whilst having a tantrum. Unusually, voicing can be seen on both the exhalation (high frequency, high energy) and inhalation (low frequency, low energy).

### *Whimper*

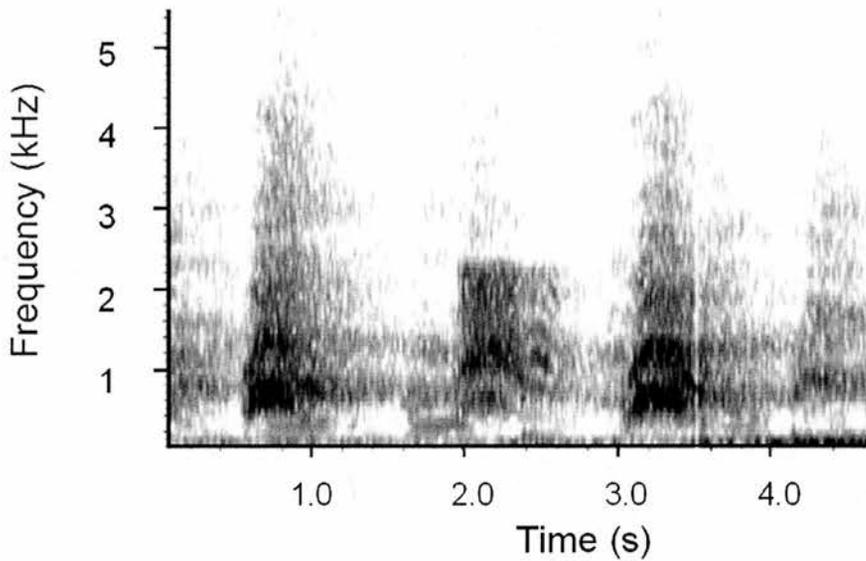
Whimpers consist of a series of soft hoo calls, where the frequency and amplitude of the whimper sequence rises and falls. Whimpers are often produced with a pout expression and are generally given by distressed individuals, typically separated or frustrated juveniles, or frustrated adults in competitive feeding or begging contexts. The example whimper is given by juvenile female, Nora, after she became separated from her mother (Figure 3.6). Nora's whimpers graded into screams when, after ten minutes, her mother failed to return to find her. Nora then began actively searching for her and after five minutes she found her mother, who had waited in the undergrowth and remained puzzlingly silent.



**Figure 3.6. A spectrogram of a whimper given by juvenile female, Nora.**

### *Bark*

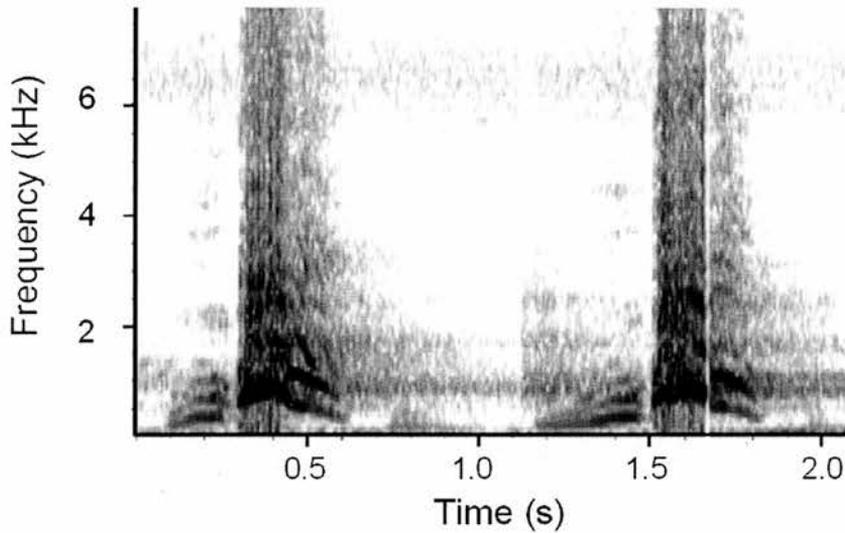
Barks are sharp, loud calls with abrupt onsets. They are often noisy and are generally low-pitched vocalisations. Barks are given more by females than males in a variety of contexts including situations of social excitement and agonistic encounters. The example barks were given by adult females, Flora and Janie, whilst watching adult male, Zefa, displaying silently beneath them, shaking vegetation (Figure 3.7). Flora and Janie had climbed up into the trees to avoid the initial charge of his display.



**Figure 3.7.** A spectrogram of barks produced by adult females, Flora and Janie, in response to adult male, Zefa, displaying. Flora and Janie gave alternate barks.

#### *Waa Bark*

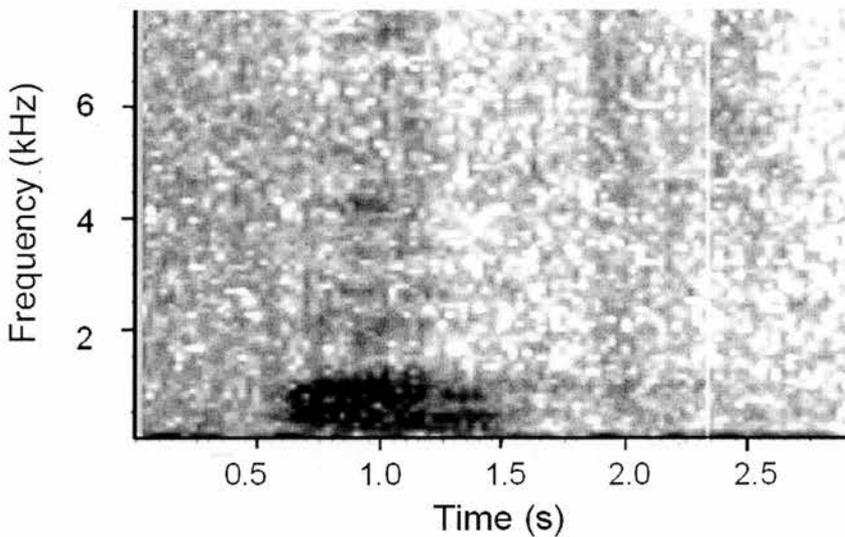
This call is a distinct loud, intimidating bark variant, in which the sound ‘waa’ is clear. Acoustically distinct from shorter bark calls and screams into which they often grade, waa barks typically have maximum energy at a low frequency at call onset and then a clear rise and short fall in pitch during the ‘aa’ element of the call. Waa barks are produced in isolation or in short series. They are commonly given by chimpanzees observing an agonistic interaction, as threats to other species including baboons and bush pigs and as threats to distant opponents, most often by victims of aggression after the aggressor has retreated. Adult female, Flora, gave the example waa barks to baboons that were attempting to displace her small feeding party from a patch of *Broussonetia papyrifera*, which had lots of ripe fruit (Figure 3.8).



**Figure 3.8.** A spectrogram of waa barks given by adult female, Flora, to baboons.

*Cough*

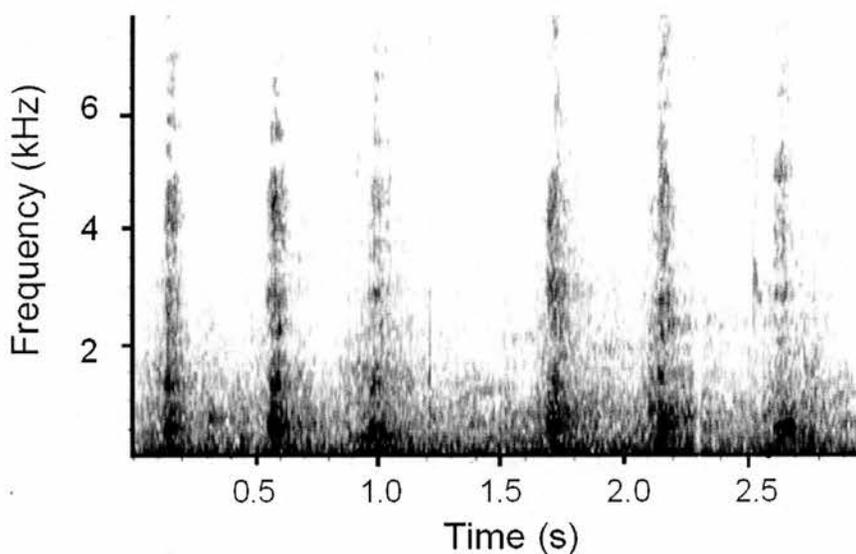
This low frequency bark vocalisation is usually given in isolation as a mild threat by an annoyed individual to a subordinate. The cough threat is usually sufficient to secure the termination of the undesirable behaviour in the subordinate. The example cough was given by adult female, Kwera, to juvenile male, Kato, when play wrestling with her juvenile son, Kwezi, got too rough (Figure 3.9). Kato stopped playing with Kwezi and oriented towards Kwera, before initiating chase play with Kwezi.



**Figure 3.9.** A spectrogram of a cough threat given by adult female, Kwera.

### *Rough grunts*

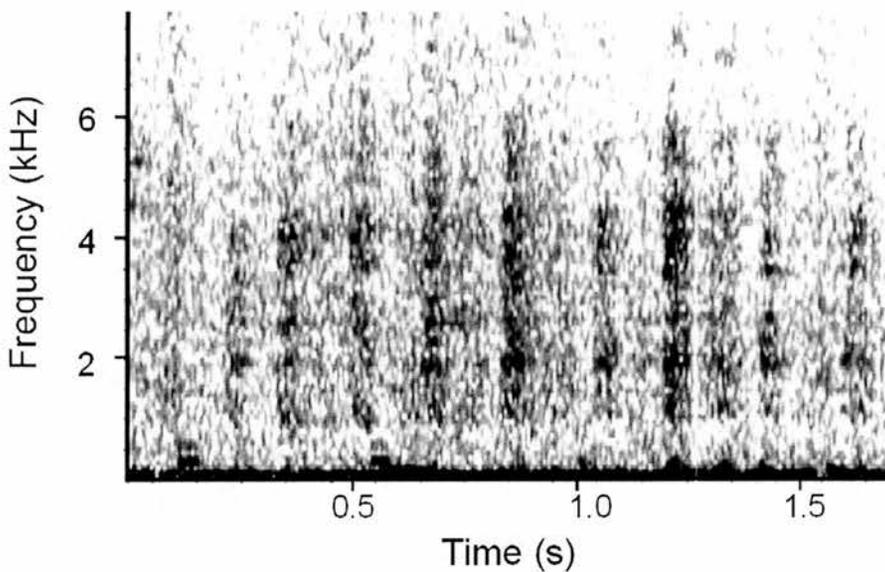
'Rough grunt' is an umbrella term that describes the vocalisations produced by individuals when approaching, collecting or consuming food. Acoustically, rough grunts grade from low frequency noisy grunts to high frequency tonal squeaks. The temporal patterning of these calls within long bouts is typically irregular. Males produce these calls more often than females and other individuals usually respond to these vocalisations with orientation and approach towards the caller. Adult male, Nick, gave the example rough grunts during the first minute of feeding on fallen fruit from a *Chrysophyllum milicia excelsa* tree (Figure 3.10).



**Figure 3.10.** A spectrogram of rough grunts given by adult male, Nick.

### *Pant*

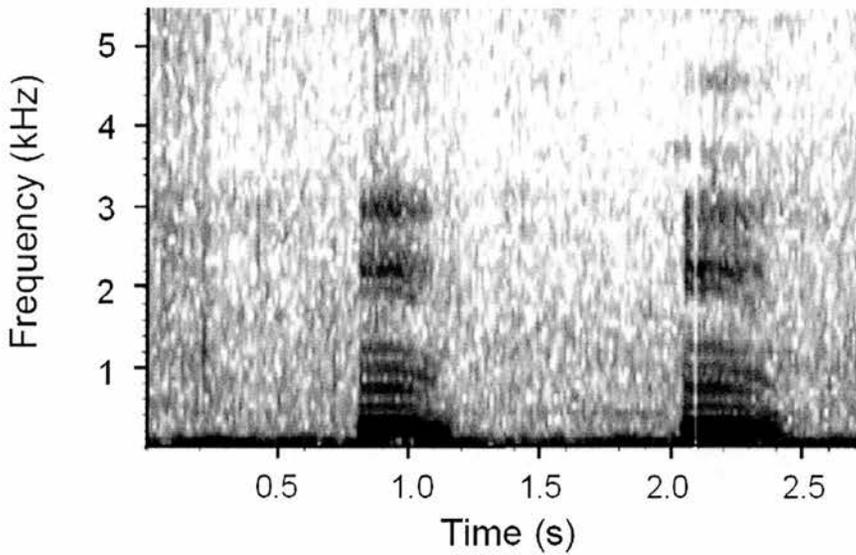
Panting is usually unvoiced and therefore the sounds are soft and low frequency. The temporal patterning of panting is regular and rapid. Panting is often given as part of a greeting. In this context the caller habitually presses their open mouth against the other individual whilst panting. Panting also occurs in males during copulation and it is in this context that the example panting bout was given. Adult male, Zefa, produced this panting bout during a copulation with adult female, Janie, that lasted 12 seconds (Figure 3.11).



**Figure 3.11. A spectrogram of a panting bout given by adult male, Zefa, during copulation.**

### *Grunt*

Grunts are soft, low frequency, short calls that are given singularly or in short bouts. These calls are produced during resting and the making of nests. Short grunt exchanges can often be heard between affiliative individuals as they initiate travel or rest, or they hear an approaching chimpanzee. The example soft grunts were given by sub-adult male, Gershom, in reply to soft grunts given by alpha male, Duane, sitting 3 metres away from Gershom on the ground (Figure 3.12).



**Figure 3.12. A spectrogram of soft grunts given by sub-adult male, Gershom.**

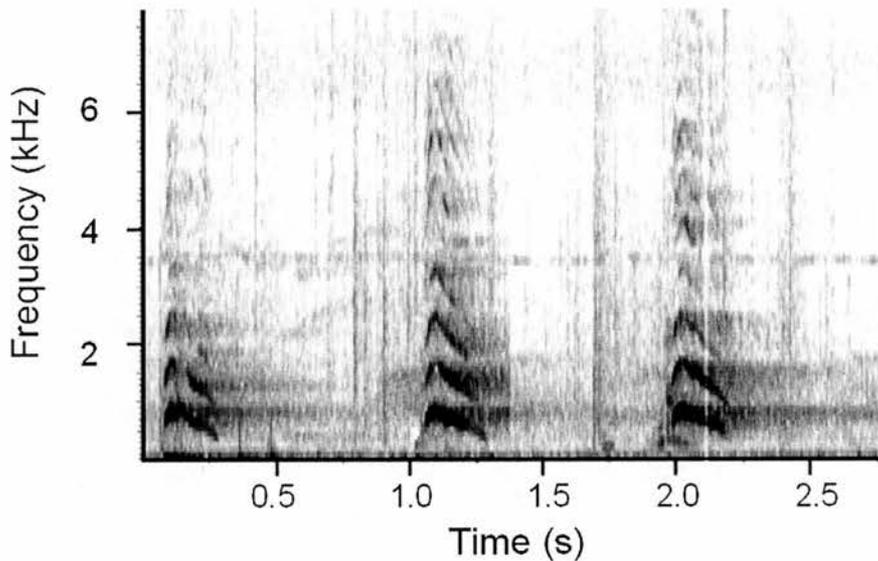
### *Wraaa*

Wraaa vocalisations are proposed to be variants of waa barks (Marler and Tenaza, 1977), where the rising 'aa' element is drawn out into a long, high amplitude howl. No spectral description or spectrograms of this vocalisation are available in the previous literature and this call was never heard during the current study, making it impossible to describe this call further. Goodall (1986) described the Gombe chimpanzees producing wraaas in response to leopard, buffalo, pythons, humans before successful habituation and paralysed or dead community members.

### *Huu*

Huu vocalisations were not included in Marler and Tenaza's (1977) description of the chimpanzee repertoire, because spectrally they were similar to the hoo calls which make up whimper bouts. However, the amplitude and duration of huu calls observed in the Budongo forest community was much greater compared to 'hoo' calls. In addition huu calls are not typically produced with a pout expression (Goodall, 1986) and they elicit much stronger responses from listening individuals than hoos. Huu calls are tonal calls, with most energy at call onset and a rise and fall in frequency over the call. These calls can be loud, sometimes carrying over a hundred metres and generally elicit approach and alert scanning behaviour from recipients. Goodall (1986)

describes them as being elicited by puzzling or unusual events. This was true for the Budongo chimpanzees who were recorded to give them in response to surprising objects and events, such as a dead monkey in a snare, earth tremors and the waterproof cloak of a new researcher. However, the Budongo chimpanzees, which have never been recorded to produce 'wraaa' calls, also gave them as alarm calls in response to buffalo, pythons and dying members of the community. The example huu calls were given by adult female, Kalema, in response to a large earth tremor (Figure 3.13). Kalema stayed in the same tree and persisted in producing these calls for several hours after the event.



**Figure 3.13.** A spectrogram of huu calls given by adult female, Kalema, in response to an earth tremor.

### *Vocal production*

The range of calls and frequency with which individuals produce calls is heavily mediated by the sex and rank of the individual, and the social context. In the Gombe population, although most call types were given by all age sex classes, there were sex-biased trends in vocal production with males giving the majority of pant hoots, rough grunts, grunts and wraaas and females giving the majority of pant-grunts, squeaks, screams and barks (Marler and Tenaza, 1977). In addition to these basic sex biases in production of different call types, a study of the chimpanzees of the Kibale forest, Uganda, revealed that rank and social context also mediates individual rates of calling (Clark, 1993). High-ranking males were highly vocal in all social contexts, but adult females and low ranking adult and sub-adult males were predominantly silent, unless they were in large mixed parties.

The degree of voluntary control chimpanzees exercise over their vocal behaviour is uncertain. Anecdotal evidence of Gombe chimpanzees having difficulty suppressing calls (Goodall 1986, p.125) and the inability of the human raised chimpanzee Viki to produce sounds on demand (Hayes, 1951, p.66) indicates that control of vocal production is highly influenced by emotion. On the other hand, the close relative of the common chimpanzee, the bonobo has demonstrated the ability to suppress food-associated calls in a naturalistic setting (Van Krunkelsven, 1996) and similarly captive common chimpanzees have been observed to abstain from producing rough grunts upon the discovery of small amounts of rare, highly-preferred food (Hauser and Wrangham, 1987). This evidence indicates that a degree of voluntary and cognitive control over vocal production is possible in chimpanzees, although in most situations vocal production is closely linked to emotion.

Chimpanzees appear no different from other primates in the restricted plasticity they have available in vocal production (Chapter 1, page 5-6). Chimpanzees are also limited in a primate typical fashion in terms of the role learning can play in the production of new vocal behaviour. However, within the confines of limited vocal learning, chimpanzees have shown the ability to modify existing calls through experience, as demonstrated by convergence of pant hoot calls within communities and between chorusing partners (reviewed in Chapter 1, page 5).

## *Vocal perception*

The auditory system responsible for sound perception in chimpanzees appears to have thresholds and sensitivities that are intermediate to humans and monkeys (Kojima, 1990). Chimpanzees are more sensitive to high frequencies over 8 kHz than humans, but are less sensitive than monkeys to very high frequencies of up to 32 kHz (Masterton et al., 1969). Chimpanzees also demonstrate greater difference thresholds for frequency and less sensitivity to sounds of 2-4 kHz and under 250Hz compared to humans (Kojima, 1990). Although these findings have been used to explain possible difficulties chimpanzees may have perceiving human speech, no research has focussed on the design and perception of their own vocalisations. In the absence of this evidence, it seems reasonable to assume that chimpanzees will perceive similar call features to humans, but with greater sensitivity to acoustic energy at higher frequencies.

Within the constraints of this hearing mechanism, one of the main challenges for chimpanzees in a low visibility environment is identifying individuals from their vocalisations. Chimpanzees produce vocalisations that are individually distinctive (Marler and Hobbett, 1975; Mitani et al., 1996). Pant hoot vocalisations produced by chimpanzees of the Gombe stream varied systematically with the sex and identity of an individual, and differences between individuals were sufficient to permit human observers to identify individuals on the basis of their pant hoots (Marler and Hobbett, 1975). Pant hoots from seven different males of the Budongo Forest were sufficiently distinctive that statistical analyses could successfully categorise calls according to the identity of the caller on 73% of occasions (Notman and Rendall, 2005). These findings were also replicated in the Mahale mountain population, with pant hoots found to be stereotyped within individuals and variable between individuals, in comparison to pant grunts (Mitani et al., 1996). These authors suggested that selection acts to encode higher degrees of individuality in elements of the vocal repertoire that are broadcast over large distances where listeners have few other cues to identity.

There is important evidence available from both wild and captive populations that chimpanzees can take advantage of these acoustic cues to identity and recognise each other on the basis of their vocalisations. Chimpanzees of the Tai Forest in Ivory Coast

responded differentially to playbacks of pant hoots given by members of their own community, neighbouring communities and strangers (Herbinger, 2004). Whilst hearing pant hoots from their own community led to approach, pant hooting and drumming, playbacks of neighbouring community members elicited a reduction in feeding, screaming and an increase in reassurance behaviours. Playbacks of strangers elicited similar but less extreme reactions compared to the playbacks of neighbours. In addition, chimpanzees retreated from the source of playbacks of stranger calls, whereas they nervously approached the speaker when they heard neighbour calls. Wild chimpanzees seem able to identify members of their own community and discriminate between disparate foreign groups. The chimpanzees' knowledge of individual identity within neighbouring communities was then tested with playbacks of neighbours in expected and unexpected locations (Herbinger, 2004). Chimpanzees displayed more evidence of disturbance to playbacks of neighbours from the incorrect location, indicating that they recognise and associate each neighbour's vocalisations with a customary spatial location. These results indicate that the network of vocal recognition in wild chimpanzees is extensive and the author speculates the study community may recognise the vocalisations of up to 100 individuals. These findings are corroborated by experiments with captive chimpanzees. Three juvenile chimpanzees showed they were able to identify six individuals on the basis of their pant hoots (Bauer and Philip, 1983) and one adult female chimpanzee showed similar abilities with the pant hoots of nine individuals (Kojima et al., 2003). This female also demonstrated that both screams and pant grunts carry sufficient cues to identity to permit individual identification, as she successfully discriminated the identity of the caller from both of these call types.

### **Functionally referential communication**

Great apes, including chimpanzees, have shown great competency with artificial languages and have demonstrated that they are able to use symbols or gestures to refer to objects in the world (Fouts and Budd, 1979; Gardner and Gardner 1975; Rumbaugh, 1977; Savage-Rumbaugh et al., 1986). The concept of reference is obviously within the grasp of these enculturated apes, but there is considerable debate over whether data from these human-raised apes is comparable to the natural abilities

of wild apes. In addition, none of these studies examine the ape's natural vocal behaviour, which is both the focus of this thesis and essential for research relevant to the evolution of language. I will therefore focus on the very limited amount of evidence available for functional reference in the natural vocalisations of chimpanzees.

Most of the research effort into this topic with wild populations has focussed on the pant hoot vocalisation. This long distance vocalisation was favoured over quieter intraparty calls because receivers of the call rarely have additional visual or circumstantial information to aid understanding of the call; thus it was assumed any information it conveyed would be confined to the acoustic structure. Uhlenbroek (1996) established the existence of four acoustically distinct pant hoot variants in the Gombe population and found that three of the four variants were most commonly given in different behavioural contexts: 'wail' pant hoots were given whilst feeding, 'roar' pant hoots were given during travel or display and 'slow roar' pant hoots were produced on arrival at a plentiful food source. A replication of this study with a comparable sample of chimpanzees from the Budongo forest yielded very similar results (Notman, 2003). Uhlenbroek (1996) interpreted these results in terms of the calls having the potential to provide listeners with information about the behavioural state of the caller and elements of the environment (e.g. the presence of a plentiful food source). Thus they were seen as context specific calls, with low referential specificity but the potential to function as referential calls. Notman and Rendall (2005) chose to interpret similar results in a different light, minimising the emphasis on referential potential and focussing instead on the mechanisms driving the acoustic variation in the calls. They propose that the height above the ground and energetic output of the caller could explain the acoustic variation observed in this call type. Regardless of the authors' interpretation, this study replicated Uhlenbroek's results and the potential of a call to function referentially is crucially not constrained by the production mechanism. Empirical evidence that does question the results from these two studies comes from the analysis of pant hoots given by chimpanzees in Kibale forest during feeding and food arrival. Although the acoustic analysis was more basic than that employed by the more recent studies, there was no evidence that this population of chimpanzees gave an acoustically distinct food arrival pant hoot (Clark and Wrangham, 1993). This directly contrasts with Uhlenbroek and Notman's work.

In conclusion, pant hoots at best have the potential to convey information about the presence of plentiful food sources in the environment and the caller's current behaviour. At minimum, pant hoots merely provide listeners with a guide to the caller's current behaviour and location in the forest. It is perhaps therefore best to conclude that pant hoots may be informative but very low in referential specificity and thus not the ideal candidate for further investigation with playback experiments.

The referential specificity of pant hoots could be increased if these calls were used in combination with other calls. Such a scenario is described by Boesch (1991b). He proposed that the alpha male of the Taï community used pant hoots and drumming sequences to impart specific information to community members about the initiation of a new travel direction or rest period. Distant recipients of such call combinations were reported to silently change direction or take rest periods. The study is limited by the cessation of the behaviour 3 months after data recording began, resulting in a small number of recorded instances. Although such communication arguably has behavioural referents, not external referents, it shows the potential power of call combination to convey very specific information to listeners. This point is elaborated upon by Crockford and Boesch (2005) who found that many call combinations were given in specific contexts, some of which were different to the contexts associated with the component calls. The authors suggested that certain call combinations had additive functions, illustrating how call sequences can increase message complexity.

The only clear empirical evidence of context specific calls, with the potential to function referentially, comes from a well-conducted study on the usage of barks by the chimpanzees of the Taï Forest, Ivory Coast. Crockford and Boesch (2003) examined the circumstances of bark production in adult males and found clear acoustic subtypes were produced in response to snakes, and whilst hunting. In addition, when the combination of the bark variants with other calls or drumming was analysed, snake, hunt and travel barks showed context specificity of between 93% and 100%. Barks, especially in combination with other call types, are sufficiently context specific to function as referential calls, but playback experiments are required to

assess whether recipients extract meaningful information from these context-specific calls.

The only remaining evidence for functional reference in the natural vocalisations of chimpanzees and bonobos comes from enculturated, human raised apes. Firstly, vocal exchanges between language competent bonobos, Kanzi and Panbanisha, have been reported to convey specific information about external events (Savage-Rumbaugh et al., 2004). Eighteen clear examples of vocalisations functioning in a referential manner are presented. The established protocol was as follows: Experimenter 1 used the lexigram keyboard to communicate with one bonobo some information (“grapes are coming”), who was then asked to ‘tell’ the other bonobo. After the second bonobo heard the vocalisation they were asked by experimenter 2 what they had been told and the second bonobo used their keyboard to impart this information to the experimenter (“grapes”). Unfortunately many aspects of the experimental set up remain unspecified, including the ability of the second bonobo to hear and smell food preparation or presentation to the first bonobo and the degree of visual contact between the animals and experimenters. The experimental protocol was not always employed and there is no indication of how many failures occurred: only successful trials or anecdotes are reported. This study thus provides anecdotal evidence that bonobo vocalisations can function referentially, but the authors argue that the subject animals have a uniquely specialised linguistic ability. It is therefore highly questionable whether these results are generalisable to the natural behaviour of Kanzi and Panbanisha’s wild cousins.

The final attempt to examine functional reference in naturally occurring chimpanzee communication focuses on rough grunt vocalisations. A number of studies report the reliable use of rough grunts in contexts of food discovery (e.g. Hauser et al., 1993; Hauser and Wrangham, 1987), however the only study to formally investigate the potential of these calls to function referentially has been conducted by Hallberg and colleagues (2003). In this study five highly trained captive chimpanzees, proficient in the use of touch screens and match-to sample tasks, were played rough grunts elicited by one of nine different foods. The chimpanzees were then presented with four

photographs of food items so they could select the matching referent of the call. Over 144 trials the chimpanzees were able to choose photos of food in the same quality category (low, medium or high) as the target food that elicited the rough grunts, at a level just higher than chance. With extensive training on three of the nine food types, three of the five chimpanzees were then able to identify the correct food item when played rough grunts to the six untrained food items at a level just higher than chance. Although this indicates that chimpanzee rough grunts can function as referential signals, potential methodological and statistical problems with the reported study make it difficult to interpret these results. In particular, the effect sizes reported seem surprisingly small given the high levels of statistical power associated with the extensive number of trials that were analysed. The authors also provided no indication of whether the marginally significant results reported were a result of one or two tailed binomial tests. If one-tailed tests have been erroneously used, most of the results would become non-significant if the correct two-tailed tests were employed. These issues are particularly unfortunate given that this study represents the only attempt to test recipient responses to chimpanzee vocalisations with playbacks. Finally, even if the results could be interpreted confidently this is a highly artificial task conducted with a small number of highly trained chimpanzees. As with the enculturated bonobos, such low ecological validity makes the relevance of these results to the natural behaviour of chimpanzees questionable.

In conclusion there is no ecologically valid evidence that chimpanzees use functionally referential calls as part of their natural communication. The most promising results to date have revealed that some bark variants are context specific, but in the absence of playback experiments we cannot conclude that these calls are functionally referential. The lack of evidence for this ability in chimpanzees is particularly puzzling considering that they are our closest living relatives and they are widely accepted to be more cognitively advanced than monkeys (Byrne, 1995). Despite the current lack of evidence for functional reference in chimpanzees, there are a number of factors, which would make functionally referential calls advantageous for this species. Wild chimpanzees live in an environment with relatively poor visibility, unpredictable predation threat, violent inter-group encounters, and a highly complex fission-fusion social system; all of which lead to contexts in which the ability to

convey specific information about external events would seem highly advantageous (Bradbury and Vehrencamp, 1998). Thus this research aims to investigate promising types of chimpanzee vocalisations for evidence of context specificity and ultimately functional reference. If successful, this research could have a significant impact on our understanding of chimpanzee behaviour, animal communication and perhaps the evolution of our own linguistic abilities.

## **Chapter 4: Agonistic screams in wild chimpanzees vary as a function of social role**

### **Summary**

As the previous chapters have illustrated, some non-human primates have demonstrated the capacity to communicate about external objects or events, suggesting primate vocalizations can function as referential signals. However, there is little convincing evidence for functionally referential communication in any great ape species. In this chapter, I begin to address this anomaly by examining the vocal behaviour of wild chimpanzees of Budongo forest, Uganda. In particular, I examine whether they encode information about their role in ongoing agonistic interactions with their agonistic screams. I demonstrate that chimpanzees give acoustically distinct screams during agonistic interactions depending on the role they play in a conflict. I analysed the acoustic structure of screams of 14 individuals, both in the role of aggressor and victim. I found consistent differences in the acoustic structure of the screams, across individuals, depending on the social role the individual played during the conflict. I propose these two distinct scream variants, produced by victims and aggressors during agonistic interactions, may be promising candidates for functionally referential signals.

The results of this chapter have been published in the following paper:

Slocombe, K. E. & Zuberbühler, K. 2005. Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *Journal of Comparative Psychology*, **119**, 67-77.

## Introduction

Primates vocalize to one another most often during evolutionarily relevant events, such as predator avoidance, defence against aggressors, and food discovery. The relationship between the function of vocalizations and their acoustic structure has been the focus of much research, with relationships reported between the acoustic structure of calls and the caller's motivational state (Morton, 1977), physical attributes of the caller (Morton, 1977; Hauser, 1993) and the occurrence of discrete external events (reviewed in Cheney and Seyfarth, 1990b). From a cognitive perspective, the most interesting studies are those showing that individuals produce calls in response to discrete external events, such as the appearance of a predator or the occurrence of a specific social context (e.g. Zuberbühler et al., 1997; Cheney & Seyfarth, 1988).

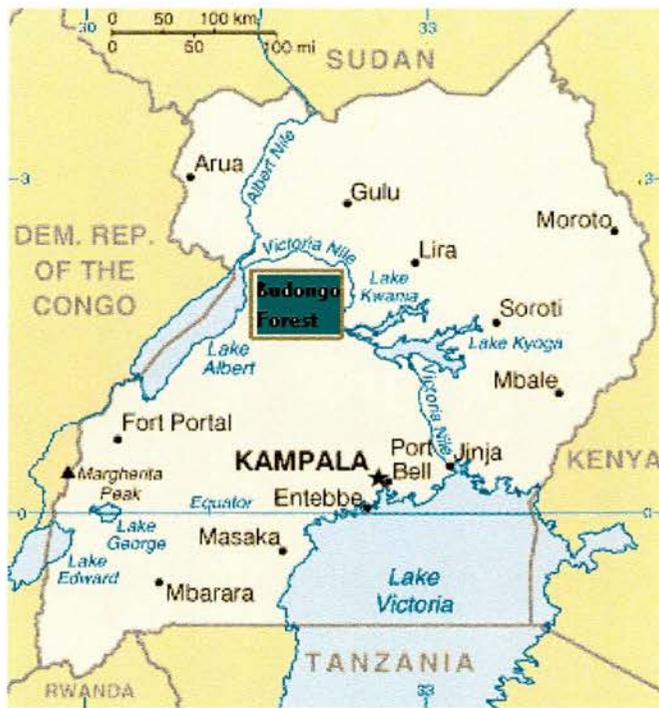
In this study, I focus on the vocal communication of wild chimpanzees, *Pan troglodytes schweinfurthii*, during agonistic encounters, in the Budongo forest, Uganda. I was particularly interested in the most common vocal signal produced during agonistic interactions: screams. Little systematic investigation of these calls has been conducted. Goodall (1986) described screams being produced in a number of different behavioural contexts, suggesting that these calls might contain crucial acoustic variation that could enable nearby listeners to assess the nature of an ongoing event. Previous work on chimpanzee screams has provided some information on the acoustic structure of these calls, particularly in relation to the two sexes (Marler and Tenaza, 1977; Mitani, 1995). However, no quantitative analysis has been conducted to relate call structure to context. Some authors have suggested that screams produced during agonistic interactions may function to recruit help or elicit reassurance behaviours from third parties (Goodall, 1968a; Marler and Tenaza, 1977). In particular, Goodall (1968a, p.308) observed that individuals sometimes responded to screams by "hurrying towards the calling individual and threatening or charging the aggressor", giving support to the notion these calls fulfilled an important function in the recruitment of allies during agonistic interactions. This has certainly been proposed to be the case for rhesus macaques (Gouzoules et al., 1984). It is suggested that this species encode the severity of the attack and the relative rank of their opponent in their screams and that potential allies are sensitive to this information (see Chapter 5 for full discussion and critique of this work).

In the present study I focus on signaller behaviour and investigate whether there is consistent acoustic variation in screams produced in agonistic encounters, which could encode socially relevant information about the ongoing interaction. I focused on the two most basic roles that individuals could take during an agonistic interaction: the aggressor and the victim. Middle and lower ranking chimpanzees produce screams in both roles. I tested whether the acoustic structure of the screams differed depending on the role the individual played in the conflict.

## **Methods**

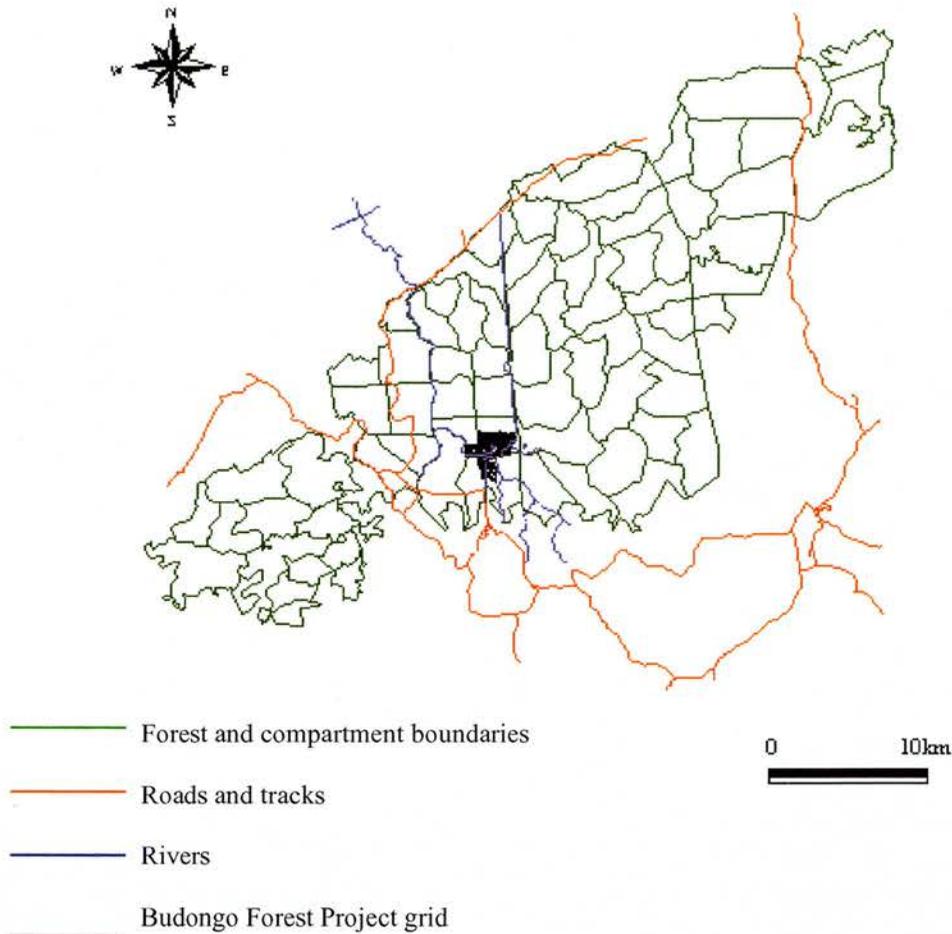
### *Study site*

Data were collected for 8 months between February 2003 and March 2004 on a habituated study group in the Sonso region (Reynolds, 1992) of the Budongo Forest Reserve, Uganda. The Budongo Forest lies between 31°8 and 31°42 East and 1°35 and 1°55 North, towards the north end of Lake Albert, in the Masindi District of Uganda (Figure 4.1). The forest covers an area 428m<sup>2</sup>, making it the largest area of tropical rainforest in Uganda. The forest is classified as moist, semi-deciduous tropical forest, containing four main forest types: mixed forest, colonizing forest, swamp forest and ironwood forest (Eggeling, 1947). Budongo Forest consists of a mosaic of these forest types, due to a history of logging (Plumptre, 1996). The study site is located at an altitude of 1,100 metres and has an annual rainfall of about 1,600 mm. There is a dry season between December and February, in between two rainy seasons (Newton-Fisher, 1999).



**Figure 4.1. Map of Uganda, illustrating the location of the Budongo Forest.**

The Sonso study site was established in 1991 and has consequently been run by the Budongo Forest Project (Reynolds, 1992). The study site is situated in the central compartment, N3, of the Budongo Forest Reserve (Figure 4.2). A trail system has been cut through the forest that covers the majority of the study community's home range. The trail system is comprised of parallel pathways running north-south and east-west (Figure 4.3). The pathways bisect the forest into blocks of approximately 100m<sup>2</sup> to allow researchers to move efficiently through the forest.



**Figure 4.2. Map of the Budongo Forest Reserve showing the 47 constituent compartments, the forest edge, rivers, roads/tracks and the trail system of the Budongo Forest Project.**

The study area supports a large diversity of fauna and flora. Six known species of primates are present: chimpanzees, *Pan troglodytes schweinfurthii*; black and white colobus monkeys, *Colobus guereza*; blue monkeys, *Cercopithecus mitis*; red-tailed monkeys, *Cercopithecus ascanius*; olive baboons, *Papio anubis* and nocturnal pottos, *Perodicticus potto*. Other large mammals include bushpig, *Potamochoerus porcus*, blue duiker, *Cephalophus monticola*, red duiker, *Cephalophus natalensis* and bushbuck, *Tragelaphus scriptus*. On very rare occasions buffalo, *Syncercus caffer* and lions, *Panthera leo*, have been observed to pass through the study area, although none were resident. Leopards, *Pantherus pardus*, seem to be absent from this part of the forest. In addition to mammals, the forest boasts a wealth of bird life and a significant number of reptiles and amphibians. A detailed description of all aspects of the study site has been provided by Newton-Fisher (1997).



**Figure 4.3.** Map of the trail system that covers the majority of the home range of the Sonso chimpanzees. Each of the blocks is labelled with a letter and number to aid navigation. The course of the river Sonso through the study area is illustrated (blue lines), as are the roads through the area (red lines). The Budongo Forest Project camp buildings are illustrated in the North-West corner of the central clearing.

### *Study community*

The Sonso community consisted of up to 66 known individuals during the study period (Table 4.1). The death of Jambo (May 2003) and the disappearance and presumed death of Nkojo (August 2003) has left the community with only six adult males to defend a large home range containing many females and offspring.

Fortuitously no encroachment by neighbouring communities has been observed. Adults were defined as individuals above 15 years of age or those with infants, sub-adults were defined as those between the ages of 10 and 15, who were regularly seen without their mothers, juveniles were classified as individuals between 4 and 9 years old who still spent the majority of their time with their mothers and infants were defined as those under 4 years old (Reynolds, 2005).

Habituation of the Sonso chimpanzees to humans began in 1990 and provisioning has never been used. At the time of the study in 2003-4, adult males were very well habituated, permitting researchers to follow them, even when traveling alone. All but the periphery adult females were confident when in mixed parties, but most remained difficult to follow when traveling just with offspring or in small female parties.

**Table 4.1. The composition of the Sonso community from February 2003-March 2004.** Deaths and births mean the total community size fluctuated between 63 and 66 individuals during the study period.

<b>Males: status</b>	<b>Name</b>	<b>Notes</b>	<b>Total</b>	<b>Females: status</b>	<b>Name</b>	<b>Notes</b>	<b>Total</b>
Adult Male	Duane Maani Black Zefa Jambo Nkojo Tinka Nick Bwoba	Alpha Beta Gamma Mother Banura Died 05/03 Died 08/03 Mother Ruhara	9	Adult female	Banura Clea Flora Harriet Janie Kalema Keway Kigere Kutu Kwera Melissa Mukwano Nambi Polly Ruhara Sabrina Wilma Zana Zimba	Alpha	19
Sub-adult males	Bob Gershom Musa	Sister Rachel Mother Nambi	3	Sub-adult females	Julliet Shida	Mother Banura	2
Juvenile males	Fred Hawa Kato Kwezi Mark Pascal Zalu Zig	Mother Flora Mother Harriet Mother Kutu Mother Kwera Mother Melissa Mother Polly Mother Zana Mother Zimba	8	Juvenile females	Beti Bahati Kana Keti Nora Rachel Rose Sally	Mother Banura Mother Kalema Mother Kutu Mother Kigere Mother Nambi Brother Bob Mother Ruhara Mother Sabrina	8
Infant males	Clint Frank Kasigwa Monday Sean Zak Zed	Mother Clea Mother Flora Mother Kutu, Born 08/03 Mother Mukwano, Died 07/03 Mother Sabrina Mother Zimba Mother Zana	7	Infant females	Helen Janet Karo Kuki Katia Kumi Night Monika Ramula	Mother Harriet Mother Janie Mother Kwera Mother Kigere Born 01/04 Mother Keway Mother Kalema Mother Nambi, Born 02/03 Mother Melissa, Born 07/03 Mother Ruhara	9

#### *Data collection*

Over the 8 months of data collection, 115 days were spent in the forest. This resulted in approximately 900 hours being spent in the forest collecting data or searching for chimpanzees. A typical day started at 0730 and finished at 1600 hours. Chimpanzees

were located in the morning by listening for calls or, if the information was available, by searching the area where the chimpanzees had been observed to nest the previous night.

### Focal Sampling

Focal animal sampling was employed (Altmann, 1974), with focal samples lasting a whole day. The target focal animals were primarily the 9 adult males and 3 sub-adult males. I also had 8 target focal adult females that I followed if male chimpanzees could not be found. These females were those who were most tolerant of being followed when not in a large mixed party. This preferential selection of males was to maximize the vocal data obtained, as males were reported to be more gregarious and vocal than females (Marler and Tenaza, 1977; Clark, 1993). The number of focal hours spent with each of the target individuals is shown in Table 4.2. The first target animal seen each morning was selected as the focal for that day. If a party was encountered, the target animal in that party with the least hours of contact was selected. All vocal behaviour of the focal individual was recorded along with the behaviour that accompanied these calls.

**Table 4.2. The number of hours spent focal sampling the vocalizations and behaviour of each of the target focal animals**

	<b>Individual</b>	<b>Hours</b>
Adult males	Duane	21.12
	Maani	67.87
	Black	25.28
	Zefa	45.12
	Nick	40.22
	Bwoba	36.18
	Jambo	1.41
	Tinka	6.67
Sub-adult males	Gershom	19.58
	Bob	32.27
	Musa	32.23
Adult females	Wilma	24.57
	Zimba	5.58
	Nambi	27.05
	Kwera	14.92
	Kalema	10.56
	Flora	1.67
	Banura	2.50
	Janie	21.38
<b>TOTAL</b>		<b>436.18</b>

### All occurrence sampling

Due to the rare nature of agonistic encounters within this community of chimpanzees, all occurrence sampling (Altmann, 1974) of this behaviour was used.

### Ad libitum sampling

In addition to focal and all occurrence sampling, vocalisations from all non-focal individuals in the party were recorded if their behaviour could be clearly observed and this did not interrupt focal sampling. Ad libitum sampling was also used when the focal animal had been lost and parties of non-focal chimpanzees were found. Following previous studies of this community of chimpanzees, a party of chimpanzees was defined as the individuals within a 35-metre radius of the focal individual (Newton-Fisher, 1997; Fawcett, 2000; Bates, 2005). The visibility in most parts of the forest was too poor to enable effective monitoring of individuals beyond this distance.

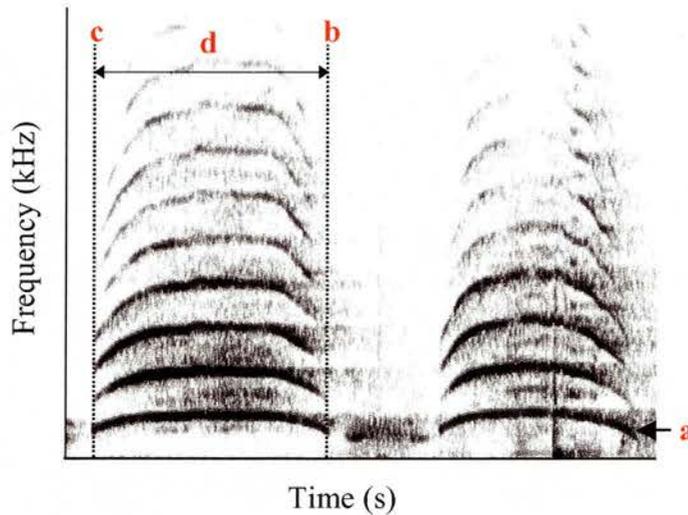
### *Acoustic analyses*

Vocalizations were recorded with a Sennheiser K6/ME67 directional microphone and a Sony TCD-D8 portable DAT recorder. Recordings of vocalizations were transferred digitally from the DAT recorder onto a PC (Toshiba, Celeron 1.8GHz). Calls were digitised at a sampling rate of 44.1 kHz, 16 bits accuracy, using Cool Edit Pro LE. Quantitative analysis of calls was carried out using Raven 1.0 with the following settings: Hanning window function; filter bandwidth: 159Hz; frequency resolution: 86.1Hz; grid time resolution: 0.113ms.

Chimpanzee screams consisted of a fundamental frequency band ( $F_0$ ) and a series of harmonic overtones. All spectral measurements were taken from the  $F_0$ . To describe the overall acoustic structure I determined the following ten parameters, which were most suitable for describing the shape and acoustic structure of the screams: two temporal parameters (Figure 4.4a) and eight spectral parameters (Figure 4.4b):

#### Temporal Parameters

- (1) Bout length: Number of calls given successively in a single bout and separated from other bouts by at least 30s of silence.
- (2) Duration of the call (s).



**Figure 4.4a. Illustration of the fundamental frequency and how temporal acoustic parameters were measured.**

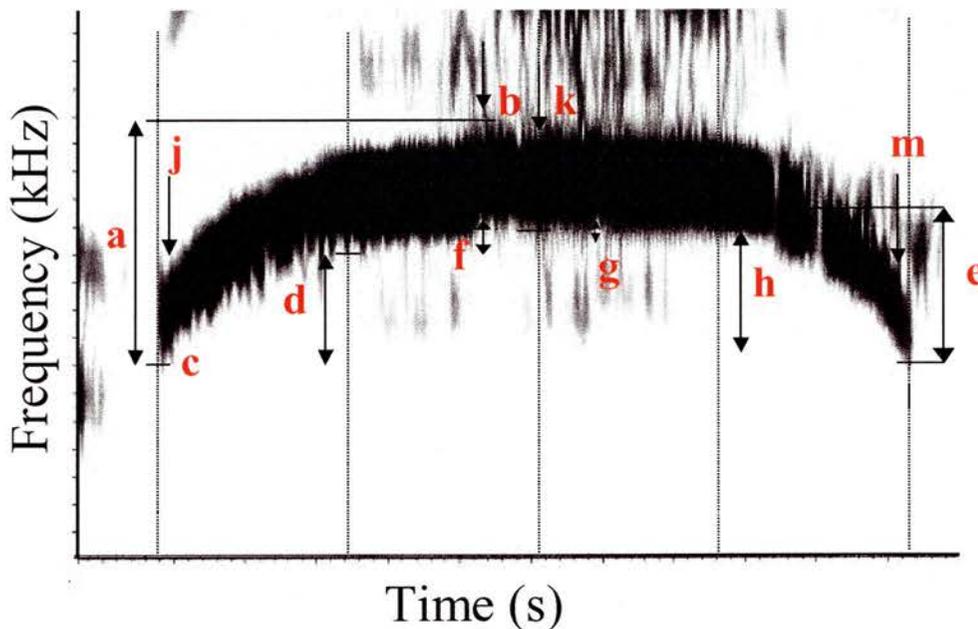
Fundamental frequency ( $F_0$ ) upon which all spectral variables were measured = a.

Call duration = b-c. Bout length is the number of calls, where one call = d.

#### Spectral Parameters

- (3) Frequency modulation: highest frequency minus the lowest frequency in the  $F_0$  (Hz).
- (4) Peak frequency: frequency where maximum acoustic energy occurs in the  $F_0$  (Hz).
- (5) Relative transition first quarter: Relative change in frequency during first quarter of the call divided by the total change in frequency occurring along the bottom edge of the  $F_0$  band, over the entire call (%);
- (6) Relative transition second quarter: Relative change in frequency during second quarter of the call divided by the total change in frequency occurring along the bottom edge of the  $F_0$  band, over the entire call (%).

- (7) Relative transition third quarter: Relative change in frequency during third quarter of the call divided by the total change in frequency occurring along the bottom edge of the  $F_0$  band, over the entire call (%).
- (8) Relative transition fourth quarter: Relative change in frequency in the last quarter of the call divided by total change in frequency occurring along the bottom edge of the  $F_0$  band, over the entire call (%).
- (9) Absolute transition onset: Frequency of maximum energy at call onset minus frequency of maximum energy at call middle (Hz).
- (10) Absolute transition offset: Frequency of maximum energy at call middle minus frequency of maximum energy at call offset (Hz).



**Figure 4.4b. Illustration of how spectral acoustic parameters were measured.**

Frequency modulation (illustrated in figure by **a**) = High frequency (**b**)- Low frequency (**c**). Relative transition first quarter =  $\Delta$  frequency in 1<sup>st</sup> quarter (**d**) /  $\Delta$  frequency along the bottom of  $F_0$  band over entire call (**e**). Relative transition second quarter =  $\Delta$  frequency in 2<sup>nd</sup> quarter (**f**) /  $\Delta$  frequency along the bottom of  $F_0$  band over entire call (**e**). Relative transition third quarter =  $\Delta$  frequency in 3<sup>rd</sup> quarter (**g**) /  $\Delta$  frequency along the bottom of  $F_0$  band over entire call (**e**). Relative transition fourth quarter =  $\Delta$  frequency in 4<sup>th</sup> quarter (**h**) /  $\Delta$  frequency along the bottom of  $F_0$  band over entire call (**e**). Absolute transition onset = Frequency of max energy at call onset (**j**) - frequency of max energy at call middle (**k**). Absolute transition offset = Frequency of max energy at call middle (**k**) - frequency at of max energy call offset (**m**). Peak frequency is not illustrated here.

Measurements of the frequencies at which maximum acoustic energy was present were obtained from creating spectrogram slices (Amplitude plotted against frequency) at the relevant points indicated in Figure 4.4b.

In order to check for co-linearity between the ten acoustic parameters I calculated variance inflation factors for each parameter. Variance inflation factors (VIF) measure the degree to which the variance of one parameter is inflated by the existence of linear and higher order correlation amongst other parameters in the model. They are therefore a sensitive measure of co-linearity and highlight potential problems of instability in a model (Howell, 1997). All ten of the acoustic parameters had acceptable variance inflation factors (VIF <8.0).

Most calling bouts consisted of three or more screams. In order to get a good estimate of the typical acoustic structure of an individual's screams I measured the first three recorded calls per bout sequence and then calculated the median values for each of the 10 acoustic parameters.

#### *Contextual variables*

Recording started whenever two individuals engaged in an agonistic interaction. The identity of the individuals involved and their respective roles during the conflict were determined. All variables were entered into a check sheet (see Appendix 1) or in some cases, spoken commentary was given and later transcribed.

The role of the participant in the interaction was determined by noting the presence of specific behaviours performed by the caller. Individuals were classified as victims if they were running or climbing away from an approaching aggressive chimpanzee, that was pursuing them individually (directed aggression). Individuals were classified as aggressors if they engaged in one of the following behaviours: charging at another individual, shaking branches or saplings at another individual, lunging at or pursuing another individual with or without subsequent physical contact (slapping, stamping or beating). Agreement between myself and experienced field assistant, Raimond Ogen, that one of these specific behaviours had occurred was required in order to classify the caller as either a victim or aggressor. If we could not both confirm the caller had

performed one of the key behaviours, the calls remained unclassified and were not used for analysis.

## **Results**

### *Behavioural observations during social conflicts*

Individuals targeted by an aggressor during a social conflict commonly produced screams. These victim screams were given in response to all kinds of aggressive behaviours ranging from simple postural threats to physical beatings. During this study aggression levels varied considerably with the season and number of females in oestrus, with the number of conflicts observed in a day ranging from 0 to 30. For this study I analysed only victim screams given in response to directed aggression, where aggressors pursued the victim individually along the ground or through the trees, but without physical contact. Aggressors also produced screams during social conflicts, although less often. For example, high-ranking males were typically silent when engaging in aggressive acts. Aggressor screams were predominantly produced by low ranking males, females or juveniles. Aggressors produced screams as they were chasing, beating or threatening an individual. Aggressor screams were often followed by “waa barks” once the interaction was terminated. Sometimes, individuals engaged in both roles during a social conflict, for example, when retaliating against an individual who initially displayed aggression towards them. On a few occasions, I observed that out-of-sight third party individuals approached and became involved in the ongoing social conflicts, presumably in response to hearing the individuals’ screams.

### *Acoustic analyses of screams recorded during social conflicts*

A total of 257 screams were recorded from 37 different individuals during a wide range of agonistic encounters of varying severity. 33 of these individuals could be classified as being in the role of either aggressors or victims of directed aggression.

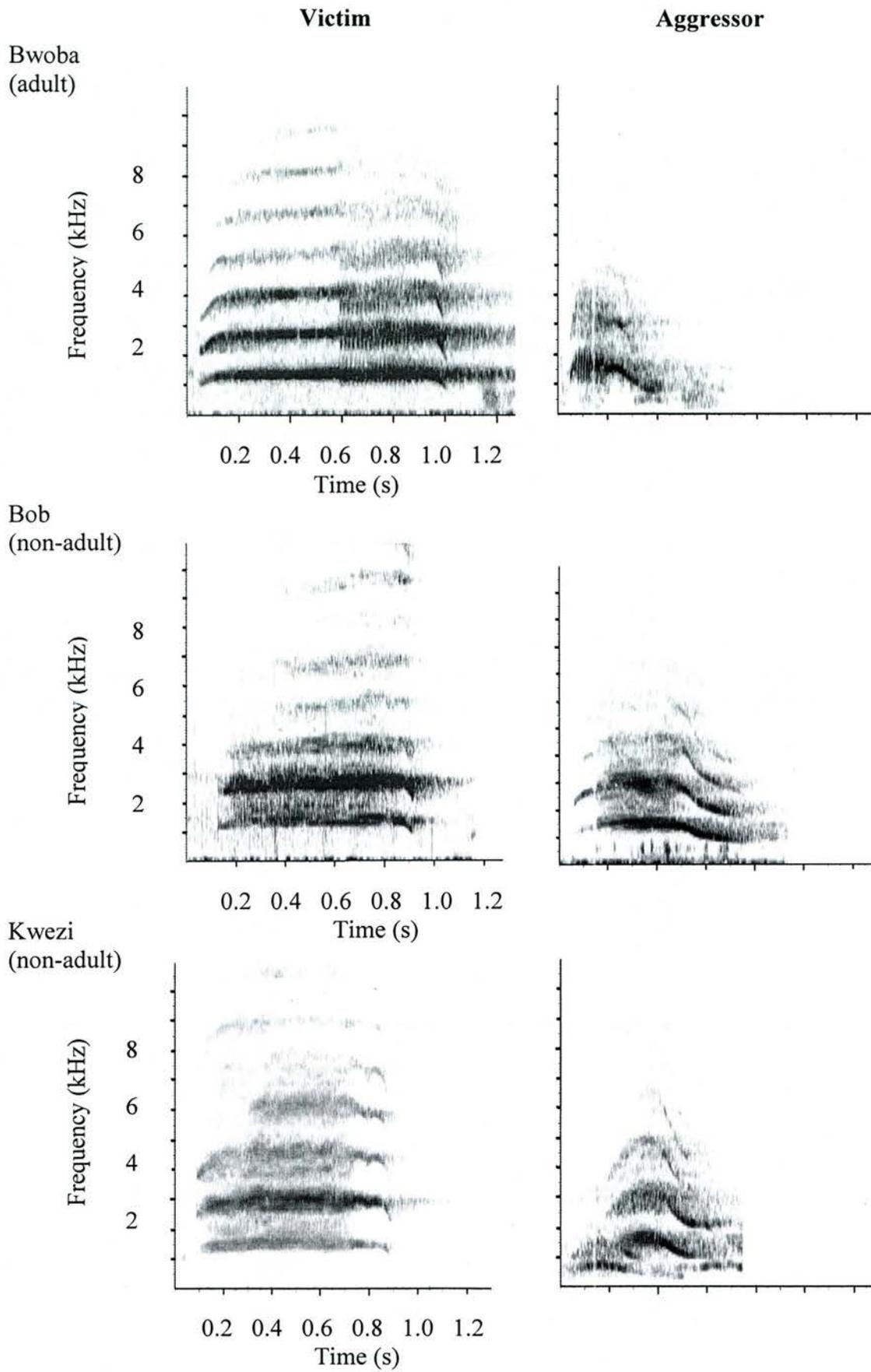
#### (a) Main Analysis

Only 14 individuals gave one or more screaming bouts in both the roles of aggressor and victim. Calls from these individuals were taken for the main analysis. These 14 individuals gave 51 scream bouts in total (range 1 to 5 per individual in each social role). In order to prevent pseudoreplication, each individual contributed one

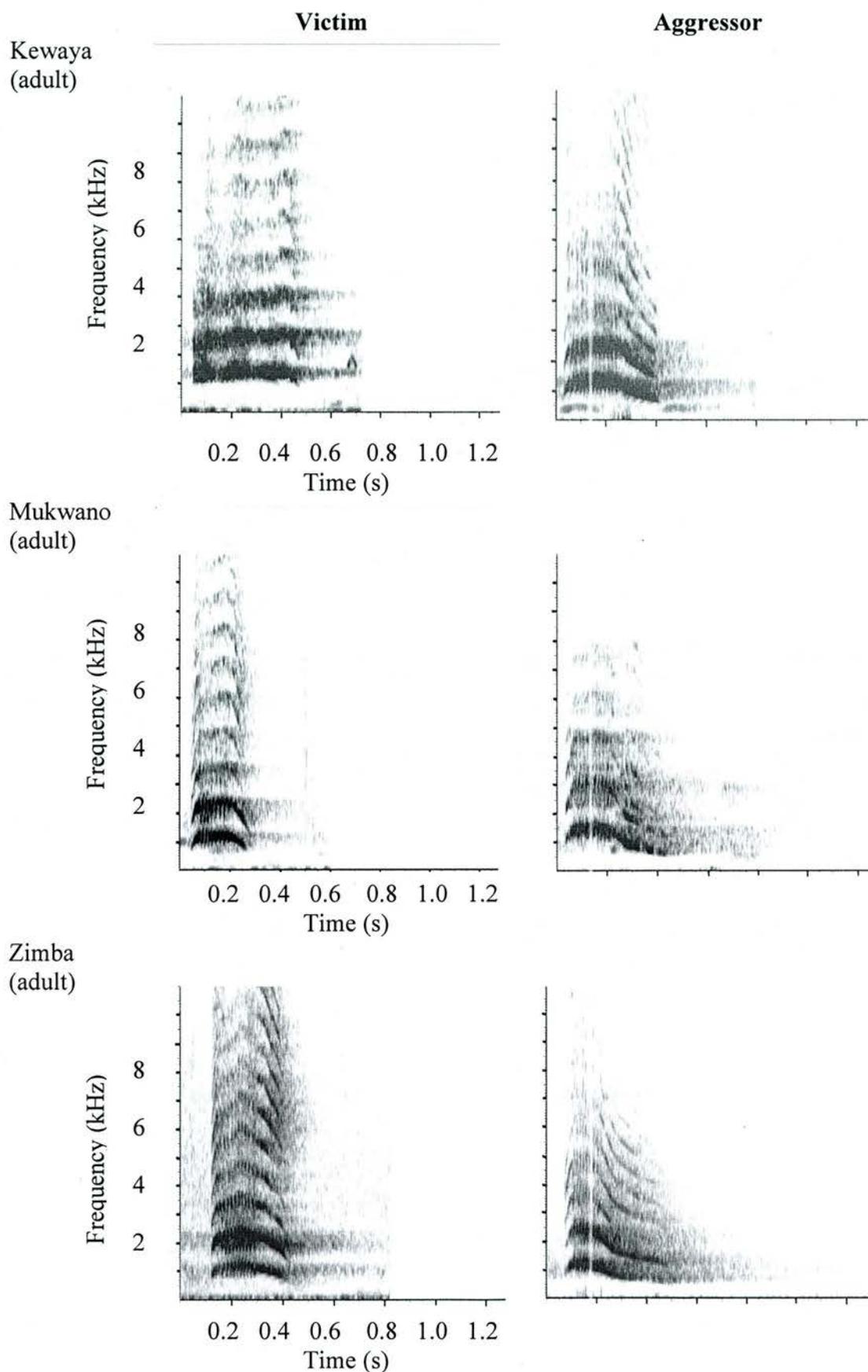
screaming bout to the sample of victim screams and one screaming bout to the sample of aggressor screams; thus, calls from 28 bouts in total were analysed in the main analysis. When more than one scream bout from an individual in a particular social role was recorded, the bout with the least overlap with other callers and minimum background noise was chosen. The 14 individuals consisted of eight adult females, one adult male and five non-adult males. Figures 4.5a and 4.5b illustrate examples of screams given by three randomly chosen males and three randomly chosen females, in both social roles.

(b) Secondary analysis

In addition to the 14 individuals who contributed screaming bouts to the main analysis, 19 further individuals gave screams only in the role of victim of directed aggression (three adult males, eight adult females, three non-adult males and five non-adult females). These 19 individuals gave a total of 38 screams (range 1 to 6 per individual). In order to prevent pseudoreplication each individual only contributed one screaming bout to this data set. For individuals with more than one screaming bout, the bout with the least overlap with other callers and minimum background noise was chosen. The calls from these 19 additional screaming bouts were then compared with the set of screams used in the main analysis.



**Figure 4.5a. Spectrograms of scream vocalizations given by three randomly chosen males.** Illustrated are screams given by these individuals during agonistic interactions where they acted as victims and aggressors.



**Figure 4.5b. Spectrograms of scream vocalizations given by three randomly chosen females.** Illustrated are screams given by these individuals during agonistic interactions where they acted as victims and aggressors.

*Main analysis: the effect of social role, sex and age-class on the acoustic structure of agonistic screams*

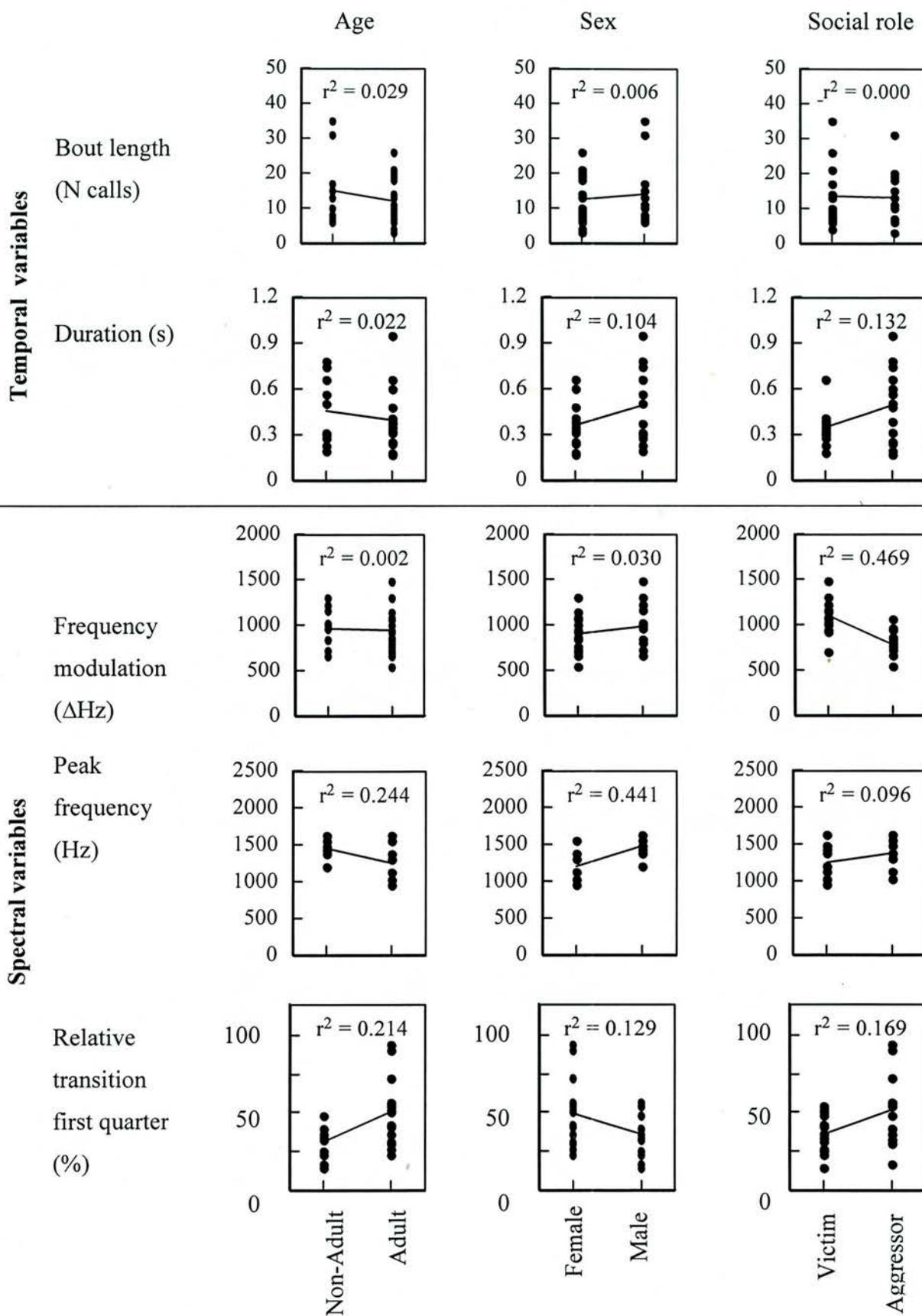
Comparing the spectrograms of screams given in both social roles (Figures 4.5a and b), similar acoustic structures became apparent, with all screams consisting of an arched tonal signal of varying duration with a variable number of harmonic overtones. Differences in the acoustic structure between the two contexts predominately arose from the calls' acoustic fine structure, particularly the shape of the calls' down-sweep. While victim screams displayed a relatively simple down-sweep, resembling the shape of the up-sweep, this was not the case for the aggressor screams. Here, calls ended with a more elaborate inverted S-shaped structure that was consistently present in all aggressor screams (Figure 4.5a and 4.5b). The acoustic analyses adequately captured these visually conspicuous differences. Victim and aggressor screams differed significantly in most spectral parameters, particularly those describing the shape of the second half of the call (Table 4.3; Figure 4.6). The independent variable 'social role' explained the largest amount of variation for most shape-related acoustic parameters.

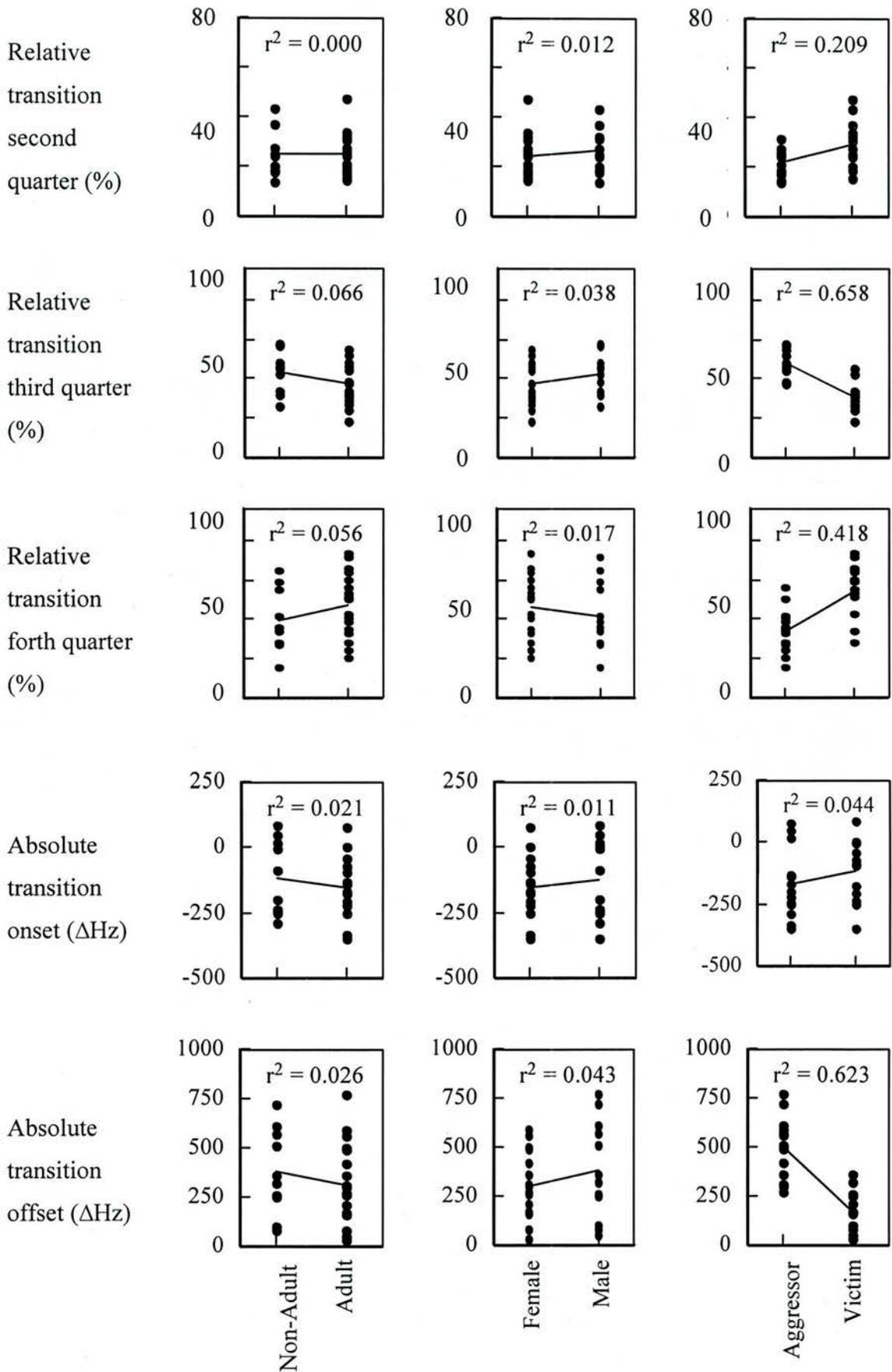
**Table 4.3. F-values from mixed design analyses of variance conducted on each of the ten acoustic parameters, as a function the callers' sex, age-class and social role during a conflict.** Social role was the within subject independent variable and sex and age were the between subject independent variables.

Acoustic parameters		Individual variables		
		Social role (Victim – aggressor)	Age class (Adult - non-adult)	Sex (Male – female)
Temporal parameters	Bout length	0.011	2.498	0.588
	Call duration	9.508*	1.368	3.557
Spectral parameters	Frequency modulation	28.069***	2.537	4.322
	Peak frequency	2.082	6.180*	30.202***
	Relative transition 1 <sup>st</sup> quarter	3.667	3.193	0.204
	Relative transition 2 <sup>nd</sup> quarter	5.816*	0.933	1.244
	Relative transition 3 <sup>rd</sup> quarter	52.511***	2.245	0.206
	Relative transition 4 <sup>th</sup> quarter	18.613***	2.375	0.815
	Absolute transition onset	3.046	0.321	0.050
Absolute transition offset	107.084***	0.072	1.104	

Degrees of freedom = (1, 11) \*p<0.05, \*\*p<0.01, \*\*\*p<0.005 (two-tailed)

**Figure 4.6**





**Figure 4.6. Scatterplots showing the values obtained for each of the ten acoustic parameters as a function of age class, sex and social role.**

Ten parameters measuring the temporal and spectral structure of the screams of 14 different chimpanzees given during agonistic interactions, plotted as a function of age class, sex and social role. Each data point represents the median value for three successive calls measured at

beginning of a scream bout, from a single individual ( $r^2$  refers to the relative amount of variance explained by the respective variable).

Mixed design analyses of variance were conducted with social role as the within subject independent variable and sex and age as the between subjects independent variables. These analyses revealed that six of the ten acoustic parameters showed significant differences as a function of the social role the caller played during the conflict (Table 4.3). Victims produced longer calls than aggressors ( $F_{(1,11)} = 9.508$ ,  $p < 0.05$ ). Victim and aggressor screams also differed significantly in the spectral structure: Aggressor screams had larger frequency modulation ( $F_{(1,11)} = 28.069$ ,  $p < 0.005$ ), greater absolute frequency transition offset ( $F_{(1,11)} = 107.084$ ,  $p < 0.005$ ) and more specifically a larger relative frequency transition in the third quarter of the call compared to victim screams ( $F_{(1,11)} = 52.511$ ,  $p < 0.005$ ). Victim screams, however, had greater relative frequency transitions in the second ( $F_{(1,11)} = 5.816$ ,  $p < 0.05$ ) and fourth ( $F_{(1,11)} = 18.613$ ,  $p < 0.005$ ) quarters of the call compared to aggressor screams. The peak frequency of screams was affected by both sex ( $F_{(1,11)} = 30.202$ ,  $p < 0.005$ ) and age ( $F_{(1,11)} = 6.180$ ,  $p < 0.05$ ), with non-adult and male callers tending to produce higher pitched screams than adult and female callers. The independent variables age-class and sex did not affect any other acoustic parameters (Table 4.3). There were no interactions between any of the three independent variables for any of the acoustic parameters. In addition, individuals did not differ in the number of calls they produced in a single bout as a function of social role, nor did individual calls differ in three of the spectral parameters as a function of social role; peak frequency, relative transition in the first quarter of the call, and the absolute transition onset (Table 4.3).

Discriminant function analysis was employed as a second method to investigate the quantitative acoustic differences between the screams produced by individuals in the two different social roles. All ten acoustic parameters were used to generate the discriminant function. This function was able to explain a significant amount of variation between calls given in victim and aggressor roles (Wilks' lambda = 0.104,  $F_{(10, 17)} = 14.71$ ,  $p < 0.001$ ). In the cross-validation discriminant analysis this function correctly classified 92.9% calls according to social role. In addition, this discriminant function was able to explain a significant amount of variation between calls given by males and females (Wilks' lambda = 0.344,  $F_{(10, 17)} = 3.247$ ,  $p < 0.05$ ). In the cross-

validation discriminant analysis this function correctly classified 78.6% calls according to the sex of the caller. Discriminant function analysis failed to find any significant effects for age class, with cross-validation discriminant analysis only correctly classifying 60.7% of cases.

*Secondary analysis: Comparison of additional victim screams with the main analysis data set.*

Screams from 19 different individuals in the role of victims were compared to the victim and aggressor screams from the 14 individuals used in the main analysis. As mentioned previously, each of the individuals involved contributed only one screaming bout to each analysis. The additional 19 victim screaming bouts were analysed in the same way as the bouts used in the main analysis.

One-way between subjects analyses of variance revealed no significant difference between the 19 'additional' victim scream bouts and the victim screams from the main analysis in any of the ten acoustic parameters (Table 4.4). In contrast, one-way between subject analyses of variance revealed that the 19 'additional' victim screams were significantly different from aggressor screams used in the main analysis in five of the ten acoustic parameters (Table 4.4).

**Table 4.4. F-values from one-way between subjects analyses of variance conducted on each of the ten acoustic parameters comparing ‘additional’ victim screams with victim screams from the main analysis and aggressor screams from the main analysis.**

Acoustic parameters		‘Additional’ victims compared to main analysis victims	‘Additional’ victims compared to main analysis aggressors
Temporal parameters	Bout length	0.878	1.839
	Call duration	1.013	0.420
Spectral parameters	Modulation frequency	0.007	33.051***
	Peak frequency	0.622	3.451
	Relative transition 1 <sup>st</sup> quarter	0.091	7.519**
	Relative transition 2 <sup>nd</sup> quarter	0.909	3.859
	Relative transition 3 <sup>rd</sup> quarter	4.125	118.388***
	Relative transition 4 <sup>th</sup> quarter	0.561	42.673***
	Absolute transition onset	0.597	0.269
Absolute transition offset	1.202	26.917***	

Degrees of freedom = (1, 31). \*p<0.05, \*\*p<0.01, \*\*\*p<0.005

## Discussion

The results of this study demonstrate that chimpanzees produce scream calls during agonistic interactions that have different acoustic structures according to the role the individual plays in the interaction. To my knowledge, this field study is the first to quantitatively distinguish an aggressor scream from a victim scream, with acoustic analysis confirming that six of the ten acoustic parameters differed significantly as a function of the social role. Subjectively, these calls are discernibly different to the human ear and this audible difference is apparent in acoustic structures of the screams (Figure 4.5). Aggressor screams were characterised by a distinctive down-sweep after mid call and a larger frequency range compared with the flatter and more symmetrically curved victim screams. Interestingly, bout length and peak fundamental frequency did not differ with social role, indicating that the overall shape of the call encoded the socially relevant information. The findings were further supported by the results of a discriminant function analysis which, after cross validation, correctly classified 92.9% of the calls into the two categories of social role: victim and aggressor. This high level of accuracy from only 10 measures of the call indicated that nearby individuals should be able to discriminate between the two screams and roles

they represented. Although individual variation is visually apparent in these calls (see Figure 4.5a and 4.5b), consistent structural differences, as a function of social role, were found throughout the sample, over a wide variety of ages and across sexes. The highly significant nature of the statistical tests performed on the acoustic analysis, despite a relatively small sample size, illustrates the differences between these two call variants: victim and aggressor screams.

The distinction between these call variants was further supported by the analysis of the ‘additional’ victim screams. These screams, taken from individuals of all four age-sex classes, were not different from the victim screams in the main analysis, indicating screams given in the role of victim of directed aggression are relatively homogenous. Furthermore, these additional victim screams varied from aggressor screams in the same way as the main analysis victim screams. Four of the six acoustic parameters that differed significantly between the main analysis victim and aggressor screams also differed significantly between the ‘additional’ victim screams and the aggressor screams (Table 4.2; Table 4.4). Although the main and secondary analyses produced different results on whether three acoustic parameters differed significantly between victims and aggressors, all ten acoustic parameters varied between victims and aggressors in the same direction in both analyses. The replication of the trends and differences in acoustic structure between victim and aggressor screams, with these additional victim screams from 19 different individuals, greatly increased the validity and strength of this finding.

The variables, of sex and age, had an effect on the peak frequency of the screams and this was probably a result of differences in body size. Previous studies had found a negative correlation between body size and frequency of vocalizations (Hauser, 1993) and a similar relationship was present in the current study: Non-adult chimpanzee screams had higher peak frequencies compared to adults’ screams. Counter-intuitively male screams also recorded a higher peak frequency than females’ screams. This contrasted with Mitani’s (1995) study, which found males produced lower frequency screams compared to females. However, Mitani (1995) also concluded this difference was likely to be a product of differences in body size and given five out of the six males in this study were non-adults, with a smaller body sizes than most females, a similar explanation is applicable to this result. The large difference between the peak

frequencies of the two sexes was sufficient for the discriminant function analysis to successfully discriminate between the calls of male and females.

From a production perspective, the chimpanzee agonistic scream system seems to be consistent with certain aspects of Morton's motivational-structural rules (Morton 1977). These rules suggest that across a large number of mammal and bird species, the motivational state of the animal has a consistent effect on the acoustic structure of vocalisations. These rules provide useful clues as to the possible evolutionary mechanisms underlying the diversification of these two scream types. In line with these rules the screams of aggressive individuals are shorter and contain larger elements of decreasing frequency patterns than the screams of attacked individuals. In addition, there is a trend for aggressive individuals to produce lower frequency screams than victims. Looking beyond the possible mechanism driving the production of these calls, this study has shown that signallers reliably produce acoustically distinct screams in specific contexts, meaning their screams are highly informative and have a relatively high degree of referential specificity.

Recipients could well use the acoustic differences in these scream variants as a basis for important behavioural decisions. It is likely that recipients not only draw inferences about the identity of the individuals involved in a conflict from their screams (Kojima, 2003), but our data also suggest that they could principally be able to infer the role each individual plays in the conflict. Although there is some controversy over the availability of identity cues in scream vocalisations (Gouzoules et al, 1984 vs. Rendall et al, 1998), I discuss previous studies and present new data that support the notion that individuals can determine individual identity from screams in the next chapter (pages 84-5, 94-5, 106-7). The vocal behaviour of signallers therefore means that information on both the role of the caller and their identity is available to listeners, permitting individuals out of sight to infer specific information about the nature of the fight from the screams. Goodall (1968) observed screams being used to recruit help and I observed several approaches of out-of-sight third party individuals rushing to aid one of the screaming protagonists. In particular, females were observed to come to the aid of other females once they started retaliating against male aggression and producing aggressor screams (Newton-Fisher, in press). These behavioural observations indicate that nearby individuals may be using acoustic

signals to make important decisions as to whether it is appropriate to intervene in a conflict. However, the hypothesis that recipients are taking advantage of the socially relevant acoustic information contained in the scream vocalizations needs to be tested with playback experiments. If recipients do use these acoustic signals to mediate their behavioural responses then chimpanzee victim and aggressor screams could qualify as functionally referential signals.

## **Chapter 5: Chimpanzee victim screams vary with the severity of aggression: potential for functional reference and audience effects.**

### **Summary**

The results of study one indicate that listening chimpanzees have the potential to infer the role of a screaming individual in an agonistic interaction from just hearing their screams. Further variables, in addition to the role of the individual in the fight, may also serve as useful sources of information for out-of-sight individuals. For example, research with rhesus monkeys has indicated that screams may provide rather complex information about an ongoing fight, including the severity of the attack and the relative rank of the opponent. In this chapter, I examine whether similar social information is conveyed in chimpanzee victim screams and whether callers are sensitive to the nature of the audience present while producing these calls.

A total of twelve chimpanzees from the Sonso community of the Budongo Forest contributed screams to the data set analysed. Chimpanzees produced victim screams, which varied acoustically according to the severity of the aggression the victim was experiencing. There was no evidence that screams varied according to the relative size of the rank difference between the victim and aggressor. Victim screams showed some evidence of being individually distinctive and reliable indicators of body size. I concluded that victim screams had the potential to function referentially in a useful manner as they encoded information about the social context and the identity of the caller. Chimpanzees gave screams that were acoustically consistent with high-risk aggression more often when a high-ranking bystander was present in the party. This indicated that vocal production was modified according to the composition of the audience and suggested that chimpanzees might be exaggerating the severity of the attack in order to increase the chances of evoking positive responses from third parties.

## Introduction

Primate signals that operate in a social context, such as agonistic screams, have been proposed to be largely under the influence of the motivational processes of the caller (Rowell and Hinde, 1962). It has also been suggested that from the caller's perspective victim screams primarily function as aversive stimuli to repel an aggressor's approach (Owren and Rendall, 1997). Nevertheless, these two hypotheses do not preclude screams from providing listeners with important information about the nature of an ongoing event and thus functioning as referential signals.

### *Agonistic screams in rhesus monkeys: referential signals?*

The question of whether screams can serve as referential signals has been addressed in free-ranging rhesus monkeys. Agonistic screams have been extensively studied in this species, but the results have been the subject of significant debate in recent years. Gouzoules and colleagues (1984) reported that victims in aggressive interactions gave five acoustically distinct screams. They hypothesized that each type of call related to the nature of the aggression experienced by the caller, as well as the dominance rank and matrilineal relatedness of the opponent. It was proposed that it was crucial to convey such social information to third parties because the recruitment of help from allies was critical to the maintenance of relative social rank in this species, which has strong matriarchal dominance hierarchies (reviewed in Walters and Seyfarth, 1987). In order for the screams to fulfil a facilitatory function in ally recruitment the screams must give the listener information about both the caller's identity and the ongoing interaction. Gouzoules and colleagues (1984) conducted experimental playback studies to test whether the calls alone contained sufficient information about the interaction to affect recruitment of help. Playbacks of single immature monkeys' screams to their mothers elicited differential responses from the mothers in terms of likelihood of responding, duration of response and latency to respond. These factors varied consistently with the type of scream played back. Mothers reacted most to noisy screams of infants receiving contact aggression from a high-ranking individual. Arched screams from infants receiving non-contact aggression from a lower ranking opponent evoked the second largest response from mothers, with the least response to pulsed screams evoked by interactions with matrilineally related opponents. Mothers' reactions therefore seemed to be motivated not only by an interest in the prevention of

harm to their offspring, but also by the need to defend their matrilineal dominance rank. The authors concluded that these screams are functioning as referential signals, encoding information about external events, and forming a vital part of aid recruitment during agonistic social interactions. Further research also revealed that scream production could also be influenced by the size of the rank difference between the aggressor and victim, not just the direction of the difference (Gouzoules et al., 1998). Although it was not known whether recipients are sensitive to these differences, the signallers seemed to distinguish between different levels of higher-ranking individuals and this was reflected in their scream bouts.

Recently, many criticisms of the study by Gouzoules and colleagues (1984) have been proposed, which call the conclusions from this research into question. There is therefore considerable controversy over whether rhesus monkey screams function as referential signals. With the advent of more sophisticated sound analysis techniques it has been suggested that the acoustic analysis of the five types of screams was oversimplistic and modern techniques indicate these categories are graded rather than discrete (Owren, personal communication). This does not necessarily create a problem, because primates are known to perceive continuous stimuli in a categorical fashion (e.g. Fischer, 1998). However, evidence from a laboratory discrimination task indicates that tonal and arched screams could not be successfully discriminated by monkeys (Le Prell et al., 2002). This result directly contrasts with the Gouzoules et al. (1984) study, which reports differential responses from recipients of these two scream variants. It should be noted, however, that the study by Le Prell and colleagues relied on data from only two monkeys kept in relatively asocial conditions.

The context specificity of the scream calls, a prerequisite for them functioning in a referential manner, has also been questioned (Owren et al., 2003). Gouzoules et al (1984) found that each of the five different types of screams was most commonly given in one of five different agonistic contexts, indicating the types of screams labelled different social events. However, if one examines the most common type of scream to occur in each of the five contexts, a different pattern emerges. Noisy screams are the most common scream produced in four of the five contexts. This indicates these screams may not have sufficient context specificity to provide listeners with reliable information.

### *Identity cues in rhesus monkey screams*

The other main area of contention is whether these screams contain sufficient acoustic cues to caller identity to play a role in recruitment of allies. Gouzoules et al (1986) played single noisy screams of immature monkeys to adult females and found that adults responded differentially to the screams as a function of the level of relatedness between themselves and the immature individual. They responded most to their own offspring, then to closely related kin and least to distantly related kin. This mirrors the naturally occurring pattern of female aid to juveniles (Kaplan, 1978). This indicated that rhesus monkeys could discriminate between different levels of kin relatedness on the basis of acoustic cues alone. Although these results supported the finding that vervet monkeys could identify individual immature monkeys from their screams (Cheney and Seyfarth, 1980), they were not replicated by Rendall and colleagues (1998). These researchers found that adult females did not show differential responses to playbacks of single noisy screams from adult female kin and non-kin. In contrast, Rendall et al. (1996) found that females responding to presentations of single coo calls showed excellent discrimination not only between kin and non-kin but also between individuals. This led the authors to argue that screams were relatively poor vehicles for information about identity in comparison to coos. This view is corroborated by Owren and Rendall (2003) who asked human participants to judge whether two successive calls came from the same or different monkeys. Human discrimination was excellent for coo calls, but relatively weak for screams. There is, however, a substantial problem with these direct comparisons of single coo and scream calls; coos occur naturally as single calls, whereas single scream calls are unnatural, as screams almost always occur in bouts. In addition to this difficulty with the previous studies, there is still strong evidence that screams do contain some cues to individual identity. Humans were able to categorise screams as coming from the same or different monkeys at a level significantly above chance (Owren and Rendall, 2003). Detailed acoustic analysis of noisy screams also indicated that a discriminant function analysis could successfully categorise screams according to individual at a rate significantly above chance (Rendall et al. 1998). As mentioned previously, one weakness of all the studies is that they examine only responses to single scream calls; a very rare natural occurrence. Gouzoules et al. (1984) report that in pilot studies playing whole sequences of screams elicited approach and attack of the speaker by adult females, thus single calls were subsequently used. This suggests that more cues

to individual identity may be available in bouts rather than single scream calls (Rendall et al. 1998). In conclusion, rhesus monkey screams can convey information about individual identity and in naturally occurring bouts, rather than single calls, this is likely to be at a level sufficient for listeners to determine their relative relatedness to or the identity of the caller.

In sum, rhesus monkeys give graded screams, which vary according to the severity of the attack and the relative rank and relatedness of the opponent. These screams may not be as context specific as previously thought, but the evidence from playbacks still suggests that listeners can extract information about the ongoing interaction from the screams. There is conflicting evidence as to whether rhesus monkeys can extract sufficient cues to individual identity from screams, in order for screams to function as effective ally recruitment signals. However, there seems to be good observational evidence that there are acoustic cues to identity in scream calls, which in a naturally occurring bout, may be sufficient to inform the listener about the identity of the caller.

#### *Agonistic screams in sooty mangabeys*

In direct contrast to the rhesus monkeys, observational studies of sooty mangabey monkeys, *Cercocebus torquatus atys*, suggest that this species does not convey a high level of social information in their scream calls (Santee, 1992). 2438 scream calls given during agonistic bouts were acoustically analysed and 96% were equivalent to noisy screams given by rhesus monkeys. Only 4% showed greater acoustic complexity. This small number of calls demonstrated that sooty mangabeys were at least capable of producing a range of sounds similar to those made by rhesus monkeys. The comparatively small subset of scream types produced by sooty mangabeys and the frequency of their use is striking. Gouzoules et al. (1995) hypothesize that this variation in call complexity between species reflects the differences in the social behaviour of the two species. Sooty mangabeys have no strong matrilineal organization in their social groups and in contrast to most other old world monkeys, there is little evidence that kinship significantly influences grooming or affiliative social behaviour of this species (Ehardt, 1988). Contact aggression is rare, with any biting usually ritualised in form and aggression is nearly always received from higher ranking individuals (Gust and Gordon, 1993). Sooty mangabeys rarely intervene in agonistic bouts, with aid to the victim only occurring in 4% of

agonistic interactions, compared to 16% in rhesus monkeys (Gust and Gordon, 1993). When third parties do interfere in interactions, they are usually higher ranking than both of the protagonists and they tend to aid the higher ranking individual in the dyad (Range and Noë, 2005). This evidence indicates that this species inhabits a complex social world, but one that is less violent and less strictly kin bound compared to rhesus monkeys. One possibility is that this social environment is not as conducive to the development of functionally referential screaming compared with other species, such as the rhesus monkey.

#### *Agonistic screams in chimpanzees*

In possible contrast to sooty mangabeys, the social environment chimpanzees inhabit seems highly conducive the development of functionally referential screaming. Chimpanzee groups have a strong male dominance hierarchy and effective alliance systems can be employed to defend and promote dominance rank (De Waal, 1998). Intraparty aggression between chimpanzees is often severe and occasionally leads to fatalities (Fawcett and Muhumuza, 2000). From a signaller's point of view, it would be advantageous to be able to recruit allies who were unable to see the agonistic interaction, especially considering the low visibility terrestrial environment in which most chimpanzees live and their fission-fusion group structure. Goodall (1968) observes that this does occur, noting other individuals sometimes respond to victim scream calls by "hurrying towards the calling individual and threatening or charging the aggressor" (pp 310). From a recipient's perspective, it would be advantageous to be able to extract information about an unseen interaction. Firstly, this could serve to ensure that potentially costly intervention only occurred when it was necessary. Secondly, it would allow individuals to monitor unseen social interactions, to increase their social knowledge of the community; information they could use to their own advantage in future social interactions.

#### *Identity cues in chimpanzee calls*

The previous chapter demonstrated that chimpanzee screams could give reliable information to listeners about the role of the caller in an agonistic interaction; that is, whether the caller was a victim or an aggressor during a fight. In this chapter I want to explore the hypothesis that victim screams provide recipients with more detailed information about the ongoing fight, similar to that which has been suggested for

rhesus monkeys. Given the similarities between aspects of the social systems of chimpanzees and rhesus monkeys, I predicted that chimpanzee victim screams might provide information on the severity of the attack and the relative rank difference between the victim and aggressor. In order for this information to be useful for listeners, there must be sufficient cues to caller identity in the screams to allow listeners to work out who is calling. Given the controversy over the level of identity cues in the acoustic structure of rhesus monkey screams, it is necessary to address this issue for the chimpanzees.

Mitani and Gros Louis (1995) identify clear sex differences in the screams of chimpanzees, with males consistently producing lower frequency screams than females; a proposed effect of relative body size. Beyond this broad cue to the sex and size of the caller, the existence of non-linear acoustic phenomena in the screams of chimpanzees indicates more complex cues to identity may be present in these calls. Riede et al. (2004) reported the common occurrence of biphonation and subharmonics in the climax screams of pant hoot calls and it may be reasonable to assume that these nonlinear phenomena could also be found in screams not embedded in a pant hoot call. Fitch et al. (2002) suggested that non-linear vocal phenomena may function as an important vehicle for individual recognition. As outlined in chapter 3, page 47, this observational work is critically supported by two experimental studies which showed that chimpanzees can recognize individuals on the basis of their vocalizations. Bauer and Philips (1983) demonstrated that three immature chimpanzees could recognize individuals on the basis of their pant hoot calls. This finding was replicated and expanded by Kojima et al. (2003) who showed that a chimpanzee could identify individuals on the basis of pant hoots, pant grunts or screams. The discrimination levels for screams were comparable to the other two call types and were significantly above the level expected by chance. The authors conclude that this ability would allow chimpanzees to have profound understanding of social interactions they could not see. Chimpanzee screams do seem to encode cues to identity, but due to the importance of and controversy surrounding this issue, I will directly examine whether chimpanzee screams contain identity cues in this study. If screams contain identity cues and vary in a reliable way with elements of the ongoing interaction as predicted, they could function as referential signals that inform and recruit potential allies.

### *The problem of intentional signalling*

To date there is limited evidence that primates vocalize with the intent of communicating about ongoing events to other individuals. There is some evidence of sensitivity to the composition of the audience in vocal production of alarm calls in vervet monkeys (Cheney and Seyfarth, 1985), but it is generally assumed that most primates vocalize in directly response to events in the environment rather than with an intention to communicate to a third party. This is in sharp contrast to human language where communication is mostly intentional, hereby bearing the potential for deception. This chasm is an argument used by many against the use of a comparative approach to language evolution that focuses on the vocal behaviour of non-human primates (e.g. Tomasello et al., in press). It is of particular interest, therefore, to investigate whether our closest relatives, the chimpanzees, modify their communication as a function of the nature of their audience.

With this study I first investigated whether screams were individually distinctive and therefore had the potential to function as referential signals to recruit kin and allies. I also examined the effect sex and age had on the acoustic structure of the calls. The focus of this study was then whether victims provided listeners with reliable information about (i) the severity of the attack and (ii) the relative rank of the opponent. Next, I determined whether certain scream variants successfully elicited sympathetic third party responses. Finally, I explored the possibility that the chimpanzees were producing screams in a way that took the nature of their audience into account; a crucial prerequisite for intentional signalling.

## Methods

### *Study site*

Data were collected for 8 months between February 2003 and March 2004 on the Sonso study group of the Budongo Forest Reserve, Uganda. A description of the study site and study community is provided in Chapter 4, pages 55-60.

### *Acoustic analyses*

Vocalizations were recorded with a Sennheiser K6/ME67 directional microphone and a Sony TCD-D8 portable DAT recorder. Recordings of vocalizations were transferred digitally from the DAT recorder onto a PC (Toshiba, Celeron 1.8GHz). Calls were digitised at a sampling rate of 44.1 kHz, 16 bits accuracy, using Cool Edit Pro LE. Quantitative analysis of calls was carried out using PRAAT software version 4.3.17 ([www.praat.org](http://www.praat.org)). The following settings were used: Pitch settings: range 50-1000 Hz, optimised for voice analysis; Spectrogram settings: window length 0.05 sec, dynamic range 70dB; Formant settings: Max formant 5500 Hz, No formants = 5, window length 0.025sec, dynamic range 30dB.

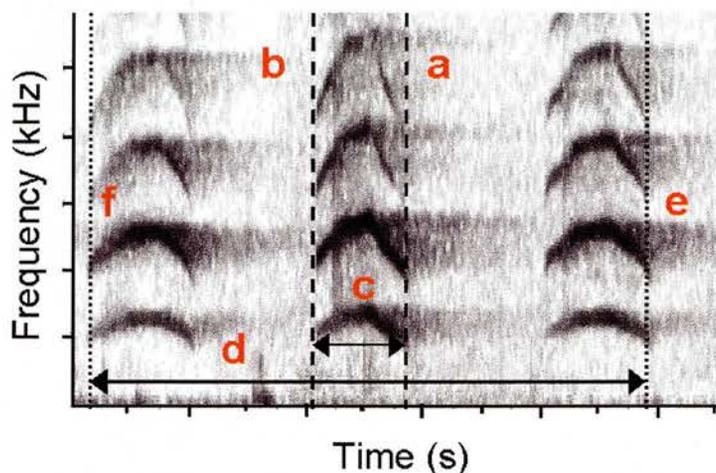
As outlined in the previous chapter, chimpanzee screams consisted of a fundamental frequency band ( $F_0$ ) and a series of harmonic overtones. Most measurements were taken from the  $F_0$ . To describe the overall acoustic structure I determined the following nine parameters, which were most suitable for describing the acoustic structure of the screams: three temporal parameters (Figure 5.1a) and five spectral parameters (Figure 5.1b):

#### Temporal Parameters

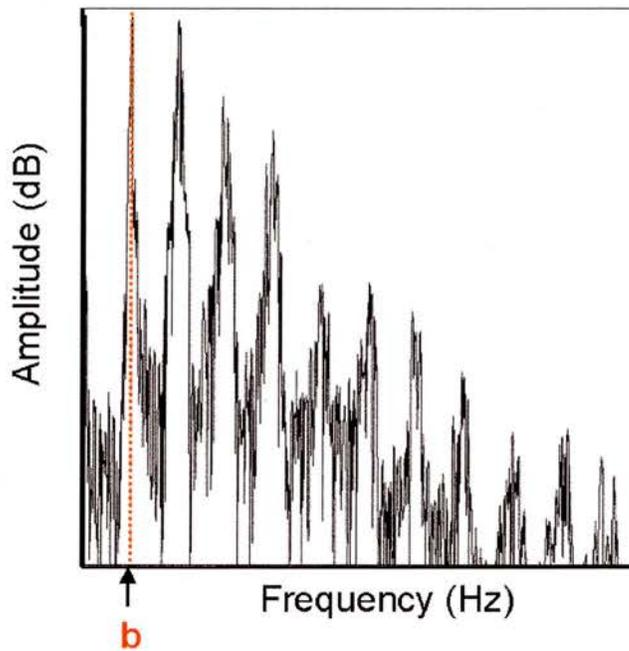
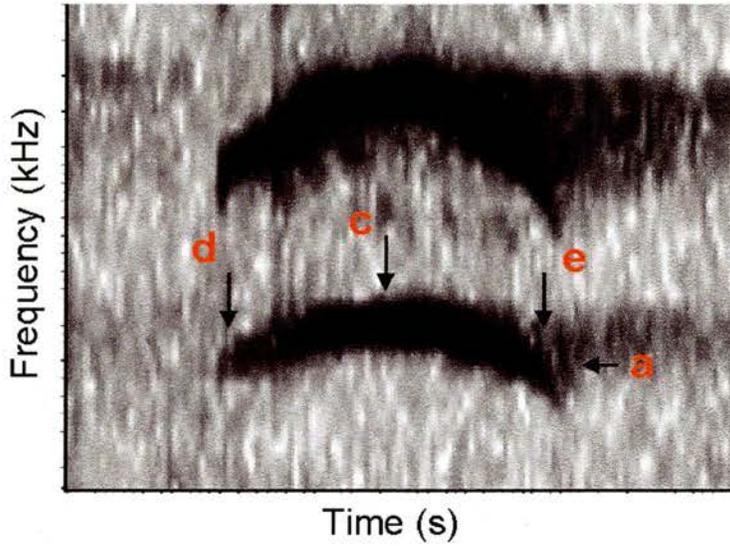
1. Bout length: Number of calls given successively and separated from other bouts by at least 30s of silence.
2. Duration of the call (s).
3. Rate: The number of calls given in the first 4 seconds of the bout divided by the time period from the start of the first call to the end of the last call. (calls/second)

## Spectral Parameters

4. Mean fundamental frequency. The mean frequency of the  $F_0$  across the call (Hz).
5. Peak frequency: frequency where maximum acoustic energy occurs in the  $F_0$  at the middle of the call (Hz).
6. Peak time: the time at which maximum acoustic energy occurs in the call: expressed as a proportion of the call duration (peak time minus start time divided by call duration).
7. First formant frequency: the mean frequency of the first formant across the call (Hz).
8. Transition onset: Frequency of maximum energy at call onset minus frequency of maximum energy at call middle (Hz).
9. Transition offset: Frequency of maximum energy at call middle minus frequency of maximum energy at call offset (Hz).



**Figure 5.1a. Illustrations of how temporal variables were measured.** Call duration = a-b. Bout length is the number of calls, where one call = c. Rate = number of calls in the first 4 seconds of the bout / duration (d) where duration is time of the end of last call (e)- time of the beginning of first call (f).



**Figure 5.1b. Spectrogram and spectral slice illustrating how spectral variables were measured.** Fundamental frequency on which most measures were taken = a. Peak frequency = frequency of max acoustic energy (b) at call middle (c). Transition onset = Frequency of max energy at call onset (d) - frequency of max energy at call middle (c). Transition offset = Frequency of max energy at call middle (c) - frequency at of max energy call offset (e). First formant frequency and Peak time are not illustrated here.

Measurements of the frequencies at which maximum acoustic energy was present were obtained from creating spectral slices (Amplitude plotted against frequency; Figure 5.1b) at the relevant points indicated in Figure 5.1b. All measurements of formant frequency reported in this thesis were derived from a script written by Owren

(1995). Formant frequencies are produced by filtering of the sound through the vocal tract (Fitch and Hauser, in press). The movement of lips and tongue alters the vocal tract through which the sound passes and the shape of the vocal tract causes some harmonics of the fundamental frequency to be enhanced, and others attenuated. These enhanced harmonics are termed 'formants'.

I performed checks for co-linearity amongst the nine parameters and found that all had acceptable variance inflation factors (VIF <8.0). In order to get a good estimate of the typical acoustic structure of an individual's screams I measured the first three recorded calls per bout sequence.

### *Context variables*

#### **Severity of aggression**

Recording started whenever two individuals engaged in an aggressive interaction or screaming began. The identity of the individuals involved and their respective roles during the conflict were determined. The type of aggression received by the victim was labelled according to the following five categories, which were based on the presence or absence of key behaviours (Table 5.1). Individuals were classified as victims of 'contact aggression' if the aggressor made aggressive physical contact with them, displaying behaviours such as beating, stamping, thumping, slapping and kicking. Victims were classified as experiencing 'directed aggression' if they were running or climbing away from an approaching aggressive chimpanzee, who was pursuing them individually along the ground or through the trees. Chimpanzees who took evasive action to avoid a male charging display were classified as victims of 'non-directed aggression' as long as the displaying male continued on his trajectory past the individual without engaging in chasing of the individual. Individuals were classified as victims of 'threat aggression' if an aggressive chimpanzee directed a low intensity threat gesture to them, such as shaking branches, arm raising and lunging without approach of more than 1m towards the victim. Finally individuals who responded to male pilo-erection, hunch walking or hunch sitting and non-directed approach were classified as victims of 'posture threats'.

All variables were entered into a check sheet (see Appendix 1); in some cases spoken commentary was given and later transcribed. As the type of aggression experienced by an individual in a single encounter could change rapidly, spoken commentary was used to mark changes in the type of aggression as it occurred.

**Table 5.1. Summary of the key behaviours which were used to classify the type of aggression received by a victim.**

TYPE OF AGGRESSION	KEY BEHAVIOURS	
	Aggressor	Victim
<b>Contact aggression</b>	Beating, stamping, thumping, slapping or kicking victim	
<b>Directed aggression</b>	Individual pursuit of victim	Rapid running or climbing away from aggressor
<b>Non directed aggression</b>	Display charge with no deviation from trajectory to pursue individuals	Run or climb out of the path of the aggressor
<b>Threat aggression</b>	Shake branches, arm raise gesture, lunge	
<b>Posture threat aggression</b>	Pilo-erection, hunch walk, hunch sit	

These five categories represented a relative scale of the risk of serious harm being suffered by the victim, with contact aggression presenting the highest risk of physical damage and posture threat aggression presenting the lowest risk of physical harm. Contact and directed aggression were classified as ‘high-risk’ and non-directed, threat and posture threat aggression were categorised as ‘low-risk’. Chimpanzees faced with low-risk aggression had a very good chance of averting the escalation of aggression to the high-risk category by responding in an appropriate manner (moving out of the way, pant-grunting, screaming, allowing themselves to be displaced).

Agreement between myself and experienced field assistant, Raimond Ogen, that one of these specific behaviours listed above had occurred was required in order to classify the caller as a victim of a certain type of aggression. If we could not both confirm the caller or the aggressor had performed one of the key behaviours, the calls remained unclassified and were not used for analysis.

### **Relative rank of chimpanzees in the Sonso community**

I did not collect systematic data on the relative rank of the each chimpanzee in the Sonso community over the course of my study. However, based on my own observations and those of four experienced field assistants I was able to assign each chimpanzee a broad rank category. I asked four field assistants, independently, to rank the chimpanzees. We then discussed these lists together and agreed on four broad groups. The highest rank group contained the most dominant males, Duane, Maani, Black, Jambo, Zefa; the second group contained the less dominant adult males, Nick, Nkojo, Bwoba, Tinka; the third group contained all the adult females and the sub-adult males; the lowest rank group contained the sub-adult females and the juvenile males. Although there were a range of dominance standings within in each of these broad groups, the four FA and I agreed that these categories reflected both the likely winners of agonistic interactions (chimpanzees in the lower rank category of the pair would lose) and the likelihood of one chimpanzee pant-grunting to another individual (pant grunts would only be given to chimpanzees in the same or higher rank groups as the caller).

Two of the high-ranking adult males Nkojo and Jambo died in the course of the study, however, these broad groupings remained stable until the end of my study period.

### Responses of third party chimpanzees to agonistic interactions

Third party interventions in agonistic encounters were rare during my study period. I recorded the following different types of responses from third party individuals: (1) approaching the victim in an affiliative manner during or immediately after the encounter (2) Displaying aggression towards the aggressor in the 10 minutes after the encounter (3) Permitting approach by the victim and subsequent grooming. These actions were all considered to be both positive and supportive of the victim. In the absence of these actions 'no response' was recorded. Third party individuals sometimes produced barks during or after the interaction. I did not include this behaviour in my analyses because the function of these calls is still unknown. In particular, although Goodall (1986) suggested that barks are given in support of the victim there is no systematic evidence for this. Hence, it is possible that barks are given in support of the aggressor or as a direct response to the aggressor, for example,

to prevent an attack on themselves. This explanation seems plausible as individuals in direct view of the fight often give barks.

### *Selection of calls*

Due to the rare nature of agonistic encounters within this community of chimpanzees, all occurrence sampling (Altmann, 1974) was employed. A total of 21 different individuals gave victim screams in response to two or more types of aggression: 203 screams in total. Nine of these individuals were not entered into any of the analyses because I did not have enough recordings of sufficiently high quality for each of the necessary categories of aggression. Only 6 individuals gave one or more scream bouts in response to all five categories of aggression. Screams from these individuals were analysed first. These individuals gave a total of 116 victim scream bouts (range 1 to 9 per individual per aggression category) but in order to prevent pseudoreplication each individual contributed only one screaming bout in response to each of the five categories of aggression. The only exception to this was the juvenile male, Kwezi, who was not recorded screaming in response to threat aggression and therefore only contributed four bouts. When more than one scream bout was recorded from an individual in response to a certain type of aggression, the first bout in the database with three calls of sufficiently high quality (minimal overlap with other callers and background noise) was chosen. This ensured unbiased selection of calls for analysis. I extracted the first three calls from each bout for analysis. A sample of 29 bouts (6 individuals x 5 bouts, with the exception of Kwezi), containing 86 calls (3 calls/bout), was used for the first analysis. The 6 individuals consisted of one adult female, three sub-adult males and two juvenile males.

Further analyses were conducted with a second larger selection of victim screams, recorded from a total of 12 individuals: 4 adult females, one sub-adult female, one adult male, 3 sub-adult males and 3 juvenile males. This larger data set was necessary to examine factors such as the responses of third parties and it also provided a higher degree of ecological validity than the smaller data set alone. Each of the 12 individuals contributed a total of four screaming bouts: two bouts in response to high-risk aggression (contact or directed aggression) and two bouts in response to low-risk aggression (non-directed aggression or posture threat). Due to the rare occurrence of

threat aggression this category of aggression was excluded from this data set and from further analysis. 180 screaming bouts were available for this analysis (range 2 to 19 per individual per high or low aggression) and as above, when a bout had to be selected, the first bout in the database with 3 measurable calls was chosen. A sample of 48 bouts containing 142 calls (12 individuals x 4 bouts x 3 calls) was used in this analysis.

## Results

### *Do chimpanzees produce individually distinctive screams?*

In order to determine if the screams of six different individuals had distinct acoustic structures that may enable listening chimpanzees to identify individuals on the basis of their screams I analysed the 29 scream bouts produced by these individuals to aggression of five different types. Firstly, a between subjects Analysis of Variance (ANOVA) revealed that six of the nine acoustic variables varied significantly between individuals. The acoustic parameters which accounted for most of the variance were measures of frequency: mean  $F_0$  ( $F_{(5,80)} = 7.178$ ,  $p < 0.001$ ,  $r^2$  adjusted = 0.267), peak frequency ( $F_{(5,80)} = 8.052$ ,  $p < 0.001$ ,  $r^2$  adjusted = 0.293) and first formant ( $F_{(5,80)} = 6.980$ ,  $p < 0.001$ ,  $r^2$  adjusted = 0.260). Other measures, including bout length ( $F_{(5,80)} = 4.773$ ,  $p = 0.001$ ,  $r^2$  adjusted = 0.182), peak time ( $F_{(5,80)} = 3.444$ ,  $p = 0.007$ ,  $r^2$  adjusted = 0.127) and duration ( $F_{(5,80)} = 2.877$ ,  $p = 0.019$ ,  $r^2$  adjusted = 0.099), also varied significantly between individuals across contexts. Post hoc tests were run with sidak corrections to control for familywise error created by running multiple comparisons. These tests revealed that there were significant differences in at least one acoustic measure between 8 of the possible 15 pairwise comparisons of individuals. I conducted a Discriminant Function Analysis (DFA) to assess if this variation in the acoustic structure of individuals' screams was sufficient to allow the screams to be classified according to the identity of the caller. The function derived from the nine acoustic parameters explained a significant amount of the variation between individuals (Wilks' lambda = 0.139,  $\chi^2_{(45)} = 152.73$ ,  $p < 0.001$ ). Screams were classified according to the individual who produced them with 43% accuracy (cross-validated), a rate significantly above that expected by chance (Binomial (0.167) = 0.001, 2-tailed).

The individual discrimination described above may have been driven by the differences in calls produced by animals of different sizes. In the sample of six there were two male juveniles, three sub-adult males and one adult female, giving a range of body sizes. Unfortunately the unbalanced nature of this data set in terms of age-sex class meant that the acoustics of the calls could not be meaningfully tested for effects of age and sex. Instead I tested the effects of age and sex on the acoustic structure of the 142 screams given by 12 individuals who offered a more balanced age-sex class distribution. These individuals comprised of 4 adult females, one sub-adult female, one adult male, 3 sub-adult males and 3 juvenile males. Firstly a between subjects ANOVA revealed that age class effected the peak frequency ( $F_{(2,139)} = 10.95$ ,  $p < 0.001$ ) and first formant frequency ( $F_{(2,139)} = 9.729$ ,  $p < 0.001$ ) of the victim screams. Post hoc tests with Sidak correction revealed that screams from juveniles ( $N = 35$ , mean = 1443Hz) and sub-adults ( $N = 47$ , mean = 1406Hz) had higher peak frequencies than adults ( $N = 60$ , mean = 1283Hz). In addition screams from juveniles (mean = 1364Hz) and sub-adults (mean = 1325) had higher first formant frequencies than adults (mean = 1243). Secondly, a between subjects ANOVA demonstrated that sex also effects the mean fundamental frequency ( $F_{(1,140)} = 21.88$ ,  $p < 0.001$ ), peak frequency ( $F_{(1,140)} = 50.16$ ,  $p < 0.001$ ), first formant frequency ( $F_{(1,140)} = 39.78$ ,  $p < 0.001$ ), transition onset ( $F_{(1,140)} = 6.08$ ,  $p = 0.015$ ) and transition offset ( $F_{(1,140)} = 4.06$ ,  $p = 0.046$ ). Males produced screams ( $N = 82$ ) with higher mean fundamental, peak and first formant frequencies as well as screams with more frequency modulation across the call than the females ( $N = 60$ ). The large proportion of non-adult males that contributed to this dataset may account for this counter-intuitive result. When taken together, the results from the age and sex analyses indicate that smaller bodied animals produce higher pitched screams possibly with more frequency modulation than larger bodied chimpanzees.

#### *Do screams vary with the severity of aggression experienced?*

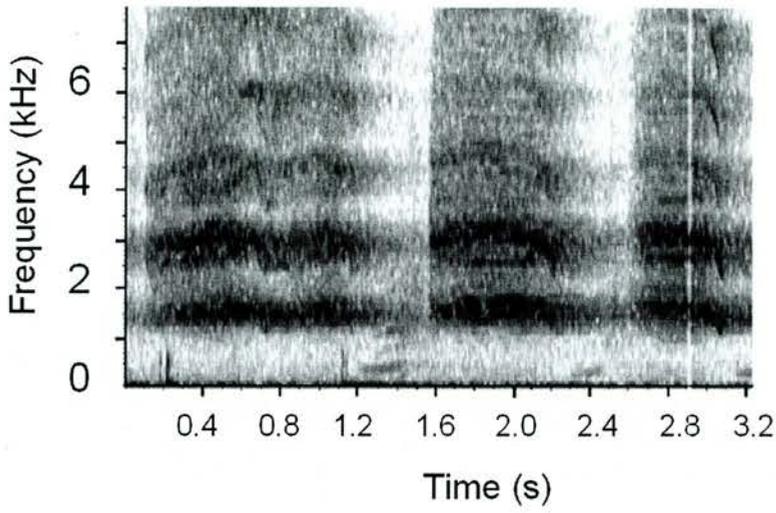
I conducted acoustic and statistical analyses on victim screams given by 6 different individuals in response to five types of aggression. Comparing the example spectrograms of victim screams given in response to the difference categories of

aggression (Figure 5.2), similar acoustic structures can be seen throughout, with all screams consisting of a tonal signal with a variable number of harmonic overtones.

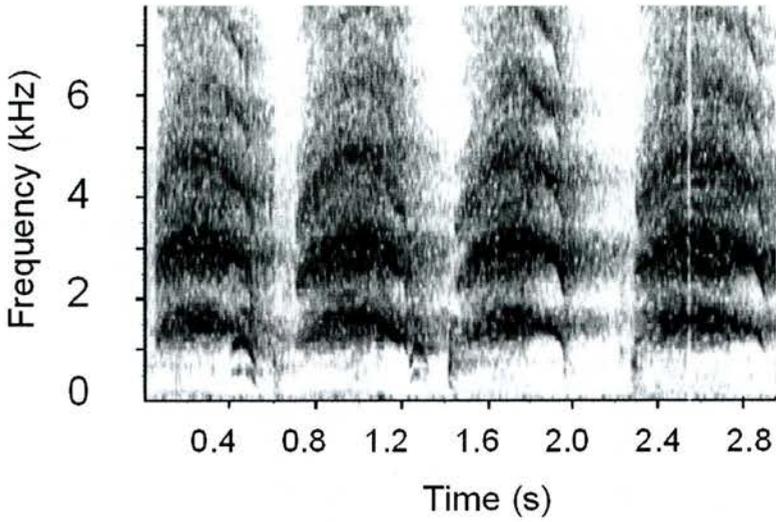
Subtle differences in the acoustic structure of these screams arose predominantly from variation in the bout length, call duration, rate, fundamental frequency, peak frequency and frequency of the first formant. In contrast to the previous analysis examining victim and aggressor screams, the shape of the call varied relatively little between these victim scream variants. Victim screams given to high-risk levels of aggression appeared to be flatter, with less frequency modulation in the second half of the call compared to screams given to low-risk aggression. No effect for onset transition was found, and most screams conformed to the flat or slightly symmetrically arched shape expected by the previous chapter's analysis. Screams given to the high severity types of aggression, such as contact or directed aggression, were long calls produced slowly within a long bout, that had high fundamental and peak frequencies and high first formant frequencies. As the level of aggression decreased the calls tended to become shorter with lower frequency measures and were produced in smaller, faster bouts.

Figure 5.2

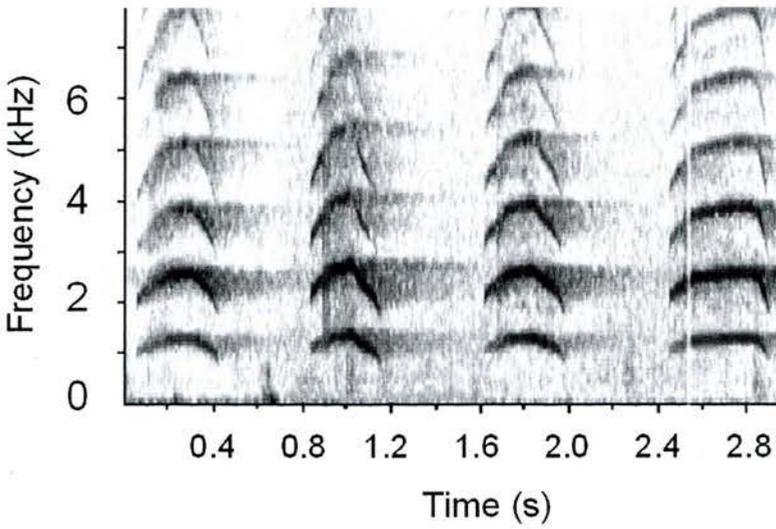
A.



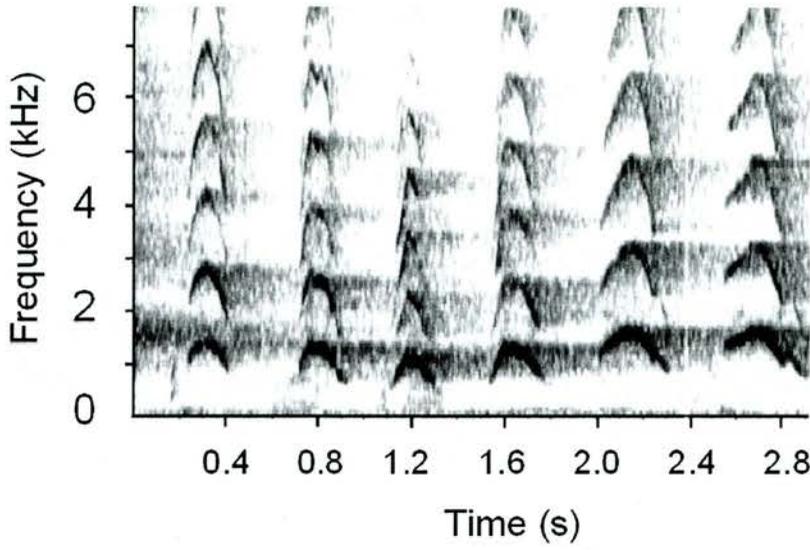
B.



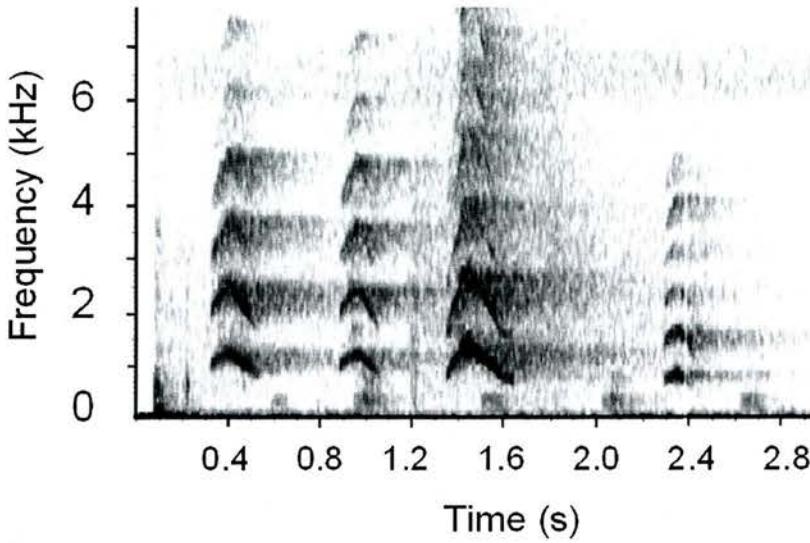
C.



D.

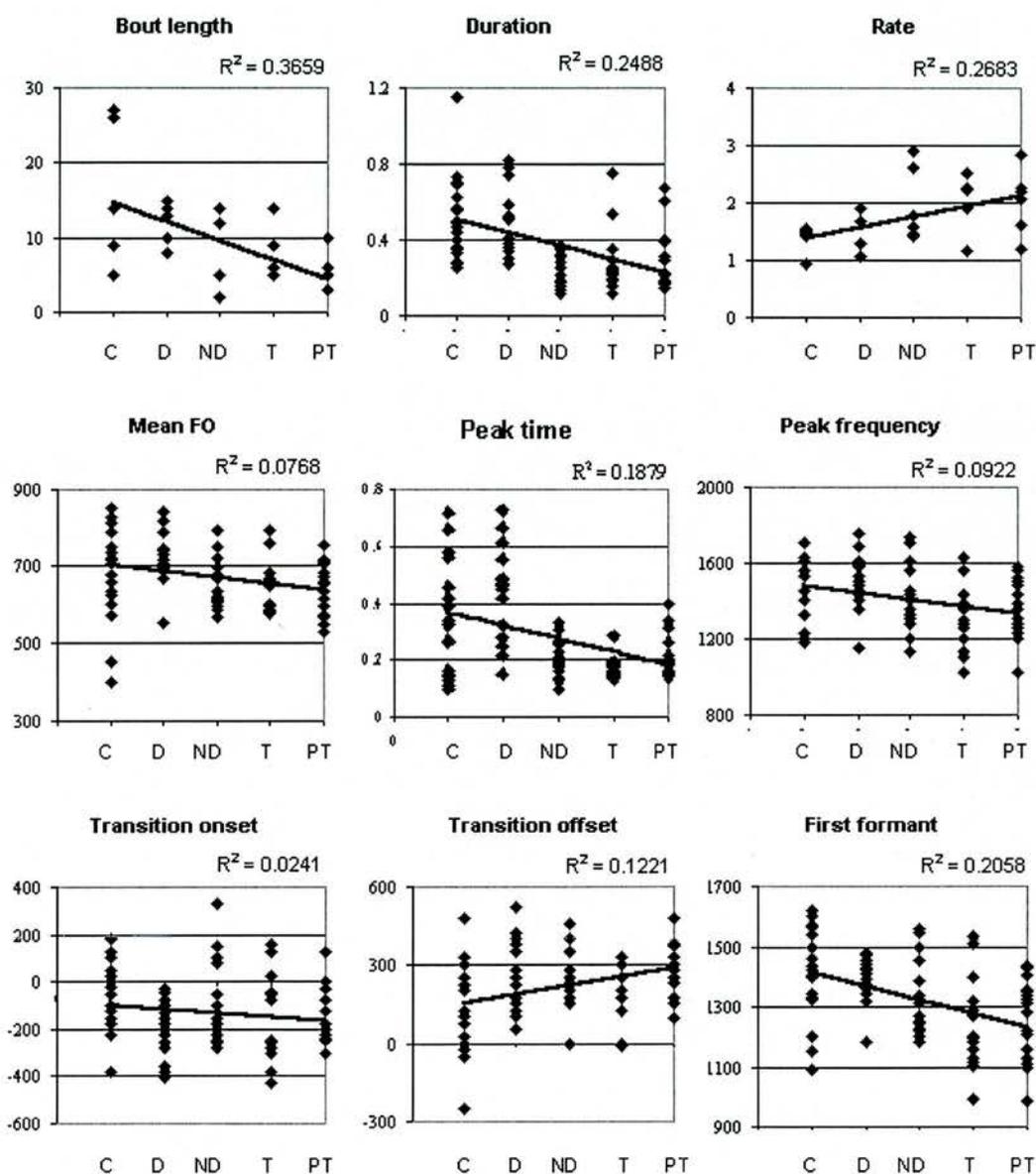


E.



**Figure 5.2. Example spectrograms of victim screams given by sub-adult male, *Musa*, in response to five types of aggression.** The screams were given in response to (a) contact aggression, (b) directed aggression, (c) non-directed aggression, (d) threat aggression, (e) posture threat aggression.

As illustrated in Figure 5.3, these changes occur in a graded manner as the level of aggression increases. I conducted a repeated measures ANOVA to establish if there were reliable differences in the structures of victim screams given to these different types of aggression.



**Figure 5.3.** Scatterplots showing the acoustic structure of 86 calls from 6 individuals as a function of the type of aggression suffered by the caller. Each point represents a value from a single call. The types of aggression plotted are C= contact, D = directed, ND = Non-directed, T = threat and PT = posture threat.

Sphericity was not assumed as some of the covariances between scores at different levels of the within subjects variable were not homogenous. This could have lead to an inflated risk of type one errors, so I have reported values from the conservative Greenhouse-Geisser test, which deals with this problem by increasing the F-value required for significance. I found that duration ( $F_{(3,41)} = 10.72, p < 0.001$ ), call rate ( $F_{(3,35)} = 7.34, p = 0.001$ ), mean fundamental frequency ( $F_{(3,37)} = 3.08, p = 0.045$ ), peak frequency ( $F_{(3,42)} = 4.05, p = 0.013$ ), peak time ( $F_{(2,33)} = 10.37, p < 0.001$ ), transition offset ( $F_{(3,38)} = 3.05, p = 0.045$ ), first formant frequency ( $F_{(2,34)} = 5.61, p = 0.005$ ) and bout length ( $F_{(2,24)} = 11.51, p < 0.001$ ) differed significantly as a function of the severity of aggression experienced by the caller. I conducted pairwise comparisons to determine between which of the five levels of aggression these differences existed. In order to minimise the risk of family-wise error encountered by performing multiple comparisons the statistics reported were calculated with a Sidak correction. Table 5.2 shows that most differences were found between the screams produced to directed aggression and the three lowest levels of aggression, with some differences apparent between screams given to contact aggression and the three lowest levels. Neither contact and directed aggression nor non-directed, threat and posture threat aggression differed on any acoustic measurement. These results confirmed the patterns observed in Figure 5.2 and indicated that our grouping of contact and directed aggression as 'high' risk aggression and non-directed, threat and posture threat aggression as 'low' risk aggression were justified.

**Table 5.2. Results of the pairwise comparisons to determine between which of the five levels of aggression the screams varied significantly.** F-values from the repeated measures ANOVA and p-values from the pairwise comparisons are reported.

Acoustic variables	ANOVA	Pair wise comparisons (p-values)									
	F-value	C-D	C-ND	C-T	C-PT	D-ND	D-T	D-PT	ND-T	ND-PT	T-PT
Duration	10.72***	1.00	0.012*	0.034*	0.059	0.003*	0.012*	0.018*	0.972	0.986	1.00
Bout length	11.51***	0.612	0.009*	0.102	0.01*	0.001*	0.042*	0.001*	0.997	0.863	0.189
Rate	7.34**	1.00	0.057	0.003*	0.015*	0.10	0.012*	0.028*	1.00	1.00	1.00
Mean F <sub>0</sub>	3.08*	0.256	1.00	1.00	0.999	0.021*	0.043*	0.082	1.00	0.998	1.00
Peak time	10.37***	0.406	0.404	0.201	0.684	0.005*	0.001*	0.008*	0.739	1.00	0.483
Peak Frequency	4.05*	0.918	0.965	0.751	0.947	0.047*	0.019*	0.02*	0.978	1.00	0.998
Transition onset	1.65	-	-	-	-	-	-	-	-	-	-
Transition offset	3.05*	0.615	0.544	0.719	0.137	1.00	0.923	0.996	1.00	8.63	0.617
First formant frequency	5.61**	1.00	0.547	0.454	0.077	0.03*	0.011*	0.006*	0.982	0.209	1.00

F-values degrees of freedom (Greenhouse-geisser) = 3,41; 3,37; 2,33; 3,35; 3,42; 3,44; 3,38; 2,34; 2,24; \* = p<0.05, \*\* = p <0.01, \*\*\* = p<0.001

Pairwise comparisons \* = significantly different

The types of aggression compared are C= contact, D = directed, ND = Non-directed, T = threat and PT = posture threat.

I then conducted a direct DFA to determine if this systematic variation would allow screams to be classified according to the type of aggression that elicited them. All nine acoustic variables were used to generate the discriminant function. This function was able to explain a significant amount of variation between the acoustic structures of the calls given in response to the different types of aggression (Wilks' lambda = 0.243,  $\chi^2_{(36)} = 110.368$ , p<0.001). In the cross-validation discriminant analysis this function correctly classified 40% calls according to the type of aggression which elicited them. A binomial test (0.2) = 0.002 (2-tailed) revealed that this was at a level significantly above that expected by chance.

In order to verify that the patterns observed were representative I ran similar analyses with a larger data set containing screams from 12 individuals. Due to the rare nature of screams given to threat aggression I collapsed the aggression categories into high and low-risk aggression; a categorisation that the previous analysis confirmed was justified. A repeated measures ANOVA on 142 calls revealed that the acoustic

structure of the screams varied in the same manner as described in the previous analysis (Table 5.3). Screams given to high-risk aggression were longer, flatter, contained higher frequencies and were given in longer, slower bouts, compared to the screams given to low-risk aggression.

**Table 5.3. Mean, standard deviation and F-values from repeated measures ANOVA examining variation in the acoustic parameters describing the 142 screams given by victims of high-risk and low-risk aggression.**

	High-risk aggression		Low-risk aggression		F-value
	Mean	Standard deviation	Mean	Standard deviation	
Duration	0.51	0.17	0.34	0.17	32.97***
Bout length	12.55	6.76	5.42	2.94	83.99***
Rate	1.39	0.24	1.79	0.50	36.30***
Mean F <sub>0</sub>	686.57	90.46	631.84	69.29	21.04***
Peak time	0.39	0.19	0.26	0.15	20.94***
Peak Frequency	1410.14	193.83	1317.03	176.34	12.51**
Transition onset	-104.78	131.28	-125.09	149.94	0.78
Transition offset	138.56	181.87	224.03	129.44	11.05**
First formant frequency	1339.66	146.17	1261.52	134.59	17.03***

Degrees of freedom = 1,70

\* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$

A DFA was conducted and the function derived from all nine acoustic variables explained a significant amount of the variation in the acoustic structure of screams given to high and low risk aggression (Wilks' lambda = 0.530,  $\chi^2_{(9)} = 85.97$ ,  $P < 0.001$ ). In a cross-validated analysis the function correctly classified 81.1% of the screams according to the level of aggression which elicited the scream. A binomial test (0.5) = 0.001 (2-tailed), confirmed that this was at a level significantly above that expected by chance.

*Are screams affected by the relative rank of the opponent?*

In order to determine whether screams varied as a function of the relative rank difference between two agonistic chimpanzees I described the 48 agonistic interactions involving the 12 individuals, in terms of the relative rank difference

between victim and aggressor. All victims and opponents belonged to one of the four broad rank groups described in the methods section, page 92. All aggressors in this study were of an equal or higher rank group compared to the victim. The relative rank difference between the two opponents was categorised as small (aggressor same rank group as victim or one rank group above) or large (aggressor 2 or 3 rank groups above the opponent). High and low risk aggression were represented in these two groups in a balanced manner, at a level not significantly different from 50% each (Small rank difference: Binomial (0.5) = 0.538, 2-tailed, Large rank difference: Binomial (0.5) = 0.566, 2-tailed). This reduced the possibility of this potentially confounding factor influencing this analysis. A between subjects ANOVA revealed little variation in the acoustic structure of the screams as a function of the relative size of the rank difference between the victim and aggressor, with only peak time ( $F_{(1,140)} = 4.09$ ,  $p = 0.045$ ) and rate ( $F_{(1,140)} = 4.73$ ,  $p = 0.031$ ) differing significantly. Screams given during interactions with large rank differences ( $N = 76$ ) were given at a faster rate and had peak energy nearer the beginning of the call compared with screams given when the rank difference between opponents was small ( $N = 66$ ). A discriminant function based on all nine acoustic variables was unable to account for a significant amount of the variation in the acoustic structure of the screams as a function of the relative difference in rank between the victim and the aggressor (Wilks' lambda = 0.895,  $\chi^2_{(9)} = 15.08$ ,  $p = 0.089$ ). The function correctly classified 50.7% (cross-validated) of the 142 screams according to the relative size of the rank difference between the caller and the opponent, a degree not significantly above that expected by chance (Binomial (0.5) = 0.675, 2-tailed).

*Do screams that elicit responses from third party chimpanzees have a distinctive acoustic structure?*

I recorded positive responses from third parties in eight of the 48 agonistic encounters examined, meaning 24 of 142 screams evoked a response from a third party. Out of the eight encounters which attracted responses, third parties responded more to the interactions where aggression directed towards the caller was high-risk ( $N = 6$ ) compared to low-risk ( $N = 2$ ). This result was mirrored by the acoustic nature of the eight screams bouts (24 calls) that evoked responses. A between subjects ANOVA showed that screams which evoked responses ( $N = 24$ ) were given in longer bouts ( $F$

( $F_{(1,140)} = 10.275$ ,  $p = 0.002$ ) and were longer in duration ( $F_{(1,140)} = 27.793$ ,  $p < 0.001$ ), slower in rate ( $F_{(1,140)} = 33.675$ ,  $p < 0.001$ ), with higher fundamental frequencies ( $F_{(1,140)} = 4.378$ ,  $p = 0.038$ ) and peak energy later on in the call ( $F_{(1,140)} = 11.756$ ,  $p = 0.001$ ) compared with screams which did not attract third party responses ( $N = 118$ ). Thus the scream variant, which elicited a response, had similar acoustic properties to the screams given in response to high-risk aggression. A discriminant function analysis confirmed that nine acoustic parameters could account for a significant amount of variation in call structure as a function of whether a third party individual did or did not respond (Wilks' lambda = 0.717,  $\chi^2_{(9)} = 45.016$ ,  $p < 0.001$ ). 72.5% screams (cross-validated) were correctly classified by this function according to whether or not they evoked a third party response, a level significantly exceeding that expected by chance (Binomial (0.5) = 0.001, 2-tailed).

*Is the acoustic structure of chimpanzee screams affected by the nature of the audience?*

In order to establish if chimpanzees modify their calling according to the composition of the audience I examined the acoustic structure of screams given by victims when chimpanzees of equal or higher rank group to the aggressor were present. It was assumed that these high-ranking third parties could have aided the victim most effectively by successfully challenging the aggressor.

A between subjects ANOVA revealed that six of the nine acoustic variables varied significantly as a function of the presence or absence of high-ranking bystanders. If chimpanzees equal or higher ranking than the opponent were present ( $N = 68$ ) the screams were longer in duration ( $F_{(1,140)} = 16.72$ ,  $p < 0.001$ ), with higher peak frequency ( $F_{(1,140)} = 9.044$ ,  $p = 0.003$ ), mean  $F_0$  ( $F_{(1,140)} = 5.018$ ,  $p = 0.027$ ) and first formant frequency ( $F_{(1,140)} = 6.507$ ,  $p = 0.012$ ) compared to interactions when they were absent ( $N = 74$ ). In addition, there were more calls in a bout ( $F_{(1,140)} = 13.707$ ,  $p < 0.001$ ), given at a slower rate ( $F_{(1,140)} = 18.970$ ,  $p < 0.001$ ) when high-ranking bystanders were present in the same party as the victim. A discriminant function derived from all nine acoustic variables accounted for a significant amount of the variation in the acoustic structure of the screams given in the presence and absence of high-ranking third parties (Wilks' lambda = 0.774,  $\chi^2_{(9)} = 34.767$ ,  $p < 0.001$ ). The

function correctly classified 68.3% (cross-validated) of calls according to whether allies were present or absent in the party at the time of the agonistic interaction, a level significantly above that expected by chance (Binomial (0.5) = 0.001, 2-tailed).

As the type of scream given when high-ranking bystanders were present resembled the acoustic structure of screams given to high rather than low risk aggression, individuals may have been exaggerating the severity of the attack to try and evoke a response from third parties. Alternatively this effect may be driven by a high correlation between high-risk aggression and the presence of high-ranking individuals in the party. I found evidence to support the confounding role of severity in this effect. When high-ranking individuals were present 65% of interactions were classified as involving high-risk aggression. In contrast, when high-ranking individuals were absent 64% of interactions were classified as involving low-risk aggression. The chance of a victim experiencing high-risk aggression when high-ranking bystanders were present was significantly higher than expected by chance (Binomial (0.5) = 0.021, 2-tailed). In order to address this confound I selected a subset of 96 calls where high and low risk aggression was balanced across the two levels of high-ranking bystander presence (Table 5.4). The 96 calls came from 12 individuals who contributed between 6 and 9 calls to the data set and these calls were selected randomly from the larger data set.

**Table 5.4. The composition of the dataset containing 96 calls which was used to examine the role of audience in victim scream production.**

	High-ranking bystander	
	Present	Absent
High-risk aggression	24 calls	24 calls
Low-risk aggression	24 calls	24 calls

A between subjects ANOVA revealed a similar, but weaker pattern of results to the original analysis. Screams given when a high-ranking individual was present (N = 48) were longer in duration ( $F_{(1,96)} = 5.960, p = 0.017$ ), slower in rate ( $F_{(1,96)} = 9.187, p = 0.003$ ) and tended to have higher peak frequencies ( $F_{(1,96)} = 3.128, p = 0.08$ ) compared to when high-ranking individuals were absent (N=48). A discriminant

function successfully classified 68.8% (cross-validated) screams according to whether they were given in the presence or absence of high-ranking bystanders, a level significantly above that expected by chance (Binomial (0.5) = 0.001, 2-tailed).

Another more parsimonious explanation for these results may be that the chimpanzees are modifying their vocalisations as a function of group size. It could be expected that in a larger party there would be a higher chance of a high-ranking individual being present and therefore the results above may be mediated by party size rather than party composition. In order to test this I looked for an effect of party size on the acoustic structure of the 96 calls, which were balanced both in terms of the number of encounters of high and low aggression and also the number of encounters where higher ranking individuals were present. I recorded the number of adult or sub-adult individuals in the party at the time of the agonistic interaction, including the victim and aggressor. Over the 32 interactions involving 12 different victims, the number of chimpanzees in the party at the time of the interaction ranged from 2 to 12 with a mean of 5.05. I thus considered 1-5 individuals to be a small party (N=63) and 6+ individuals to be a large party (N=33). Both high and low risk aggression and the presence and absence of high-ranking individuals were represented roughly equally in these two groups: each level of the two variables was at a level not significantly different from 50% (Small party: Binomial (0.5) = 0.538, 2-tailed, Large party: Binomial (0.5) = 0.728, 2-tailed). A between subjects ANOVA revealed that the relative size of the party had no significant effect on any of the nine acoustic variables. A DFA analysis failed to account for a significant amount of the variation in the acoustic structure of the screaming bouts (Wilks' lambda = 0.917,  $\chi^2_{(9)} = 7.77$ ,  $p = 0.557$ ). 46.9% of screams were correctly classified (cross-validated) according to the relative party size in which they were given, a level below that expected by chance.

## **Discussion**

### *Identity cues in chimpanzee screams*

Our results corroborate previous research that indicates that there are some cues to caller identity in the acoustic structure of scream calls. Both temporal and spectral acoustic variables differed between 6 individuals examined and a discriminant

function analysis was able to classify 43% screams correctly according to the identity of the caller; a level significantly above the 16.7% expected by chance. Although statistically significant, this level of discrimination is not as high as might be expected given that aid by kin or allies rely on accurate identification of the individual calling. There are several reasons why this may have occurred. Firstly, our acoustic analysis only covered nine basic measurements of the calls. It has been suggested that individual identity cues are most likely to be contained in the formant structure of the call (Owren and Rendall, 2003), the fundamental frequency (Owren and Rendall, 2003, Kojima et al., 2003) and the pattern of non-linear phenomena (Fitch et al., 2002). Whilst our analysis captured aspects of the fundamental frequency and the first formant frequency it did not offer analysis of the higher formants or the relationships between them or any analysis of non-linear phenomena. Thus our analysis may only have reached a small proportion of the cues available to listening chimpanzees in the real world. In addition our data set provided only three calls from each bout, which is less than the average number calls in a bout (mean = 10 for the 29 bouts analysed from 6 individuals). As screams are habitually given in a bout, not as single calls, it might be expected that cues to individual identity may be distributed across the bout. Thus analysing only a small proportion of each bout may have also reduced the available acoustic cues to individual identity.

It was also possible that due to the range of ages in our sample of 6 individuals the discrimination of individuals was largely driven by differences in body size and related frequency differences in the calls. Although an analysis of the effects of age and sex confirmed that the smaller bodied individuals produced screams with higher frequency measures, there was no evidence that age or sex affected any of the temporal acoustic structures in these scream bouts. It therefore seems that the discrimination of individual identity was driven by both differences in body size and temporal cues to identity. In conclusion, it seems our limited analysis was sufficient to detect some spectral and temporal cues to caller size and identity, which may represent some of the acoustic properties chimpanzees use to correctly identify individual callers from their screams (Kojima, 2003). This is a fundamental prerequisite in order for screams to function referentially and affect aid recruitment; unless listeners can identify the caller, the nature of the agonistic interaction they are involved in is irrelevant. Having established that chimpanzees do provide some cues

to identity in their screams, it is now possible to consider whether the screams provide the listener with information about the nature of the agonistic interaction.

#### *Screams and severity of aggression*

The results of this study demonstrate that chimpanzees produce victim screams with acoustic structures that vary systematically according to the type of aggression the caller encounters. Although five distinct types of aggression were identified and screams could be classified successfully according to these five categories, it is clear that the acoustic structure of the calls grade between these categories in a predictable fashion (Figure 5.2). This gradation mirrored the continuum of risk of serious physical harm to the caller associated with different types of aggression. As this risk increased, the scream calls became longer in duration, higher in frequency, flatter in shape and were given in longer, slower bouts. In contrast to the information regarding the role of the caller in an interaction, which was conveyed in the shape of the call, information about the severity of the attack seemed to be encoded in the temporal and absolute frequency aspects of the calls. Elements of this acoustic variation were consistent with the idea that these calls were driven by differences in arousal, including the increase in pitch as the risk of danger increased. This was consistent with Morton's structural-motivational rules, which proposed that frequency and tonality increase as fear levels rise (Morton, 1977). However, the decrease in rate, the lengthening of calls and the flat shape of the calls that accompanied high-risk contexts were not consistent with a simple motivational-structural relationship. Regardless of the mechanism producing these calls, our results provide evidence that listeners have access to reliable information about the severity of an attack suffered by a victim in the acoustic structure of the victim screams.

#### *Screams and relative rank of opponents*

Contrary to our predictions there was no evidence that screams varied reliably according to the relative rank difference between victim and aggressor. There are several possible reasons for this. Firstly, my basic classification of rank within the community may have conflated several levels of rank that are significant to the chimpanzees. However, given that there was no difference in the acoustics of screams given to opponents in the same or adjacent rank group and opponents of two or three rank groups higher than the victim, it is unlikely that more fine grain distinctions

would have arisen, had the analysis been possible. Secondly, there are differences between some aspects of the rhesus monkey and chimpanzee social systems, which make rank less important to third parties in chimpanzee society. Rank in rhesus monkeys is strictly defined by matriline, therefore kin have a vested interest in protecting the rank of their matriline against lower ranking families. In contrast, determination of rank in chimpanzees is an individual process, in which mainly males use a combination of intimidation and affiliative behaviour to increase their individual rank within the group (Goodall, 1986). In addition, in our sample, no aggression was recorded from individuals of a lower ranking group than the victim. In these chimpanzees at least, third party interventions in an agonistic interaction could not have been motivated by the protection of a common rank from a lower ranking individual. As such, the relative rank of the opponent may be of less importance to listening individuals. This result does, however, directly contrast with the effect the rank difference size between victims and higher-ranking aggressors had on rhesus monkey scream production (Gouzoules et al., 1998). It could be argued that the danger to the victim increased as the rank difference between the opponents increased and therefore it was still important information to impart to listening individuals. If this were true then chimpanzees might simply use the severity of attack encoding system to take account of this information.

#### *Potential for functional reference?*

From a production perspective, these results indicate that chimpanzee victim screams may function in a referential manner. The acoustic structures of the screams contained subtle but systematic variation and the chimpanzees used this variation in a context specific way. From a recipient perspective, this vocal behaviour has the potential to provide listeners with information on the severity of the aggression encountered by the caller. Evidence from this study and previous work (Kojima, 2003) indicates that there are sufficient cues to individual identity for listeners to be able to discern the identity of the caller from the screams. In theory, this provides listeners with a rich source of information about a social interaction they are unable to see, but playback experiments are needed to establish that chimpanzees do take advantage of this available information, before these calls can be described as functionally referential.

One argument against agonistic screams functioning in a referential manner has been the low level of third party intervention observed in agonistic encounters in wild chimpanzees (Fitch, personal communication). I suggest there are two principle reasons why this argument is not valid. Firstly, in this study I report eight cases (17% of cases) where a third party gave a positive response to a victim of aggression. While this proportion is low, it is not insignificant. I showed that responses were more likely to be given to victims of high-risk aggression, where the aid has most benefit for the victim, but unfortunately I have no evidence that the third parties responded on the basis of the screams they heard. I cannot rule out that the third parties could see the interaction and responded to what they saw, rather than what they heard. This highlights the need for playback experiments to fully understand the ability of recipients to extract information from calls and use it to influence their behaviour. Secondly, even if a chimpanzee does not respond there are still advantages to understanding the details of the interaction they are unable to see. This ability would enable chimpanzees to respond appropriately to screams of an ally, investing potentially costly intervention in encounters when the risk to the ally is high and ignoring screams evoked by minor aggressive acts. This analysis has shown that chimpanzees commonly scream in response to a large range of aggressive acts, most of which are not serious. Chimpanzees could waste a lot of time and energy if they responded naively to the frequent victim screams of kin and allies. It has also been suggested that chimpanzees are efficient social monitors, with great sensitivity to weaknesses in the chimps ranking above them, so they are “ready to take advantage of a senior if he should show signs of ill health or aging, or if he loses an ally” (Goodall, 1986, p.415). Extracting key details about agonistic encounters occurring in neighbouring parties, out of sight, would broaden the pool of social knowledge a chimpanzee possessed. This knowledge of third party relationships and alliances could be used to advantageously influence their own future social interactions.

### *Intentional signalling?*

From the signaller’s perspective the primary function of producing victim screams is still unclear. Whilst some argue individuals use screams as ‘acoustic bludgeons’ to discourage the aggressor (Owren and Rendall, 1997), others posit that callers scream to inform and recruit aid from their kin and allies (Gouzoules et al., 1984). The issue of intentional signalling is a highly contentious and important one and this study has

highlighted the possibility that chimpanzees modify their calling behaviour according to the composition of their audience. Whilst the relative size of the party did not affect the acoustic structure of the screams, the composition of the party did. Once I had controlled for the large effect of severity of aggression on the acoustic structure of the screams, by using a data set with high and low aggression equally represented in all groups, I found that chimpanzees gave different screams depending on whether a high-ranking individual was present in the party. The definition of 'high-ranking bystanders' relied on the ability of a third party chimpanzee to challenge the aggressor in terms of being of equal or higher rank than the aggressor. The definition did not take into consideration the inclination of a third party chimpanzee to come to the victim's aid. Nevertheless, when a high-ranking bystander was present, there was a chimpanzee capable of helping the screaming individual and this seemed to influence the calling behaviour of victims. When high-ranking individuals were present victims gave longer, higher pitched screams at a slower rate than when they were absent. Our results examining the effect of severity of aggression revealed that it was the slower, longer, higher pitched screams that were given in response to high-risk aggression. I also found that 75% of responses from third parties were given to victims of high-risk aggression. It seems that the chimpanzees were giving screams that indicated the aggression they faced was more severe when high-ranking bystanders were present; the type of screams that were most likely to elicit a response. This result suggests that chimpanzees may be using calls, which exaggerate the severity of the situation, in order to increase their chances of receiving aid from third parties.

## Chapter 6: Chimpanzee rough grunts are functionally referential signals

### Summary

The observational studies focussing on signaller behaviour presented in the last two chapters have highlighted agonistic screams as promising candidates for functionally referential signals. I now turn my attention to the assessment of rough grunt vocalisations produced in feeding contexts. This chapter, in contrast to the previous ones, focuses on the behaviour of recipients and thus provides the first complete test of functional reference in chimpanzees. I tested whether chimpanzee rough grunts, were produced and, crucially, perceived as functionally referential signals with a combination of observational and experimental work. I conducted this study with the captive population of chimpanzees housed at Edinburgh Zoo. Individuals produced acoustically distinct types of 'rough grunts' when encountering different foods. In a naturalistic playback experiment, a focal subject was able to use the information conveyed by these calls to guide his search for food, demonstrating that the different grunt types were meaningful to him. This study provides experimental evidence that our closest living relatives can produce and understand functionally referential calls as part of their natural communication.

The results presented in this chapter have been published in the following paper:

Slocombe, K. & Zuberbühler, K. 2005. Functionally referential communication in a chimpanzee. *Current Biology*, **15(19)**, 1779-1784.

## Introduction

Food-associated calls have been documented in many different taxa, including non-human primates (see Chapter 2 for a comprehensive review). Food-associated calls have a great potential to function as referential signals: they can inform listeners about the presence of food (e.g. Evans and Evans, 1999), and they can also provide information about the nature of a discovered food source (e.g. Hauser, 1998). Despite this potential very few studies, to date, have provided the necessary experimental evidence to confirm that listeners do use and understand the information available in context-specific calls. The most convincing evidence for functional reference comes from studies of rhesus monkeys. This species produced different calls types to foods of different qualities (Hauser et al., 1993). Playback experiments demonstrated that these macaques habituated across acoustically different calls with the same referent (i.e. high quality food), and only showed dis-habituation when the referent of the call changed (i.e. low quality food). This showed that listeners extracted information about the quality of a food source from the calls and attended to this information rather than just the different acoustic structure of each call.

Chimpanzees produce food-associated calls whilst eating or approaching a desirable food (Reynolds, 1965; Goodall, 1968; 1986). Listeners habitually respond with orientation towards or approach of the caller (Goodall 1968, 1986). Acoustically, these food-associated calls grade from soft grunts to high-pitched shrieks, typically described under the umbrella term 'rough grunts' (Marler and Tenaza, 1977, p. 987). Captive chimpanzees are more likely to give rough grunts when discovering a large and divisible food source compared to a small or indivisible one (Hauser et al. 1993) and callers may adjust call production depending on the audience present (*Pan troglodytes*: Hauser and Wrangham, 1987; *Pan paniscus*: Van Krunkelsven et al., 1996). Many have suggested that rough grunts may function as referential signals, because they are produced exclusively in feeding contexts and are therefore context-specific (Hauser and Wrangham, 1987; Hauser et al., 1993). Unfortunately the only study to systematically test this hypothesis with the necessary playback experiments (Hallberg et al., 2003) is limited by several methodological and statistical problems (see Chapter 3, pages 50-51, for full discussion).

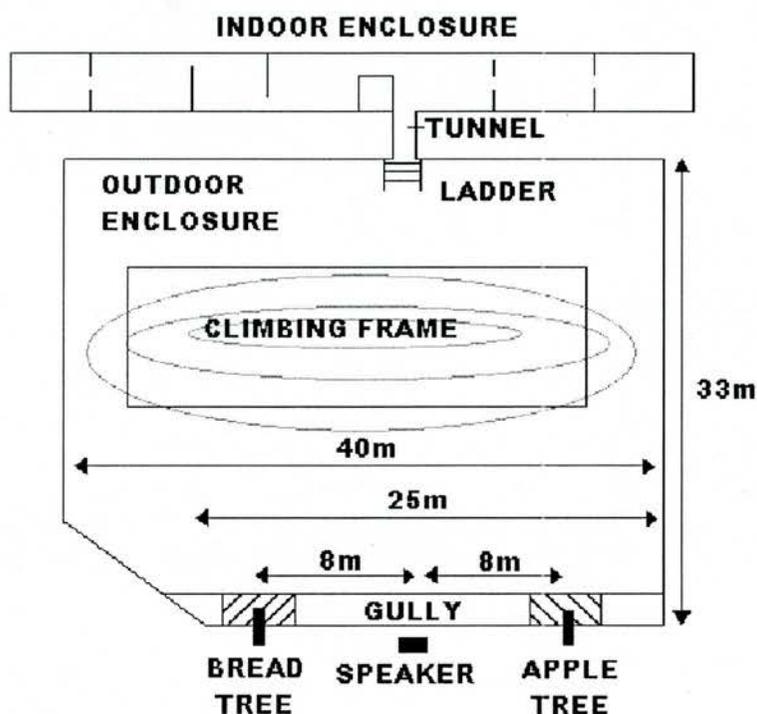
This study aimed to investigate whether chimpanzees use the acoustic variation present in this call type (Marler and Tenaza, 1977) in a systematic, context specific way to label food quality or type. I chose to conduct this study with a captive population rather than a wild population for several reasons. Primarily, I needed to be able to objectively determine food quality and individual food preferences and this was only possible in a captive environment where provisioning was habitual and controlled. It was also unfortunately impossible to obtain permission to conduct playback experiments in the wild. In order to address both the production and perception criteria for functional reference, this study investigated the behaviour of both the signallers and receivers. Within the captive setting, I first conducted an observational study to establish whether chimpanzees produce acoustically distinct rough grunts to high and low value food. I then tested whether recipients extracted referential information from the calls with a naturalistic playback experiment in which chimpanzees were played a sequence of rough grunts that mimicked the discovery of food by another group member. My goal was to determine firstly, whether other individuals hearing these call sequences could draw inferences about the calls' referent (that is, the food found by the caller) and secondly, whether recipients used this information to guide their own search for food.

## **Methods**

### *Study site*

Data were collected for four months between May 2004 and September 2004 on the captive chimpanzees housed at Edinburgh Zoo, Scotland. The eleven chimpanzees were housed in an outdoor area measuring 1452m<sup>2</sup> and an indoor area of 90m<sup>2</sup> (Figure 6.1). A tunnel with opaque flaps at each end connected these two areas. Chimpanzees had free access through the tunnel at all times except during cleaning. The tunnel exited into the outdoor enclosure at a height of 2.5m and a ladder connected the tunnel with the ground (Figure 6.4). The indoor enclosure consisted of a series of interconnected cages, with visual barriers separating most adjacent cages. This meant that most of the time an individual could not see all other group members. The outdoor enclosure had a central mound, upon which the climbing frame was built, and a concrete gully running along one of the walls (1.2m deep; 2m wide). Due to the

slope of the ground the chimpanzees could not see into the gully from the ladder or any other place on the ground in the enclosure, except for a 2m strip of ground running alongside the gully.



**Figure 6.1. Plan of the chimpanzee enclosures at Edinburgh Zoo.** Illustrated are the indoor/outdoor enclosures, the location of bread and apple trees, and the corresponding feeding sites underneath. All measurements are in metres (m).

### *Study animals*

The study group consisted of eleven animals ranging from 5 to 44 years in age (Table 6.1). In contrast to the wild, the ages of all captive individuals were known, so purely age-based criteria could be used to define the age classes. Adults were defined as individuals over 15 years, sub-adults were individuals 10-15 years, juveniles were 4-9 year olds and infants were 0-4 years old (Reynolds, 2005). This group lacked a clear alpha male. Adult males, David and Louis, had amicably shared dominance for many

years (MacDonald, personal communication), but during the study period sub-adult, Quafzeh, challenged the two older males for dominance. Although his prematurely large size allowed him to physically dominate all single members of the group, David and Louis often supported each other against him. The females also occasionally intervened to support the older males. No consistent pattern of pant grunting emerged between the three males during the study and the struggle for dominance remained largely unresolved. Due to his age, Liborius was the only member of the group who did not attract any serious aggression from the adult males. This five-year old was shown a large degree of tolerance by all group members, even during feeding.

**Table 6.1. The composition of the chimpanzee group at Edinburgh Zoo.**

Males: status	Individuals	Total	Females: status	Individuals	Total
Adult male	Louis Ricky David	3	Adult female	Cindy Emma Lucy Lyndsay	4
Sub-adult male	Quafzeh	1	Sub-adult female	Kilimi	1
Juvenile male	Liborius Kindia	2	Juvenile female		0

### *Study design*

To determine whether chimpanzees produced and understood functionally referential vocalisations in response to food I conducted a study that consisted of the following elements: (1) determination of individual food preferences, (2) acoustic analysis of rough grunts (3) establishment of two artificial food trees, (4) playback experiments and matching controls.

#### **(1) Food preferences**

Mixed feeds containing two types of food were scattered in the outdoor enclosure between 1100 and 1800 hours each day, by a caretaker. The feeding events were filmed and the first choice of each individual was recorded. I systematically tested pair-wise combinations of seven food types (bread, apples, carrots, greens, bananas,

chow pellets, pears) to establish individual food preference hierarchies. Bread was unanimously chosen as the most preferred food item, relative to the other six foods. Some of the low ranking foods, such as carrots and greens, rarely elicited rough grunts so I did not consider them any further. Apples regularly elicited rough grunts, but they were ignored when bread, bananas, chow pellets or pears were available, making them the least preferred food that reliably elicited a vocal response. If directly compared, all individuals unanimously preferred bread to apples. Bread was chosen as a high-value food and apples as a low-value food in the following experiment. Both food types were relatively non-odorous, thus reducing the chances of olfactory cues compromising the experiment.

## *(2) Acoustic analysis of rough grunts*

Rough grunts were recorded and analysed in order to examine whether signallers produced acoustically distinct rough grunts to food of different values and thus met the production criteria of functional reference. The rough grunt recordings were then edited to form the playback stimuli.

Vocalisations were recorded from chimpanzees in the outdoor enclosure with a Sennheiser MKH 815 directional microphone and a Sony TCD-D8 portable DAT recorder. Recordings were transferred digitally onto a TOSHIBA (Celeron 1.8GHz) laptop computer, using Cool Edit Pro LE (sampling rate 44.1 kHz, 16 bits accuracy). I took recordings from the first feed of the day to try and keep the novelty value of the food and the hunger levels of the chimpanzees constant across recording events. I obtained 19 bouts of rough grunts with minimal interference from other sounds sources (children screaming, gibbon song, keeper talks broadcast to the public). Ten bouts were in response to apples and nine bouts were in response to bread. Each calling bout was from a separate feeding event in which either only apples or only bread were provided in the outdoor enclosure. Only bouts given whilst the animal was collecting or eating the target food were used. I used the first three seconds of each bout that was free from interference by other callers and extraneous background noise, once the animal had made physical contact with the food. Each of the 3-second bouts contained between 3 and 8 calls and the 19 calling bouts consisted of a total of 95 rough grunts. Three individuals contributed bouts to the dataset (adult female Emma:

$N_{\text{apples}}=1$ ;  $N_{\text{bread}}=2$ ; adult male Louis:  $N_{\text{apples}}=5$ ;  $N_{\text{bread}}=3$ , sub-adult male Quafezeh:  $N_{\text{apples}}=4$ ;  $N_{\text{bread}}=4$ ), representing a range of the main age-sex classes.

Acoustic analyses were carried out using PRAAT software version 4.3.17 ([www.praat.org](http://www.praat.org)). The following settings were used: Pitch settings: range 50-1000 Hz, optimised for voice analysis; Spectrogram settings: window length 0.005 sec, dynamic range 70dB; Formant settings: Max formant 5500 Hz, No formants = 5, window length 0.025sec, dynamic range 30dB. Rough grunts consisted of both voiced and unvoiced calls. I found 13 unvoiced calls, in which insufficient proportions of the call were voiced to enable accurate measurement of fundamental frequencies. Of the ten bouts given in response to apple, five contained unvoiced calls. None of the nine grunt bouts given to bread contained any unvoiced calls. For the remaining 82 voiced calls I determined the following seven parameters:

#### Temporal parameters:

1. Duration of the call (s).
2. Rate of calling in the bout (calls/s): number of calls/duration of bout.

#### Spectral parameters:

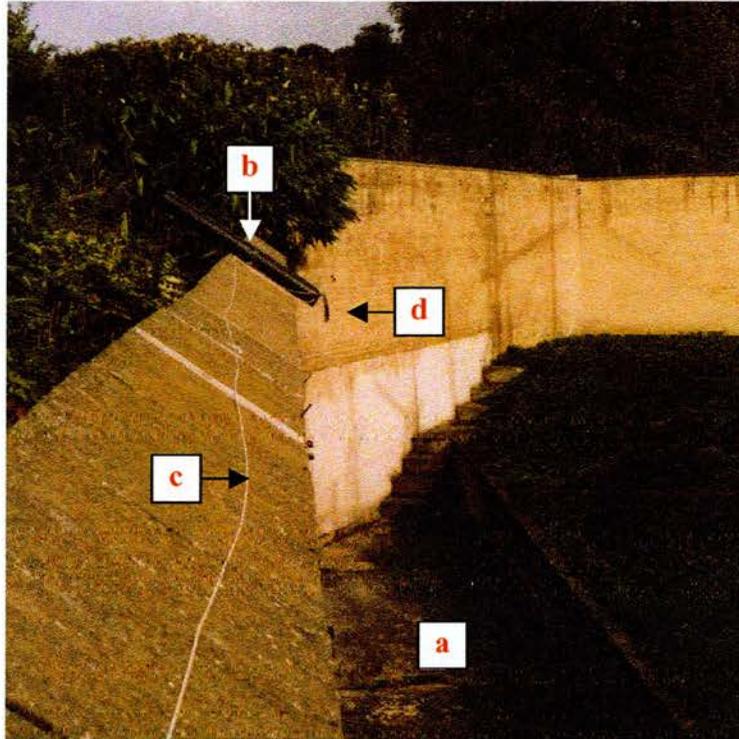
3. Fundamental frequency: mean frequency of the fundamental across the call (Hz).
4. First formant frequency: the mean frequency of the first formant across the call (Hz).
5. Second formant frequency: the mean frequency of the second formant across the call (Hz)
6. Third formant frequency: the mean frequency of the second formant across the call (Hz)
7. Noise to Harmonic ratio: the proportion of the signal that was non periodic.

I used the 19 bouts I analysed to create the playback stimuli. The 3-second recordings, containing between 3 and 8 calls, were edited to reduce background noise in the inter-call period, whilst the temporal patterning of the call bout remained unchanged. The amplitudes of all recordings were edited so that they fell within a common amplitude range. Recordings were taken from a range of locations in the enclosure, suggesting

that differences in calling behaviour could not have been caused by particular locations. There were 19 playback stimuli: ten grunt bouts given in response to apples and nine grunt bouts given in response to bread. Three individuals produced these playback stimuli (Emma:  $N_{\text{apples}}=1$ ;  $N_{\text{bread}}=2$ ; Louis:  $N_{\text{apples}}=5$ ;  $N_{\text{bread}}=3$ ; Quafezeh:  $N_{\text{apples}}=4$ ;  $N_{\text{bread}}=4$ ).

### ***(3) Artificial food trees***

On 10<sup>th</sup> June 2004, I introduced two artificial ‘food trees’ adjacent to the enclosure, an ‘apple tree’ and a ‘bread tree’ (Figure 6.1). The ‘trees’ consisted of opaque black tubes attached to the wall of the enclosure, in which four small cardboard tubes containing food (or no food) could be stored (Figure 6.2). The ‘tree’ tubes were made of plastic and measured 110cm in length and 11cm in diameter. The tubes were opaque and the ends were covered with an opaque flap to prevent chimps from seeing the contents of the trees (Figure 6.2). A metal pin at the bottom of each opaque tube, which prevented the tubes from falling out, was attached to the speaker by string (Figure 6.2). The experimenter, standing by the speaker, could therefore release the tubes from both trees into the enclosure simultaneously and remotely, by pulling the strings. Food was delivered regularly into the enclosure in this manner over a period of six weeks. The chimpanzees could not climb into the artificial trees, but they had unrestricted access to the food items dropped into the concrete gully below (Figure 6.2). Within this gully the apple and bread tubes fell into two areas at opposite ends of the gully, both measuring 4x2 metres.



**Figure 6.2. Photo of the ‘bread tree’ from the perspective of the experimenter standing next to the speaker.** Illustrated are (a) the concrete gully into which the tubes fell, (b) the opaque tube ‘tree’, (c) the string connecting the release pin of the ‘tree’ to the speaker, (d) the opaque flap at the end of the ‘tree’ to prevent chimpanzees seeing if the tubes inside were baited or not.

To avoid detection of food at a distance, and to encourage food-searching behaviour, pieces of apple or bread were consistently concealed in cardboard tubes (Figure 6.3). The tubes were made from tough 3mm cardboard measuring 20cm in length and 6.8cm in diameter, with four holes and two bamboo sticks forming a cross at each end. These tubes were purposefully constructed out of materials that were not harmful to the chimps if ingested.



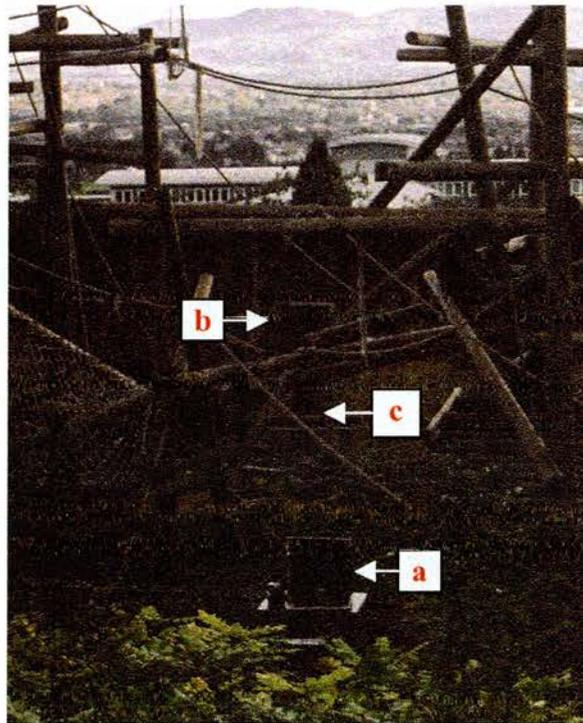
**Figure 6.3. Photos illustrating the cardboard tubes that were dropped from the trees, either baited or unbaited.** In order to access the bread or apples contained in baited tubes the chimpanzees either ripped the cardboard with their teeth or removed the bamboo sticks.

During each feeding event, four tubes were dropped from both food trees remotely and simultaneously, but only one set of tubes was baited in any one trial. Baiting of tubes was predetermined according to a randomly generated binomial sequence. This simulated the situation in the wild in which food is patchily distributed in time and space. Tubes were loaded into the trees with the experimenter's hands concealing the open ends so observing chimps couldn't see what the tubes contained. In order to control for chimps watching the loading process and gaining clues about which tree was baited the apple tree was always loaded first.

To determine whether or not a tube was baited, individuals had to lift the tube (to assess the weight), squash the tube or to visually inspect it; thus physical contact with the tube was essential. Baited tubes contained either two slices of bread or three apple halves; non-baited tubes were always empty. I consistently dropped series of four tubes in each location to make the amount of available food substantial and divisible. Previous research has indicated these two variables may mediate the production of rough grunts in chimpanzees (Hauser et al., 1993).

Tubes were released both in the presence of chimpanzees (visible) or whilst they were inside (hidden). If tubes were released in the presence of chimpanzees, individuals immediately approached to inspect the tubes and, if available, extract food items. If tubes were released whilst the chimpanzees were inside, discovery of the tubes was opportunistic. These 'hidden' trials were important to establish that food could spontaneously appear in the enclosure without a visible feeding event. I filmed the

in the chimpanzees' environment. Once all the equipment had been introduced, the chimpanzees were then allowed to habituate to all the items for a further week before the first test trial.



**Figure 6.4. Photo of the outdoor enclosure showing the speaker and tunnel exit into the outdoor enclosure.** Illustrated are (a) the speaker and laptop (b) the tunnel exit into the outdoor enclosure covered with an opaque flap, (c) a chimpanzee descending into the outdoor enclosure on the ladder.

#### Trial Procedure

The experimental phase consisted of test and control trials. Control trials provided a baseline of search behaviour. A maximum of one playback and one control trial were conducted each day, in addition to baited reinforcement trials. All trials were separated by at least one hour.

Before each trial the group was given a small feed in their indoor enclosure. Once all chimpanzees were inside, four empty tubes were simultaneously and remotely dropped into each location (i.e. eight empty tubes total; no food available under either tree). The first individual emerging from the inside area was the subject. Then, a test stimulus (a 3s sequence of rough grunts) or no stimulus was played back (control trial) and the response of the subject was filmed. Filming of the trial began as the tubes were dropped into the gully and continued until the trial was complete. The trial

terminated when the subject finished searching the gully and climbed out or they went back inside. I filmed with a SONY video camera recorder (CCD-TR728E). I stood in the same location beside the speaker on all trials and filmed the movements of the subject using the eyepiece of the video camera. This made eye contact impossible, reducing the chances that I gave any cues as to which location was possibly 'represented' by the playback stimuli.

Test and control trials were conducted only if the following conditions were met: (a) The subject was not involved in a social interaction (play or aggression) (b) no more than two other group members followed him/her (c) no individuals were sat closer than 25 m from the speaker (d) the individual who provided the grunts for the playback stimuli was still inside and out of hearing range. The trial was terminated if another chimp entered the gully before or whilst the subject was searching in the gully or if another chimp vocalised during the trial.

### Subjects

It was possible to systematically test only one subject, five-year old male Liberius, (LB). This was partly due to my attempt to minimise the interference the testing regime imposed on the natural behaviour of the group. It was impossible to separate individuals from the group without the individuals subsequently encountering high levels of aggression from other group members. When individuals had to be separated for veterinarian reasons, severe and prolonged social upheaval was the normal outcome, suggesting that in such a situation animals would not pay attention to subtle acoustic stimuli, the focus of this study. Therefore I did not restrict the movements of the chimpanzees and thus focussed on testing the first individuals who chose to come outside after an indoor feed. During the experimental phase, LB was always one of the first individuals outside after any feed and so was the subject on most occasions. On a few occasions another animal emerged first, heard the playback without LB present and began to approach the gully. However, on all these occasions LB emerged shortly afterwards, saw another animal approaching the gully and rushed to overtake the subject animal to enter the gully before them. LB thus prevented trials of other individuals, by emerging first on most occasions, responding first to the playback when other target animals were present and aborting other target individual's trials by

entering the gully before them. Prior to the experimental phase LB had considerable experience with apple, bread and unbaited tubes (See results).

Although the single subject is a potential limitation, studies of single animals have crucially contributed to our understanding of a species' cognitive capacities (Harley et al., 2003; Janik et al, 1994; Kenward et al, 2005; Poole et al, 2005; Weir et al, 2002)

### *Measures of response*

I analysed the videotapes and measured various response parameters in both test and control trials. My initial prediction was that, after hearing a playback stimulus, LB would rush to the food tree that corresponded to the rough grunts used as playback stimuli. This was true during four of the six initial playback trials, but thereafter LB developed an idiosyncratic search strategy. He consistently approached the bread tree first, presumably because there were no costs involved in visiting both trees (note that no food was provided during any of the experimental or control trials). I therefore analysed a number of subtler behavioural measures:

*Time on ladder:* Time from when the chimpanzee's head emerged from the tunnel to when the chimpanzee climbed off the ladder on to the ground.

*Number of tubes searched:* The number of tubes searched within the target area as a proportion of the total number of tubes in the target area. 'Searching a tube' constituted picking up, rolling or squashing a tube;

*Search time:* The time from touching the first tube to when the last tube to be searched was first touched. This time was then expressed as a proportion of the total number of tubes in the target area.

The number of tubes present in each location could vary from one trial to the next and between the two target areas: chimpanzees removed and moved tubes and retrieval of old tubes was only possible if the chimpanzees could all be locked inside, which only occurred 1-3 times a week. Thus both the measures of the number of tubes searched and the search time were potentially confounded by the varying number of tubes in each location (e.g. if one location had five tubes in and the other had twenty the maximum possible values for these measures was very different at the two locations).

As such, each measure was expressed as a proportion of the total number of tubes available in each location to control for this factor.

I extracted these measures from a total of 17 test trials (9 apple, 8 bread), which I compared to 10 control trials. 19 test trials were originally conducted, but only 17 trials are presented for analysis. The other two trials were aborted as the subject went back inside after hearing the playback without approaching or searching the gully.

To ensure that my coding of the video tapes was accurate I asked an independent person, who was blind to the trial type and to the hypothesis of the study, to code four randomly chosen test trials and three randomly chosen control trials (25% of the total trials). Written instructions were presented to the coder explaining the criteria used to obtain each measure. The coder was then left to extract the seven measures from each of the chosen trials. These independently coded measures were then compared to the original measures using a Cronbach's alpha test of inter-observer reliability. A score of 0.87 across all trials and measures was obtained, indicating the trials had been reliably measured.

## **Results**

*Acoustic structure of rough grunts varies as a function of the food encountered by the caller.*

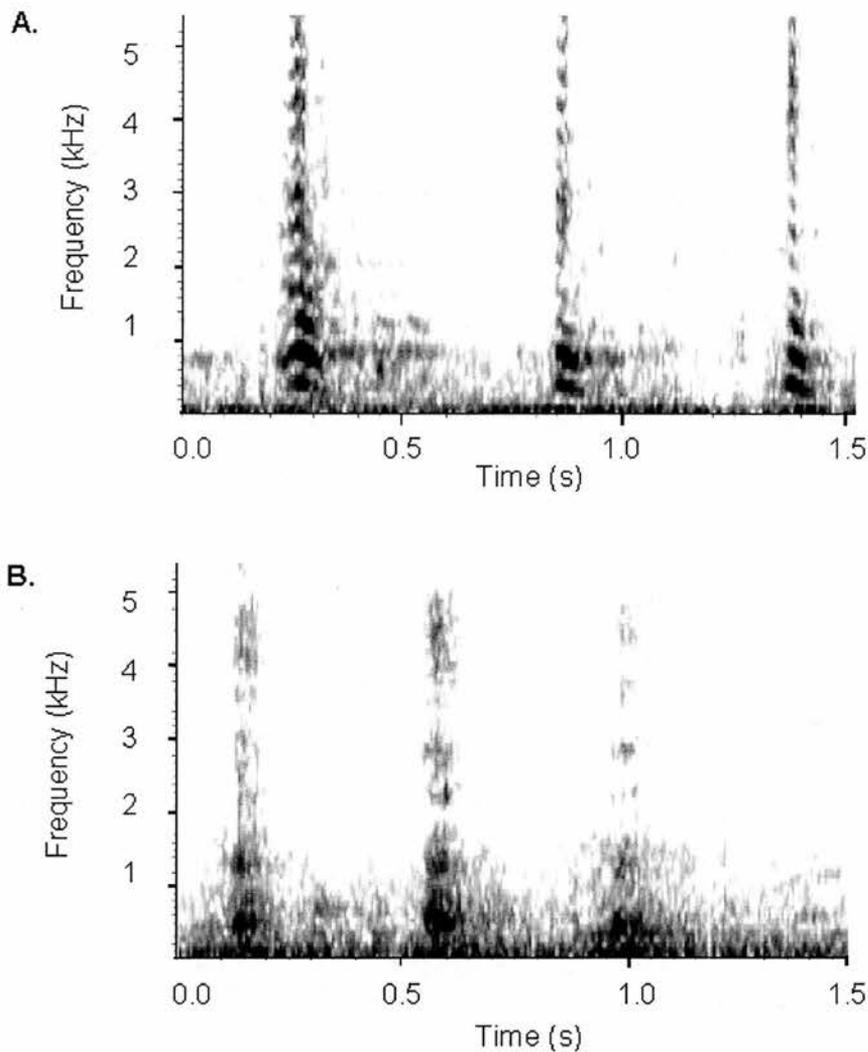
I conducted an acoustic analysis, which showed that rough grunts given to bread and apples fell into two acoustic subtypes with relatively little overlap (Table 6.2; Figure 6.5). I analysed 82 calls from 19 different bouts recorded from three different individuals. Univariate analysis of variance revealed that six out of the seven parameters varied significantly as a function of the food, which elicited them (Table 6.2). Rough grunts given to apples were characterised by a low fundamental frequency, a high level of non-periodic sound, a low first formant frequency and a high second and third formant frequency. In contrast, rough grunts given to bread were characterised by a high fundamental frequency, a low level of non-periodic sound (high noise to harmonic ratio), a high first formant frequency, and a low second and third formant frequencies. There were no differences in call duration.

**Table 6.2. Descriptive statistics and univariate analysis of variance for 82 analysed rough grunts given in response to apples or bread**

	Apples (n=42)		Bread (n=40)		ANOVA	
	Mean	SD	Mean	SD	F	p-value
Call rate (calls per second)	2.23	0.517	1.89	0.411	10.45	0.002
Call duration (s)	0.13	0.110	0.11	0.056	0.85	0.360
Fundamental frequency (Hz)	365.60	218.853	559.15	160.226	20.71	<0.001
First formant frequency (Hz)	684.07	143.581	739.05	97.983	4.06	0.047
Second formant frequency (Hz)	1661.12	267.113	1490.35	174.856	11.61	0.001
Third formant frequency (Hz)	2973.57	256.530	2705.95	246.187	23.19	<0.001
Noise to Harmonic ratio	0.54	0.167	0.28	0.197	38.54	<0.001

Degrees of Freedom =1, 80

I then conducted a discriminant function analysis to explore whether rough grunts given to apples and bread could be statistically grouped. The seven acoustic parameters had variance inflation factors of less than 8, indicating that there were no co-linearity problems. The discriminant function resulting from the 7 parameters explained a significant amount of variation between grunts given in response to bread and apples (Wilks lambda=0.187,  $F_{(6,12)}=8.005$ ,  $p=0.001$ ). The function correctly classified 100% of the calls according to the foods, which elicited them (78.9% using cross validation discriminant analysis). In sum, my analyses clearly demonstrated that there is subtle, but consistent, acoustic variation present within this particular call type, which can be explained by the nature of the food encountered by the caller.



**Figure 6.5. Time-frequency spectrograms of rough grunt calling bouts given by the adult male Louis: (a) to bread, (b) to apples.** Grunts given to bread have more energy (depicted by the darkness of the image) at higher frequencies and have a clear harmonic structure, compared to the lower pitched, noisy grunts given to apples.

#### *LB's learning history*

90 baited trials were conducted during the course of this study: 45 bread trials (14 hidden and 31 visible) and 45 apple trials (16 hidden and 29 visible) in a random order. This provided the opportunity for unbiased learning. Records of direct and vicarious learning about each type of tube were taken for each baited trial. Prior to test trials LB gained considerable experience with apple and bread tubes (Table 6.3).

**Table 6.3. The number and type of learning experiences LB had with baited tubes prior to the beginning of the test and control trials.**

Type of tubes	Baited apple tubes (17)				Baited bread trials (13)			
Type of trial	Hidden trials (11)		Visible trials (6)		Hidden trials (5)		Visible trials (8)	
Type of experience	Direct (9)	Vicarious (2)	Direct (5)	Vicarious (1)	Direct (4)	Vicarious (1)	Direct (3)	Vicarious (5)

In addition he had experience of 14 unbaited apple tubes and 16 unbaited bread tubes, which reinforced the fact that only one location was ever baited. It is evident that LB learnt from all types of trials in a relatively balanced manner and on a few occasions during the latter stages of this phase it was apparent he had learnt the correct associations. For instance, baited apple tubes were dropped into the enclosure and retrieved by Lyndsay, in his absence. LB then entered the outdoor enclosure, approached the female with the apple tube, saw the contents and ran to search under the apple tree.

During the baited trials that continued during the experimental phase LB gained a further 18 experiences of baited apple tubes, 20 experiences of baited bread tubes and 22 experiences of unbaited tubes. In order to control for the possibility that the subject was using his previous baited trial to inform his search strategy in the playback trials, we checked that there was no systematic matching between the baited location in the previous trial and the target location indicated by the playback stimulus in the experimental trial. The results from 17 experimental trials were analysed and there was only a match between the previously baited location and the target playback location on 9 of the 17 occasions. This makes it very unlikely Liberius was simply adopting a search strategy based on the preceding baited trial.

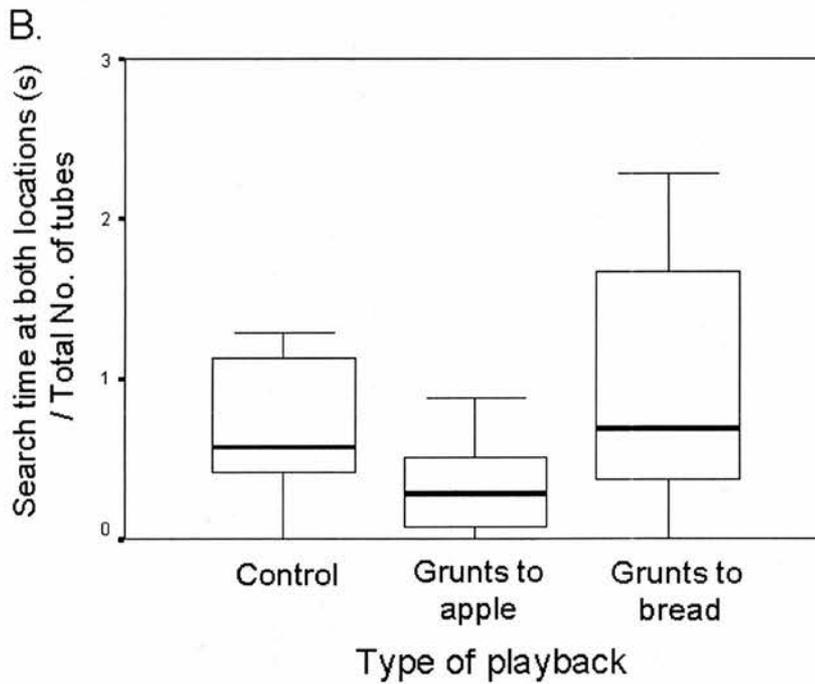
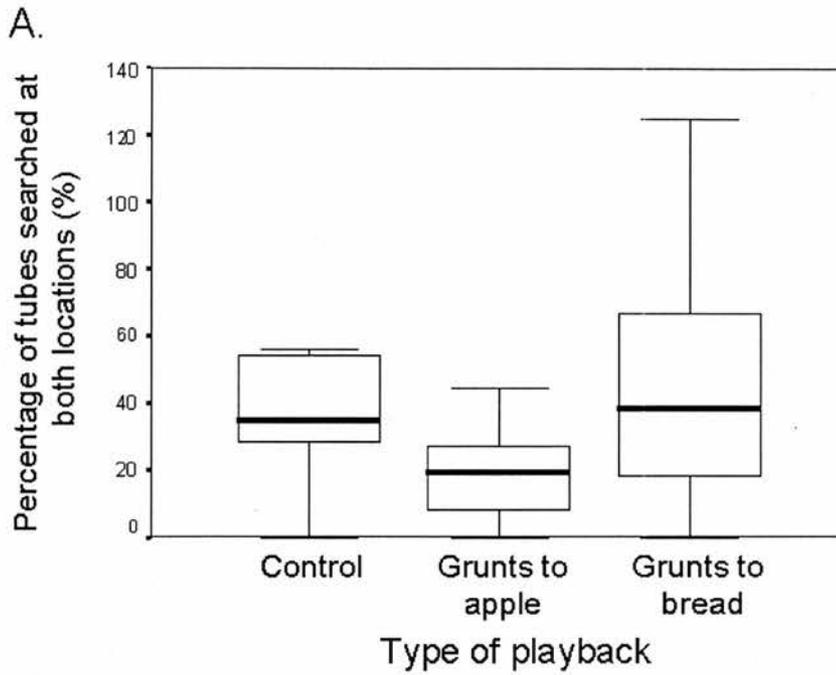
*Playbacks had a significant effect on the subject's behaviour*

LB completed 17 test trials (9 apple, 8 bread) and 10 control trials. Hearing a series of grunts had a number of effects on LB's behaviour (two-tailed, Mann-Whitney U-tests). Firstly, before approaching the trees, LB remained on the ladder significantly longer in test than control trials ( $mean_{test} = 9.33$ ,  $mean_{control} = 5.40$ ,  $U = 42.50$ ,  $p =$

0.031), demonstrating that he perceived and presumably processed the playback stimuli.

I then analysed whether rough grunts affected his overall search efforts (Figure 6.6). As predicted, LB searched more tubes ( $\text{mean}_{\text{bread}}=48.87\%$ ,  $\text{mean}_{\text{apple}}=21.15\%$ ,  $U=85.5$ ,  $p=0.043$ ) and searched for longer ( $\text{mean}_{\text{bread}}=1.13\text{sec}/\text{tube}$ ,  $\text{mean}_{\text{apple}}=0.36\text{sec}/\text{tube}$ ,  $U=81.5$ ,  $p=0.030$ ) underneath both trees after hearing grunts given to bread compared to grunts given to apples. Somewhat surprisingly, his search behaviour in control trials did not differ from bread trials (tubes searched:  $\text{mean}_{\text{control}}=49.3\%$ ,  $U=179$ ,  $p=0.983$ ; search time:  $\text{mean}_{\text{control}}=1.44\text{sec}/\text{tube}$ ,  $U=178$ ,  $p=0.960$ ), although he searched significantly more in control than apple trials (tubes searched:  $U=71.0$ ,  $p=0.004$ ; search time:  $U=77.0$ ,  $p=0.007$ ). To correct for multiple pair-wise comparisons I adjusted the critical alpha level from 0.050 to 0.017 using a Sidak correction ( $\alpha_{\text{FW}} = 1 - (1 - \alpha_{\text{COMP}})^{\text{No COMP}}$ ).

These differences in global search effort indicated LB was searching with clear expectations. In particular, they seem to reflect LB's expectations of finding highly prized bread. Due to the ongoing baiting procedure, finding bread was more likely during control trials (when new tubes were present, but no grunts were heard), than after apple trials (when new tubes were present, and grunts given to apples were heard). It was therefore only after hearing grunts given to apples that LB could safely abandon the possibility of finding bread and his overall search effort was accordingly reduced.

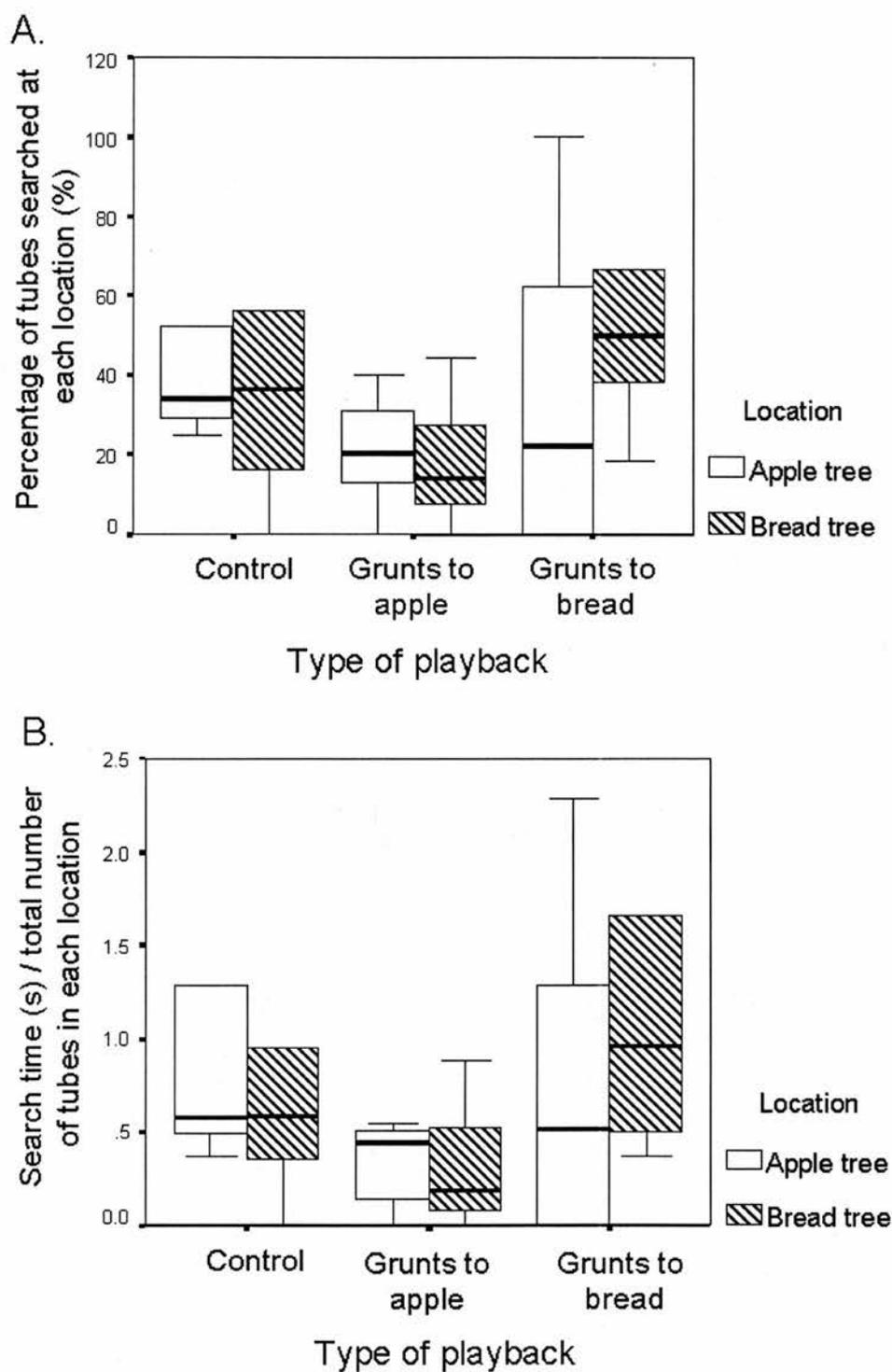


**Figure 6.6. Box plots illustrating (a) number of tubes searched, (b) time spent searching, at both locations, controlling for total number of tubes available.** Illustrated are medians; inter-quartile ranges and highest and lowest values, excluding outliers. Each tube searched was scored as a search event, even if it had been searched previously in the trial (i.e. relative scores could be higher than 100%).

*Deployment of search effort was affected by the type of rough grunts heard by the subject*

In a final analysis I compared the search efforts LB deployed under each tree (two-tailed Wilcoxon-matched pair tests). For control trials, I predicted no difference in search effort under the two trees, which was the case (tubes searched:  $W=21.0$ ,  $p=0.556$ ; search time:  $W=21.0$ ,  $p=0.556$ ). For test trials, I predicted more intense searching underneath the correct tree, i.e. the one referred to by the grunts. This was also the case. After hearing grunts given to apples, LB searched significantly longer and tended to search more tubes underneath the apple than the bread tree ( $W=4.0$ ,  $p=0.028$ ;  $W=5.0$ ,  $p=0.078$ ; Figure 6.7). In contrast, after hearing grunts given to bread, he searched significantly more tubes and tended to search longer underneath the bread tree than the apple tree ( $W=6.0$ ,  $p=0.046$ ;  $W=7.0$ ,  $p=0.074$ ; Figure 6.7).

I conducted a power analysis to assess how meaningful the p-values of 0.10-0.05 were. An a-priori test revealed that in order to achieve a moderate level of power (0.500), a total of 183 trials would have been required (effect size 0.3, alpha level 0.05, 2-tailed t-test, Pitman Asymptotic Relative Efficiency score 0.955 for non-parametric testing). Since the sample sizes for analysis only ranged from 8 to 27 trials the corresponding power levels were much lower, ranging from 0.063 to 0.219. Hence, it seems safe to conclude that the failure to reach significance at the  $\alpha=0.05$  level is attributable to the low statistical power associated with the small number of trials. Simply running more trials on LB was not an option, as in the last weeks he was already beginning to show signs of frustration when responding to playback stimuli (which never lead to finding any food, due to the experimental design). Continuing with more trials would have simply lead to extinction.



**Figure 6.7. Box plots illustrating (a) percentage of tubes searched and (b) time spent searching in each location after hearing playbacks of grunts given to bread or apples.** Illustrated are medians; inter-quartile ranges and highest and lowest values, excluding outliers. Each tube searched was scored as a search event, even if it had been searched previously in the trial (i.e. relative scores could be higher than 100%).

## Discussion

These results have demonstrated that chimpanzees produce acoustically distinct rough grunts to different foods and that a listener can extract information about the nature of a food source encountered by conspecifics by listening to their calls. The focal animal adjusted his foraging behaviour on the basis of the calls he heard, in the absence of any additional contextual information. Crucially, this study was not based on any training or conditioning regime, nor did it rely on artificial segregation of individuals. Instead, animals were given the opportunity to use and respond to vocalisations freely and spontaneously within an ecologically relevant framework.

The results are consistent with the hypothesis that chimpanzee rough grunts are functionally referential signals. Rough grunts appear to meet both the production and perception criteria necessary for functional reference (see Chapter 1, pages 13-14). This study indicates that rough grunts reference food type or food value; however, an alternative hypothesis is possible. The chimpanzees might have learnt to associate rough grunt variants with spatial locations (i.e. grunts given to bread function to reference the gully below the right hand tree, not any aspect of the food). I believe this alternative hypothesis is highly improbable for two reasons. Firstly, as outlined in the methods, page 122, the chimpanzees continued to receive regular scatter feeds that included apples and bread throughout the study period. Rough grunts given to apples and bread were therefore routinely produced by individuals all over the enclosure. This suggests that it was impossible to form a simple association between a particular type of rough grunt and a specific spatial location. Secondly, LB experienced only 7 trials, over the 6-week period prior to the experimental phase, in which he observed others finding baited tubes and giving rough grunts whilst approaching, searching or leaving the corresponding location. Thus, it seems very unlikely that LB could have formed a simple association between the occurrence of one particular acoustic stimulus (e.g. the rough grunts given to bread) and the one particular location (e.g. the area underneath the bread tree); the necessary contingencies were simply not there.

In what ways are these findings of functional reference important for understanding the origins of linguistic reference, a core feature of human speech? As reviewed in chapter 1, non-human primate vocal behaviour, in contrast to speech, is probably not

the result of a conscious desire of individuals to inform one another. In this sense, nonhuman primate signals differ from human speech in an important way: Signallers and recipients may not know that producing a signal is the same as receiving one (Seyfarth and Cheney, 2003). Nevertheless, primate calls can be functionally referential because individuals produce acoustically distinct vocalisations in response to distinct external events. Recipients can therefore infer specific information about external events witnessed by the caller. While this process appears to mirror human semantic capacities from the perspective of the recipient (Zuberbühler et al., 1999), the production of signals may well be driven by a substantial motivational component. Chimpanzees may experience unique psychological states when finding apples or bread, which drive their vocal production more or less directly. Nevertheless, since the grunts vary reliably with the kind of food encountered, the calls obtain functional relevance as referential signals and become meaningful to recipients. The same argument also applies for the better-known cases of the vervet or Diana monkey alarm calls (Seyfarth et al., 1980; Zuberbühler et al., 1999) or the functionally referential food calls of rhesus monkeys (Hauser, 1998). Further work will have to explore the nature of the psychological mechanisms that drive call production. Currently, this study shows that a chimpanzee can infer information about external events from conspecifics' rough grunts, demonstrating that these vocalisations qualify as functionally referential signals.

There are two principal limitations in this study. Firstly, the exact nature of the calls' referents are difficult to describe. Currently, it may be most parsimonious to assume that the grunts were labelling some aspect of food value ('good food', 'bad food'). However, the calls could also be specific to particular food types ('bread', 'apple'). I attempt to address this problem and determine the referential specificity in these calls in the next chapter. Secondly, as explained earlier, because I did not isolate individuals from the rest of the group I could only collect data from one individual. This limits the generality of these findings, particularly because it remains unclear whether the behavioural capacity described is a general feature of chimpanzee communication or an isolated skill of an exceptionally gifted individual. However, given the reports from the wild (Marler and Tenaza, 1977; Goodall, 1986) it is very plausible that these results apply to chimpanzees in general. Lastly, the acoustic analysis performed here was limited as it only dealt with calls to two food types and it

did not rigorously balance the relative input of the three individuals to the data set. This occurred because it was vital to analyse all calls that were used as playback stimuli, in order to check that the stimuli used met the production criterion of context-specificity. A more detailed and thorough acoustic analysis of rough grunts, produced to nine different foods, is presented in the next chapter. Both analyses provide comparable results.

In conclusion, this study has shown that chimpanzees produce acoustically distinct rough grunt variants in response to different foods. Crucially, a listening chimpanzee used the rough grunts to infer the nature of the food discovered by the caller and then used this information to guide his own search for food. The ecologically valid playback experiment presented here is the first to demonstrate that spontaneous chimpanzee communication can be functionally referential.

## **Chapter 7: Rough grunts in chimpanzees: Responses to food types or food preferences?**

### **Summary**

Chimpanzees produce rough grunt vocalisations when encountering food. The previous chapter demonstrated that these calls vary acoustically depending on the nature of the food discovered by the caller and that listeners are able to extract useful information about the food source from these vocalisations. It is unclear, however, whether these calls function to reference food preferences or food types. Here, I investigate this issue by examining whether rough grunt variants are reliably produced in response to (a) specific food types or (b) relative food preferences. I recorded calls from captive individuals in response to nine different food items, which could be ranked as high, medium, or low preference. Individuals consistently produced three acoustically distinct grunt variants to the three food preference classes, but there was no evidence that chimpanzees produced individual labels for food types of low and medium preference. However, calls to high preference food types differed significantly in their acoustic structure. These acoustic patterns remained stable over trials, suggesting rough grunts have the potential to serve as referential labels for individual food types. I was unable to replicate these findings with a set of recordings from the wild, although most other aspects of calling behaviour remained identical. I discuss these discrepancies between the results from the wild and captivity and suggest that referential labels of food items may be a by-product of the special circumstances found in captive settings.

The results of this chapter have been accepted for publication in *Animal Behaviour*: Slocombe, K. & Zuberbühler, K. Accepted. Food-associated calls in chimpanzees: Responses to food types or food preferences? *Animal Behaviour*.

## **Introduction**

Chimpanzees produce rough grunt vocalisations when approaching, discovering and consuming desirable food sources. The previous study indicated that rough grunts are functionally referential calls; however, there is some controversy concerning the nature of the information encoded by chimpanzee rough grunts. The playback experiment presented in the last chapter was unable to distinguish whether rough grunts were referencing food type (apples or bread) or food preference or value (good food or bad food). Another captive study suggested that individuals produce acoustically distinct rough grunt variants to different food types and that these signals served as referential labels for recipients (Hallberg et al., 2003). Both studies are consistent with the idea that chimpanzee rough grunts inform recipients about the type of food encountered by the caller. If chimpanzees were labelling specific food types, then this would represent a rather sophisticated type of functionally referential communication. Not only would the calls have an unprecedented level of referential specificity, but a substantial degree of social learning would also be required both by the signaller and recipient. These attributes would make the rough grunting system more analogous to humans communication than any other system known to date. Alternatively, a more parsimonious hypothesis suggests that the results of these previous studies can also be explained by calls reflecting an individual's relative preference for the food encountered. With this study I examine data from captivity and the wild to test these two hypotheses.

## **Methods**

### *Study sites*

*Edinburgh chimpanzees:* I collected data for four months between May 2004 and September 2004 from a captive group of chimpanzees housed at Edinburgh Zoo, Scotland. The group consisted of 3 adult, 1 sub-adult and 2 juvenile males and 4 adult and 1 sub-adult females, ranging from 5 to 43 years. A full description of the study site and community is provided in Chapter 6, pages 114-116.

*Budongo chimpanzees:* I collected data for 6 months, during the dry seasons (January-March) of 2003 and 2004 from the Sonso community of the Budongo Forest Reserve, Uganda (Reynolds, 1992; 2005). A full description of the study site and community is provided in Chapter 4, pages 55-60.

#### *Data collection*

##### **Food preference hierarchy**

*Edinburgh chimpanzees:* To determine the food preferences of the captive study animals, I systematically tested nine food types (bread, banana, mango, grape, plum, chow, apple, greens and carrot) in pair-wise comparisons. During these events, a caretaker scattered two types of foods in roughly equal amounts throughout the outdoor enclosure. The feeding events were filmed and the first choice of each individual was recorded. The chimpanzees were habituated to the presence of the observer and the video camera before data collection began. I recorded the individuals' choices from a total of 55 feeding events. For each individual, I determined a food preference hierarchy. I counted how many times a particular food item was chosen relative to the other eight food types. These scores were then converted to percentages, ranging from 100% (i.e. always chosen above all other 8 foods), to 0% (i.e. never chosen in comparison to the other 8 foods). The foods were then ranked for each individual on the basis of the percentage scores.

*Budongo chimpanzees:* I identified the three most highly preferred food items during the dry season study period, based on the proportions of their feeding time consuming these items: 30.9% Cynometra alexandri (CYN), 24.3% Ficus exasperata (Fe), 15.6% Ficus sur (Fsu) (data from Bates 2005). It was not possible to objectively determine food preferences in the wild population, in a comparable way to the captive population. However, based on the feeding time data I was confident that the three foods chosen could be ranked as medium-highly preferred foods. I recorded the rough grunts produced by four adult males in response to these three foods.

### Recording rough grunts

For the Edinburgh chimpanzees, rough grunts were recorded from individuals feeding exclusively on one type of food in the outdoor enclosure. For the Budongo chimpanzees, I tried to follow a focal individual all day to record rough grunts whilst the individual was feeding from the three selected species. All recordings were made with a SENNHEISER directional microphone (Wild: ME67/K6; Captive: MKH816) and a SONY TCD-D8 portable DAT recorder. Recordings were transferred digitally from the DAT recorder onto a PC (TOSHIBA, Celeron 1.8GHz) with a sampling rate of 44.1 kHz, 16 bits accuracy using COOL EDIT Pro LE.

### Selection of calls for analysis

*Edinburgh chimpanzees:* I excluded all calling bouts that suffered from heavy interference, either from other chimpanzee calls or extraneous background noise such as other zoo animals or visitors. This resulted in a set of 76 calling bouts, which were suitable for acoustic analysis (range 1-3 bouts per individual per food type). I selected the first 15 seconds of each bout starting from when the focal chimpanzee first made physical contact with the food. Within these segments, I selected the first three calls, which were free from other chimpanzee calls or masking noise. I analysed calls from four different chimpanzees, one from each of the four age sex classes (Louis, adult male; Emma, adult female; Quafzeh, sub-adult male; Kilimi, sub-adult female).

*Budongo chimpanzees:* I recorded calls from four adult males (Black, Maani, Nick and Zefa). This resulted in a total of 38 bouts from the four males (range 1-6 bouts per individual per tree species). As with the captive individuals, I selected the first 15 seconds of a calling bout once the chimpanzee was collecting food or feeding. I then measured the first three calls per bout, which were free from other chimpanzee calls and other masking noise.

### *Acoustic analysis*

Acoustic analyses were carried out using PRAAT Version 4.2.23 ([www.praat.org](http://www.praat.org)) with the following settings: Window length: 0.005 seconds, dynamic range: 70 dB. Rough grunts consisted of both voiced and unvoiced calls. For unvoiced calls, it was impossible to determine the fundamental frequency, so I excluded all measures related

to this, otherwise commonly used, parameter from further analyses. The following four measures could be reliably taken from all calls:

Temporal parameters:

1. Duration of call, (s)
2. Rate of calling in the bout, (calls/s): number of calls divided by the time from the start of the first call to the end of the last call during the first fifteen seconds of the bout.

Spectral parameters:

3. Peak frequency, (Hz): frequency at which most acoustic energy was present in the call.
4. First formant frequency (Hz), the mean frequency of the first formant across the call .

*Statistical analyses*

*Call structure and food preferences*

In order to establish if there was any relationship between the acoustic structure of the rough grunts and individual preferences I analysed a sample of 108 captive calls (4 individuals x 3 preference categories x 3 bouts x 3 calls). Each individual contributed an equal number of bouts for each preference category, but the food types within those categories were chosen randomly. I then ran a multiple regression analysis on the 108 calls with peak frequency, call rate, duration, and first formant frequency as independent variables and the caller's preference for the food item (%) as the dependent variable.

*Call structure and food types*

I analysed high, medium and low preference food types separately in order to minimise the confounding effects of preference. Firstly, rough grunts given to the highly preferred food types, bread, mango and banana, were analysed to investigate whether calls varied reliably with type of food. Each of the four captive individuals contributed one calling bout (containing 3 calls) for each food type. Thus a total of 36 calls were analysed, with each food type represented by 12 calls. Secondly, for the rough grunts given to the medium preferred food types, grapes, plums and chow, each of the four individuals contributed one bout (containing 3 calls) for each food type.

Two exceptions to this were the calling bouts given to plums by Kilimi and Quafzeh, which only contained two measurable calls each. Thus a total of 34 calls were analysed, with grapes and chow represented by 12 calls each and plums represented by 10 calls. Finally, I analysed rough grunts given to the least preferred food types, apples, greens and carrots. The two female chimpanzees were never observed giving rough grunts to greens or carrots, therefore this analysis was based only upon the data from the two males. A total of 18 calls were analysed, with each food type represented by 6 calls.

If an individual had more than one suitable calling bout for each food type I randomly selected the bout to be used (range 1-3). In order to obtain a more representative view of the larger available data set, I generated three randomly chosen data sets for each food type analysis. I thus ran three iterations for each type analysis, which used a wider selection of randomly chosen calls than a single iteration permitted.

The data sets used in the food type analyses were smaller than those used in the first food preference analysis. In order to provide a fair and direct comparison of the two competing hypotheses matching food preference data sets were produced for each of the nine food type analyses (3x 3 iterations). These data sets contained the same number of calls from each individual as each of the 'type' analyses. The calls in each of the 'preference' data sets were randomly selected in the same way reported for the first preference analysis.

I conducted univariate analyses of variance to investigate which of the four acoustic variables varied reliably with the type of food or preference category of food. I then conducted direct discriminant function analyses (DFA) to assess how well the four acoustic variables, when taken together (providing a quantitative description of the sound), could discriminate between the food type or preference associated with the call.

## **Results**

### *Food preference hierarchy*

For the Edinburgh chimpanzees, I tested preferences to all nine foods in all possible combinations, i.e. 36 pair-wise comparisons. Some pairings were tested multiple

times. There was high consistency in individual choices over time, suggesting that individual preferences were stable. The four study animals showed a high degree of agreement on preference, with differences only appearing between individuals for the high preference foods (Table 7.1). On the basis of the mean group ratings, these nine food items were divided into three broad group preference categories: high (67-100%), medium (34-66%) and low (0-33%).

**Table 7.1. The individual food preferences of the four focal captive chimpanzees and the average preferences of this group of four animals.** The percentage associated with each food represents the number of times that food was chosen over the other 8 foods in pairwise comparisons. The ranks are assigned on the basis of the percentages for each individual.

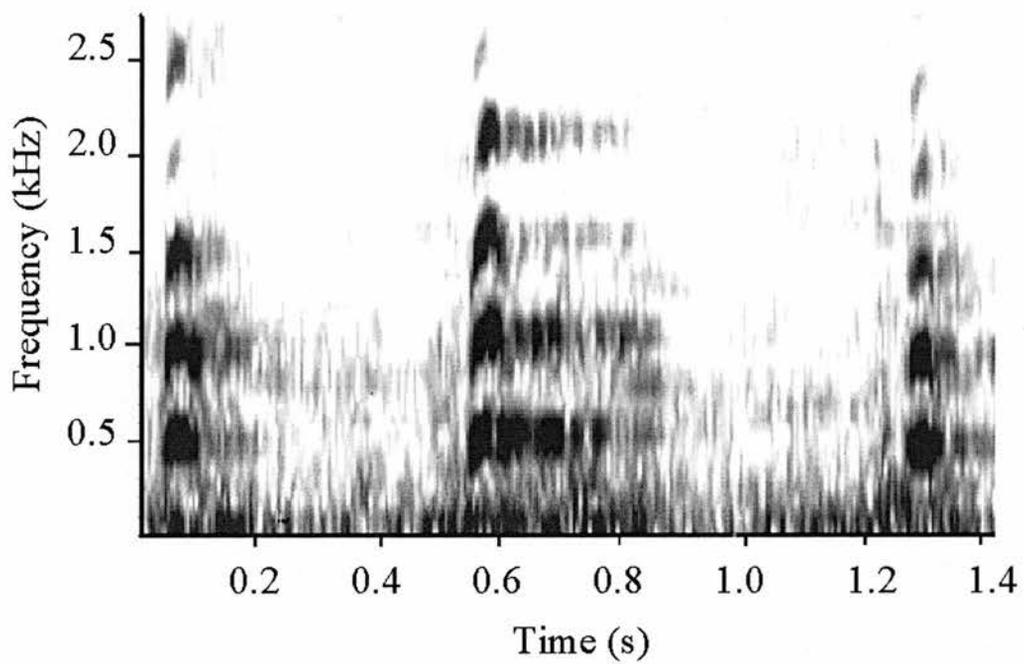
		Group mean		Emma		Kilimi		Louis		Quafzeh	
		%	Rank	%	Rank	%	Rank	%	Rank	%	<i>Rank</i>
<b>High</b>	<b>Bread</b>	95.31	1	100	1	100	1	81.25	2	100	1
	<b>Mango</b>	87.5	2	75	3	87.5	2	100	1	87.5	2
	<b>Banana</b>	76.56	3	81.25	2	75	3	75	3	75	3
<b>Med</b>	<b>Grapes</b>	62.5	4	68.75	4	56.25	4	62.5	4	62.5	4
	<b>Plum</b>	51.56	5	50	5	50	5	56.25	5	50	5
	<b>Chow</b>	37.5	6	37.5	6	37.5	6	37.5	6	37.5	6
<b>Low</b>	<b>Apple</b>	26.56	7	25	7	31.25	7	25	7	25	7
	<b>Greens</b>	12.5	8	12.5	8	12.5	8	12.5	8	12.5	8
	<b>Carrot</b>	0	9	0	9	0	9	0	9	0	9

*Do rough grunts label food preference?*

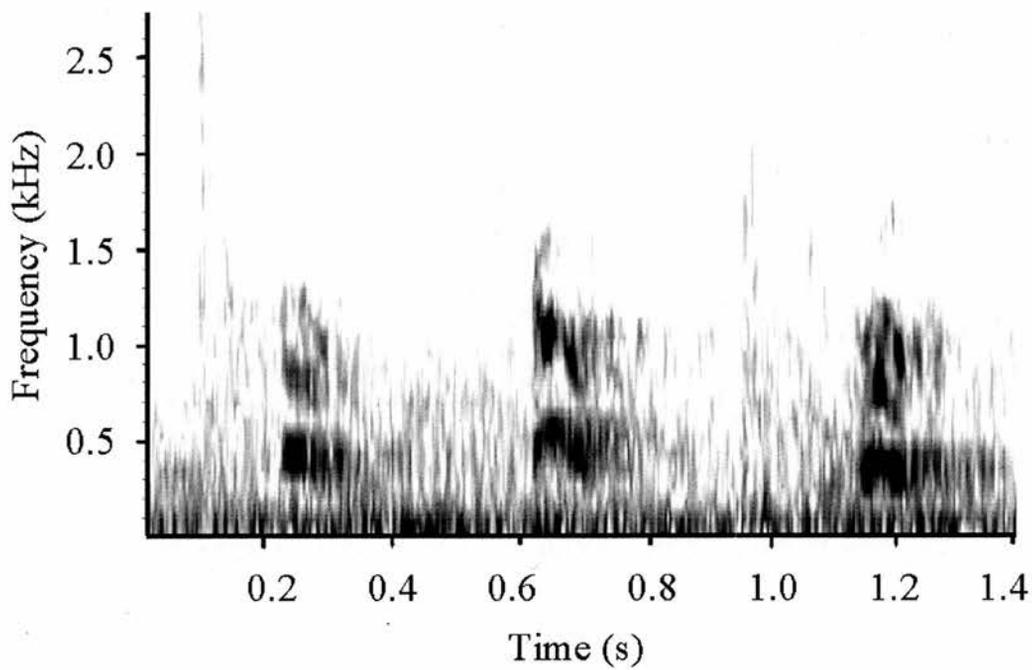
Rough grunts produced in response to foods of different preference categories had subtly, but distinctly, different acoustic structures (Fig. 7.1). Visual examination of the spectrograms indicated that high preference foods elicited calls with a clear harmonic structure, a high peak frequency and a long duration (Figure 7.1a), whereas low preference foods elicited noisy signals with no clear harmonic structure, a low peak frequency and a short duration (Figure 7.1c). Medium preference foods elicit calls with structures that were intermediate to these two variants (Fig. 7.1b).

**Figure 7.1**

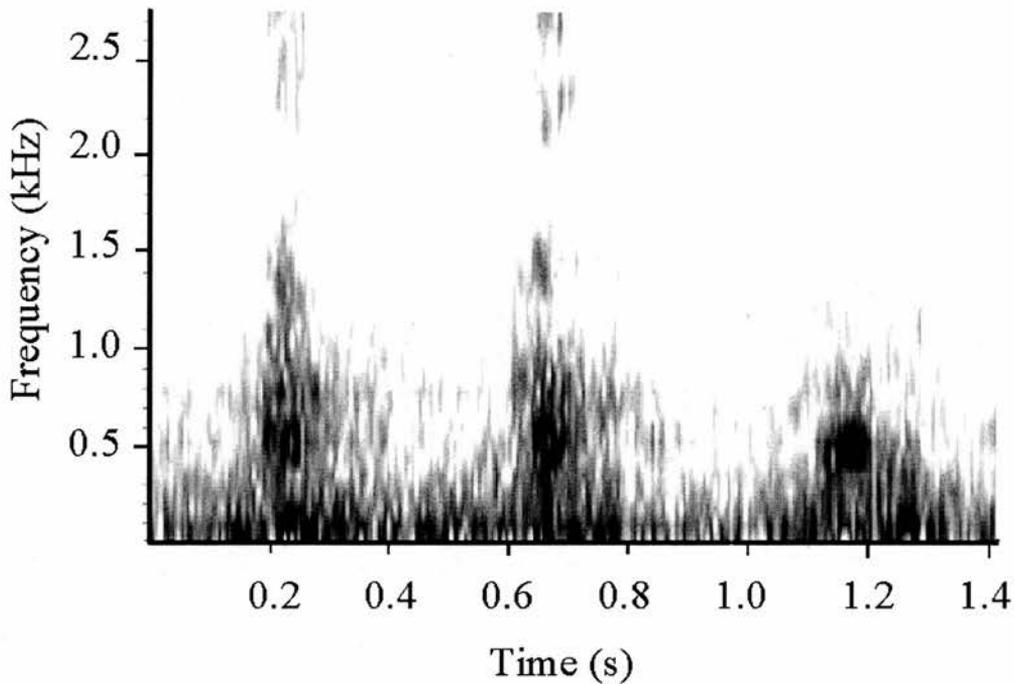
**A.**



**B.**

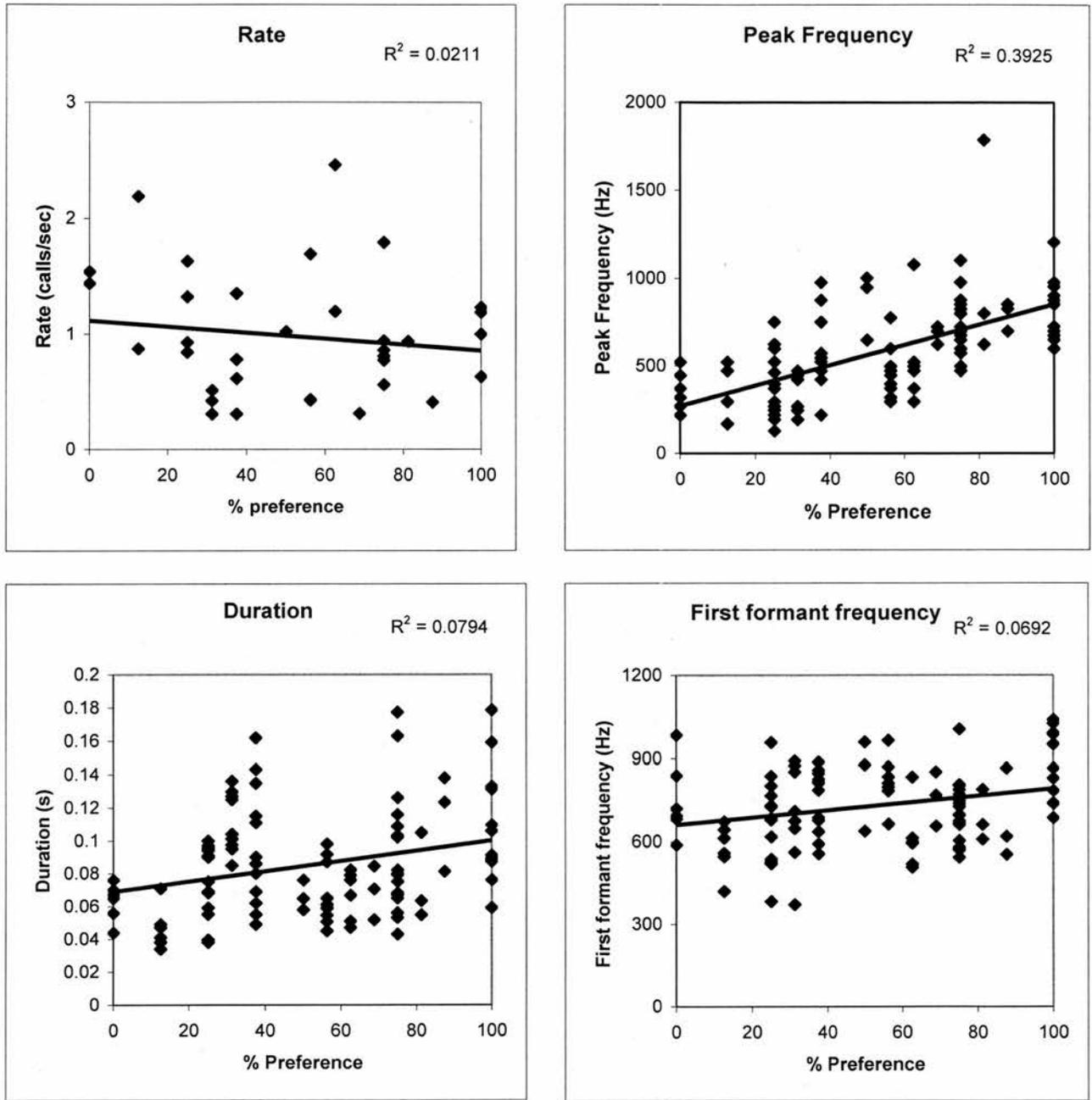


c.



**Figure 7.1. Example spectrograms illustrating rough grunts given by captive adult male Louis in response to (a) bread (b) chow (c) carrots.** Bread was a high preference food, chow was a medium preference food and carrots were a low preference food. The spectrograms depict a representative 1.4 second section of a 15 second calling bout given to bread, chow and carrots respectively. Acoustic energy is depicted by the darkness of the image.

Figure 7.2 further illustrates the graded nature of rough grunt calls. Peak frequency increased as preference increased ( $r^2 = 0.39$ ). Duration ( $r^2 = 0.08$ ) and first formant frequency ( $r^2 = 0.07$ ) also produced positive relationships with preference. There was no obvious relationship between the rate of calling and preference ( $r^2 = 0.02$ ).



**Figure 7.2. Scatterplots showing four acoustic measures, that describe the calls elicited by different foods, plotted against the individual preference ratings for each food (%).** Each data point represents a value from a single call (108 calls in total). Each of the four individual contributed 9 bouts each containing 3 calls.

Multiple regression analysis was run on 108 calls with peak frequency, call rate, duration, and first formant frequency entered as independent variables. The variance inflation factors (VIF) of the variables were less than 1.5, indicating that co-linearity was not a problem. When combined in one model, the variables successfully predicted

the individuals' preference ratings for the food that elicited the grunts ( $F_{(4,103)} = 22.45$ ,  $p < 0.001$ ,  $R^2$  adjusted = 0.445). This indicated that the acoustic structure of the rough grunts varied significantly with individual preferences. Peak frequency made the most important contribution (Beta = 0.587,  $t_{(1,101)} = 7.42$ ,  $p < 0.001$ ), followed by call duration (Beta = 0.144,  $t_{(1,101)} = 1.82$ ,  $p = 0.071$ ). Call rate and first formant frequency did not vary significantly with preference (call rate: Beta = -0.102,  $t_{(1,101)} = -1.347$ ,  $p = 0.306$ ; first formant frequency: Beta = 0.033,  $t_{(1,101)} = 0.413$ ,  $p = 0.741$ ), consistent with the patterns observed in Figure 7.2.

These patterns remained consistent with the smaller preference data sets provided to match the food type analyses. More specifically, calls given to foods of the three different preference categories differed significantly in peak frequency (Table 7.2). In addition, more than half the analyses revealed significant differences in the duration and first formant frequencies of the calls given to foods of different preference categories (Table 7.2). All the discriminant functions, derived from the four variables describing the acoustic structure of rough grunts given to high, medium and low preference food, explained a significant amount of variation between grunts given in response to foods from the three different preference categories (Table 7.2). The functions all correctly classified calls, according to the preference category of food that had elicited them, at a level significantly above that expected by chance (Table 7.2). This confirms that rough grunts given to foods of different preferences have consistently and significantly different acoustic structures.

**Table 7.2. The results of univariate analyses of variance and discriminant function analyses conducted to test differences between and discrimination of the acoustic structure of rough grunts given to foods of different types and foods of different preference categories.**

Analysis	Iteration	F-values from Univariate analyses of variance				Discriminant function analyses			
		Rate	Peak Freq	Duration	F1	Wilks Lambda	X <sup>2</sup>	% correctly classified (x-validated)	Binomial test (0.33) p-value (2-tailed)
HIGH TYPE (N=36)	1	6.147**	4.147*	5.221*	2.413	0.373	31.072***	61.1	0.001
	2	2.087	0.114	1.603	2.385	0.565	18.005*	44.4	0.202
	3	3.859*	0.694	5.872**	4.769	0.346	33.416***	66.7	0.001
	<b>Mean</b>	<b>4.031</b>	<b>1.652</b>	<b>4.232</b>	<b>3.189</b>	<b>0.428</b>	<b>27.498</b>	<b>57.400</b>	
	std dev	2.035	2.180	2.300	1.368	0.119	8.304	11.601	
Matched Preference (N=36)	1	1.714	7.543**	4.954*	3.333*	0.356	32.571***	61.1	0.001
	2	3.078	33.380***	3.146	10.788***	0.259	42.509***	69.4	0.001
	3	1.442	7.552**	3.355*	1.494	0.442	25.710***	61.1	0.001
	<b>Mean</b>	<b>2.078</b>	<b>16.158</b>	<b>3.818</b>	<b>5.205</b>	<b>0.352</b>	<b>33.597</b>	<b>63.867</b>	
	std dev	0.877	14.914	0.989	4.922	0.092	8.446	4.792	
MEDIUM TYPE (N=34)	1	0.715	0.180	5.424*	1.393	0.641	13.118	44.1	0.234
	2	0.634	1.561	1.190	0.780	0.754	8.316	26.5	0.808
	3	0.675	1.053	1.200	1.714	0.793	7.299	30.6	0.540
	<b>Mean</b>	<b>0.675</b>	<b>0.931</b>	<b>2.605</b>	<b>1.296</b>	<b>0.729</b>	<b>9.578</b>	<b>33.733</b>	
	std dev	0.041	0.698	2.442	0.475	0.079	3.108	9.209	
Matched Preference (N=34)	1	1.635	7.929**	4.216*	2.893**	0.356	30.496***	64.7	0.001
	2	0.951	13.290***	0.635	1.839	0.420	25.172**	52.9	0.026
	3	2.875	15.190***	0.791	4.432*	0.398	26.700**	58.8	0.004
	<b>Mean</b>	<b>1.820</b>	<b>12.136</b>	<b>1.881</b>	<b>3.055</b>	<b>0.391</b>	<b>27.456</b>	<b>58.800</b>	
	std dev	0.975	3.765	2.024	1.304	0.033	2.741	5.900	
LOW TYPE (N=18)	1	1.217	0.003	4.454*	3.576	0.380	13.048	50.0	0.228
	2	1.371	0.077	6.596**	2.513	0.378	13.130	50.0	0.228
	3	3.466	0.309	3.922*	3.271	0.324	15.215	50.0	0.228
	<b>Mean</b>	<b>2.018</b>	<b>0.130</b>	<b>4.991</b>	<b>3.120</b>	<b>0.361</b>	<b>13.798</b>	<b>50.000</b>	
	std dev	1.256	0.160	1.415	0.547	0.032	1.228	0.000	
Matched Preference (N=18)	1	15.185***	3.099	4.363*	2.043	0.152	25.449**	77.8	0.001
	2	1.379	24.938***	21.182***	0.770	0.091	32.343***	77.8	0.001
	3	13.079***	5.784*	11.710***	7.499**	0.088	32.763***	72.2	0.002
	<b>Mean</b>	<b>9.881</b>	<b>11.274</b>	<b>12.418</b>	<b>3.437</b>	<b>0.110</b>	<b>30.185</b>	<b>75.933</b>	
	std dev	7.438	11.910	8.432	3.575	0.036	4.107	3.233	

Analysis of variance degrees of freedom: High = 2,33; Medium = 2,31; Low = 2,15

Chi square degrees of freedom = 8

\* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.001

*Do rough grunts label food type?*

Given the high correlation observed between food type and preference rating (Table 7.1), I had to control for preference, in order to investigate whether rough grunts label specific food types. I therefore examined the high, medium and low preference food types separately. I found that different types of high preference foods elicited rough grunts that differed subtly, but significantly, in their acoustic structures. Analyses of variance revealed that bread, banana, and mango calls can vary significantly in their rate, peak frequency and duration (Table 7.2). This variation was sufficient for two of the three discriminant function analyses to correctly classify the calls according to the type of food which elicited them, at a level above that expected by chance (Table 7.2). In contrast, there was no evidence that the rough grunts given to different types of medium or low preference foods differed in their acoustic structures. Only duration differed significantly in some analyses of the three different food types in the medium and low preference categories (Table 7.2). This variation was insufficient to enable the discriminant function analyses to correctly discriminate between calls given to plums, chow and grapes or between calls given to carrots, greens and apples (Table 7.2).

The results obtained so far indicate that chimpanzees may be labelling specific food types, at least within the highly preferred class (bread, banana, mango). For this to be of theoretical importance (i.e. whether calls function as labels for food items), however, acoustic structures need to be consistent from one feeding event to the next. Thus, in the next analysis I compared three separate calling bouts given on separate days to bread and banana for three of the individuals (Emma, Louis and Quafzeh). I analysed a total of 27 calls given to bread (3 individuals x 3 feeding events x 3 calls/bout) and another 27 calls to banana. If the chimpanzees were labelling food types, then there should be no difference between the calls given in response to the three different feeding events. Consistent with this hypothesis, the analyses of variance failed to reveal any significant differences across feeding events in response to bread or bananas in the four acoustic variables (Table 7.3).

**Table 7.3. The results of univariate analyses of variance and discriminant function analyses conducted to test differences between and discrimination of the acoustic structure of rough grunts given to bananas and bread across three different feeding events.**

Analysis	F-values from Univariate analyses of variance				Discriminant function analyses			
	Rate	Peak Freq	Duration	F1	Wilks Lambda	X <sup>2</sup>	% correctly classified (x-validated)	Binomial test (0.33) p-values (2-tailed)
Bread	0.918	2.420	0.068	0.873	0.542	13.766	44.4	0.290
Banana	0.012	1.135	0.699	0.471	0.835	4.055	37.0	0.810

Analyses of variance degrees of freedom: 2,24

Chi square degrees of freedom = 8

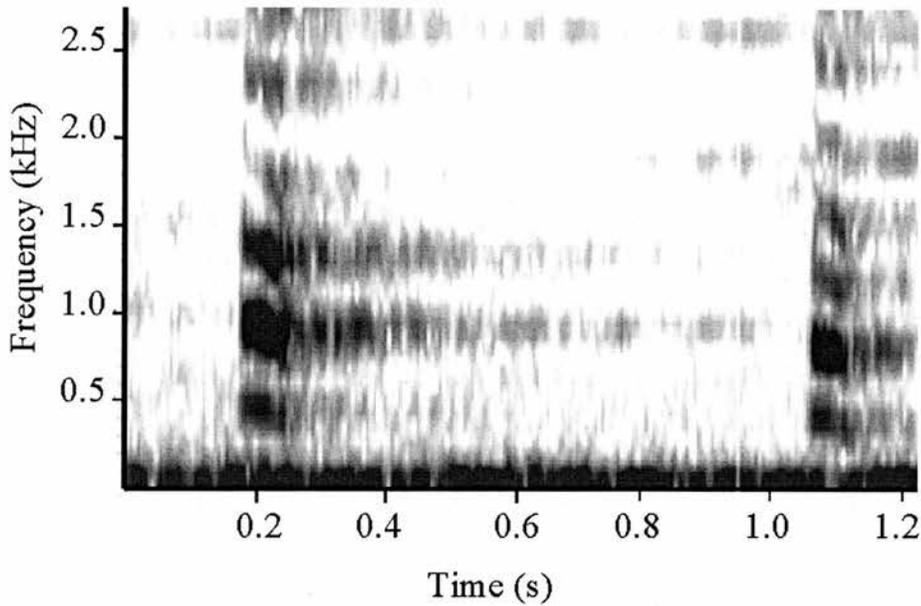
\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$

A discriminant function analysis was equally unable to account for a significant amount of the variance between calls given to bread or banana over three different feeding events. The functions could not correctly classify calls according to the feeding event they were given in at a level above that expected by chance (Table 7.3).

#### *Food-associated calls in wild chimpanzees*

A major criticism of work with captive animals is that findings may not be ecologically relevant. This is of particular concern for scientific problems of an evolutionary nature, for example those relating to the cognitive bases of language evolution. I therefore analysed a set of rough grunts recorded from wild chimpanzees in Budongo forest, Uganda, during natural feeding events. The data set composition was identical to the high preference data set from the captive individuals, allowing direct comparisons.

Rough grunts recorded from the wild chimpanzees, in response to the top three food species during the study period, were acoustically very similar to the ones given by captive chimpanzees to high or medium preference foods (Figures 7.1, 7.3; Table 7.4).



**Figure 7.3. Example spectrogram illustrating rough grunts given by wild adult male Black in response to *Ficus exasperata*.** The spectrograms depict a representative 1.2 second section of a 15 second calling bout given whilst feeding on *Ficus exasperata*. Acoustic energy is depicted by the darkness of the image.

The mean peak frequency and duration of these wild calls were intermediate to the mean values of calls given to high and medium preference foods in captive individuals. In addition, the first formant frequency of wild calls matched values obtained from grunts given to high and medium preference foods in captivity. Wild chimpanzees, however, gave rough grunts at a faster rate than captive chimpanzees (Table 7.4).

Our previous analyses showed that captive chimpanzees gave acoustically distinct rough grunt calls to three highly preferred food types. However, I found no evidence that the rough grunts elicited by CYN, Fe and Fsu fruits differed in peak frequency ( $F_{(1,33)} = 1.666$ ,  $p = 0.205$ ), duration ( $F_{(1,33)} = 1.999$ ,  $p = 0.151$ ) or first formant frequency ( $F_{(1,33)} = 0.297$ ,  $p = 0.745$ ). The only parameter that differed significantly between the three food types was call rate ( $F_{(1,33)} = 3.931$ ,  $p = 0.029$ ). A discriminant function analysis was unable to account for a significant amount of variance between calls given to the three food types (Wilks Lambda = 0.642,  $X^2 = 13.953$ ,  $p = 0.083$ ). The function only correctly classified 44.4% calls (cross-validated) according to the type of food that elicited them; a level expected by chance (Binomial (0.33),  $p = 0.202$ ).

**Table 7.4. The mean values of the four acoustic variables, as measured for the three wild food types and the captive high and medium preference food types.** The mean of all preference categories in the captive population and the mean of all the wild food types are provided.

		Peak freq	Duration	First Formant Frequency	Rate
<b>Captive</b>	Bread	1085.50	0.13	813.35	1.09
	Mango	743.50	0.09	688.18	1.26
	Banana	763.42	0.13	715.18	0.84
	<b>High Mean</b>	<b>864.14</b>	<b>0.12</b>	<b>738.91</b>	<b>1.06</b>
	Grapes	569.50	0.06	699.98	0.81
	Plums	624.20	0.07	788.10	0.99
	Chow	579.83	0.10	747.92	0.76
	<b>Med mean</b>	<b>591.18</b>	<b>0.08</b>	<b>745.33</b>	<b>0.85</b>
	<b>Low mean</b>	<b>358.72</b>	<b>0.06</b>	<b>643.15</b>	<b>1.30</b>
<b>Wild</b>	CYN	683.25	0.07	759.50	1.38
	FE	698.58	0.10	753.33	1.84
	Fsu	789.42	0.16	788.92	1.53
	<b>Wild mean</b>	<b>723.75</b>	<b>0.11</b>	<b>767.25</b>	<b>1.58</b>

## Discussion

This study demonstrates that chimpanzees produce rough grunt calls with different acoustic structures according to the relative preference of the food encountered. Rough grunts varied systematically with food preference, which consistently accounted for more of the variance in the acoustic structure of the calls than the type of food. Differences in preferences affected the peak frequency and duration of rough grunts, with highly preferred food eliciting long harmonic signals with high peak frequencies, while least preferred food elicited short signals with low peak frequencies. Medium preference foods elicited calls with an acoustic structure intermediate to these two call variants.

My data from the wild population of Budongo Forest showed that the rough grunts given to high preference foods were acoustically equivalent to rough grunts given by captive chimpanzees to medium or high preference foods. This provided the captive results a degree of ecological validity. More complex comparisons were not possible due to the difficulties in accurately assessing food quality or preference in the wild.

Although the psychological mechanisms underlying call production are not well understood, my data suggest that calling behaviour may not be a simple function of the excitement experienced by the animal when discovering a particular type of food. In chickens and some new world primates, calling rates are directly dependent on the quality of food (Gyger and Marler, 1988; Elowson et al., 1991; Gros-Louis, 2003), suggesting that calling behaviour could be directly driven by the excitement experienced by animals discovering a highly preferred food. Surprisingly, in chimpanzees, call rates were unaffected by food preference, suggesting that no such direct link exists. The rough grunt system may thus be more analogous to the macaque monkey calling system where call type varies acoustically with food preference, while call rate is mediated by hunger (Hauser et al., 1993). Of course, I cannot exclude the possibility that differences in excitement still mediate the frequency or the type of call produced in both chimpanzees and macaques.

This study also revealed that captive chimpanzees produce acoustically distinct rough grunts to different types of high preference food, suggesting a process of vocal individuation for food items. Comparable findings were not available for rough grunts given to medium or low preference foods, suggesting that individuals only make fine-grained distinctions between highly preferred foods. Calls produced to the highly preferred foods bread and bananas were structurally consistent across feeding events, suggesting that these calls could provide recipients with reliable labels for specific food types. The fact that rough grunts are graded signals does not preclude call variants from serving as referential signals. As reviewed in chapter 3, pages 31-2, animals can perceive acoustically graded calls as discrete units (e.g. Fischer et al., 2001).

Our findings thus seem to support the interpretation that rough grunts can function as labels for particular food items (Hallberg et al., 2003), although ecologically valid playback studies are needed to elucidate the exact informational content of these calls from the listener's perspective. It is, however, important to note that I was unable to find comparable results with data from the wild. There was no evidence that the Budongo chimpanzees used acoustically distinct labels for different types of highly preferred foods. Why then were the captive chimpanzees able to do this? I can think of at least three explanations for this. Firstly, my preference judgments for the three foods in the wild may have been inaccurate. I had no way of objectively testing food preferences in the wild and although proportion of time spent eating certain items is accepted as a good index of preference it has limitations. It cannot be used to determine relative preferences of common and rare foods, or the preference of foods eaten in the study period compared with those available at other times of the year. The categorisation of the three species of food as 'high preference' may therefore have been an overestimate. Rough grunts produced to these three foods fell somewhere in between the grunts given by captive individuals to high and medium preference foods, supporting this view. If the three foods were in fact only of medium preference then, in line with the captive findings, I would not have expected to see any differentiation between food types.

A second, and perhaps more parsimonious, explanation suggests that the previously proposed process of vocal individuation for food items is an unlikely event in wild due to the immense variation in food sources encountered by individuals. The situation in captivity is very different because food availability, quality and quantity are very predictable. During the study period the captive population regularly received 20 different foods in sufficient quantities for all individuals to be able to obtain some. They received four food types every day, eleven food types at least once a week and five other food types at least once every month. The food was always of high quality (fresh, ripe) and the quantity only varied between a whole and half a bucket. In addition, individuals in captivity could always see all other members and observe their choices and calling behaviour closely. In contrast, in the wild the quality, quantity and availability of food is very variable. The quality of a food source is reliant on the ripeness of the fruit or the age of the leaves. The quantity of the food source is determined by the size of the tree or food patch and also its state of depletion. Foods

are usually highly seasonal (e.g. *Cynometra alexandri*) or follow unpredictable fruiting patterns (e.g. *Ficus* species). This means that the probability of obtaining a certain food has to be tracked over seasons, not just a few weeks, or it is highly unpredictable. In addition, wild chimpanzees forage over a large home range, in a fission-fusion social system, often in a low-visibility habitat; it is therefore not possible for individuals to observe all the feeding choices and calling behaviour of all community members, as it is in captivity. The scale of variation that wild chimpanzees are confronted with in terms of number of food types (e.g., tree species, fruits, leaves, flowers), quality (e.g. ripeness), quantity (e.g. patch size, depletion state) and availability (e.g. seasonal variation) is simply enormous. In light of these factors the emergence of individualised food labels seems to be a rather unlikely event. In contrast, for captive animals food type automatically becomes the key factor in determining the relative value of a food source, since all other variables remain fairly constant. This may explain why I was able to associate some acoustic variants with particular food types (Table 7.2).

Third, it may not even be necessary for individuals in the wild to provide individual labels for particular food types. It has repeatedly been suggested that wild chimpanzees possess sophisticated knowledge of the distribution of key food trees throughout their home range (Goodall 1986; Boesch & Boesch-Achermann 2000; Bates 2005). A communication system capable of encoding the relative value of a food source, rather than the actual food type, may thus be adequate since experienced listeners may be able to infer the type of food from the location of the caller.

In sum, the findings are probably most compatible with the idea that captive chimpanzees can converge on idiosyncratic semantic conventions, in which particular rough grunt types become meaningful labels by referring to specific food items, such as bread or bananas. However, this may only be possible in a setting where most aspects of feeding events are predictable and regular and the type of food becomes the principal determinant of food value. When the differences in the relative preferences for foods are sufficiently large, as bread, mango and banana were in this study group, a preference driven calling system can differentiate between them. Equally, these differences in calling can become meaningful to listeners in captivity because individuals usually eat in sight of one another and can observe individual food choices

and calling behaviours. It therefore may be possible for listeners to infer the type of food referenced by a call, although it is still essentially a marker of relative food value.

In conclusion, chimpanzees produce rough grunts with acoustic structures that vary as a function of preference for the food they discover. In the restricted setting of captivity this system can obtain naming functions, in which calls may refer to particular types of foods. Data from the wild show a broad similarity between the calling behaviour of wild and captive chimpanzees, providing the captive results with ecological validity. However, unlike the captive chimpanzees, there is no evidence that wild chimpanzees produce acoustically distinct calls to different food types. In the wild, the exact meaning of calls may be the product of call type and context (e.g. Smith 1977).

## **Chapter 8: General discussion**

### **Summary**

This chapter brings together the findings from the previous four chapters and reflects on how this research has helped to answer the main question posed: Do chimpanzees produce and understand functionally referential calls as part of their natural communication?

I discuss how vocal communication and this research relates to other better-studied aspects of chimpanzee behaviour and cognition. I consider the relevance of this research for understanding the complexity of other chimpanzee behaviours and reflect on the possibility that chimpanzees may communicate intentionally and deceptively.

Finally, I examine the impact these findings may have on the evolution of language debate. Specifically, I discuss my research in the light of the vocal and gestural theories of language evolution. I explore the nature of future work that is needed to strengthen the body of empirical evidence that could ultimately help elucidate the origins of human language.

## **Do chimpanzees produce and understand functionally referential calls as part of their natural communication?**

As discussed in chapters 1-3, there is a startling absence of evidence for functionally referential signals in the natural communication of great apes. I aimed to address this anomaly by examining the natural vocal communication of wild and captive chimpanzees. Chimpanzees have a graded vocal repertoire, containing at least 13 call types. I chose to focus on two call types: agonistic screams and rough grunts. Both of these call types appeared to be promising candidates for functionally referential signals. There seemed to be an evolutionary advantage for chimpanzees to be able to communicate with kin and allies about the nature of both a discovered food source and ongoing agonistic interactions. In addition, previous work with rhesus monkeys indicated that screams and food-associated calls could function referentially (Gouzoules et al., 1984; Hauser, 1998).

### *Agonistic screams*

Agonistic screams are acoustically variable signals and my observational work has demonstrated that chimpanzees use this variation systematically to produce acoustically distinct calls in specific social contexts (chapters 4, 5). I found systematic differences in the acoustic structure of screams given by victims and aggressors, meaning the production of these calls was specific to the social role the caller played in the conflict (chapter 4). The acoustic structure of victim screams varied systematically with the severity of the attack experienced by the victim (chapter 5).

From the signaller perspective agonistic scream variants appear to be acoustically distinct signals that are given in context-specific ways. Thus, they have the potential to encode information about external events to listeners. This observational work, conducted in the wild, complements the research into context-specific bark calls in the chimpanzees of the Taï Forest (Crockford and Boesch, 2003). This research revealed that chimpanzees produce acoustically distinct barks when encountering snakes and whilst hunting. Barks and now screams have been identified as excellent candidates for functionally referential signals. Unfortunately it has not been possible to test recipient responses to these calls and without this information, it is impossible to state conclusively that these signals function in a referential manner.

Despite the absence of formal testing, behavioural observations indicated that listening chimpanzees were able to extract meaningful information about an ongoing fight from listening to the screams of the protagonists. For instance, on 28<sup>th</sup> October, 2003 I observed the following event: The adult male 'Nick' attacked the adult female 'Wilma' who gave victim screams. Once Nick relented, Wilma then began charging and lunging at Nick, whilst giving aggressor screams. Nambi, the alpha female, then appeared and joined Wilma in attacking Nick. After retaliation from Nick, the females succeeded in chasing him away. A fellow researcher who had followed Nambi to the scene of the fight confirmed that she could not have seen the beginning of the fight when she began her approach. This indicated she had based her decision to come and intervene on the available auditory information: the screams. Unfortunately, I was only able to collate a couple of observations like this, as it was very rare that a second observer was able to confirm that the third party individual had approached from out of sight of the fight. During most observations of third party interference, I was unable to exclude the possibility that they were reacting to visual cues, rather than the information gained from listening to the screams.

In order to address the perception criteria of functional reference, systematic data need to be collected on recipient responses to these different scream variants. A promising preliminary step towards this critical goal would be to collect more systematic responses to naturally occurring fights. Several observers would be required for this to increase the chances that data on the identity and roles of the fighting individuals were known and could be matched to the reactions of a focal individual. Ultimately, playback experiments testing whether recipients can extract information about the role of the caller and the severity of the attack suffered by the victim are needed. Given the potential difficulties with conducting playback experiments with such potent social stimuli in the wild, captivity perhaps presents a more suitable environment in which to conduct such experiments.

In conclusion, this research has provided ecologically valid evidence from the wild that chimpanzees produce acoustically distinct scream variants in specific social contexts. Although behavioural anecdotes indicate that listeners can access the referential information encoded in these calls, more systematic observations of

recipient responses in the wild, in conjunction with playback experiments, are needed to confirm that these calls function referentially.

### *Rough grunts*

The acoustic variation in this call type and its context specific production has been previously documented (Marler and Tenaza, 1977; Goodall 1986; Hauser and Wrangham, 1987). This research indicated that the chimpanzees reliably gave acoustically distinct rough grunt variants in response to foods of different quality: high preference foods elicited long, high frequency, tonal calls and low preference food elicited short, low frequency, noisy calls (chapters 6, 7). Although in captivity this preference driven calling system discriminated between some high preference food types, I was unable to find comparable results in the wild (chapter 7). The rough grunts given by wild chimpanzees to three high preference food types did not vary in acoustic structure, although the calls were similar in structure to the those produced by the captive population to high or medium preference foods. Further systematic investigation of rough grunts in wild populations may eventually yield comparable findings, but it currently seems most parsimonious to conclude that this high level of referential specificity was an artefact of captive living. It is not possible to present wild chimpanzees with alternate choices as it is in captivity and currently methods of quantifying the quality of food sources in the wild are subjective or inadequate. In order to successfully address this issue in the wild, a new way of quantifying food quality in the wild needs to be developed.

From a signaller perspective, acoustically distinct rough grunt variants were produced in response to foods of different values. Thus, although the system is graded, the grunt variants were produced in a context specific manner. In contrast to the research on screams, I was able to systematically address the perception criteria of functional reference with the rough grunt calls. I conducted a naturalistic playback experiment with a captive population which revealed that a listening chimpanzee could infer information about the kind of food a caller had discovered, from their rough grunt calls (chapter 6). This provided the first evidence that chimpanzee calls can satisfy all of the established criteria for functional reference. Future studies should aim to replicate this finding with a larger sample size to clarify that this finding is representative of the larger population.

As discussed in chapter 6 and 7, the exact nature of the referent of these rough grunt calls remains uncertain. The observational evidence of signaller behaviour indicated that rough grunts function to refer to food quality, through a preference driven system. However, the exact meaning extracted by the listener remains unclear. Future research needs to address this issue of referential specificity from the receiver perspective with playback experiments.

In conclusion, this research has begun to answer the question of whether chimpanzees use functionally referential calls as part of their natural communication. I have provided evidence of functional reference with an investigation of chimpanzee rough grunt calls. My research has also demonstrated that agonistic screams satisfy the production criteria of functional reference, making them excellent candidates for functionally referential signals. Chimpanzees seem capable of functionally referential communication and future research may build on these findings to elucidate the details of the referential specificity of these calls and perhaps reveal more call types that function in a referential manner.

### **Chimpanzee communication and cognition**

Our current understanding of chimpanzee vocal communication is very poor (Chapter 3). We lack an objective, acoustic based classification system for their complex graded vocal repertoire and we know very little about how they use their calls and the cognitive abilities that underlie vocal production and comprehension. The demonstration of functional reference in the chimpanzee vocal system indicates that signallers are producing calls in a predictable and context-specific manner and that receivers can extract important information about their environment from the calls of others. This research will hopefully inspire future work on chimpanzee vocal communication, which will enhance our understanding of this hitherto neglected area of chimpanzee behaviour. The considerable research effort that has been devoted to many other aspects of chimpanzee behaviour has produced findings that indicate that chimpanzees are a cognitively advanced species (e.g. Tomasello et al., 2003). I therefore suggest that their sophisticated cognition may also influence their vocal communication. I will now briefly outline the key areas of cognition that have

provided evidence to fuel the assumption that chimpanzees are special and cognitively advanced.

Chimpanzees seem to have an excellent understanding of the physical world that surrounds them, and it has been suggested that they possess causal understanding of actions (Horner and Whiten, 2005), as well as a capacity for insightful problem solving (Köhler, 1925). Chimpanzees also select and modify tools to aid them in a number of different situations. Chimpanzees use tools to aid potentially difficult or painful foraging tasks including drinking (Goodall, 1986), and extracting termites (McGrew et al., 1979), ants (Goodall, 1964), honey (Goodall, 1986) and nut kernels (Sugiyama and Koman, 1979). Tool use appears to be planned, as suitable tools are often carried some distance to the foraging site. For example Taï chimpanzees are reported to transport suitable hammer stones hundreds of metres to nut cracking sites (Boesch and Boesch-Achermann, 2000). A number of reports also indicate that chimpanzees use a 'tool kit' for complex tasks, such as extraction of honey from usually impenetrable nests of Meliponni bees. In this situation three different types of tools (chisel, bodkin and probe) are used in sequence to break into the nest and extract the nutritious honey (Brewer and McGrew, 1990; Bermenjo and Illera, 1999). Tool use also extends beyond the procurement of food: Chimpanzees use a variety of tools to attend to their bodies: sticks to clean and maintain others' teeth (McGrew and Tutin, 1973), leaves to dab bleeding wounds and to clean their ano-genital region (Goodall, 1986) and in one instance twigs were used to elicit sneezing to clear nasal blockages (Nishida and Nakamura, 1993). Leafy twigs are used as fly whisks (Boesch and Boesch-Achermann, 2000) and sticks and stones are used as weapons against predators and non-compliant conspecifics (Goodall, 1986).

It is not only in interactions with the physical world that chimpanzees have demonstrated remarkable skill. Chimpanzees live in a complex fission-fusion social society, so it is no surprise perhaps that they also show advanced levels of social cognition. Chimpanzees appear to understand the distinction between other and self, as they normally pass the mirror self-recognition test (Gallup, 1970). They also seem to have some understanding of the visual perspectives of others (Hare et al., 2000) and they can extrapolate lines of gaze (Tomasello et al., 1999). These abilities may enable chimpanzees to tactically deceive one another. Tactical deception has been defined as

“acts from the normal repertoire of the agent, deployed such that another individual is likely to misinterpret what the acts signify, to the advantage of the agent.” (Byrne and Whiten, 1992, p. 612) and it includes behaviours such as concealment and distraction. A review of observational records of tactical deception revealed that chimpanzees demonstrated this type of behaviour more than most other well-studied primate species (Byrne and Whiten, 1992). Observations of intentional deception, where the agent had insight into the beliefs of the victim, numbered only eighteen and these were all attributable to chimpanzees and other great apes (Byrne, 1995). Recent evidence from behavioural experiments has corroborated the view that chimpanzees understand something about what others know (Hare et al., 2001). Together this evidence indicates that chimpanzees have a rudimentary theory of mind.

Many of the skills adult chimpanzees possess are complex and have to be learnt. For instance, in the Tāi Forest, chimpanzees are reported to hunt cooperatively (Boesch and Boesch-Achermann, 2000). Chimpanzees who block or ambush the hunted monkey need to learn to anticipate the speed and direction of the monkey’s escape route, in order to be in the correct place to effectively contribute to the hunting effort. In this context, learning these skills seems to be done progressively over as many as twenty years. The mechanisms that mediate learning in chimpanzees have been the subject of much research. Although there are a few anecdotal observations of active teaching of nut cracking by mothers to juvenile offspring (Boesch, 1991c), it is generally accepted that active teaching does not play a significant role in chimpanzee skill acquisition. Chimpanzees can certainly learn individually through trial and error, but a more powerful mechanism appears to be available to them, which allows them to acquire skills socially, through observational learning (Whiten et al., 2004). The strength of social influences on learning in chimpanzees means that even when members of a group find a valid way of solving a novel task individually, they revert back to using the common group technique; thus conforming with their group members (Whiten et al., 2005a). The ability of chimpanzees to learn through social mechanisms vastly increases the number of complex skills they can acquire in a lifetime (Whiten et al., 2005b) and it also leads to local traditions or ‘cultures’ within different communities of chimpanzees (Whiten et al., 1999; Whiten et al., 2001). This has been observed both in terms of material culture (McGrew, 1992) and social

customs, such as handclasp grooming (McGrew et al. 2001) and social scratching (Nakamura et al., 2000).

Chimpanzees have also shown remarkable abilities in mastering artificial, human taught languages. After the initial failure of trying to teach chimpanzees to articulate human words (Hayes, 1951), considerable success has come from teaching chimpanzees sign language (Washoe; Gardner and Gardner, 1969) or artificial symbol based languages (Sarah; Premack and Premack, 1972; Lana; Rumbaugh, 1977). The ability of these individuals varied, but Washoe, for instance, learnt over 130 signs in her first five years of life. These chimpanzees were able to associate symbols or signs with objects and actions, and use them in simple sequences to request food items or initiate play and tickling. These projects working with common chimpanzees used reinforcement regimes to explicitly teach the apes the meaning of symbols. These studies can tell us how well a chimpanzee can be conditioned, but they do not tell us very much about what chimpanzees naturally communicate about. In contrast, the project involving the bonobo Kanzi has never used systematic teaching and reinforcement; simply being exposed to the use of the lexigram keyboard and human speech from birth has enabled this individual to spontaneously acquire an understanding of spoken English and the use of over 250 symbols (Savage-Rumbaugh et al., 1986). As mentioned previously, Kanzi has an understanding of human semantics and syntax surpassing that of any other language trained ape (Savage-Rumbaugh, 1993); equivalent to that of a two and a half year old child. This project reveals the potential of the cognitive capacities of this remarkable individual that has been raised in an optimum environment for language acquisition. Unfortunately, these conditions were not available to our last common ancestors, so ecologically valid research into naturalistic communication is still needed to aid our understanding of human language evolution.

How does my research relate to this considerable body of literature, which suggests that chimpanzees possess advanced cognitive abilities in both the material and social world? The natural vocal communication of these tool-using, deceptive, insightful, social learners seems remarkably basic in comparison to their otherwise advanced social cognition. Even if, as my research suggests, chimpanzees are communicating with functionally referential signals, this is an ability shared with many monkey

species. In most other spheres of behaviour chimpanzees are significantly more capable than their monkey cousins (Byrne, 1995). So why are comparable findings of complex cognition not available in the realm of vocal communication? It could be that vocal communication is just not important to this species and that the relevant selective pressures have not been present to shape the vocal behaviour into a complex system. However, chimpanzees are a highly vocal species, with vocalisations given in most behavioural contexts, so it is hard to believe that they are irrelevant or unimportant. In addition, the habitat, social structure and daily difficulties facing chimpanzees, in terms of finding food, defending a territory and avoiding predation, mean that a complex communication system would endow these advanced animals with a considerable evolutionary advantage. As noted before, a startlingly small amount of research effort has been dedicated to the study of chimpanzee vocal behaviour. I propose that the highly graded nature of their vocal system combined with the lack of vocal plasticity and imitation in this species has led many to dismiss the topic as too difficult to study and unworthy of systematic investigation. Until much more empirical research is conducted on this topic, I believe it is far too early to conclude that chimpanzee vocal communication is basic and uninteresting, in comparison to other elements of their behaviour and cognition. My research has revealed several findings, such as functional reference and the potential for intentional signalling that contradict the view that chimpanzee vocal behaviour is cognitively uninteresting. I suggest that more work on this topic will yield more stimulating findings that could eventually provide the currently missing links to the existing literature on the advanced cognitive abilities of this species.

This research has highlighted the possibility that chimpanzee signallers are calling with sensitivity to the composition of their audience. In particular, victims seem to alter the acoustic structure of their screams as a function of whether high-ranking individuals are present who could effectively stop or punish the aggressor (chapter 6). Third party intervention occurred more when victims suffered high-risk aggression. As the screams given when high-ranking bystanders were present mirrored the screams given to high-risk aggression there is a possibility that the victims were signalling dishonestly in order to increase the chances of third party interference. This highlights the benefits of studying functional reference: it allows more complex communication issues to be probed. The study of intentionality in signalling and

ultimately the possibility of deception in vocal behaviour is only possible once we have a good understanding of what the calls mean to recipients and what responses they evoke. Intentionality and deception are extremely important and exciting issues in the study of communication, due to the complexity of the cognitive mechanisms assumed to underlie them. Unfortunately, neither is well understood in the field of animal communication, but this research has highlighted chimpanzees as a species that definitely warrants further investigation. There are still only a limited number of anecdotal examples to support the notion that chimpanzees are capable of intentional deception (Byrne, 1995). Ultimately, vocalisations may prove to be an ideal way to further investigate this issue in chimpanzees.

My research may have implications for the study of many aspects of chimpanzee behaviour, as some of the results presented here suggest that chimpanzee listeners may be able to draw inferences about their social and ecological world that they cannot see. We may have previously underestimated the role information about distant events, gained from auditory cues, has on the behaviour of these animals. Effective monitoring of third party relationships may be possible simply by listening to screams and submissive and affiliative calls made by others. Knowledge of the presence and quality of food patches may be obtained from the calls of others and this information may affect future travel patterns and foraging behaviour. Previously it has been accepted that interparty vocalisations aid co-ordination of travel between distant individuals (Goodall, 1986), but it is plausible vocal behaviour provides individuals with much more complex information about social interactions and food patches. In addition, chimpanzees may not respond to this information immediately; they may remember it and use this knowledge base to guide their future decisions and behaviour. This poses a potential problem in studying the importance of information gained about distant events through the auditory channel, as responses may not be executed immediately. It may be necessary to conduct focal observations lasting several days in order to begin to assess the influence information extracted from others calls has on the natural behaviour of listening chimpanzees.

In conclusion, this research has furthered our understanding of both signaller and receiver behaviour in chimpanzees. Our current understanding of the complexity of vocal behaviour indicates it falls short of that found in many other aspects of

chimpanzee cognition and behaviour. However, my research has revealed some promising aspects of chimpanzee vocal behaviour. I believe in the future, with more research effort on the topic, we may discover chimpanzee vocal communication shares the complexity of many other aspects of chimpanzee cognition. In particular, the issue of signaller intentionality and potential for deceptive vocal behaviour is a very exciting prospect. My research also indicates that numerous aspects of chimpanzee behaviour could be influenced by the ability of listeners to extract information from the calls of others; a possibility researchers may have previously overlooked.

### **Evolution of Language**

Finding an evolutionary explanation for the origins of human language is an extremely difficult challenge. Spoken language has left no fossil remains and very few clues as to when and how it emerged. Deacon aptly summarises “it is a mystery with all the fingerprints wiped off.” (In Holden, 2004, p.1316). It is unsurprising, therefore, that extensive speculation has led to the proliferation of a great number of theories of language evolution. Many different origins for modern language have been suggested, including vocal grooming in social groups (Dunbar, 2003), production of motherese (Falk, 2003) and aimed throwing of objects (Bingham, 1999). Although elements of many of these theories are appealing, they deal with the pressures that drove language evolution in our hominid ancestors, and do not discuss the details of how the different elements of language evolved. In this chapter, I consider the comparative approaches of language evolution that focus on the mechanisms involved in the origins of human language. I will discuss my findings in relation to the vocal theory of language evolution and contrast it with its principal competitor, the gestural theory of language evolution.

The comparative approach to language evolution searches for precursors to human language in animals, commonly primates, in order to model the capacities of our common ancestors. It is greatly strengthened by several lines of evidence that indicate that human language only emerged in our very recent evolutionary history. Evidence from Crelin (1987) on the reconstruction of early hominids’ vocal tracts, including *Homo erectus* and *Australopithecus*, indicates that the anatomy required to produce

the flexible range of sounds associated with modern speech was not present until the advent of archaic *Homo sapiens*, about 250 000 years ago. Enard and colleagues (2002) also propose that spoken human language appeared in this time period. It is likely that the mutations that caused changes in two amino acids coded by the human FOXP2 gene, which now differentiate this gene from the corresponding DNA structure in the chimpanzee, stabilized in the population at about this time. The human FOXP2 gene is thought to be significant in the coordination of fine orofacial movements and the expression and comprehension of spoken language, as individuals with mutations in this gene fail to acquire normal spoken language (Fisher et al., 1998). Modern language not only requires speech abilities, but also symbolic representation. Archaeological records indicate that 50,000 years ago there was an unprecedented proliferation of symbolic artefacts left by our ancestors, in the form of representational cave art and bone carvings (Deacon, 1997). When all this evidence is considered, it seems reasonable to assume that language, as we know it, originated between 250 000 and 50 000 years ago. This timeline represents a relatively short phylogenetic period, making it highly unlikely that human language is a *de novo* invention. This supports the comparative search for the cognitive skills, essential for modern language, that may have been present in our primate ancestors and that represent the building blocks necessary for the emergence of modern human language in the last 250 000 years.

The inherent structure and nature of language is not tied to a particular mode of production, as the existence of spoken and sign languages in modern humans demonstrates. Ultimately, the modality in which the cognitive mechanisms underlying language developed is not important, in comparison to understanding when and how these cognitive abilities contributed to the emergence of language. However, for empirical comparative research we are forced to concentrate on either the vocal or gestural modality of communication in other animals. This has led to substantial debate over whether human language built upon cognitive skills involved in gestural or vocal communication. These two theories will be discussed before the relevance of my research to these theories is examined.

Proponents of the gestural theory of language evolution suggest that primate gestural communication is more analogous to human language than primate vocalisations are

(Hewes, 1973; Corballis, 1999). Gestures of the great apes have been shown to be adaptable and generative, with individuals able to invent new gestures through a flexible process of ontogenetic ritualization (reviewed in Tomasello and Zuberbühler, 2002; Pika et al., 2003). In this process, a gesture develops communicative meaning through the signaller and receiver shaping each other's behaviour with repeated social interactions. Firstly, the recipient responds consistently to a sequence of gestures and behaviours from the signaller. The recipient then learns to anticipate the signaller's behaviour from the initial gesture and the signaller soon learns that this is sufficient to elicit a response in the recipient. Thus the signaller learns to produce the initial gesture in a ritualised fashion to elicit the desired behaviour in the recipient. Chimpanzees seem to be sensitive to the attentional state of the recipient and they tend to use visual gestures when others are already attending to them (Liebal et al., 2004). The flexibility and generative nature of this system reflect some of the key aspects of modern human language.

Gestural theories of language evolution also draw support from research on the mirror neuron system. Neurophysiological experiments on rhesus monkeys have revealed neurons in the macaque homologue of Broca's area, which respond to goal directed actions such as grasping. These neurons are special because they respond both when the monkey performs the action and when he watches another individual execute the action (Di Pellegrino et al., 1992). It is proposed that these neurons provide the basis for representing and understanding actions of others by forming a link between sender and receiver (Rizzolatti and Arbib, 1998). The authors suggest that this link enabled intentional gestural communication between our hominid ancestors and that once the gesture system became complex, sound was paired with the manual gestures and later became the dominant system. Speech control thus developed at a much later date, in the cortical regions initially responsible for controlling and understanding gestures. In contrast, primate vocal behaviour is thought to be mainly controlled by non-cortical structures (Sutton and Jürgens, 1988) and so the evolution of cortical control of modern speech is difficult to address for vocal theories of language evolution. However, one of the outstanding problems for the mirror neuron story is why monkeys with these neurons do not demonstrate intentional communication in the manner proposed by this theory. In addition these neurons can match the actions of oro-facial movements as well as manual actions (Ferrari et al., 2003); mirror neurons

could have enabled facial gestures and then the vocalisations that accompanied them, to become intentional. The need to implicate manual gestures as the primary mode of early complex communication therefore remains unsubstantiated.

Ape gestures seem to mirror the flexibility of language production and gestural theories provide an important contribution to understanding the origins of some aspects of language. However, I believe one of the core features of human language is our ability to use words to refer to events and objects in the world and our imagination; be they spatially distant or in the past or future. A promising precursor to this ability is functional reference, but unfortunately, there is no evidence that naturally occurring primate gestures function to reference entities in the environment (Tomasello and Zuberbühler, 2002). In contrast, studying the vocal communication of animals has revealed considerable evidence of naturally occurring functional reference. I therefore examined the natural vocal behaviour of chimpanzees for evidence of functional reference: work which contributes to the vocal theory of language evolution.

Vocal theories of language evolution suggest that it is more parsimonious to propose a direct evolutionary trajectory from ancestral primate-like vocal behaviour to fully developed human language, rather than assuming a more complex route involving an intermediate stage of gestural communication. In contrast to primate gestures, primate vocalisations function referentially in a number of contexts (as reviewed in chapter 2, pages 20-27). As discussed previously (chapter 1, page 18), proponents of the vocal theories of language evolution argue that functional reference may be the evolutionary precursor to elements of human semantic abilities.

There are, however, several criticisms of the vocal theories of language evolution. Primate vocal behaviour has been characterised as cognitively uninteresting, as this quote from Lieberman demonstrates “non human primates engage in a number of stereotyped calls...they don’t have the interactive or combinatorial quality of language” (Holden, 2004, p.1317). Although chimpanzee calls have been regarded as closely tied to emotion (Goodall, 1986), my research shows that chimpanzee vocal communication can still function in complex ways. Not only can calls function to reference events in the environment, but evidence of audience effects indicate that

chimpanzees have a degree of control over their vocal output. This work may lead to more research, which may ultimately prove the current criticisms untrue: we do not currently have sufficient knowledge about chimpanzee vocal communication to confidently state that their calls are not interactive, combinatorial or intentional.

Another concern focuses on the relationship between functional reference and linguistic reference. Some argue that without intentionality on the part of the signaller functional reference is qualitatively different from the referential nature of human words (Tomasello, in press). This leads some to conclude that functional reference can shed little light on the evolutionary path of human semantics (Corballis, 1999). I agree that the lack of intentional denotation of external objects through any modality in non-human primates contrasts with even a very young child's gestures and words. However, I still believe that functional reference can help explain the evolution of the basic semantic abilities of listeners. In addition, my research adds to the body of evidence that suggests that primates modify their vocal behaviour in response to their audience (Cheney and Seyfarth, 1985; Mitani and Nishida, 1993). It may therefore be premature to conclude that apes, with a higher degree of theory of mind ability than monkeys (Byrne, 1995; Tomasello et al., 2003), do not use functionally referential signals intentionally.

Perhaps a more fundamental flaw in the vocal theories relating functional reference to the evolution of human semantics has been the lack of evidence for this ability in great apes. It might be the case that this does not pose a problem since the absence of language-like communication in non-human primates does not necessarily mean that language did not evolve from a primate-like communication system (Pinker, 1994). But then how should the monkey evidence be interpreted? For comparative approaches to language evolution, this creates an anomaly both because apes are more closely related to humans and because they are commonly thought to be cognitively more advanced than monkeys (Byrne, 1995). It is difficult to exclude the possibility that the functionally referential skills of many monkey species represent convergent evolution of these skills. This appears to be what happened in the case of vocal learning, which seems to have evolved independently in three groups of birds, marine mammals, some bats and humans. In this context my research has contributed to the field by addressing the anomalous absence of evidence for functional reference in the

vocal behaviour of great apes. The evidence of functional reference in chimpanzees and the identification of call types with potential to function referentially has highlighted the interesting and possibly complex nature of this species' vocal communication system. I am confident that future work will reveal that other call types function referentially and that chimpanzees will prove to have levels of vocal functional reference comparable to that of better studied monkey species. My research therefore offers support for the vocal theory of language evolution and begins to address one of its previous weaknesses. In the long term, the impact of this research is not limited to addressing issues of functional reference. I believe it has made a start towards the investigation of the evolution of more complex linguistic abilities such as syntax.

So far, there is no convincing evidence that apes combine their gestures or vocalisations in a meaningful, rule governed way. As discussed previously (Chapter 1, pages 10-11), the only suggestion of lexical syntax in any primate comes from the Campbell's monkey alarm call system (Zuberbühler, 2002). I would argue that lexical syntax is the closest approximation to basic human syntax known in any animal communication system; therefore discovering whether ape communication naturally includes elements of lexical syntax would represent a huge leap forward for the comparative approach to language evolution. The critical definition of lexical syntax is that the meaning of the call or gesture sequence is independent of its constituent elements. Although there is no evidence for this currently in apes, Hauser (1996) suggests that concluding non-human primates do not have natural syntactic structures in their vocalisations is premature. Until we understand what the individual calls mean to recipients, how can we infer whether call combinations change those meanings? I believe that work on functional reference is therefore a necessary precursor to work on lexical syntax in non-human primates. This research is the first necessary step towards examining call combinations and assessing if call sequences modify the meaning of the constituent calls. As such, my research has hopefully made a contribution to laying the groundwork required for the successful study of the evolutionary origins of syntax.

In the future, research that increases our knowledge of chimpanzee vocal communication could play a vital role in furthering our understanding of the origins of

human language. More research is needed to examine the diversity of chimpanzee calls that function referentially. We then need to examine audience effects and devise experiments that will test the degree of intentionality in caller behaviour. Finally and perhaps most importantly, we can examine call combinations, which often occur in the wild (Crockford and Boesch, 2005), to see if calls are combined to form sequences with meanings independent from those of the constituent elements.

## **Conclusion**

The aim of this research was to investigate whether chimpanzees produce and understand functionally referential calls as part of their natural communication. My research has begun to address this aim, although much more research is needed to examine the diversity of situations in which such communication occurs. The investigation of agonistic screams indicated that these calls make excellent candidates for functionally referential communication, but playback experiments are needed to test this hypothesis. Chimpanzee rough grunts vary reliably with the quality of the food discovered by the caller and listeners can infer the kind of food available from listening to these calls. Thus rough grunts appear to function referentially; the first evidence of this ability in the natural communication of any ape species.

This research indicates that chimpanzee vocal communication may be more complex than previously thought. However, currently chimpanzee vocal communication still falls short of demonstrating the involvement of advanced cognition, which has been shown to influence many other aspects of chimpanzee behaviour. More research effort, particularly that focussed on signaller intentionality and deception, may reverse this current view of chimpanzee vocal behaviour. In addition, other elements of chimpanzee behaviour such as foraging and social interactions may be influenced by information about the ecological and social environment gained through listening to the calls of others.

Finally, this research provides support for the vocal theory of language evolution. By focussing on the anomalous lack of evidence for functional reference in apes, a critical weakness of the theory has been addressed by the current research. Functional reference appears to be a general feature of primate cognition, indicating that the ability of human listeners to infer meaning from words has its evolutionary roots deep in the primate lineage. This research also paves the way for future work examining the issues of signaller intentionality and lexical syntax, which are potentially crucial precursors to language; abilities we currently know virtually nothing about in apes.

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**Appendix 1. Example checksheets used to record the context and behaviour that accompanied each vocalization recording**

**FOCAL ANIMAL SAMPLING**

**Date:** \_\_\_\_\_ **Time start:** \_\_\_\_\_ **Time finish:** \_\_\_\_\_ **Time in:** \_\_\_\_\_ **Observers:** \_\_\_\_\_ **Focal individual:** \_\_\_\_\_

<b>Block</b>	<b>Call type</b>	<b>Context</b>	<b>Behaviour of focal individual</b>	<b>Other individuals and proximity to focal ind.</b>	<b>Behaviour of others</b>

# AD LIBITUM SAMPLING

Observers:

Date:

Time	Block ID	Call type	Context	Behaviour of focal individual	Other individuals and proximity	Behaviour of others

**VICTIM CONTEXT**

Date	Time + Block	ID & (F/ AD)	Charged /Pursued individ?	Run/climb away? Speed? Distance?	Fear Grim.	Crouch	Physical contact? Type?	Aggressor beh.		3 <sup>rd</sup> Party behaviour		Food?
								PH / scream / silent?	Shake veg / drum?	Barking ID / timing / duration	Approach Timing / from where/ support who?	

**AGGRESSOR CONTEXT**

Date	Time	Block	ID & (F/AD)	Charge others / Pursue individual?	Pant hoot / silent / scream	Pilo erect?	Drum?	Shake veg?	Physical contact? Type?	3 <sup>rd</sup> party interference		Food	Copulation? Distance from couple? Length cop? Cop interrupted?
										Barking – ID / timing / duration	Approach – timing / from out of sight?		