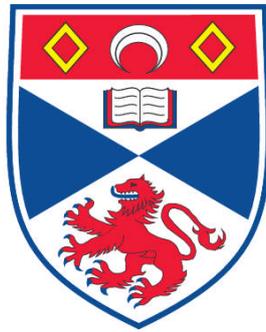


**ANTI-PREDATOR BEHAVIOUR OF GUEREZA COLOBUS MONKEYS  
(COLOBUS GUEREZ)**

**Anne Marijke Schel**

**A Thesis Submitted for the Degree of PhD  
at the  
University of St. Andrews**



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**Anti-predator behaviour of Guereza colobus monkeys**  
*(Colobus guereza)*

**Anne Marijke Schel**

**Thesis submitted to the School of Psychology of the  
University of St. Andrews for the degree of Doctor of  
Philosophy**

**February 2009**

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To my parents, who shared this exceptional experience with me  
and Gophine Mwale Erickson, who made it exceptionally valuable and fun

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## Abstract

Black-and-white colobus monkeys are renowned for their impressive vocal behaviour, but up to date there have been only very few systematic efforts to study this. These monkeys are able to produce loud and low-pitched roars that transmit over long distances, which has led to the assumption that these calls function in inter-group spacing and male-male competition. The fact that the monkeys sometimes produce the same calls to predators as well, has not received much attention so far.

This thesis presents a detailed description of the form and function of the anti-predator behaviour of one species of black-and-white colobus monkeys, the Guereza (*Colobus guereza*), with a specific focus on their alarm calling behaviour. A second aim was to determine the effects of predator experience on their anti-predator behaviour, with a specific focus on call comprehension and production. Data were collected from two populations of Guereza monkeys in the Budongo Forest Reserve, Uganda, that differ in predation pressures experienced by their main predators: leopards, eagles and chimpanzees. Results showed that Guerezas use a basic form of zoo-syntax in order to compose predator-specific call sequences that vary in the number of roaring phrases and snorts. These sequences are meaningful to recipients, at least at the level of the predator class, but there were also indications for additional levels of encoded information: Guerezas appear to have evolved a second system, based on acoustic variants of individual phrases, which allows them to narrow down the information content of call sequences, generating the potential to communicate highly specific information by using a mix of syntactic and semantic cues. The monkeys' vocal behaviour was influenced by predator experience, but not strongly so. Monkeys without prior experience with leopards lacked some of the behavioural nuances seen in leopard-experienced monkeys, but they nevertheless responded appropriately to visual and acoustic leopard models, suggesting they had retained the basic capacities to recognise this predator type as relevant and dangerous.

Results are discussed in light of the comparative approach to the study of human language evolution. Although human language is unique in a number of ways, for example through its use of complex syntax and intentional semantics, some animal communication systems have revealed similar features, and Guerezas, the first member of the colobine family to be studied in this respect, are no exception. The Guerezas' alarm calling behaviour is complex and flexible, and these monkeys have provided another piece of empirical evidence that is directly relevant for the comparative approach to human language evolution.

## **Chapter 1**

### **General Introduction**

#### **Vocal animal communication: human language from a comparative perspective**

One defining aspect of ‘what it means to be human’ concerns our extraordinary capacity to share knowledge by using referential vocal communication. Humans possess the unique capacity to produce an infinite number of meaningful spoken messages by assembling a small set of basic sounds, the phonemes, according to a number of language-specific rules (Tomasello, 2003). The rich expressive power generated through the capacity of human language is generally thought to set us apart from other animals that make use of sophisticated communication systems.

#### ***Animal communication systems vs Human language***

##### **Communication and signal content**

Many different animal species have evolved complex communication systems that employ highly specific visual, olfactory and/or vocal signals. Over the years, studies conducted within several distinct scientific disciplines have generated many definitions for the term ‘communication’, as well as many debates concerning this topic (reviewed in Hauser, 1996). Consequently, definitions of communication are often based on intra-disciplinary points of view and restrictions related to the study species or genus (e.g. through cognitive limitations). They therefore cannot always be generally applied in just any given study on animal communication. However, most of the more specific definitions will have basically incorporated the more fundamental concept of ‘communication’ being an interaction between a signaller and a receiver, in which information is transmitted through the external environment by one individual through the use of a signal (vocal, visual, or olfactory) that significantly alters the behaviour of receivers (Smith, 1977; Marler, 1967; Hauser, 1996; Noble & Cliff, 1996; Seyfarth & Cheney, 2003). Most signals produced in such communicatory events have evolved in cooperative contexts (Marler, 1967; Seyfarth & Cheney, 2003), although it has been

suggested that some signals may function in more selfish, manipulative, contexts beneficial only for the sender (Krebs & Dawkins, 1984).

In cooperative communication systems, natural selection usually acts on both signaller and recipient, who co-evolve and adapt their production and comprehension skills to generate the most efficient communication strategy beneficial for both parties (Hauser, 1996). Such a co-operative communication system evolved under strong selection pressures can, for example, be found in predatory situations (Lima & Dill, 1990; Stanford, 1998). Efficient alarm communication between signaller and receiver in such situations will usually be beneficial to both parties, because it will increase their survival chances (Seyfarth & Cheney, 2003). In such evolutionary highly important contexts, the relations are often quite complex. For example, recipients may include members of other species that eavesdrop and associate the alarm signals, triggered by a particular event in the environment, with specific experiences of their own. Such examples range from a predator hearing a prey species' vocalization and thus simply confirming its location, to more complex cognitive abilities that allow a receiver to extract highly specific information from hetero-specific signals (Hauser, 1988; Hauser, 1996; Zuberbühler, 2000b; Rundus et al., 2007).

Sophisticated psychological processes may be at work in these situations, although this does not necessarily have to be the case. Animals may rely on rather basic processes when responding to each other's signals (e.g. Byrne, 1995; Owren & Rendall, 2001). Information contained in an animal signal may result purely from "the association of each signal with a particular referent, which could include the identity, behavioural tendencies, or external circumstances of the signaller" (Smith, 1977; Wiley & Richards, 1978). A recipient's response may be adapted to the specific situation, but this could be caused merely by the physical acoustic characteristics of the signal and the emotional effects it causes in recipients, and not necessarily through any specific information content incorporated into the signal by signallers (Owren & Rendall, 2001; Hauser et al., 2002). Nevertheless, in such situations the recipient's behaviour *is* altered after hearing the sound, which still, in the most basic sense of the term, constitutes a communicative event. Moreover, this interaction may not be intended, nor may it convey any highly specific information about a situation in the signaller's external environment (Cheney & Seyfarth, 1990; Byrne, 1995). The most basic definition of

communication does, accordingly, not assume that animal communication is intentional, nor that animal signals contain any specific referential information. However, in the highly complex and adaptive situations that can be observed in some animal species' communication, these assumptions are sometimes easy to forget (or, arguably, contra-indicated: see below).

Thus, different animal species have evolved different communication systems ranging in complexity, that seem constrained by a species' cognitive abilities, and are the evolutionary product of the social and physical environment in which these animals live in (e.g. Waser & Brown, 1986; Macedonia & Evans, 1993; Rundus et al., 2007). In contrast to human language, animal communication is usually not thought to be 'intentional', but described as 'affective'. Moreover, many theorists argue that animals are unable to produce referential (or semantic) signals, while syntax and recursion are generally considered to be beyond any animal's capacities (reviewed in Tomasello 2003; defined below). Furthermore, animal communication is usually regarded as innate and inflexible (Robinson, 1984; Cheney & Seyfarth, 1990).

Consequently, human language, with its extra-ordinary 'design features' and its use of advanced cognitive capacities that allow for grammar and recursion (reviewed e.g. in Hauser, 1996; Tomasello, 2003), has long been regarded as disconnected from the natural selection processes that have shaped the design and function of animal signals.

### **Discontinuity and continuity**

This 'discontinuity stance' emphasises that human language is a unique communication system that did not emerge out of any form of animal communication system in a continuous line of evolution (e.g. Lenneberg, 1967; Hill, 1974; Aitchison, 1998). Instead, humans are thought to possess an 'innate language faculty' or 'language organ' that generates a 'universal grammar' to which every natural language conforms (reviewed in Chomsky, 1980). This language organ is only present in the human mind and without it language cannot be learned (Hill, 1974; Chomsky, 1980; Pinker & Bloom, 1990). Lenneberg (1967) further proposed that language is a self-contained biological system that is not shared with other animals. According to this and other authors, the emergence of language is not obvious in the evolutionary record, suggesting that there are no relevant precursors of language in the animal kingdom.

In contrast, the ‘continuity stance’ emphasises the Darwinian heritage of human language, e.g. by searching for its predecessors in animal communication systems. Hockett (1959), for example, identified a number of general ‘design features’ (e.g. arbitrariness and displacement) that characterise human language, allowing researchers to chart the similarities and differences between human and animal communication systems. According to this scenario, progressive additions of crucial design features gradually lead to the emergence of human language of the kind present today. Furthermore, Hockett & Ascher (1964) proposed that the open-ended communication system used by humans evolved by the mechanism of blending two calls into a new one with a specific meaning. These then gradually became established in the repertoire if functionally useful. Pinker and Bloom (1990) argued that human language is a clear example of a product of natural selection, by meeting the two criteria that normally attribute a trait to the process of evolution: a complex design and the absence of alternative processes that are capable of explaining this complexity.

The continuity theory is supported by studies on the anatomy and neural capacity required for modern speech, an ability that only became present in our ancestral line around 250.000 years ago, with the appearance of *Homo sapiens* (Lieberman, 2001). Recent clinical-genetic studies further supported this idea (Enard et al., 2002; Zeesman et al., 2006), by suggesting that the FOXP2 gene is involved in the development of orofacial movement control, which is needed to develop normal articulate speech (Fitch, 2000). In one study it was shown that two mutations occurred in this gene after humans separated from the common ancestor with the chimpanzee around 6 million years ago. The mutated version of the gene became fixed in the human population around 200.000 years ago, which is around the time when anatomically modern humans emerged. This event may have been crucial for the human ability to develop language (Enard et al., 2002).

In evolutionary terms, 200.000 years is a very short period to evolve the complete extra-ordinary cognitive and physical apparatus needed for human language. One possibility is that the capacity to use modern human language has its base in neural structures and cognitive capacities that were already present in the primate lineage, although perhaps used for other purposes (Zuberbühler, 2003).

**Comparative method**

In an attempt to bring biology and linguistics closer together, Hauser et al. (2002) proposed an intermediate view in the continuity-discontinuity debate. Using a comparative approach they identified capacities needed for human language which were inherited unchanged from the common ancestor with chimpanzees, as well as the ones that were qualitatively new. One conclusion from this analysis was that the basic features of the faculty of language were mostly shared with non-human animals. Examples are the internal sensory-motor system that is concerned with speech perception and –production, the imitation-learning system, and the conceptional-intentional system, that handles representations of referential vocalisations. The computational mechanisms of syntax and recursion, however, are thought to have evolved much more recently, long after the approximately 6 million years since our divergence from a chimpanzee-like common ancestor (Hauser et al., 2002). This theory thus embraces both the discontinuity and continuity theories, and encourages the comparative approach initially introduced by Hockett (1959). Studies on non-human primate communicative abilities are considered of particular interest because of their close phylogenetical relationship to humans.

***Recapitulation: capacities needed for human language***

To recapitulate, the main difference between animal communication and human language are thought to be found in humans' extra-ordinary capacities to generate grammar and recursion. It seems that “no species other than humans has a comparable capacity to recombine meaningful units into an unlimited variety of larger structures, each differing systematically in meaning” (Hauser et al., 2002). Semantics, vocal learning, vocal flexibility, and intentionality are often included in this distinction as well, generating a set of criteria for defining human language (reviewed in Tomasello 2003). The traditional contrast to such ‘learned, flexible, intentional, semantic, grammatical human language’ is embodied by the classic view of ‘affective’ animal communication, in which signals simply represent an animal’s motivational state, its general arousal or its imminent behaviour. According to this view, animals are not thought to refer to objects in the external environment, nor to generate patterns that could qualify as grammar. Signallers are thought to use a fixed, finite number of discrete vocalisations in an inflexible, stereotyped way when communicating to one another. However, more and more studies suggest that this simple dichotomy between

animal communication and human language is inaccurate. Before reviewing some of these studies, some key terminology is defined first.

### **Definitions**

Many of the terms used in studies on animal communication were derived from those used in linguistics. In the following, the purely linguistic definition of a term is given first, followed by the more generally used definition.

**Semantics** (or symbolism) is defined as “the study of meaning in human language” (O’Grady et al., 1997). More generally it is defined as “(the study or analysis of) the relationships between symbols and their meanings” (OED, 1989). As an ability in communication, it describes the use of arbitrary symbols referring to objects in a signaller’s external environment, i.e. the relationship between words and things (e.g. Robinson, 1984; reviewed in Hurford, 2007).

**Syntax** (or grammar) is defined as “the system of rules and categories that underlies [understanding and producing] sentence formation in human language” (O’Grady et al., 1997). More generally the term is defined as “the arrangement of words (in their appropriate forms) within sentences, by which their connection and relation in a sentence are shown” (OED, 1989). Syntax shapes the meaning of strings of symbols through word order.

**Recursion** (or ‘recursivity’) is defined as “a property of grammars whereby a finite set of rules can generate an infinite set of structures” (Akmajian et al., 1990). Palmatier (*Gloss. Eng. Transformational Gram.* 142; OED, 1989) described “a recursive rule [as] a rule which reapplies indefinitely to its own output... The recursive property of a grammar... is its provision for embedding sentences within other sentences”.

Thus, following syntactic and recursive rules, meaningful units can be recombined into a unlimited variety of larger structures, each differing systematically in meaning (Hauser et al., 2002; Fitch & Hauser, 2004). This leads to the capacity to communicate an endless variety of thoughts, generating a limitless expressive power.

**Vocal learning** refers to “instances where the vocalizations themselves are modified in form as a result of experience with those of other individuals” (Janik & Slater, 1997). This type of learning involves imitation of sounds that are novel to the species’ repertoire. It is also termed ‘vocal production learning’ (Janik & Slater, 2000).

**Vocal flexibility** (or – plasticity) seems related to vocal learning and can be described as the capacity to subtly modify the structure of existing vocalizations according to specific contexts, or to voluntarily elicit or inhibit sound production (Egnor & Hauser, 2004; Lemasson et al., 2005; Egnor et al., 2007).

**Intentionality** is defined as “the distinguishing property of mental phenomena being necessarily [or purposefully] directed upon an object” (OED, 1989). More generally it can be described as a directed action which may lead to profit by manipulating another’s knowledge (reviewed in Byrne, 1995; Hurford, 2007). The use of a ‘theory of mind’ (the attribution of mental states to others) is often assumed inherent with this definition.

## **Defining characteristics of human language in animal communication**

### ***Recent work: syntax***

Basic syntax-like patterns have been described in primate communication for monkey species such as wedge-capped capuchins (Robinson, 1984), titi monkeys (Robinson, 1984), Campbell’s monkeys (Zuberbühler, 2002), putty-nosed monkeys (Arnold & Zuberbühler, 2006), and gibbons (Mitani & Marler, 1989; Clarke et al., 2006). These species appear to possess the ability to produce and understand specific combinatorial rules applied to a fixed number of call types, leading to a variable number of distinct sequences that differ in distinct contexts. One further relevant study described sequential use of vocalizations by pygmy marmosets, which follow some ‘conversational rules’ (Snowdon & Cleveland, 1984). Those primates take turns in the production of call sequences, and keep to an ordering in terms of calling individuals, with one particular individual usually starting a call sequence.

A useful distinction for such cases of ‘zoo-syntax’ has been made by Marler (1977), who introduced the terms ‘phonological syntax’ and ‘lexical syntax’. Phonological syntax refers to the rules that control the combination of meaningless call units into

higher-order sequences that possess meaning; it is analogous to the formation of different words through the rearrangement of phonemes. Lexical syntax, in contrast, is present if the components that are used in different combinations possess separate meanings, such that higher-order sequences derive their meaning from the combined meaning of the components, as for example in human language (e.g. cat chases dog vs dog chases cat). According to this classification, Robinson (1984) argued that wedge-capped capuchins used lexical syntax, while titi monkeys used phonological syntax. More recent work, however, usually refrained from classifying findings according to either one of these two categories. Furthermore, most authors acknowledged that the rules used by these primates to produce compound signals are not analogous to the grammatical rules used in human language, and can broadly be seen as ‘concatenation’ processes (based on an understanding of transition probabilities between a finite number of calls, Fitch & Hauser, 2004) or ‘the simple addition of meaning’ ([cf. Byrne, 1982], Robinson, 1984). More recent work addressed this topic in cotton-top tamarins (Fitch & Hauser, 2004) and confirmed that non-human primates may indeed have the capacity to process sequential regularities in acoustic sequences, but that they cannot master to use and understand the highly hierarchical phrase structures as found in human language, where components at one end of a sequence are related to other components further away in the sequence.

***Recent work: semantics***

Several studies have argued that the notion of ‘semantics’ can be a useful concept in the study of animal communication. Some animal vocalisations are evoked by specific external events (also called ‘referents’: Seyfarth & Cheney, 1980; Macedonia & Evans, 1993) and elicit specific responses from recipients (Evans & Marler, 1995). If there is a tight and reliable link between the production of a unique vocalisation and the appearance of a distinct object or event in the environment, then these calls can provide fairly specific information for conspecifics to respond appropriately, even when no additional contextual information is available (Seyfarth et al., 1980; Evans & Marler, 1995). Such signals are usually referred to as ‘functionally’ referential signals. According to one definition, to be functionally referential the calls must meet a ‘production criterion’ (the signal is produced in a context-specific way) and ‘perception criterion’ (the signal alone is sufficient to evoke the appropriate response from listeners in absence of the eliciting stimulus (Macedonia & Evans, 1993).

The word ‘functional’ in the term ‘functionally referential’ acknowledges the constraints inherent in the study of animal vocalisations (Evans, 1997), especially the fact that it is usually not possible to determine whether a signal is produced to inform a receiver. Even in humans it is difficult to establish if such a process takes place, but at least humans can be interrogated about it. In animal studies one can only establish that the animals behave *as if* the vocalisations encode external information (Evans, 1997). One related issue concerns the information content actually communicated with such calls. Some researchers have argued that a recipient’s adaptive response is caused merely by the physical acoustic characteristics of the signal, and not by any specific information content incorporated into the signal (Owren & Rendall, 2001; Hauser et al., 2002). Even if the recipients behave *as if* the vocalizations encode external information, this may be based on very basic stimulus-response processes. Finally, and equally important, it is never entirely possible to establish if an animal calls with the *intention* to inform ignorant conspecifics, i.e. whether it takes the audience into account (Seyfarth & Cheney, 2003; Zuberbühler, 2003).

Evidence for functionally referential communication in animals has come from several species in social and food contexts (e.g. Gouzoules et al., 1984; Hauser, 1992; Slocombe & Zuberbuhler, 2005). However, the vast majority and strongest evidence has come from studies on predator alarm call systems, which will be discussed in the following section (Table 1.1).

## **Referential alarm call systems**

### ***Primates***

The classic example of the use of functionally referential alarm calls comes from the work of Struhsaker (1967) and Seyfarth et al. (1980) on vervet monkey alarm calls. These monkeys produce acoustically distinct vocalisations in response to a number of predator types. Playback experiments revealed that call recipients have a refined understanding of these calls’ meaning (i.e. the predator type usually associated with a call), even in absence of the eliciting stimulus (i.e. the predator itself). For example, after hearing a conspecific’s snake alarm call, receivers tend to react just as they do when confronted with a real snake: standing on their hind legs and peering down at the ground around them. Because these calls evoked the same reaction in listeners as would the real predator, they are thought to have semantic content, i.e. to refer to an external

object in their environment. Similar findings were reported for several other primate species, such as ringtailed lemurs (Pereira & Macedonia, 1991), mustached tamarins (Kirchhof & Hammerschmidt, 2006), Diana monkeys (Zuberbühler et al., 1997; Zuberbühler, 2000c), Campbell's monkeys (Zuberbühler, 2001), and blue monkeys (Papworth et al., 2008).

An elegant field experiment (the prime-probe design) on the referential capacities of Diana monkeys addressed some of the questions raised by the notion of semantics in animals, as mentioned before (reviewed in Zuberbühler, 2003). The basic experimental design in this study was as follows: monkeys were exposed to a first playback consisting of a series of conspecific predator alarm calls (the prime stimulus). After a period of silence, a second series of identical predator alarm calls or corresponding/non-corresponding predator vocalisations were played from the same location (the probe stimulus). It was found that Diana monkeys primed with conspecific predator alarm calls no longer responded to the vocalizations of the corresponding predator. This suggested that the semantic component of the prime stimuli, not their acoustic feature alone, explained the response patterns of the listeners to the probe stimuli. Secondly, it suggested that the recipients had formed a mental representation of the corresponding predator; they had acted as if they already knew about its presence (Zuberbühler et al., 1999).

### ***Non-primate mammals***

Referential alarm calling has also been reported for non-primate mammals of the *Sciuridae* (squirrels, chipmunks and marmots), *Herpestidae* (mongoose), and *Muridae* (mice, rats and gerbils) families (Slobodchikoff et al., 1991; Greene & Meagher, 1998; Manser, 2001). However, when applying the definition of referential communication in terms of the 'production' and 'perception' criteria (Macedonia & Evans, 1993), the majority of species from these families display alarm call behaviour that does not qualify as 'functionally referential'. Ground squirrel alarm calls, for example, have only 'probabilistic' semantic content (California ground squirrels: Owings & Virginia, 1978; Macedonia & Evans, 1993; Belding's ground squirrels: Mateo, 1996). These animals appear to emit specific calls for raptors and specific calls for terrestrial predators, but this call pattern is reversed if ground predators 'suddenly' attack the squirrels, or when eagles are spotted at a distance (Leger et al., 1980). Because most of

the raptor encounters normally involve a ‘sudden’ attack and the ground predator encounters usually are spotted from a distance, the calls are mostly observed in these instances, but they are not exclusive. Instead, the calls seem to vary with the animal’s experienced level of threat (related to the distance and/or hunting technique of the predator) (Owings & Virginia, 1978). They thus appear associated with the emotions experienced by the caller when perceiving the predator, or with the ‘response urgency’, i.e. the time constraints for escape behaviour that different predators impose on their prey (Robinson, 1980). Alarm call systems of this kind have been termed *response-urgency* or *urgency-based alarm call systems*. Urgency-based alarm call systems have been described in several primate species as well, such as the redfronted lemur (Fichtel & Hammerschmidt, 2002), the ruffed lemur (Macedonia, 1990), and putty-nosed monkeys (Price et al., 2008).

Manser (2001; Manser et al., 2001) reported that suricates produce alarm calls that contain both information about the predator type *and* about the level of urgency. Playback experiments showed that the acoustically different alarm calls given to different predators and their faeces evoked qualitatively different responses from listeners. In addition, alarm calls recorded in situations of high, medium, and low urgency respectively evoked the strongest, intermediate and weakest responses from listeners (Manser et al., 2001). The results indicated that call recipients extracted specific information not only about the predator type but also about the level of urgency from the acoustic structures of alarm calls in the absence of the eliciting stimuli. Because the calls were production-specific (Manser, 2001), they qualified both as functionally referential and as urgency-based.

The case of urgency-response based non-referential alarm communication in squirrels lead to the idea that urgency-based signals have been selected for in species that seek their refuge in a single plane (but see Manser 2001). In contrast to squirrels, most primates such as vervet monkeys and Diana monkeys need to take more complex decisions about where to seek refuge (on the ground or in the trees). The most adaptive response will thus depend on the predator type that has been spotted by the alarm call-signaller, its hunting-techniques, and the situation the receiver is in. The calls therefore must convey additional information that makes it possible for the listeners to decide immediately where to hide (Macedonia & Evans, 1993).

**Birds**

Finally, the use of a functional referential alarm call system has also been reported in birds, particularly chickens. Evans & Marler (1995) argued that chicken alarm calls meet both the production and perception criteria for functional reference, although some other studies showed that the animals may actually take into account the direction of attack (Gyger et al., 1987). Black-capped chickadees use an anti-predator call system with two different call types, that seem to function referentially in the sense that they communicate the type of encounter (Templeton et al., 2005). Alarm calls ('seet') refer to a rapidly moving predator, and mobbing calls ('chick-a-dee') refer to stationary predators. Within their mobbing calls, these birds additionally seem to indicate predator size, by producing relatively longer or shorter sequences of their mobbing vocalizations.

**Alarm call systems using different strategies**

In primates, one other common finding is that one alarm call type has a narrow reference (i.e. is given to highly specific events, typically dangerous raptors), while a second one is given to all sorts of disturbances, including terrestrial predators but sometimes also inter-group encounters, suggesting that the underlying psychological processes are relatively complicated (lemurs: Fichtel & Kappeler, 2002; e.g. white-faced capuchins: Digweed et al., 2005; sifakas: Fichtel & van Schaik, 2006). Because this system does not meet the criteria put forward by Macedonia and Evans (1993), it has been termed a *mixed alarm call system* (Fichtel & Kappeler, 2002).

Another type of system is found in species such as Chacma baboons and sooty mangabeys. Here, individuals produce only one general call type to predators, with much acoustic variation. Some call variants are also produced in non-predation contexts. Experiments have shown, however, that receivers are perfectly capable of associating discrete events to such acoustically *graded signals*, suggesting that discrete call types are not a prerequisite for encoding specific external events (Fischer et al., 2001; Range & Fischer, 2004).

Yet, other primates follow a different strategy and convey predator information by assembling a small repertoire of call types into more complex *call sequences*. Campbell's monkeys, for example, indicate low levels of threat, or signals aimed at

competitors, by adding a pair of boom calls to subsequent loud call series, which are regularly given to predators (Zuberbühler, 2002). Another example comes from putty-nosed monkeys, which produce two basic types of alarm calls to predators. Unlike Diana or vervet monkeys, both calls are regularly given to both leopards and eagles, but the monkeys assemble them into sequences specific to the presence of eagles, sequences specific to the presence of leopards, and sequences that indicate group travel (Arnold & Zuberbühler, 2006a; Arnold & Zuberbühler, 2006b; Arnold et al., 2008). White handed gibbons, finally, use some of their vocal behaviour, the songs, not only in pair bonding but also to indicate the presence of predators. Experiments have shown that predator-induced songs consist of the same types of notes as normal songs, but that differences in the arrangement of notes are meaningful to other gibbons. This suggests that this primate is able to use simple combinatorial rules to convey whether or not a caller is singing in response to the presence of a predator (Clarke et al., 2006).

Thus, discrete call types, graded signals and/or call sequences/ combinatorial rules can be used in predator communication. These signals may subsequently be classified as used in one of three types of alarm call systems: referential-, urgency-based- or mixed alarm call systems (Table 1.1.)

**Table 1.1.** Studies that investigated the alarm call systems of different mammal species, organised by the type of alarm call system used by these species. ‘Signal type’ indicates the type of signal used in the alarm responses produced by these animal species.

Species	Alarm Call System (PRIMATES)			Signal type		
	Functionally Referential	Urgency Response	Mixed	Discrete signals	Graded signals	Call Sequences
<b>Lemuroids</b> <i>Propithecus verreauxi</i>			Fichtel & Kappeler, 2002	+		
<i>P. v. coquereli</i>			Fichtel & v. Schaik, 2006	+		
<i>Lemur catta</i>	Macedonia, 1990			+		
<i>Eulemur f. rufus</i>			Fichtel & Kappeler, 2002	+		
<i>Varecia variegata</i>		Macedonia, 1990		+		
<b>Callitrichids</b> <i>Saguinus fuscicollis</i> <i>Saguinus mystax</i>	Kirchhof & Hammerschmidt, 2006			+		
<b>Cebids</b> <i>Cebus capucinus</i>			Fichtel et al., 2005 Digweed et al., 2005	+		
<b>Cercopithecines</b> <i>Cercocebus atys</i>		Range & Fischer 2004			+	
<i>C. aethiops</i>	Struhsaker, 1967 Seyfarth et al., 1980			+		
<i>C. campbelli</i>	Zuberbühler, 2001, Zuberbühler, 2002			+(2001)		+(2002)
<i>C. diana</i>	Zuberbühler et al., 1999			+		
<i>C. nictitans martini</i>		Arnold & Zuberbühler 2006 ; Price et al., 2008				+
<i>C. mitis</i>	Papworth et al. 2008			+		?
<i>Papio c. ursinus</i>		Fischer et al. 2001			+	
<b>Hylobatids</b> <i>Hylobates lar</i>	Clarke et al. 2006					+

Species	Alarm Call System (NON- PRIMATES)			Signal Type		
	Functionally Referential	Urgency Response	Mixed	Discrete signals	Graded signals	Call Sequences
<b>Sciurids</b> <i>Cynomys guunisoni</i>	Slobodchikoff et al., 1991			+		
<i>Marmota spp.</i>		Blumstein & Armitage, 1997; Blumstein, 1999		+		
<i>Spermophilus beecheyi</i>		Owings & Virginia, 1978		+		
<i>Spermophilus beldingi</i>		Leger et al., 1984		+		
<i>Tamiasciurus hudsonicus</i>	Greene & Meagher, 1998			+		
<b>Murids</b> <i>Parotomys brantsii</i>		Le Roux et al., 2001			+	
<b>Herpestids</b> <i>Suricatta suricatta</i>	Manser, 2001	Manser, 2001		+		

**Motivational-referential continuum**

The described studies on alarm call systems thus suggest a dichotomy within animal communication, with referential call systems in some species and response urgency call systems in others (or a mix of the two). Related to this, Marler et al. (1992) suggested that the terms ‘referential’ and ‘motivational’ should be viewed as varying along a continuum. Alarm calls, just like human words, can contain highly specific referential information, but will most likely display some elements of the caller’s emotions as experienced at that particular moment. Vice versa, even in the most prototypical motivational signals a certain degree of stimulus specificity is likely to be present, because the behaviour was most probably triggered by something in the animal’s environment (Macedonia & Evans, 1993). Seyfarth & Cheney (2003), however, argue that affect and referentiality are two distinct and independent dimensions, and it thus seems inappropriate to classify alarm calls either as ‘motivational’ *or* ‘referential’. Calls may be triggered by affective situations (such as stressful or aversive situations), and they therefore may indeed contain motivational or emotional content, but this does not mean that the call cannot also be highly stimulus-specific, and potentially referential. According to these authors, the affective properties of a signal depend on the call production of the signaller, whereas the referential properties of a call depend on the listener’s ability to extract information from these calls, associated with the events in its environment. Although both signaller and recipient are engaged in the same communicative event, the recipient is the one that links sound with its supposed meaning. As argued before, the recipient’s physical and cognitive abilities will determine what information can be extracted from a signaller’s call: a ‘clever’ recipient may extract information about the specific external event, in addition to information about the emotions of the signaller when producing the call.

**Affect intensity**

According to Rendall (2003) affect is “the activity dimension of emotion”. Affect intensity is further described as “the relative intensity of generalized (i.e. nonspecific) psycho- physiological arousal (affect) in different circumstances”. In accordance with Morton’s motivation-structural rules (Morton, 1977), this author suggested that the emotional state of an animal can be reflected in its vocalizations as it becomes aroused. Thus, affect intensity influences call production, e.g. through changes in respiration, facial musculature, and vocal folds, influencing amplitude, resonance and fundamental

frequency. For primates, the influence of affect intensity on acoustic call parameters has most notably been investigated in baboons (Fischer et al., 1995; Rendall, 2003) and squirrel monkeys (Fichtel et al., 2001). The studies showed that affect in the broad sense (including e.g. aggressiveness, aversion, fearfulness) generally influenced a signaller's total call number, call rate, amplitude, noisiness, fundamental and peak frequency, frequency range and formant frequencies. Clara et al. (2008) furthermore suggested that the production of a high amount of calls may effectively reduce cortisol levels. The trouble with such studies is that affect is difficult to quantify. As Zuberbühler (2003) describes, “the empirical study of affect relies on proxies, such as behavioural responses or brain activity, and can probably never be based on more than analogies derived from human psychology”. This does not mean, however, that they are not interesting to study from a comparative perspective. Moreover, it should not be assumed in such studies that humans can look into a monkey's brain and witness its mental processes: it is just possible to, again, conclude that monkeys merely behave *as if*.

***Recent work: intentionality and vocal flexibility***

Seyfarth & Cheney (2003) argued that primates most likely do not call through a mechanism of ‘mental state attribution’, i.e. by assuming that providing information will change the listener's behaviour, by altering its knowledge. In contrast, signals produced “without flexibility, strategic choice, or voluntary control” (Tomasello & Call, 1997) may indicate that the underlying cognitive processes are rarely more complex than simple stimulus-response mechanisms. Tomasello & Call (1997) argued that intentional communication only takes place when signals are used as part of ‘flexible communicative strategies’, directed at recipients.

Recent work on alarm calls in Thomas' langurs (Wich & Sterck, 2003; Wich & de Vries, 2006) and blue monkeys (Papworth et al., 2008) showed indications of such flexibility. For example, Wich & de Vries (2006) showed that, after being presented with predator stimuli, resident male Thomas langurs persisted with their alarm calling until all its females had counter-called, but that lone males remained silent in similar predator situations. In these studies signallers generally adjusted the production of calls depending on the identity or presence of their relative audiences. The flexibility in call production in response to the presence and composition of an audience can thus

potentially indicate whether a signal is a pure sign of arousal, or a more deliberate attempt to inform a recipient. The latter case could be taken as evidence for intentional communication. The langur study mentioned before appeared to indicate an intention of the signaller to inform all group members through monitoring their response. Such observations can be classified as cases of first-order intentionality (reviewed in Byrne, 1995; Cheney & Seyfarth, 1990), for which no theory of mind is required: the signaller recognises the effects of its call on the audience's behaviour, and it might call simply because of this. This does not imply anything concerning a signaller's knowledge about the effects of its calls on a recipient's mind (Cheney & Seyfarth, 1990). The signaller thus calls with the intention to change the recipients' behaviour, not their knowledge state. Apart from these observations, up to the present, the issue of intentionality and/or mental state attribution in primate alarm communication has remained obscure. More convincing evidence for this comes from work on tactical deception, mostly studied in the great apes (Byrne, 1995). However, this topic will not be further discussed here.

***Recent work: Vocal learning***

As defined earlier, vocal learning refers to “instances where vocalizations are modified in form as a result of experience with those of other individuals” (Janik & Slater, 1997). This type of learning is also termed ‘*vocal production learning*’ (Janik & Slater, 2000).

*Contextual learning* refers to instances in which an existing signal is associated with a new ‘context’ (used in a broad sense: e.g. a new signal context through novel sequence use, social rank, affective state, or referent) as a result of experience with the usage of this signal by other individuals (Janik & Slater, 2000). It is divided in ‘usage learning’ (the pre-existing signal is produced in a new context as the result of experience with such usage by other individuals) and ‘comprehension learning’ (a novel meaning is extracted from the pre-existing signal as a result of the novel use of signals by other individuals).

In non-human primates, the two parts of contextual learning, vocal comprehension learning and vocal usage learning, are both present. For instance, infant vervet monkeys learn the appropriate contexts of production by individual experience and learning. When still very young, they produce alarm calls in a wide range of contexts, some of which are inappropriate. Their responses then gradually narrow down, until reaching a

narrow reference state, in which they only produce one particular type of alarm call in one highly specific context (Seyfarth & Cheney, 1986). Similarly, the comprehension of calls is also learned by experience. The same patterns have been described for some other primate species, e.g. baboons (Fischer et al., 2000).

Vocal production learning is often linked to human's and songbird's early sensitive period, in which animals need to be exposed to some critical auditory experience with the species-specific vocal repertoire in order to develop normal adult vocal behaviour. Non-human primates do not appear to have such a sensitive period in their early life. Rather, some studies have shown that some primate species (reviewed in Newman & Symmes, 1982) produce nearly all of the species' vocal repertoire within the first week of life. Vocal production learning in primates can occur in adulthood, but the evidence is generally weak (Sutton et al., 1973).

**Vocal flexibility**, however, has been observed more widely, mainly in social contexts. Examples range from matrilineal-specific calls (pigtail macaques: Gouzoules & Gouzoules, 1990; rhesus macaques: Hauser, 1992) to population-specific dialects (e.g. chimpanzees: Mitani et al., 1992). In these cases, group specific vocalisations have been found, which are different from the species-specific vocal repertoire. However, it is difficult to rule out that such group differences have a genetic base, since the necessary cross-fostering experiments have not been done (Egnor & Hauser, 2004). 'Acoustic convergence' in the vocalisations of unrelated animals may thus provide a better example of vocal flexibility. Such studies have shown that, when paired, animals subtly adjust the vocal characteristics of some of their calls to match the call characteristics of a conspecific (e.g. chimpanzees: Mitani & Gros-Louis, 1998; pygmy marmosets: Snowdon & Elowson, 1999), but use their own individual call again when calling alone. Other examples of vocal flexibility concern differences in call rates, as mentioned before (Wich & Sterck, 2003; Wich & de Vries, 2006; Papworth et al., 2008).

### ***Predation risk and vocal flexibility***

Predation risk is defined as the probability that a prey animal will be killed during an encounter with a predator (Stanford, 1998). Some important factors that influence predation risk are the density of predators of various species, the openness of the

terrain, and the grouping pattern of prey species. Primates can only actively modify the latter, for example by the formation of large multi-male groups (Stanford, 1998) or mixed species associations (Noë & Bshary, 1997) to increase their vigilance and benefit from other anti-predation benefits. Apart from forming large groups, most primate species use a range of different anti-predator tactics in order to avoid predation, including mobbing (e.g. Ross, 1993) and alarm calling.

The usage and comprehension learning of predator specific functionally referential alarm calls has already been described in the previous paragraphs. There is good evidence that primates not only react to the calls of conspecifics, but also take into account the alarm calls of other species, including those of non-primates (Seyfarth & Cheney, 1990; Zuberbühler, 2000b; Zuberbühler, 2000a; Fichtel, 2004). Zuberbühler (2000b), for example, showed that Diana monkeys can use the predator information that is conveyed in male Campbell's monkeys' alarm calls to adjust their anti-predator behaviour. Similar findings were reported in studies that focussed on non-primate alarm calls. For example, playbacks of guinea fowl alarm calls elicited the corresponding predator alarm calls from Diana monkeys (Zuberbühler, 2000a). Vervet monkeys are known to behave in a similar way (Cheney & Seyfarth, 1985). These monkeys respond with their own anti-predator behaviour in response to the predator calls of superb starlings, birds that inhabit the same areas as the vervet monkeys. Hauser (1988) found that vervet infants that have been exposed to higher rates of starling alarm calls (because of higher predator pressure) responded to these calls at an earlier age than infants in areas with lower encounter rates. This suggests that higher predation pressures may lead to increased behavioural flexibility in prey's vocal and cognitive capacities (Zuberbühler, 2000b; Zuberbühler & Jenny, 2002).

It has been argued that primates may possess a predisposition to learn to give alarm calls only to those stimuli that pose an actual threat to them (Fichtel & van Schaik, 2006). Differences in predation pressure and predator experience might then influence the vocal flexibility in comprehension and production of alarm call usage. Work on prosimians by Fichtel & van Schaik (2006) and Fichtel (2008) showed that low exposure rates to particular predators could lead to weak associations between alarm calls and predator types. Additionally, comprehension of particular alarm calls differed

between populations depending on predator pressures. This topic is further discussed in chapter 6 of this thesis.

In sum, the traditional dichotomy between animal communication as simple, stereotyped, and fixed, and human language as complex, variant and open has been challenged increasingly. Traditionally, animals were assumed to lack the cognitive capacities that would enable them to perform the kinds of computations fundamental to human language: semantics, syntax, vocal learning and intentionality. However, the comparative method has revealed that many primates and other animals possess (rudimentary) mechanisms that resemble these domains and exhibit vocal behaviour that compares well with that of humans. A number of studies have provided evidence that different animal species use basic forms of (zoo-) syntax, follow flexible strategies affecting the production and perception of vocal behaviour, and possess well developed (functionally) referential communication systems. The underlying cognitive capacities may be the foundations for the complex and cognitively advanced mechanisms involved in syntax, complex semantic communication, and vocal learning in human language.

One fundamental difference between animal communication and human language remains, however. Although there is some evidence for the use of intentional signals in great apes, the case is much less clear for other non-human primates and other animals, where it is usually impossible to assess what is going on in the mind of a signalling animal. Research is usually limited to observational studies in which the relationship between specific calls and specific external events are determined. Playback experiments are then used to determine the functional properties of the calls by studying the recipients' reactions. These data are then interpreted as a whole to assign the call's 'meaning', a process that will probably always generate debate and disputes. Nevertheless, as the only major avenue to investigate the mind of a non-linguistic animal, this approach is used in this thesis.

### **Main aims of study and thesis outline**

As a part of a greater effort to investigate the origins of referential communication in primates, the principal goal of this thesis was to systematically investigate and describe the form and function of roaring in the predation context by black-and-white colobus

monkeys, followed by the classification of their alarm call system based on current theory as discussed in the previous paragraphs. Results will be used to gain a better understanding of the possible cognitive processes underlying the production of the vocalizations under differing ecological circumstances, most importantly predation pressure. This is done by comparing Guereza colobus monkeys' behavioural and vocal responses to different predator types at two field sites that differ in predation pressure.

The African *Colobinae* are an especially interesting group in this respect, because they have largely been ignored by previous studies investigating this topic. Studies on prosimians and the *Cercopithecinae* subfamily of the Old World primates (such as guenons, baboons and mangabeys), as well as members of some subfamilies of New World primates, such as the *Callitrichinae*, *Cebinae* and *Alouattinae*, have revealed many interesting aspects concerning communication in the predator context, such as the use of complex cognitive mechanisms, which have been used to draw parallels between animal communication and human language. Because of a lack of studies on *Colobinae*, it remains unclear whether the cognitive precursors for human language can be found in primate vocal behaviour in general or if they are a specialised trait of a handful species of Old World- and New World primates. A better understanding of the behavioural patterns and the underlying cognitive processes of Colobine monkey alarm communication will help to obtain a more complete view of the evolutionary origins of complex communication systems in the primate lineage, with possible relevance for theories of hominid language evolution (Hauser et al., 2002).

Chapter 2 introduces the study species and previous work investigating their vocal behaviour. It furthermore introduces the two main field sites, the study populations, the predation risks posed by the different predator types, the basic methods used in data collection, and the statistical tests used in data analyses. Chapter 3 describes a pilot study investigating the ecological and social parameters influencing dawn chorusing in Guerezas. The chapter reveals some of the socio-ecological factors that influence the monkeys' calling behaviour and general responsiveness to playback experiments. Chapter 4 describes the results from a study conducted with acoustic predator models at the study population in Kaniyo Pabidi, the field site containing all predator types that pose a threat to the Guerezas. Chapter 5 reports the results from a study conducted with visual predator models in Kaniyo Pabidi. It compares the locomotor and vocal

responses to visual predator models with the responses to acoustic predator models and discusses some theoretical implications. Chapter 6 investigates the effects of predator experience on anti-predator behaviour of Guereza populations living under differing predation pressures. To this end, it first describes the results of the basic acoustic and visual predator model experiments conducted at the second field site, Sonso, where one major predator, the leopard, is absent. After having established the locomotor and vocal responses produced at both sites, a comparison is made between sites that is discussed in the light of differing predation risks and predator experience. Chapter 7, finally, establishes how the alarm calling system as described for the Guerezas should be classified with regards to the wider theory, i.e. whether it qualifies as ‘functionally referential’, ‘urgency-based’, a ‘mixed system’ or a different system altogether. Chapter 8 summarises and discusses the main findings of this study, and draws a comprehensive conclusion about the form and function of Guerezas’ alarm call responses, and how this might be influenced by differences in predation pressures. The importance of the results are discussed within the major framework of comparative research related to human language evolution as discussed in the introduction.

## Chapter 2

### Methodology

#### Study species

A review of the literature (Table 1.1) indicates that most studies on primate alarm communication have focussed on prosimians, cercopithecines, and some New World monkeys. Very little is known about the alarm communication of the various species of colobines, despite being a major group of Old World monkeys. In order to gain a clearer and more complete understanding of the phylogenetic distribution and evolutionary origins of alarm communication in the primate lineage, this thesis focuses on the vocal behaviour of Guereza colobus monkeys (*Colobus guereza*).

#### *The Colobine family*

##### General characteristics

Colobine monkeys are members of the subfamily *Colobinae*. Together with the *Cercopithecinae* subfamily, they form the *Cercopithecidae* family of Old World Monkeys. Colobines are found in Asia and Africa, where they respectively are classified as members of the 4-9 genera of Asian Langurs and African Colobus monkeys. All colobines are diurnal and highly arboreal, generally only coming to the forest floor to feed on minerals in the soil or to drink (Struhsaker & Leland, 1987). Typically, hind limbs of colobine monkeys are much longer than forelimbs, and almost all colobine species have characteristically long tails (Oates & Davies, 1994; Rowe, 1996). The family name *Colobinae* symbolizes the short or absent thumbs found in most African colobine species; the word 'kolobos' in Greek means 'mutilated' or 'cut short' (Oates & Davies, 1994; Rowe, 1996; Kingdon, 1997).

Most colobines have an enlarged, sacculated forestomach, which accommodates a complex microflora capable of cellulose digestion, granting access to plant fibres and cell contents protected by plant cell walls, as well as the detoxification of certain components present in a diet including substantial quantities of leaves, seeds and unripe

fruits (Kay & Davies, 1994). Because of their specialized digestive tract and relatively high leaf intake, colobine monkeys are also known as ‘the leaf eating monkeys’ (Rowe, 1996). Their ability to subsist on a diet of low quality mature leaves allows the colobines to survive in areas that are ecologically deprived of key food resources, such as young leaves, fruits and seeds. This, in turn, is reflected by their generally higher biomass in such deprived areas when compared with the other primate species inhabiting the same area (Oates et al., 1990; Oates & Davies, 1994; Fashing et al., 2007).

### **African Colobus monkeys**

The differences in the African Colobus species were described in detail by Oates et al. (1994) and Groves (2007). African colobines are divided into three genera: the black-and-white colobus monkeys (genus *Colobus*), the red colobus monkeys (genus *Piliocolobus*), and the olive colobus monkeys (genus *Procolobus*). The genera are distinguished by some clear differences in anatomy, such as the presence of a subhyoid sac and a large rather than small larynx found in the *Colobus* genus when compared with the other two genera (Hill & Booth, 1957). These last two anatomical differences have been linked to the production of the conspicuous, resonant, low-pitched vocalizations, which are characteristic of the *Colobus* genus. This feature has been studied most extensively in *Colobus guereza* (further called ‘Guereza colobus’ or simply ‘Guereza’ throughout this study), which is one of the classified *Colobus* species, and the focus of this thesis (Marler, 1972; Oates, 1977; Oates & Trocco, 1983; Harris, 2006; Harris et al., 2006).

### **Genus *Colobus***

Although there have been many disputes about the species-classification of the different forms of *Colobus*, the genus is now thought to consist of five different species: *C. satanas*, *C. polykomos*, *C. vellerosus*, *C. guereza* and *C. angolensis* (Oates & Trocco, 1983; Oates et al., 1994; Groves, 2007). *C. vellerosus* and *C. polykomos* are found in West Africa, whereas the other three species are found in Central- and East Africa (Rowe, 1996; Groves, 2007). Acoustic analyses of temporal patterning, frequency, and modulation of the vocalizations of these five species by Oates and Trocco (1983) and Oates et al. (2000) suggested that they are grouped in three clusters. *C. vellerosus* and *C. guereza* share a recent common ancestor, with *C. guereza* having

the largest number of derived features among the members of the black-and-white colobus group. *C. polykomos* and *C. angolensis* seem to be more primitive, but have diverged rather little from each other, whereas *C. satanas* is a form that has not had a recent common ancestry with any other form, but is most closely related to the *angolensis-polykomos* pair. *C. vellerosus* is suggested to be an intermediate form between *C. polykomos* and *C. guereza*.

### **Species *C. guereza***

Guereza colobus monkeys have been studied in detail over the past decades. Reviews about the early studies of these animals, as well as new data on their vocalizations, ecology and social lives, were most notably given by Marler (1969; 1972), Oates (1977), (Davies & Oates, 1994), Fashing (Fashing, 2001b; Fashing, 2001a) and Harris (Harris, 2006; Harris & Chapman, 2007).

Guereza colobus monkeys are medium sized arboreal primates, with moderate sexual dimorphism (weight: ♀ 7.9-9.2 kg, ♂ 13.5 kg; head and body length: ♀ 576 mm, ♂ 615 mm; tail length: ♀ 667 mm, ♂ 687mm; Rowe, 1996). Both sexes have a characteristic pelage consisting of a white mantle of long fur on the shoulders and around the back, a white brow and full beard surrounding the grey-black face, and a white bushy tail-tip. Infants are born with an all-white coat and pink face, which gradually darkens to the adult pattern. In addition to the all-white infants, three other age classes are normally described: juveniles, ranging from 6 months to two years of age, sub-adults, ranging from two to four years of age, and large sub-adults, ranging from 4 to 6 years of age. Maturing males disperse from their natal group, and sometimes form all-male bands before taking over a group of their own. Guerezas predominantly live in one-male multi-female groups, but multi-male multi-female groups have also been described. A typical group contains 6-11 individuals, with a composition of one adult male, 3-4 adult females, perhaps one large sub-adult male and one large sub-adult female, a sub-adult male and female, one juvenile and one infant.

Guereza colobus monkeys are distributed across equatorial Africa, from Ethiopia to northern Tanzania and west to the Nigeria-Cameroon border (Oates, 1994). Over this range, several subspecies of *C. guereza* have been classified (*C. g. occidentalis*, *C. g. guereza*, *C. g. gallarum*, *C. g. dodingae*, *C. g. percivali*, *C. g. matschiei*, *C. g.*

*kikuyuensis*, and *C. g. caudatus* (Groves, 2007), that differ characteristically in the length and degree of white in their tail-tuft and the length of their mantle. These subspecies inhabit a diverse range of habitats, such as moist lowland forests, montane forests, riverine forests, dry coastal forests, and gallery forests of the savanna zones (Oates, 1994). Guereza colobus monkeys thrive extremely well in secondary forests, and often they are actually found at higher densities in heavily logged forest compartments than in unlogged or lightly logged forest compartments (e.g. Plumptre & Reynolds, 1994; Chapman et al., 2000).

Despite their reputation as ‘strict leaf eaters’, most *Colobus spp.*, including *C. guereza*, are not restricting themselves to a diet purely consisting of leaves. Although the proportion of leaves in their diet can be high (ranging from 53% to 94%), some Guereza populations also eat considerable quantities of fruits (ranging from 2 to 39%), flowers and flower buds (ranging from 0.5 to 5.5%), and bark (ranging from 0.5 to 3.2%), which shows that they possess a certain degree of dietary flexibility (Oates, 1994; Fashing, 2001b; Fashing, 2001a). Nevertheless, the Guerezas’ high leaf-intake provides relatively little energy and requires long fermentation periods after feeding, which has been linked to the monkeys’ peculiar, highly inactive, life-style: to cope with their dietary constraints, Guerezas display energy-conserving behaviour with 57% or more of their time spent resting, around 20% feeding and only 5% moving (cf. Dasilva, 1992; Oates, 1994; Fashing, 2001a). Day journey length of Guerezas, consequently, only averages around 550 m per day (Oates, 1977b; Oates, 1994; Fashing, 2001a). Related to this, Guerezas are generally found to occupy rather small home ranges (Oates, 1994). Average home range sizes range from 10 to 35ha, with actively defended core territories of around 1 to 2ha in some study populations (Marler, 1969; but see Harris, 2006; Harris & Chapman, 2007). Home range size generally shows a clear inverse relationship with population densities (Oates, 1977b; Dunbar, 1981, but see Oates et al (2000); Oates, 1994; Fashing, 2001a). In larger forest blocks, home ranges often are larger and overlap extensively (Oates, 1977; Oates, 1994; Fashing, 2001a; Harris & Chapman, 2007).

### ***Vocal behaviour of black-and-white colobus monkeys***

A detailed description, spectrographic representation, and acoustic analysis of the vocal repertoire of black-and-white colobus monkeys was first given by Marler (1972) for the Guereza colobus monkeys. Following this study, more or less detailed descriptions of black-and-white colobus vocalizations were provided by Groves (1973) on *C.*

*angolensis*, Oates (1977) on *C. guereza*, and Walek (1978) on *C. polykomos/angolensis*. Five different vocalisations and one non-vocal sound were described in all of these studies: 1. roaring, 2. snorting, 3. cawing, 4. grunting or purring, 5. squeaking or screaming, and 6. tongue clicking. Two of these vocalisations, snorting and roaring, are found in alarm responses of the male black-and-white colobus monkeys and will be discussed in more detail later on.

**Cawing** is only produced by adult females, juveniles and infants, often together with squeaking and screaming. It consists of a rapid train of pulses, with a dominant frequency around 1 kHz or less. The pulse trains can be very short, although trains of more than 100 pulses have been observed (Marler, 1972). Cawing can be produced during inhalation, but also during exhalation, when it often grades into squeaking and screaming, in a continuous sequence. Cawing in infants and juveniles is observed in situations of mild distress, such as abandonment, insecurity, or weaning, and is used by adult females during defensive threats to other adult females or the adult male.

**Squeaking** and **screaming** are produced by infants, juveniles, and adult females. The sounds last around 0.1s, have a fundamental frequency between 1 and 2 kHz, and can be either tonal or harsh. Infants sometimes couple squeaks together, producing a continuous tone that oscillates in frequency. These individual tones can be interrupted by cawing. Bouts of several squeaks and screams combined together can sometimes last several seconds, especially when produced by infants. Squeaks and screams are given in similar situations as cawing, but are associated with stronger distress. They are most typical for newborn white infants, producing them for example when abandoned on a tree branch, or when the mother grabs it very suddenly in a dangerous situation (personal observation).

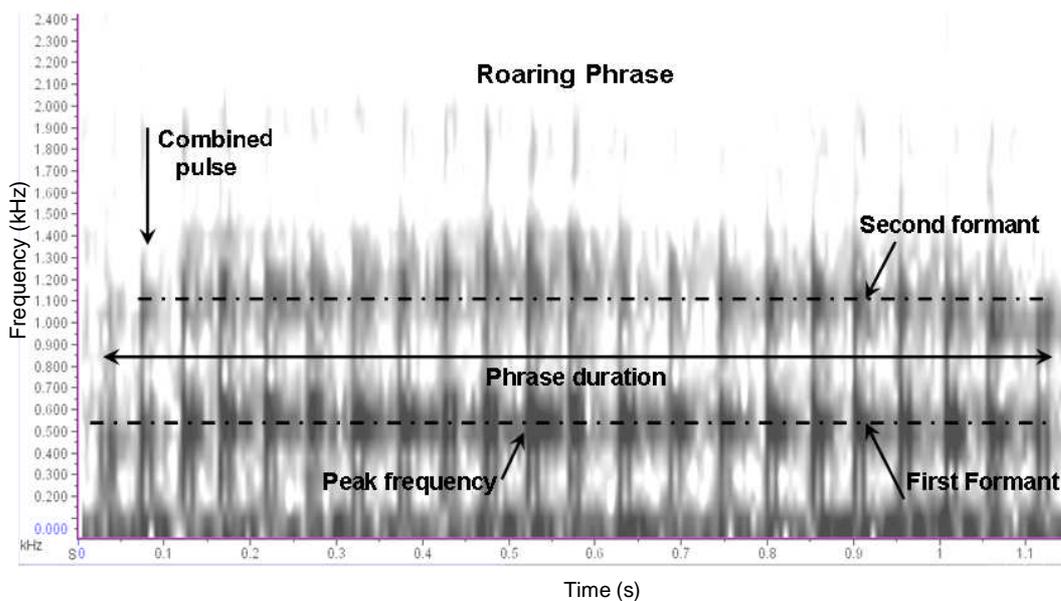
**Grunting (purring)** was observed by Marler (1972) to occur as a prelude to group locomotion and possibly serves to co-ordinate movements. It is produced mostly by females but has also been observed in males. Additionally, grunting is frequently observed in situations of increased alertness, in which the animals might have noticed a disturbance (Oates, 1977, personal observation *C. guereza* and *C. polykomos*), such as predators, observers, or stranger males.

**Tongue clicking** is a non-vocal sound produced by adults of both sexes during mild aggressive interactions. It is often used by the dominant male to other males in his group, but also in between-group encounters, and in potential dangerous situations, such as the presence of an observer or predator (personal observation, Marler, 1972; Walek, 1978). It appears to be part of an aggressive strategy, serving to evoke withdrawal or submissive behaviour in another individual. It appears to function as a threat in the first stage of aggressive interactions, and may be accompanied by glaring and lunging. The threshold for production seems lower than that for the snort (described below), and the animals sometimes switch from tongue clicking to snorting as they become more aroused.

**Snorting** consists of broadband acoustic energy with a sudden, ‘explosive’ onset, ranging in frequency up to about 4 kHz with the main frequency at around 1 kHz. Snorts are low-amplitude, a-periodic sounds, audible over short distances only. Snorts are dominantly given by males, but they have also been documented for females (Marler, 1972; Sicotte et al., 2007). These signals, when given alone, are often associated with approach, glaring, lunging and bouncing from branch to branch. This signal is most frequently given in response to potential predators on the ground, such as leopards, human observers and (more exceptionally) chimpanzees (Marler, 1972, personal observation). As mentioned, they can be given alone, but are also often preceding roaring sequences. When preceding roaring sequences, they have also been observed to appear in the response to raptors. Snorts were proposed to function as an alarm call by Hill & Booth (1957), Marler (1972), and Walek (1978). It can evoke approach and inspection from group members that are up in the canopy, but escape and alarm from group members that are below their customary level in the canopy.

**Roaring**, the characteristic loud, low pitched vocalizations for which the black-and-white colobines are well-known, was called the species’ ‘full call’ by Hill & Booth (1957). They described it to sound like a deep ‘rurr rurr rurr rurr’. Although it is usually referred to as ‘roaring’, its pulsed character also gives it some similarity with ‘croaking’ of frogs, albeit much louder (Hill & Booth, 1957; Oates, 1977; Walek, 1978). It is the most conspicuous sound in the black-and-white colobus’ vocal repertoire, audible through the forest over more than one kilometre, and is produced only by the adult males (Marler, 1969; Marler, 1972, but see Harris et al. 2006;

Korstjens, 2001; Sicotte et al., 2007). The basic structural features of roaring were described by Marler (1972), Oates & Trocco (1983) and Oates et al. (2000) for *Guereza colobus* monkeys and confirmed to be similar in *C. angolensis* by Walek (1978). Individual **roaring phrases** ('phrases', 'calls') are the result of about a dozen **compound pulses** (also called syllables), which appear in the spectrogram as compound units with an average duration of about 700 ms. Each compound pulse is composed of 2-4 short distinct glottal pulses, with an average duration of 10 ms. The main acoustic energy in each phrase tends to appear as two discrete frequency bands on the spectrogram, at around 600 Hz and 1200 Hz, with a varying emphasis on either band (Figure 2.1). A recent study by Harris et al (2006) revealed that these two frequency bands are the first and second formants resulting from resonances of the vocal tract after call production.

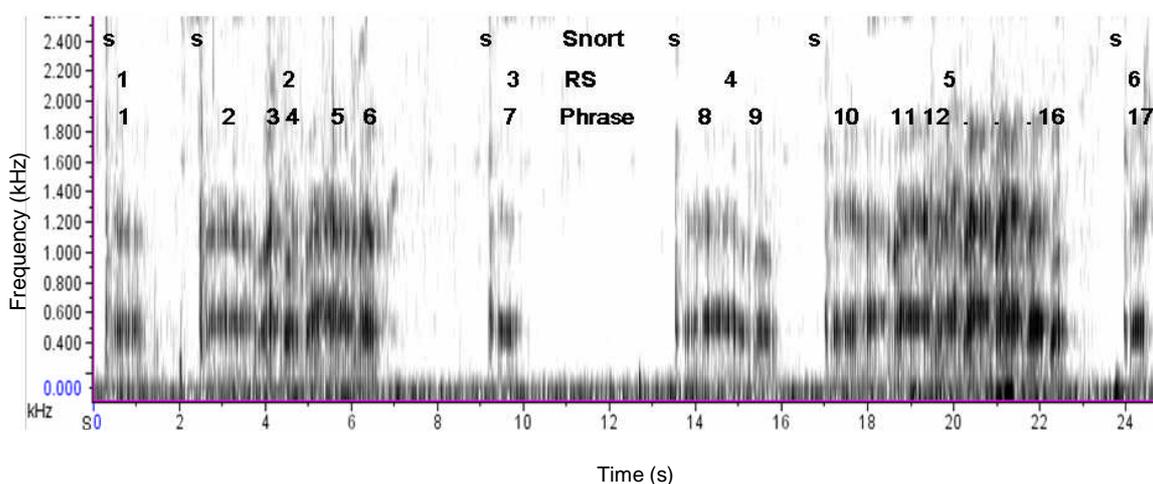


**Figure 2.1.** Roaring phrase of an individual *Guereza colobus* male. Indicated are the different components described in this study. The x-axis represents time in seconds, the y-axis frequency in kHz.

Individual roaring phrases are usually assembled into **roaring sequences** (called 'roars' in the studies of Harris (2006) and Harris et al. (2006)), which together form a bout. A bout is separated from another bout by a non-roaring period of at least one minute. The first phrase in a roaring sequence can be preceded by one or more snorts. Roaring sequences vary substantially in the number of roaring phrases they consist of, ranging from one or two to 20 or more given in rapid succession with intervals of around 200

ms between them (Figure 2.2). Marler (1972) distinguished between ‘low intensity roaring’ and ‘high intensity roaring’. Low intensity roaring consists of a snort and one or two phrases repeated in intervals of several seconds. In more intense roaring the calls are often grouped together in sequences of 4 or 5, with a snort before the first phrase. In the most intense display, sequences of up to 20 or more calls may be given in rapid succession, with intervals of around 0.2 seconds between them.

Individual roaring phrases can vary in their acoustic structure, especially when comparing the first and last phrase in a sequence. The final phrase in a roaring sequence often is lower pitched, which generates a perceptually conspicuous marker to terminate the sequence (Marler, 1972; Oates & Trocco, 1983).



**Figure 2.2.** Spectrographic illustration of the structural composition of roaring, depicting a continuous recording of an adult Guereza colobus male responding to a leopard with snort-introduced roaring sequences of low and intermediate intensity. 'S' stands for snort, and RS for roaring sequence. The x-axis represents time in seconds, the y-axis frequency in KHz.

Roaring is used in a variety of contexts by the different black-and-white colobus species, such as dawn- and night choruses, in response to the calls of other males and/or species, and in response to major disturbances, such as falling trees or the presence of predators (Hill & Booth, 1957; Marler, 1969; Groves, 1973; Oates, 1977b; Oates, 1977a; Walek, 1978, personal observation; Oates, 1994). There has been a longstanding view that the main function of roaring is the maintenance of inter-group spacing (Marler, 1969; Marler, 1972), although intimidation of predators has also been proposed as a function (Hill & Booth, 1957; Marler, 1972; Oates, 1977a; Walek, 1978;

Oates, 1994). Additionally, recent research on morning chorus characteristics suggested that variation in the number of phrases per RS ('roar') produced by different males varies negatively with group rank (i.e. effectively male rank) and might indicate a male's fighting ability (Harris, 2006). Formant dispersion in the roars produced in these morning choruses was argued to be an honest indicator, relative to con-specifics, of body mass. In relation to non-specifics, however, Guerezas have exaggerated, low formants and formant dispersion (Harris et al., 2006), and might appear much larger than they really are. Finally, there is some recent evidence for an association between the number of phrases per RS ('roar') produced by a male and the time to presumptive ovulation of his females, suggesting a mate-defence function of roaring as well (Harris, 2006).

### **Roaring: the species-specific loud call**

The production of these characteristic loud roaring vocalizations by Guerezas and the other black-and-white colobines could be costly in terms of time and energy expenditure and is therefore likely to be an honest signal of a male's quality or condition and, as suggested by Harris (2006), his competitive abilities (Gautier & Gautier, 1977; Zahavi, 1977; Zahavi & Zahavi, 1997; Steenbeek et al., 1999; Wich, 2002; cf Delgado, 2006). The frequent use of these costly loud vocalizations, together with the anatomical adaptations (sub-hyoid sac and enlarged larynx) for producing them, presume an important function of roaring in the monkeys' every-day lives, especially because of their otherwise highly energy-saving life style. As described before, one important function of roaring is believed to be inter-group spacing and/or long range male-male competition (Marler, 1969; Marler, 1972; Waser & Waser, 1977; Oates et al., 2000). In a large variety of studies, vocalizations used for this purpose are described to be of low pitch and high amplitude, which enables them to travel far through the dense forest environment, while advertising the callers' relative positions and/or fighting abilities to extra-group males (Gautier & Gautier, 1977; Waser, 1977; Waser & Waser, 1977; Robinson, 1981; Waser & Brown, 1986; Whitehead, 1987; Steenbeek et al., 1999; reviewed by Delgado, 2006). Because of their loud character, and the long distances over which they are audible, calls of this type have been termed 'loud calls' or 'long (distance) calls' (Gautier & Gautier, 1977). Over the years, a lot of studies have investigated the function of loud calls in several different species. Thus, based on their acoustic characteristics, loud calls were traditionally thought to function

in inter-group spacing, intra-group rallying and long range male-male competition (e.g. Gautier & Gautier, 1977; Delgado, 2006). More recently, however, evidence for an additional, very different, function of loud calls has emerged: communication in predatory contexts in the form of conspecific warning and perception advertisement to the predator (e.g. Zuberbühler et al., 1997; Zuberbühler, 2001; Wich & Sterck, 2003; Arnold & Zuberbühler, 2006a; Clarke et al., 2006).

Surprisingly, little research has been conducted on the production and function of black-and-white colobus roaring, which is also classified as a loud call (Gautier & Gautier, 1977). Although several authors have speculated about the function of this conspicuous vocal behaviour (Marler, 1968; Groves, 1973; Gautier & Gautier, 1977; e.g. Oates, 1977b), systematic studies are hard to find. In the following, an overview is provided of the few studies that have specifically focussed on black-and-white colobus vocalizations in the years after Marler's (1972) and Oates' (1977) initial reports.

A vocalization study on black-and-white colobus on the coast of Kenya by Walek (Walek, 1978) argued that the vocalizations were remarkably similar to those of the Guereza colobus described by Marler (1972). Walek (1978) identified the study animals as *C. polykomos*, or King colobus monkeys, but following more recent taxonomy (e.g. Oates et al., 1994; Groves, 2007), the species under study probably was the Angola black-and-white colobus. The most important finding of this study was the fact that the organization of the vocalizations of this species was remarkably similar to that of the Guereza colobus monkeys. The contexts in which the vocalizations were used were also highly similar to those in Guerezas, with the exception of their production in early morning and night choruses, which was absent in the Angola colobines (but see Groves, 1973). Interestingly, Walek (1978) presented some more detailed, but anecdotal, data on roars produced in the presence of eagles and dogs, indicating already that roars might have a function in alarm communication.

Another study compared the vocalizations of the five different species of black-and-white colobus monkeys (*C. satanas*, *C. polykomos*, *C. vellerosus*, *C. guereza* and *C. angolensis*), mainly for taxonomic purposes (Oates & Trocco (1983). In a follow-up study (Oates et al., 2000) the spectral and temporal characteristics of the roars of all five species were compared to determine the monkeys' phylogenetic relationships. The

authors concluded that these vocalizations were evolutionary relatively stable and displayed species-specific characters, but also contained enough measurable differences between the species that could serve as taxonomic indices. Even though all five species displayed a similar basic organization of their vocalizations into roaring sequences and bouts (Marler (1972), the species' vocalizations differed in temporal characteristics, such as bout composition and the total number of phrases per sequence. One problem with this conclusion was that no information was available on calling context (Walek, 1978). To properly compare the different species' temporal patterning of vocalizations, the call-eliciting context needs to be standardised. Furthermore, Oates et al. (2000) described that the roars were used to serve different main functions in the five different species. In the Ituri Forest (DRC), *C. guereza* and *C. angolensis* live sympatrically. Here, the Guerezas were found to roar much more than the Angola colobines, especially in their use of morning choruses, suggesting a role in long-range intergroup communication (Oates et al., 2000). Based on such observations, the authors suggested a relationship between the acoustic characteristics of the vocalizations and social evolution of the *Colobines* (Oates et al. (2000). The most primitive species, *C. satanas*, produces roars with a much higher frequency and faster tempo than the other species, mainly in predatory contexts. *C. angolensis*, a more derived species, uses roars also for social purposes in multi-male groups, suggesting that male-male competition has led to louder and lower pitched calls indicating a male's strength and condition. In the most derived *C. guereza*, finally, selection has favoured long-distance calling, which enabled males to communicate and compete over long distances, concurrent with a shift in the calls' primary function. Oates et al.'s (2000) notion of an 'evolutionary sequence' implies that the derived function (long range male-male competition as present in *C. guereza*) is different from the original function (alarm communication as seen in *C. satanas*), and that the derived function thus might be present most clearly in the most derived species and the original function most clearly in the most conserved species. This rationale does, however, not make any predictions how roars are used in predator related contexts in *C. guereza* and the other species.

Harris (2006) focussed on the function of morning roars and suggested that variation in the number of phrases per RS ('roar') produced by different males varied negatively with male rank as an indicator of male fighting ability. Harris (2006) also reported an

association between the number of phrases per RS ('roar') and the time to presumptive ovulation of the caller's females, suggesting a mate-defence function of roaring.

Harris et al. (2006) showed that formant dispersion in the morning and predator roars produced by Guerezas was an honest indicator of body mass, and therefore possibly strength and competitive power. Indeed, Guerezas appear much larger than they really are: based on a cross-species comparison of formant dispersion, Guerezas would have an estimated vocal tract length three times longer than it actual is. This observation is consistent with the scenario proposed by Oates et al. (2000). It is also possible that colobus monkeys advertise perception to the predators (one of the ideas that will be tested in this thesis), and evolved low formants to deceive predators about their body size and intimidate them. Finally, it is equally possible that low formants evolved to facilitate long distance communication in a dense forest environment (e.g. Waser & Waser, 1977; Waser & Brown, 1986). Since most black and white colobus species appear to use roars in predatory situations (*C. angolensis*: Groves, 1973; *C. polykomos*: Walek, 1978; *C. angolensis*: Sicotte et al., 2007; *C. guereza*: Schel et al., 2009), predator intimidation seems a plausible way to explain the black-and-white colobine roar characteristics.

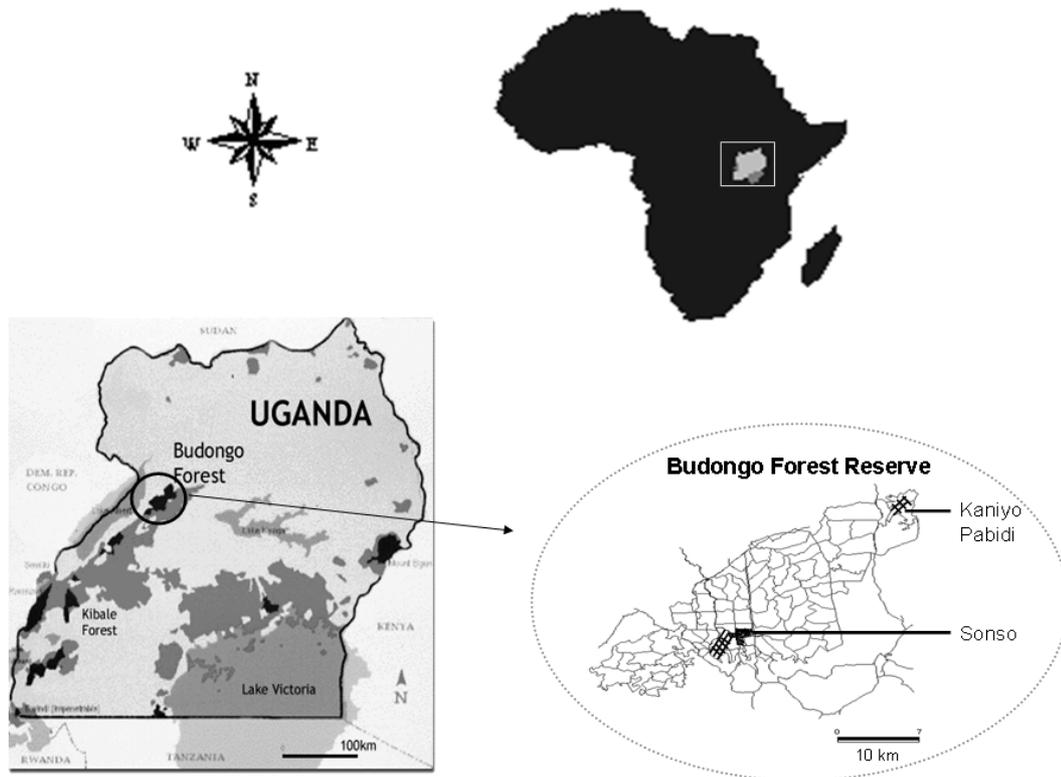
Finally, Sicotte et al. (2007) described roaring in *C. vellerosus* in relation to a male takeover and infanticide, although the study only described one case. In the days before his group was taken over by an all male band of 7 individuals, the resident male's roaring rate dropped dramatically, which could have advertised to the all male band that he was weakened or vulnerable, not able to produce the energetically costly roars, and therefore probably not able to prevent a takeover. This observation is in accordance with a function of roaring in advertising male condition or strength.

An other interesting finding of that study concerned the observation of female roaring produced after a second takeover in the same area. It was hypothesised that, by roaring, the females force the resident male to roar as well, to advertise his physical condition and ability to keep potential male intruders away, and thus preventing costly aggressive takeovers and potential infanticide.

### **Study area and field sites**

Fieldwork was conducted at two field sites within the Budongo Forest Reserve, Western Uganda, Africa (Figure 2.3). The first site was Kaniyo Pabidi, a pristine forest

block located in the North of the Reserve (co-ordinates at camp site: N 01° 55', E 31°43'). The second site was Sonso, located in the South of the Reserve (co-ordinates at camp site: N 05° 49', E 31° 32'). The sites differ considerably in their natural history and ecology, mainly due to their logging history (Plumptre et al., 1997).



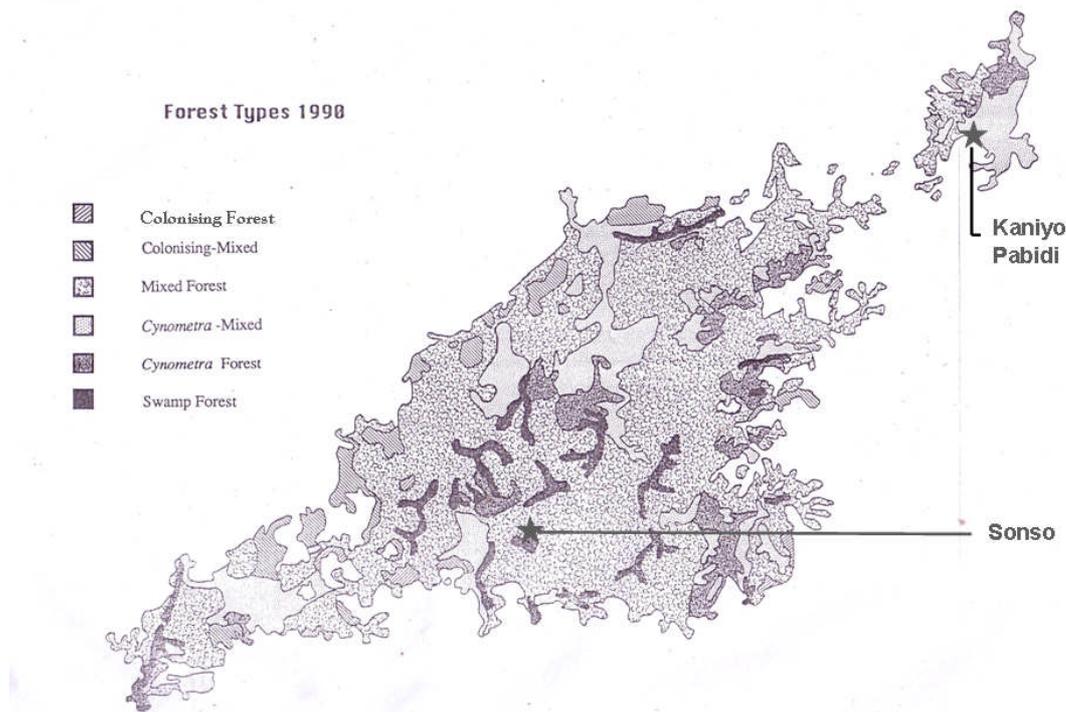
**Figure 2.3.** Map of Uganda, with the geographical location of the Budongo Forest Reserve encircled, and the Kaniyo Pabidi site and Sonso site highlighted. The hatched areas indicate unlogged sections of the Reserve: N15 in the South and KP in the North (copied from Plumptre et al. 1997, and <http://www.budongo.org/>, with permission).

### ***The Budongo Forest Reserve***

#### **Classification and forest types**

The Budongo Forest Reserve is located on the edge of the Western Rift Valley, and covers a total area of 793 km<sup>2</sup>, of which 428 km<sup>2</sup> is forested (Paterson, 1991; Plumptre & Reynolds, 1994; Plumptre, 1996). It is classified as medium altitude moist semi-deciduous tropical rainforest (Eggeling, 1947; Paterson, 1991; Plumptre & Reynolds, 1994), with an average altitude of 1100 m. Eggeling (1947), Paterson (1991), and

Plumptre & Reynolds (1994) described the ecology of the forest in detail, and classified four main types of forest in the area: 1. swamp forest, 2. colonizing forest or woodland, 3. mixed forest and 4. ironwood (*Cynometra*) forest, which follow an ecological succession from woodland forest at the edge of the reserve, through mixed forest, to the climax ironwood forest type dominated by *Cynometra alexandrii* (Fig. 2.4).



**Figure 2.4.** Forest types within the Budongo Forest Reserve (copied from Plumptre, hard copy BCFS, with permission.)

Colonizing forest/woodland mainly contains *Maesopsis eminii*, *Cordia milenii*, and *Diospyros abyssinica*. Mixed forest (the largest component of the forest and recognized by 'its four canopy layers, its high species diversity, and its abundance of large trees 20 to 55 m high'; (Paterson, 1991) is dominated by *Celtis midbraedii*, *Celtis zenkeri*, *Funtumia elastica*, *Khaya anthotheca* (a mahogany species), and *Chrysophyllum albidum*. Swamp forest (the least common forest type) mainly contains *Raphia farnifera*, *Mitragyna stipulosa*, and *Pseudospondias microcarpa*. Swamp forests are found around the forest streams, two of which intersect the Budongo Forest Reserve: the Sonso river and the Waisoke river, which both flow all the way into Lake Albert.

### Climate

The climate is tropical, with a mean annual rainfall of 1600 mm. The Budongo Forest has a double peaked rainfall pattern, with peaks from March to May and from September to November, and a pronounced dry season from December through to February. The mean maximum temperature within the forested areas lies around 27° C and the mean minimum temperature around 16-17° C.

### Fauna

Recent studies by Howard et al. (2000) and Plumptre et al. (2001) reported a rich fauna for the Budongo Forest Reserve. According to these studies, there is a total of 359 bird species, 254 butterfly species, 130 large moth species, 17 species of small mammals, and at least 8 species of larger mammals present in the reserve. Five species of diurnal primates occur in the forested areas of the Budongo Forest Reserve: chimpanzees (*Pan troglodytes schweinfurthii*), olive baboons (*Papio anubis*), redtail monkeys (*Cercopithecus ascanius schmidtii*), blue monkeys (*Cercopithecus mitis stuhlmannii*), and black-and-white colobus monkeys (*Colobus guereza occidentalis*). Vervet monkeys (*Cercopithecus aethiops*) occur in the grasslands surrounding the forested areas of the Reserve.

### Logging history

Most parts of the Budongo Forest Reserve have been part of a polycyclic logging scheme that started in the 1920's, aiming to sustainably harvest valuable timber species (such as different species of mahogany) from the Reserve at 40 year intervals, as well as to replant timber species for future harvest. In the 1950's, this scheme was changed to a monocyclic felling scheme with an 80 year interval, and the replanting of mahoganies stopped. In the 1960's, arboricides were introduced, aiming to get rid of non-marketable species regarded as 'weed' (e.g. *Cynometra*). Using this harsh method, the canopy was opened up to aid and speed up the mahogany re-growth and prevent the forest from converting into a climax forest consisting mainly of ironwood. Arboricide treatments stopped during the years of heavy political unrest in the 1970's (cf. Plumptre, 1996).

The Sonso sawmill, near the Sonso river in the south of the Reserve, was the most important sawmill participating in felling trees and processing timber of Uganda, and

was functioning until the early 1990's. Two forest compartments, N15 and Kaniyo Pabidi (indicated as the hatched areas on Figure 2.3), were left untouched by the logging companies, and can still be considered as more or less pristine forest compartments of the Budongo Forest Reserve. In these unlogged forest compartments, densities of blue monkeys, redbtail monkeys, and Guereza colobus monkeys are lower than the corresponding densities in the logged compartments (up to 5 times lower for *C. ascanius*, 4 times lower for *C. mitis* and 2 times lower for *C. guereza*). Chimpanzees and baboons occur at equivalent densities in both logged and unlogged forest compartments (Plumptre & Reynolds, 1994).

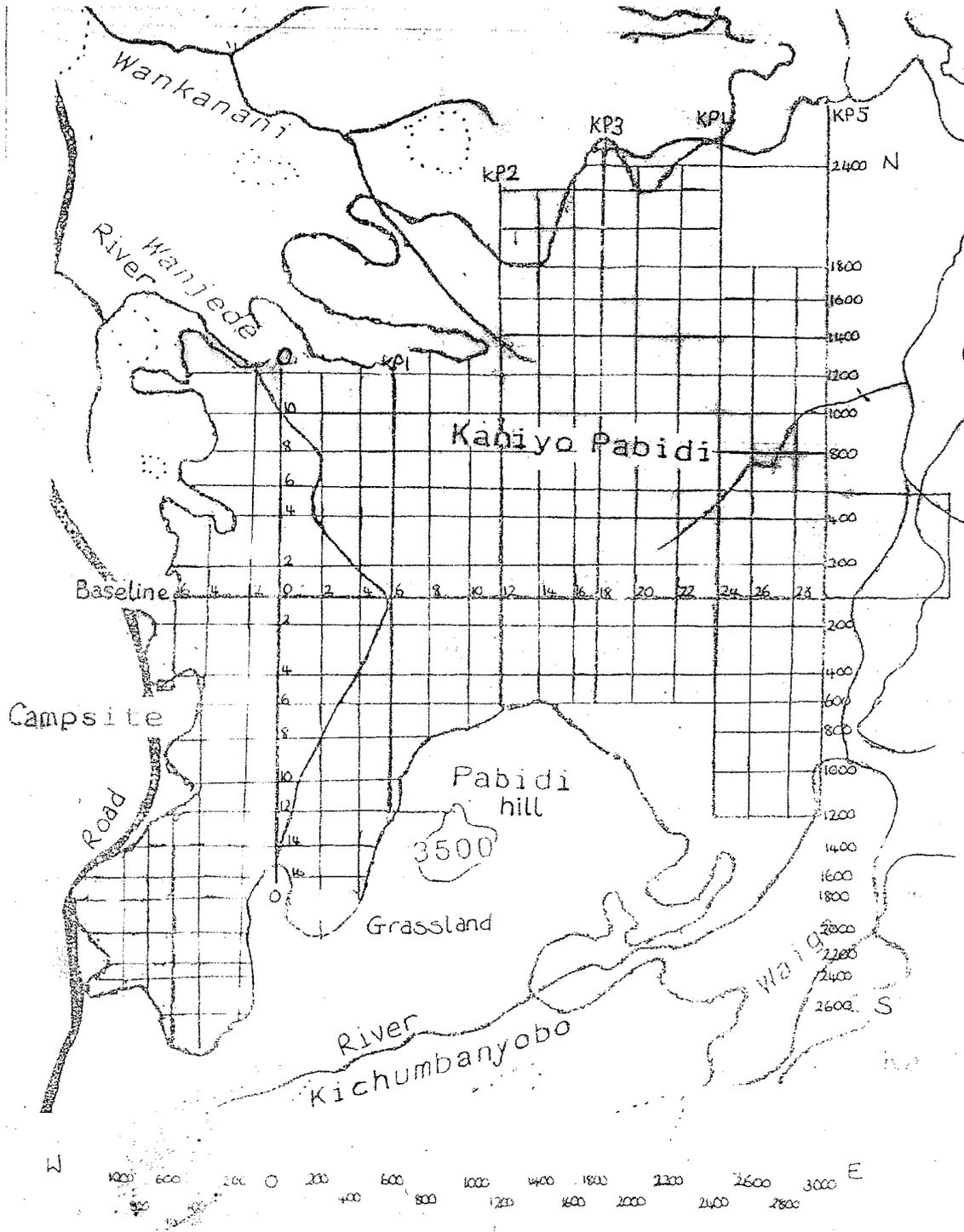
### ***Study sites***

#### **Study site 1: Kaniyo Pabidi**

##### ***Characteristics and Location***

The Kaniyo Pabidi Ecotourism Site is currently run by the Jane Goodall Institute-Uganda, which offers chimpanzee treks, as well as bird watching and nature walks along specified trails. The study site in the Kaniyo Pabidi area of the Budongo Forest Reserve (compartments K11, K12, and K13, see Plumptre, 1996, for a detailed map indicating the forest compartments) consists of approximately 11 km<sup>2</sup> of primary tropical moist semi-deciduous rainforest, accessible through a well maintained trail system with a total length of around 115 km (Fig. 2.5).

The study area contains patches of all types of forest described by Eggeling (1947), Paterson (1991), and Plumptre & Reynolds (1994). The core area of the grid system consists of cynometra-mixed forest, whereas there are cynometra dominated patches to the north and swampy areas to the south. Colobus monkey groups seemed to occur at lower densities in the cynometra dominated patches and swampy areas, which can be explained by the fact that Guereza density is correlated with the presence of *Celtis durandii* in any particular area; this tree species mostly occurs as part of mixed forest vegetation (Plumptre et al., 1997).



**Figure 2.5.** Grid system and study area of the Kaniyo Pabidi Ecotourism site of the Budongo Forest Reserve (printed with permission JGI-Uganda).

***Primate densities***

Despite the lower overall density of primates in this pristine forest area, recent primate density estimates (Plumptre et al., 1997; Plumptre & Reynolds, 1994; Plumptre, 2000) estimated Guereza colobus groups in Kaniyo Pabidi to occur at relatively high densities of around 30 individuals per square kilometre (equal to approximately 3 to 5 groups (Plumptre & Reynolds, 1994; Plumptre, 2000)). Blue monkeys occurred at densities of around 16 individuals per square kilometre (equal to approximately 1 to 3 groups: Plumptre, 2000; Pazol & Cords, 2005), red tail monkeys at densities of around 8 individuals per square kilometre (equal to approximately 1 group: Chapman & Chapman, 2000, personal observation), and baboons at densities of around 14 individuals per square kilometre (equal to approximately 1 group; personal observation (Plumptre & Reynolds, 1994)). The habituated chimpanzee community at Kaniyo Pabidi contains approximately 85 individuals, of which 39 individuals are identified males, 35 individuals are identified females, and 9 are identified infants (personal communication K. McQualter).

Strikingly, however, in the field periods during the present research in this area (7 years after the last line transects were conducted in this area), only one blue monkey individual was ever observed. This unusual observation was confirmed by the site's experienced field guides (having more than 20 years guiding experience in the area), who pointed out that this was the only blue monkey ever seen in the area recently (personal communication Chombe and Cipriano), suggesting a rapid recent decline of this species in this area.

***Predator species***

The mammalian and avian fauna in Kaniyo Pabidi include predator species that form a permanent threat to the Guereza colobus monkeys: chimpanzees (*Pan troglodytes schweinfurthii*), crowned eagles (*Stepanoaetus coronatus*), and leopards (*Panthera pardus*), Fig. 2.6. Humans do not have access to the forest in Kaniyo Pabidi apart from the trail system, and poaching is a relatively minor threat to the animals in this area (personal observation).



**Figure 2.6.** Primate predators of Kaniyo Pabidi: (A) African crowned eagle, (B) chimpanzee, (C) leopard footprint. Photos by A.M. Schel, or printed with permission.

### **Study site 2: Sonso**

#### ***Characteristics and Location***

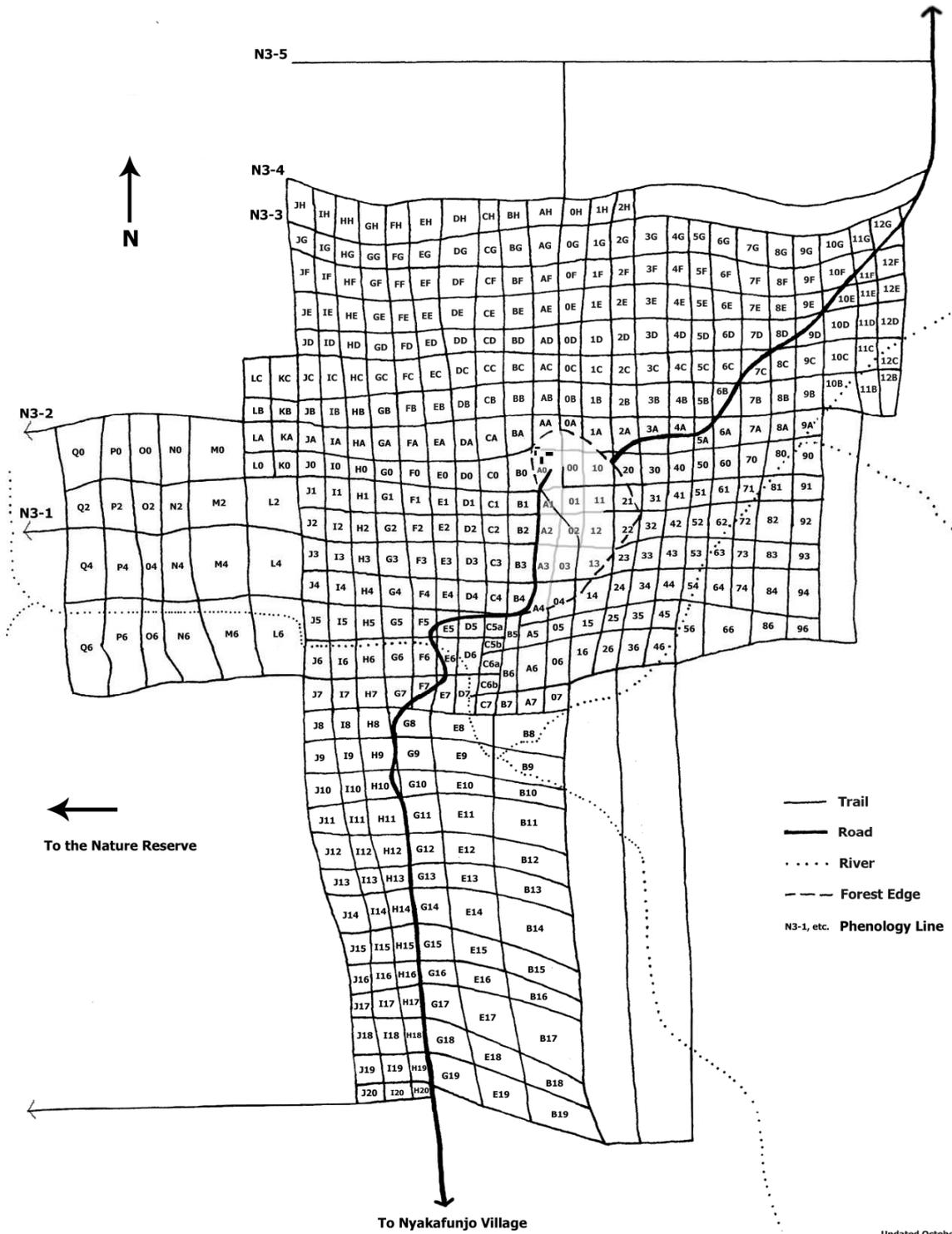
The Sonso fieldsite is located in the South of the Budongo Forest Reserve (Fig. 2.3 and 2.4). It is home to the Budongo Conservation Field Station (BCFS), which was partly rebuilt from the remnants of the disused Sonso sawmill that operated from the 1920's until the early 1990's.

The site is named after the river Sonso, which crosses the study area at several locations. The Budongo Conservation Field Station (BCFS), formerly named the Budongo Forest Project (BFP) was founded in 1990 by Prof. V. Reynolds, with the aim to investigate the responses of wildlife to habitat modification post-logging, and to ensure sustainable management and utilisation of the Budongo Forest Reserve as a model for tropical rain forest management ([www.budongo.org](http://www.budongo.org)). Over the years, its main focus was on studying wild chimpanzees, focusing on topics ranging from their social lives, feeding preferences and habitat use, to their vocalizations, conservation,

and cognitive capacities. Conservation work and research on other primates and birds have also been successfully undertaken in this area, and the project is currently expanding its aims and interests.

The study area at Sonso ranges across forest compartments N1, N2, N3, and N4 (Plumptre, 1996), and consists of approximately 9 km<sup>2</sup> of secondary tropical moist semi-deciduous rainforest, accessible through a well maintained trail system (100m blocks). The study area contains all types of forest described by Eggeling (1947), Paterson (1991), and Plumptre & Reynolds (1994), which, moreover, is reflected in the variability of habitat use by different species in specific parts of the forest (personal observation, cf. Plumptre et al., 1997). An old logging road (called the Royal Mile in the South, which is well maintained and used extensively) runs through the study range, and continues up to the North, where it is somewhat overgrown (Fig. 2.7).

A school at the sawmill terrain, that provided education for the children of the Sonso sawmill personnel was still functioning at the time of this study. Therefore, children were found walking through the forest almost every morning and afternoon during the term time. Furthermore, humans are allowed to harvest *Raphia spp.* in the area, and are often found walking through the forest. People also enter to set illegal snares aimed to catch small mammals such as duikers and big rodents, but, unfortunately, chimpanzees, baboons and occasionally the more arboreal primates get trapped in these snares, leading to serious injuries or death.



**Figure 2.7.** Sonso study area of the Budongo Conservation Field Station, indicating the grid system and block names (printed with permission).

***Primate densities***

Densities of primates in Sonso are generally higher than in the unlogged Kaniyo Pabidi compartment of the Reserve. Based on line transect data conducted in the area, Guereza colobus groups occurred at densities of around 60 individuals per square kilometre (equal to approximately 6-10 groups, Plumptre & Reynolds, 1994; Plumptre, 2000; Preece, 2001). Blue monkeys also occurred at densities of around 60 individuals per square kilometre (equal to approximately 10 groups, Plumptre, 2000; Plumptre & Reynolds, 1994), red tail monkeys at densities of around 45 individuals per square kilometre (equal to approximately 2-5 groups, Chapman & Chapman, 2000), and baboons at densities of around 11 individuals per square kilometre (equal to approximately 1 group; personal observation). The habituated chimpanzee community at Sonso contained approximately 75 individuals at the time of study, of which 8 were identified adult males and 25 identified adult females. Two neighbouring chimpanzee communities with an unknown number of individuals were present in the area, one to the north and the other to the southwest of the Sonso community.

***Predator species***

The mammalian and avian fauna reported for Sonso include two predator species that form a permanent threat to the Guereza colobus monkeys; chimpanzees and crowned eagles. In this area, roaring was also two times observed in the presence of a harrier hawk, *Polyboroides typus*. In contrast to Kaniyo Pabidi, leopards are most probably less relevant as predators in Sonso. There have not been any signs of this felid in this part of the forest for over 40 years. One unverified sighting of a reportedly 'old' leopard walking on the Royal Mile near the Sonso river, as well as some plausible leopard tracks on the old logging road to the north have been reported by field staff in the last two years, but it is likely that most monkeys within the study area have never, or rarely, encountered this predator species. Humans do have (limited) access to the forest surrounding the Sonso fieldsite, and therefore poaching is a possible threat to the primates in this area. Even though poaching often is not aimed at primates because these are not eaten by the local population, monkeys and chimpanzees do occasionally get caught in the snares set for duikers and other small mammals, which can be lethal to Guerezas (Plumptre et al., 1997, personal observation).

## **Predator abundance, predation risks, predator hunting techniques, and Guereza anti-predator behaviour**

In the present study, previously published data were combined with personal observations in order to classify the predator abundance and predation risks for both sites as accurately as possible. Plumptre et al. (1997) described the predation risks for the primate species in Sonso, including the unlogged N15 compartment. Data for the unlogged Kaniyo Pabidi compartments are not available. Following Struhsaker (2000), relative abundance and corresponding predatory threats of the predator species were classified as '*common*: seen at least once a week, often daily', '*less common*: seen every 1-3 months', '*infrequent*: seen every 4-8 months', '*uncommon*: seen every 8-12 months', '*rare*: seen approximately once every two to three years', or '*absent*: no sightings'.

### ***Predator abundance and predation risks***

#### **Chimpanzees**

Chimpanzees can pose serious predation risks to monkey populations, as reported for red colobus monkeys in Gombe, Tanzania (reviewed in e.g. Stanford, 1996), Kibale, Uganda (Watts & Mitani, 2002), and the Tai Forest, Ivory Coast (e.g. Noe & Bshary, 1997). In Gombe, the predation risk caused by chimpanzees can reach relatively high levels of up to 36% of annual mortality of red colobus monkeys (Stanford, 1996). In Kibale, 6-12% of the red colobus population is killed each year by chimpanzees, with the second-most frequent prey species in this area being the Guereza colobus monkeys. The risk appears to be lower in Tai, but the red colobus monkeys are still exposed to an average of 26.4 high risk chimpanzee encounters per year (Noe & Bshary, 1997). Shultz et al. (2004) showed that the Tai chimpanzees mainly hunt arboreal prey, and that, depending on the prey species, they were responsible for the removal of 1-4% of total prey biomass per year.

In the period of 1991-1997 chimpanzees posed just a mild threat to the Guereza colobus monkeys in the Sonso area of the Budongo Forest, with only five recorded observations of Guereza kills and –eating (Plumptre et al. (1997); Newton-Fisher (2002)). Between 1997 and 2006, another 6 events of chimpanzee predation on monkeys were observed, but this pattern changed dramatically in 2007 and 2008, when

colobus kills- and/or -eating happened much more frequently. For example, between April and June 2008 a total of 13 successful black and white colobus hunts- and kills were reported, with an average catch of 3 individuals per attempt. Therefore, the predation risk by chimpanzees for the Guerezas in Sonso seems to have increased over the years and is higher than previously thought.

Hunting and meat eating by chimpanzees has been less well documented for Kaniyo Pabidi, but it can happen on a daily basis at certain times of the year (personal communication K. McQualter).

The number of chimpanzees present is more or less equal at the two sites, but the number of adult male chimpanzees is probably higher in Kaniyo Pabidi than in Sonso. As mentioned earlier, primate prey biomass per km<sup>2</sup> is lower in Kaniyo Pabidi than in Sonso, and home range sizes of the chimpanzees and the monkey species is suggested to be larger in Kaniyo Pabidi (Plumptre et al., 1997). Based on these observations, chimpanzees can be classified as a ‘common’ threat for Guerezas at both sites, that pose a considerable risk at both sites.

### **Crowned Eagles**

Studies on crowned eagles have shown that a large proportion of this raptor’s diet consists of primate prey (e.g. Kibale: Struhsaker & Leakey, 1990: 83.7%; Mitani et al., 2001: 82%; Taï: Shultz, 2002: 49%), although they can pose an important threat to much of the other mammalian community in tropical forests as well (e.g. Shultz, 2002; Schulz et al., 2004). Based on the dietary requirements of about 340kg of prey per year (cf Brown (1982): 340 kg, Shultz, 2002; Schulz et al., 2004), average home range size (6.5-10 km<sup>2</sup>: Struhsaker & Leakey 1990; Shultz, 2002), number of kills observed, and the respective prey biomass present in the studied areas, crowned eagle predation was estimated to be responsible for an annual offtake of 2.4% of the available mammalian prey biomass in Kibale, and 4-9% in Taï. Crowned eagles in Taï hunt terrestrial and arboreal prey at equal rates, removing between 2-14% of prey biomass per year (Shultz et al. 2004). In Budongo Forest, the annual offtake of mammalian prey was estimated at 7.5% in the unlogged (N15) compartment, and 3.7% in the logged compartment (N3; Plumptre et al. 1997). These estimates depend on the home range sizes, which can vary from 10 km<sup>2</sup> (cf. Struhsaker & Leakey, 1990), to 6.5 km<sup>2</sup> (Shultz, 2002) and 3.8 km<sup>2</sup>

(Mitani et al. 2001), depending on the study site. In order to estimate the current impact of crowned eagles in Sonso, an observational study of 11 months (September 2006-August 2007) was conducted in this area. During this study the entire study area was searched for eagle nests. Once a nest was found, it was monitored with intervals of 2-3 weeks. Two, possibly three, active nests were present in the Sonso grid area, indicating a crowned eagle density of more than 1 pair per 10 km<sup>2</sup> (i.e. average home range size 5 km<sup>2</sup>). Eagle circling displays could be observed at least once per week in the Sonso study area. Silent flight through the canopy and monkey-eagle encounters were also observed frequently, but actual kills have never been observed directly. However, the remains of eagle colobus kills were encountered a few times. Based on these facts and observations, eagle predation in Sonso can be classified as ‘common’.

In Kaniyo Pabidi, eagle abundance appeared much lower. Eagle circling displays were observed less frequently than in Sonso (approximately once every 1.5 month), and eagles were never directly observed flying through the canopy. One natural monkey-eagle encounter was observed in four months, no actual kills were observed, and no remains of eagle colobus kills were ever found in the area. Based on these observations in the area, relative to Sonso, eagles were classified as a ‘less common’ threat in Kaniyo Pabidi. For a more accurate estimate, sampling of eagle nests will have to be carried out, although conclusions are unlikely to change.

One important additional point is that predation risk by eagles might not be uniformly distributed throughout a study area. A study by Shultz & Noë (2002) showed that eagle hunting activity is often located close to the nest, and that monkeys’ alarm calling rates decreased with increasing distance from an eagle’s nest. This suggests that prey animals in a specific area might experience variable levels of predation risk, depending on their location within the predator’s home range.

### **Leopards**

Few studies on leopard density and predatory behaviour have been carried out in African rainforests (Jenny, 1996; Zuberbühler & Jenny, 2002; Henschel & Ray, 2003; Jenny & Zuberbühler, 2005). Forest leopards primarily hunt during the daytime, and around 20-30 % of their diet consists of primate prey (Ray & Sunquist, 2001; Zuberbühler & Jenny, 2002; Henschel & Ray, 2003; Jenny & Zuberbühler, 2005;

reviewed in Hayward et al., 2006). Shultz et al. (2004) reported that leopards in Taï Forest mainly hunt terrestrial prey, and were responsible for an annual removal of 2-17 % of prey biomass. Based on footprint analyses, Prins & Reitsma (1989) estimated leopard density in the rainforest of South-western Gabon to be 1 leopard per 5 km<sup>2</sup>, while in the Taï National Park a density of 1 leopard per 9-14 km<sup>2</sup> was reported (Jenny, 1996).

In Budongo, leopards were probably locally driven to extinction during the civil unrests in the country in the seventies and eighties, although roaming individuals can occur. A leopard's home range can extend to 90 km<sup>2</sup>, and usually overlaps to some extent with home ranges of other leopards in the area (Jenny, 1996). Core areas that are most extensively used by the animals often just comprise around 30-40 % of their actual home range, but they will use their entire home range when needed (Jenny, 1996). This information, together with the fact that the two study sites in the Budongo Forest only lie apart 50km from each other, makes it entirely possible that leopards inhabiting a core area in or near Kaniyo Pabidi could roam through the forest around Sonso, although Kaniyo Pabidi is separated from the rest of the forest by open terrain (Fig. 2.4).

Leopard sightings and/or leopard signs have been extremely scarce in Sonso. Therefore, they have been classified as 'rare/ absent' in this area. In Kaniyo Pabidi, reports of direct leopard sightings and/or signs of their presence happen more frequently, at least every few months, and leopards are therefore classified as a 'less common' threat in this area.

**Table 2.1.** Classification of threats posed by the three different predator types at the two different field sites.

Field Site	Predator Type		
	Chimpanzee	Crowned Eagle	Leopard
<i>Kaniyo Pabidi</i>	<i>common</i>	<i>less common</i>	<i>less common</i>
<i>Sonso</i>	<i>common</i>	<i>common</i>	<i>rare/ absent</i>

### **Predator hunting techniques**

As described briefly in the general introduction, differences in the predators' hunting techniques have been implicated as an important factor in shaping different animals' anti-predator behaviours, including the use of alarm call systems. Prey species that are predominantly terrestrial will experience different risks from predators than species that can move in more than one dimension (Macedonia & Evans, 1993). To be able to understand the anti-predator behaviour of Guerezas, an understanding of their predators' hunting techniques is needed and described below.

### **Chimpanzees**

Chimpanzees can be described as 'pursuit hunters' that often hunt in groups, but they have also been found to hunt individually and opportunistically (e.g. Zuberbühler et al., 1997; Boesch & Boesch-Achermann, 2000; Newton-Fisher et al., 2002; Watts & Mitani, 2002). When hunting, the chimpanzees move through the forest extremely silently, apparently in search for a suitable target monkey group. Once a target group has been identified by the hunting party (usually the adult males of the community), they will climb in the tree where a specific individual monkey is residing and singled out. This prey animal is then driven through the canopy, into the trees where other chimpanzees are waiting to capture it. Just before or during the hunts, the chimpanzees may start vocalizing (personal observation). As mentioned before, at most sites, the prey species most frequently hunted by chimpanzees is the red colobus monkey, followed by black-and-white colobus monkeys (Stanford, 1996; Boesch & Boesch-Achermann, 2000; Watts & Mitani, 2002). The lack of red colobus monkeys in the Budongo Forest has been suggested to be responsible for the relatively lower levels of hunting observed in this forest compared to other forests, but *if* hunts take place, the Guerezas are the most frequently hunted species (Newton-Fisher et al., 2002).

### **Crowned Eagles**

Crowned eagles are usually described as 'stealth' hunters, and have been observed to hunt in pairs as well as alone. In the paired hunts, one of the individuals is usually observed to drive the target monkeys towards the other, by which it is unexpectedly attacked (Plumptre et al., 1997, Dr. E. P. Willems: personal communication). Other observations describe a 'sit-and-wait' technique (e.g. Shultz & Thomsett, 2007). By using this strategy, an eagle will sit silently perched on a branch, waiting until it has

spotted an unwary prey target that it can attack by surprise. Eagles can manoeuvre themselves remarkably swiftly and silently through the canopy, which generates the essential surprise element of the final attack.

### **Leopards**

Forest leopard are described as ‘ambush predators’, hunting during the daytime by means of stealth (Henschel & Ray, 2003; Jenny & Zuberbuhler, 2005). They have been suggested to strike from the lower branches of a tree (Zuberbühler, 2007), but also from the thick bush where they hide silently and remain hidden from sight until an unwary prey species has moved close enough to be attacked by surprise (Jenny & Zuberbuhler, 2005). The animals can be found to hide at places where many monkeys are usually present (Jenny, 1996; Jenny & Zuberbuhler, 2005), and may strategically hide at places that many prey species will eventually visit, such as salt lakes. Even highly arboreal primate species will come down to drink and forage on the soil at such lakes, to obtain their necessary mineral requirements (personal communication Chombe, field assistant Kaniyo Pabidi).

### ***Behavioural response characteristics during natural predator encounters***

Since one aim of the present study was to monitor the monkeys’ vocal and locomotor behaviour in the presence of simulated predators, it is important to also describe the behavioural responses of the monkeys to the presence of the naturally occurring predators. Because of the difficulties of observing naturally occurring predator-prey interactions, this could not be studied systematically, and naturally occurring predator encounters were observed and described opportunistically. From these observations, as well as discussions with other researchers and field staff of the two camp sites and descriptions of monkey responses at other sites, the following behavioural patterns concerning anti-predator behaviour emerged.

### **Chimpanzee encounters**

During chimpanzee encounters, the Guerezas were usually observed to climb up in the tree, after which they silently continued what they were doing, keeping a close eye on the chimpanzees that were present. Once, the Guerezas were observed to run straight into the opposite direction of the chimpanzees that suddenly arrived in their area. This behaviour seems conform that described for other forest monkeys, such as Diana

monkeys and red colobus monkeys of the Tai forest in the Ivory Coast (Zuberbühler, 2007). At times when the chimpanzees would enter a location where a Guereza group resided, and produced arrival pant hoots, the Guerezas were observed to produce snorts and roars (Z. Machanda, personal communication). Other studies have revealed that the Guerezas can actively chase away chimpanzees that are travelling in small parties, and that they can produce vocalizations while doing this (Bates, 2001; Reynolds, 2005, personal observation).

### **Eagle encounters**

It was frequently observed that eagles displayed high up in the air: in these displays the eagles circle around in pairs and emit high pitched vocalizations, the ‘circling calls’. These vocalizations usually did not evoke any reaction from the monkeys, other than an infrequent and occasional glance upwards by some individuals while continuing what they were doing (e.g. feeding, but also sleeping!; personal observation: unpublished data). They normally seemed rather ignorant about the eagles’ presence in this form, and were never observed to produce any roaring sequences in this context. However, when an eagle was observed flying silently over or through the canopy, or silently sitting perched on a branch, fierce roaring was usually observed once the monkeys had detected it. In the majority of such observed monkey-eagle encounters, there was at least one individual, presumably the adult male, pursuing the eagle through the canopy while fiercely roaring and chasing it away from the group. Once, upon hearing the roars of the male that detected an eagle, the other monkeys were observed to jump down and hide in denser canopy, while the male was chasing away the eagle. When the eagle was chased satisfyingly far enough from the group, the individual that was roaring and had chased the eagle would return to the group.

### **Leopard encounters**

Leopard encounters were never observed directly, and the natural behavioural responses on the presence of a leopard could therefore only be deduced from other studies that worked with habituated leopards that could be tracked through the forest (e.g. Zuberbühler & Jenny, 2002), and anecdotal information. Zuberbühler (2007) described monkeys to respond upon detecting a forest leopard with alarm calls and sometimes approaching the predator in the lower canopy.

## **Data collection**

### ***Field periods***

Data were collected during one pilot study in Sonso from August - December 2005, and two main studies in both Kaniyo Pabidi and Sonso: one from March - September 2006, and one from March - September 2007. During these seasons, different kinds of data were collected.

In Sonso, playback experiments with all different acoustic predator models (leopard growls, eagle shrieks and chimpanzee pant hoots) were conducted, as well as control experiments with acoustic models of hyena howls and elephant rumbles. Trials with visual leopard and chimpanzee models, as well as trials with a green sheet with flower print as a control were carried out. Finally, playback experiments with conspecific predator alarms and morning choruses were carried out. In Kaniyo Pabidi, the acoustic predator model experiments (chimpanzee, leopard, eagle), visual model experiments (chimpanzee and leopard) and conspecific monkey alarm experiments were conducted.

During all seasons, natural occurring predator events were recorded and noted down. At the end of the second field season (September 2006), a field assistant started collecting observational data on two active eagle nests in the study area in Sonso at intervals of three weeks, lasting until September 2007. Weather data (temperature and rainfall) and behavioural data of the chimpanzees of the Sonso community, including predatory behaviour, were collected by the field assistants of BCFS during all the field seasons and the periods in between.

### ***Study populations***

One of the most important principles of the experimental protocol (see later in this section), was that each monkey group had to be naïve to a particular experimental condition. This meant that, e.g. during the acoustic model experiments, monkey groups that had heard a specific acoustic model before (e.g. leopard growls), could not be tested with this same model again. They could, however, be tested with acoustic models of a different predator type, e.g. eagle shrieks. Yet, if the same group was to be tested again with a different stimulus type, a period of at least one week had to separate

the two events. To implement this condition, all Guereza groups in the study area were mapped during the first week of a field season, as well as during the experiments. A group located at least 300m from a previously mapped group in the same area was classified as ‘distinct’, but only if encountered on the same day. If a potentially new group was encountered in a similar area to a group that was previously mapped on a different day, then these groups were only classified as ‘distinct’ if they were separated by at least 500m. Additional to the implementation of the restrictions of the protocol, this procedure provided for a means to obtain an estimate of the number and distribution of Guereza groups participating in this study, and facilitate the search for Guereza groups while staying undetected by the monkeys in the experimental phase. Accordingly, in the core study area of Kaniyo Pabidi, at least 21 distinct Guereza groups were identified and in the core study area of Sonso at least 25 distinct Guereza groups.

### ***Experimental protocol***

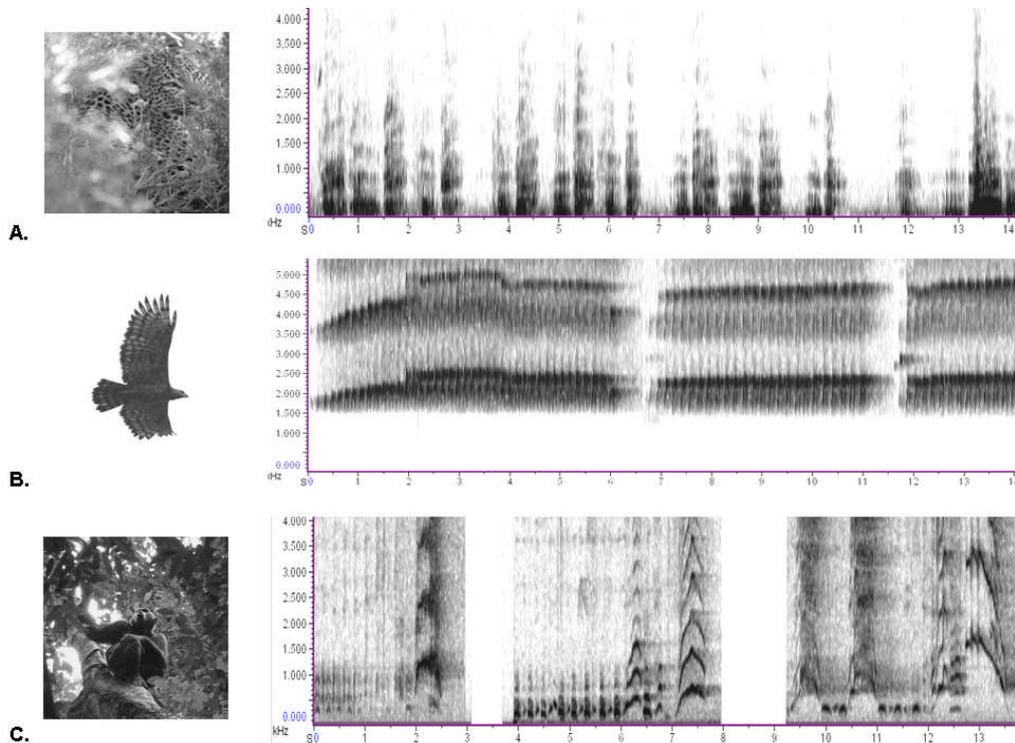
The same experimental protocols were used at both study sites. A normal work day would start around 7h30 and last until around 16h30, but some days could last until 18h00. Before setting out in the morning, it was decided which experiment type (leopard growls, eagle shrieks, chimpanzee pant hoots, corresponding monkey alarms, visual leopard model or visual chimpanzee model) would be used during the day, and which area of the forest would be searched for monkeys. Groups were often found resting silently high up in a feeding tree (using the monkeys’ conspicuous tail tufts as a cue), or by hearing the soft intra-group vocalizations or rustling of trees where they resided. Once found, their exact geographical location was determined using a Garmin GPS 76 and a detailed map to ensure that the group had not been tested before following the previously described protocol. Subsequently, the monkeys’ vocal behaviour was monitored for at least 15 min to make sure that they were unaware of the observers’ presence. An experimental trial followed only if during this period (1.) no animal (including monkeys, duikers and guinea fowls) in the group’s surroundings had produced any alarm calls, (2.) no naturally occurring predator vocalizations had been heard nor any silent predator had been seen, (3) the monkeys had not accidentally detected the observers or the playback equipment, and (4.) no other field worker had walked into the experimental area. If the monkeys saw the observer or equipment

during the experiment, or if there was another disturbance during the course of the experiment and the trial was completed, it was classified as ‘invalid’.

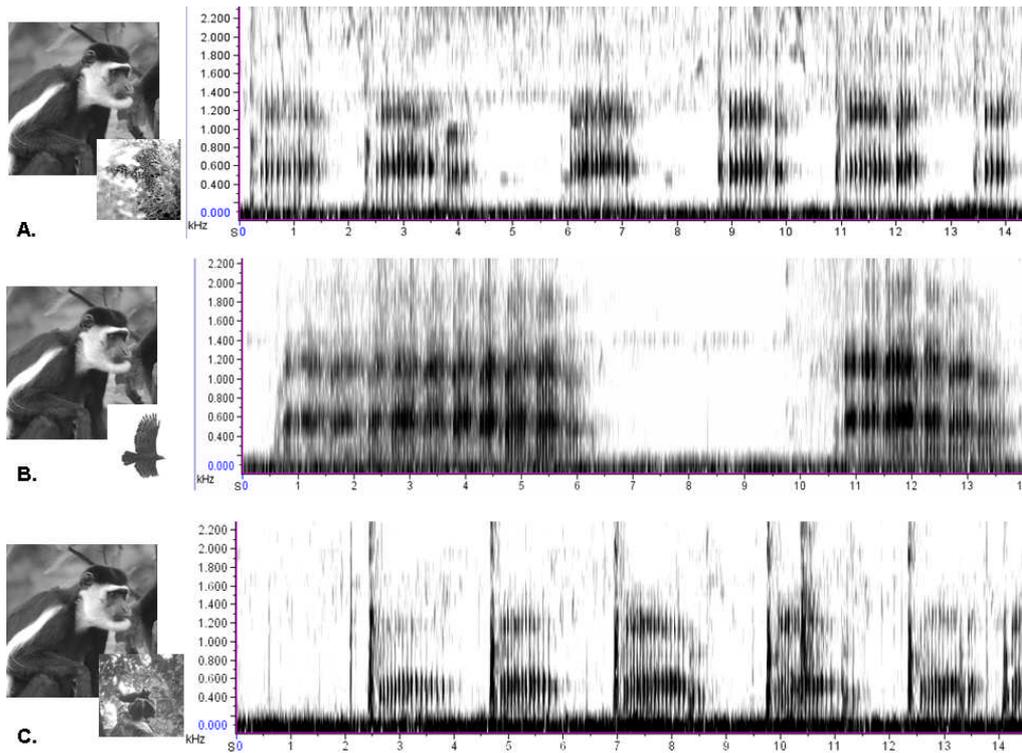
## Experiments

### *Acoustic model experiments*

Predator vocalizations used to create the predator playback stimuli were either purchased from the British Library of Wildlife Sounds, London, by K. Zuberbühler (leopard growls: African leopard; BBC master tape number MM 35 © South African Broadcasting Corporation), or recorded in the Taï forest with a Sony professional Walkman WMD6C and Sennheiser 70mm microphone (K3U +ME88) by K. Zuberbühler (eagle shrieks and chimpanzee pant hoots; Fig. 2.8). Eagle vocalizations used to produce the playback stimuli did not comprise the eagle circling calls. The calls that were used to fabricate eagle playback stimuli consisted of calls emitted by these raptors from within the canopy, e.g. when sitting on the nest. Conspecific monkey alarm vocalizations used for the production of playback stimuli were randomly chosen from the subsets of vocal responses that were recorded in both study areas, using a Sony TCD D8 DAT recorder connected to a Sennheiser K6/ME66 directional microphone (Fig. 2.9).



**Figure 2.8.** Spectrographic representation of predator vocalizations used as playback stimuli: A. leopard growls (14s), B. eagle shrieks (14 s), and C. chimpanzee pant hoots (14s). The x-axes in the figures represent the time in seconds, the y-axis the frequency in kHz.



**Figure 2.9.** Spectrographic representation of Guereza roars to different predators used as playback stimuli: A. leopard alarm roars (14 s), B. eagle alarm roars (14 s), and C. chimpanzee alarm roars (14s). The x-axes in the figures present the time in seconds, the y-axis the frequency in kHz.

All predator and conspecific playback stimuli were edited such that they consisted of 5 min silence prior to approximately 15s of predator vocalizations. To avoid pseudo-replication (McGregor, 2000; Kroodsma et al., 2001), several exemplars of the different playback stimuli were used (N=6 leopard growls, N=6 chimpanzee pant hoots, N=3 eagle shrieks, N=4 Guereza leopard alarms, N=3 Guereza chimpanzee alarms, N=4 Guereza eagle alarms, N=4 hyena howls and N=4 elephant rumbles). The main aim of every experiment was to collect at least 10 vocal responses from different groups to each stimulus.

In 2005 and 2006, playback stimuli were broadcast with a Panasonic SL-SX320 discman connected to a NAGRA DSM speaker-amplifier. In 2007, an Apple Ipod Nano was used to broadcast the sounds via the NAGRA. The volume of the discman and Ipod were always kept constant, whereas the NAGRA amplifier was adjusted so that all playback stimuli were broadcast within their natural amplitude range. Stimulus amplitude was measured with a Radioshack Sound Pressure Level Meter at 2 metres from the source in the natural environment in which the playback was broadcast.

Leopard growls were broadcast within a range of 70-90 dB, eagle shrieks within 80-100 dB, chimpanzee pant hoots within 90-100 dB, and conspecific monkey alarms within 60-70 dB. During broadcasting of the predator stimuli, the playback equipment was usually positioned close to the forest floor (0-2m) at a distance of circa 20-40m from the group, outside their visual range. During broadcasting of the conspecific monkey alarms in Kaniyo Pabidi the playback equipment was positioned close to the forest floor, but during a significant number of playback trials with conspecific monkey alarms in Sonso, the equipment was hoisted up into the trees using a catapult, fishing rod, spindle, fishing wire and lead bullets, resulting in the stimuli being played back from a height of 12-15m. Recordings of the monkeys' responses started after the observers had found a hiding place from the group, about 3 minutes before the actual playback played, and lasted at least 15 min, regardless of whether or not the focal animals responded vocally. The recorded roars were transferred digitally from the DAT recorder onto a PC at a sampling rate of 48 kHz, 16 bits accuracy with Cool Edit 2000 (Syntrillium Software Cooperation).

### ***Visual model experiments***

During the visual predator model experiments two different predator models were presented to the monkeys: one leopard model and one chimpanzee model. To accommodate for the inactive lifestyle of Guerezas, moving predator models were used in this study (e.g. Wich & Sterck, 2003; Arnold et al., 2008).

For the two models, commercially produced material ('fake fur') was used, that was draped over the head, shoulders and torso of a field assistant (GE). If the experimental protocol allowed for an experimental trial, GE would start moving slowly towards the target monkey group, while the other observer (AMS) recorded and observed the monkeys from the hiding place. In case of the leopard model, GE moved on all fours, and in case of the chimpanzee model, he moved in a hunched position on two legs. The size, shape, posture, and colouration of both models matched those of the real predators in their natural environment well (Fig. 2.10). In exceptional cases, GE arrived unnoticed under the tree in which the monkeys were residing. He then gently shook some branches and made rustling noises while moving, to get the monkeys' attention. After the monkeys had seen him, he lingered around in sight of the group for about 15 minutes, before slowly moving back towards the observers' hiding place. The recorded

roars were transferred digitally from the DAT recorder onto a PC at a sampling rate of 48 kHz, 16 bits accuracy with Cool Edit 2000 (Syntrillium Software Cooperation).



**Figure 2.10.** Predators and predator models. A. a forest leopard in its natural environment (photo © [www.dye.no/gallery](http://www.dye.no/gallery), printed with permission), followed by two photographs of the leopard model (photo's © A.M. Schel), and B. a chimpanzee in its natural environment (photo © C. Hobaiter, printed with permission), followed by two photographs of the chimpanzee model (photo's © A.M. Schel).

### Behavioural data and additional information

For all experiments, locomotor data of the monkeys was recorded. For each trial, it was scored whether the majority of the visible individuals had moved at all during the trial, and if so, whether this was up or down the tree ('vertical movement', in metres), and/or further from or closer to the stimulus ('horizontal movement', in metres). Vertical movement data was not collected during the pilot study in 2005 and during trials in 2006. All behavioural responses to the stimuli were classified qualitatively as either 'strong' or 'weak'. If animals expressed either extreme of the possible movements in a significantly higher proportion of the experimental trials than the other ('movement' *or* 'no movement'/ 'up' *or* 'down'/ 'further' *or* 'closer'), then a 'strong' response was reported. If the animals behaved ambiguously, then a 'weak' response was reported, or it was described as being ambiguous/ random.

General information was recorded, such as the date, time, stimulus type and location of the experiment, distance of visible individuals to the stimulus, other monkey species present in the area, and whether these other species called in response to the stimulus.

General illumination during the experiment was scored on a 1-4 scale (1. sun, 2. bright/no sun, 3. overcast/no rain, 4. overcast/start rain), as well as the general density of the forest from the observer's point of view (1-3 scale: 1. open, 2. intermediate, 3. dense), the forest stratum in which the Guerezas were located (0-3 scale: 0. ground, 1. lower canopy, 2. middle canopy, 3. tree top), the elevation of the speaker (in metres from the forest floor), and the approximate angle at which the playbacks were broadcast to the group.

## **Data analyses**

### ***Locomotor data***

Locomotor data were analysed within and between contexts. First of all, it was determined whether the monkeys preferred to move or stay still within a specific predator context ('movement' vs 'no movement'), and if movement occurred, whether there were differences in movements in the horizontal and vertical plane.

Because no prior predictions could be made concerning the monkeys' locomotor behaviour, the test probability used during statistical testing was set at chance level ( $p=0.5$ ), and the critical significance level  $\alpha=0.05$ . For comparisons within the contexts a two-tailed Binomial Test was used, with the data divided into two discrete categories (e.g. 'movement' vs 'no movement', or 'up' vs 'down'). A 'trend' was reported if a critical significance level larger than 0.05 but smaller than 0.08 was found, indicating that there was a general tendency of the monkeys moving into a particular direction during the trials.

To compare the movements between contexts, two-tailed Fisher's exact tests were used, by dividing the data into two categories (e.g. 'movement' vs 'no movement'), but this time two different conditions were compared (e.g. eagle shriek playback vs leopard growl playback). The test probability was set at  $p=0.5$ , and the critical significance level  $\alpha=0.05$ . A Fisher's exact test is recommended over a chi-squared test if any of the cells in the contingency table used in the test are expected to contain a value of 0, or more than one-fifth of the expected values are less than 5 (Siegel & Castellan, 1988).

**Vocal data****General acoustic analyses**

If more than one individual called in response to the predator models, the vocal response of the individual that called first was used for subsequent analyses; vocalizations of other calling individuals were not used in any analyses. In all trials further used for temporal and structural analyses, the calling individuals could be clearly distinguished.

**Structural measurements**

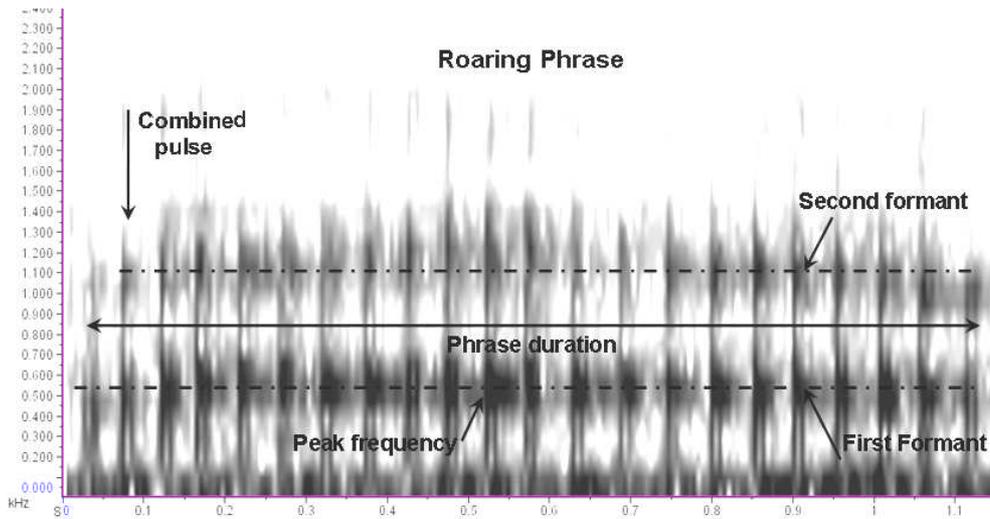
From the vocal responses produced in each trial, the following six structural parameters were determined using spectrograms generated on RAVEN 1.2 (Cornell Laboratory of Ornithology, Ithaca, New York; Hanning window function; filter bandwidth: 124 Hz; frequency resolution: 86.1 Hz; grid time resolution: 5.80 ms): (a) total duration of the vocal response (s), (b) total number of roaring sequences, (c) total number of roaring phrases, (d) mean number of roaring phrases per roaring sequence, (e) number of snorts, and (f) call delivery rate (phrases/s); cf. Oates & Trocco, 1983.

**Spectral measurements**

To compare the acoustic structure of individual roaring phrases given to the two different predator playbacks, 7 different acoustic variables were measured from individual phrases (Fig. 2.11), considered suitable to describe general call characteristics after inspection of the vocal responses and based on previous work by Oates and Trocco (1983), Oates et al. (2000) and Harris et al. (2006). The following temporal measures were determined using Raven 1.2 (Cornell Laboratory of ornithology, Ithaca, New York; Hanning window function; filter bandwidth: 124 Hz; frequency resolution: 86.1 Hz; grid time resolution: 5.80 ms): (a) phrase duration (ms): time interval from the first to the last produced combined pulse; (b) number of combined pulses per roaring phrase; combined pulses were counted by playing back the roar at 10% of the original speed; (c) fundamental frequency (Hz): number of combined pulses per second. The following spectral measures were extracted using PRAAT 4.3.12 (Boersma et al., 2005) (Spectrogram settings: Hanning window shape; window length = 0.05 s, maximum frequency = 3000 Hz, time step = 0.002 s, frequency step = 20 Hz; Formant settings: burg algorithm; time step = 0.05 s; maximum number of

formants = 3; maximum formant frequency = 2700 Hz; window length = 0.025 s., pre-emphasis from 50 Hz (cf. Harris et al., 2006); (d) harmonics-to-noise ratio (HNR, dB), defined as the degree of acoustic periodicity; this represents the energy distribution of periodic signals versus noise (e) first and (f) second formants (Hz), representing the first and second peaks in the frequency spectrum, which result from the resonant frequencies of the fundamental frequency of the call, and (g) peak frequency (Hz), defined as the frequency at which maximum acoustic energy occurs in the dominant frequency band of the phrase.

Because the Praat software was originally developed to measure acoustic parameters in human speech, the values of parameters (e), (f), and (g) of Guereza vocalizations measured with Praat were double checked using Raven. It was not possible to measure HNR as a standardized function of the Raven software, and other software programs or methods to measure or calculate HNR more accurately (e.g. Riede et al., 2001) could not be accessed at the time of analyses. Furthermore, it appears that ‘methods for characterizing and quantifying noise are less well established than methods applicable to harmonically structured aspects of signals’ (Riede et al., 2005). Because of the difficulties in measuring HNR, this study relied on the measurement of the harmonics-to-noise ratio as calculated by Praat, using the rationale that at least in the present study the same methods for HNR measurement were used to calculate HNR in every single experiment. Thus, differences in HNR between contexts could thus be roughly determined. One other question concerns to which extent the recordings are comparable, when it is taken into consideration that background noise can change relatively fast from site to site and during the day. This factor could nevertheless not be controlled for in the present study, due to the small overall sample sizes when conducting field experiments, the cryptic nature of Guerezas, and the consequent relatively low response rates of these monkeys.



**Figure 2.11.** Phrase of an individual Guereza colobus male, illustrating the various acoustic variables considered in this study.

After a preliminary analysis of the data collected in this study, similar to findings of studies on *C. polykomos* and *C. angolensis* (Walek, 1978; Schel et al., 2008), results indicated that monkeys predominantly reacted with one bout of roaring to leopard growls, consisting of a large number of roaring sequences, each typically containing only one or two roaring phrases each. To eagle playbacks, the response was the opposite. Although the monkeys mostly produced only one roaring bout in response to eagles, it generally contained only two roaring sequences but they consisted of a large number of roaring phrases each. For systematic comparisons, the focus for spectral analyses was therefore put on the first and last phrases of the first two roaring sequences, provided they contained at least two roaring phrases (i.e. four roaring phrases per response). Both the first and the last phrases were measured, because of Marler's (1972) notion that last phrase in a sequence had a distinctive lower pitch.

A matched-pair design (every group contributing responses to all experimental stimuli to the final dataset) would have been an obvious choice for the intended comparisons. However, this approach was methodologically not feasible because the exact ranging behaviour of the different unhabituated groups was not known, and individuals were not always eager to respond vocally. As indicated in the experimental protocol, great care was taken to ensure that every group was only tested once with a particular stimulus, and therefore would not contribute more than one response per experimental dataset.

***Statistical comparisons***

Datasets were checked for normal distribution both within and between group responses using the SPSS Software Package 12.0. Conditions for parametric analyses were generally not met, therefore non-parametric analyses were used throughout. For spectral comparison within the contexts, in order to test the differences between first and last phrases produced in a sequence, a Wilcoxon matched pairs test was used. For the comparison of spectral and temporal parameters between the predator contexts a Mann Whitney U Test was used. Critical p-values were adjusted with a Bonferroni correction to  $p=0.05/n$ , when the same dataset was used for  $n$  different comparisons. All reported p-values were exact p-values and all testing was two-tailed (Brace et al., 2000 ; Maltby & Day, 2002; Hawkins, 2005 ).

99% confidence intervals for means were calculated using the descriptive statistics option in SPSS, and non-parametric effect sizes (ES,  $r$ ) were estimated from the performed statistics. Effect size is a standardized measure of the magnitude of an observed effect, also defined as the standardized mean difference between groups (reviewed in Cohen, 1990). For the non-parametric Wilcoxon signed ranks test and Mann-Whitney U test, it is calculated by dividing the z-score by the square root of the total number of observations (Field, 2005). Values of  $r$  can lie between 0 (no effect) and 1 (perfect effect), with the widely used accepted standards of  $r= 0.10$  (small effect),  $r= 0.30$  (medium effect) and  $r= 0.50$  (large effect).

## Chapter 3

### Morning chorus roaring

#### Introduction

Roaring by *Guerezas* is most impressively displayed during the species' highly contagious early dawn choruses. Studies on dawn chorusing have mainly concentrated on songbirds (reviewed in Burt & Vehrencamp, 2005). Here the phenomenon is usually attributed to intrinsic, social, or environmental conditions, which are not mutually exclusive (reviewed in Burt & Vehrencamp, 2005). Intrinsic conditions, such as a circadian testosterone cycle that peaks at dawn, or an energy surplus after nights that were not as energy-demanding as anticipated (reviewed in Hutchinson, 2002), could explain the occurrence of dawn chorusing at a proximate level. Environmental conditions, such as a possible lower predation risk, reduced foraging efficiency in low light conditions, or enhanced acoustic transmission at dawn (e.g. Henwood & Fabrick, 1979; but see Dabelsteen & Mathevon, 2002; Hutchinson, 2002) could also proximately explain the occurrence of morning choruses. However, these explanations do not offer an ultimate explanation for why dawn chorusing is selectively advantageous to the animals that produce them. Social conditions such as mate attraction, male-male competition, social dynamics, or territory defence have been mentioned in this respect (reviewed in Burt & Vehrencamp, 2005; Harris et al., 2006).

Several primate species produce loud calls before or at dawn (Waser & Waser, 1977; Sekulic, 1982; Whitten, 1982; Horwich & Gebhard, 1983; Wich, 2002; da Cunha & Byrne, 2006), which are often part of elaborate choruses. Such choruses produced by *Guerezas* have been explained to function in the social domain, for example by regulating spacing between groups, as well as long-range male-male competition and mate-defence (Marler, 1969; Marler, 1972; Gautier & Gautier, 1977; Henwood & Fabrick, 1979; Harris et al., 2006). The contagiousness of roaring (with males starting to counter-roar after roaring was initiated by neighbouring males) and its stereotyped and ritualized emission pattern both are consistent with these supposed ultimate functions. The low acoustic frequency of roaring and the evolution of resonating airsacs

in Guerezas additionally reveal important adaptations which enable long-distance communication.

The relation between the unique structure of acoustic long-range signals and the ecological circumstances under which they are produced was studied extensively in the seventies and eighties in several studies on habitat acoustics (e.g. Morton, 1975; Waser & Waser, 1977; Waser & Brown, 1984; Waser & Brown, 1986), comprehensively reviewed by Henwood & Fabrick (1979), Brown & Waser (1988), and Brown et al. (1995). To briefly summarise: the distance over which a sound is audible is dependent on the sound pressure level at the source, the level of background noise at the receiver, the auditory acuity of the listener, and the attenuation rate of sound travelling through the environment. Temperature, wind, and humidity are the principal abiotic factors determining the attenuation of sound in any environment (on top of the usual, overall, attenuation that sound faces when travelling through the environment). Call frequency, volume, and complexity, as well as a recipient's auditory acuity are important biotic factors that can influence the transmission distance of a sound, as are specific behavioural adaptations of the vocalizing monkeys themselves, such as the time of calling and calling from elevated locations or more open canopies. Background noise at the location of the receiver, e.g. produced by other animals in the vicinity such as cicadas, will determine the minimum sound pressure level needed at the source, below which transmitted sounds are not identifiable (Egnor et al., 2007). Moreover, these and other studies have shown that sound of lower frequency is absorbed less rapidly by humid air, and that low frequency sounds are reflected less easily by obstacles in their transmission path. Furthermore, a stereotyped emission of long distance calls is thought to be an important feature enhancing auditory acuity in recipients. By using a stereotyped temporal pattern, e.g. through repetition of call elements separated by uniform pauses or by systematically producing the calls at a specific time of day, maximum perception efficiency is achieved in the recipients of the calls, because there is a higher probability of them detecting the sounds if they are repeated and/or emitted at specific, predictive, times.

Waser & Waser (1977) argued that the fact that colobus roars are stereotyped signals that are repeated *and* chorused between individuals 'tunes' a recipient's auditory expectations most optimally. The recipient will thereby ignore possible signals that do

not fit into the pattern of call emission in the morning consisting of roar repetitions followed by answers from neighbouring groups. Interestingly, Waser & Waser (1977) argued that this is the reason why playbacks of recorded roars to a colobus monkey will only evoke a vocal response during the early morning, but unfortunately no empirical data exist for this statement.

In sum, timing (background noise vs. no background noise), location (obstacles vs. no obstacles in the way), and structure (single sound vs. repetitions, chorusing vs. no chorusing, and low frequency vs. high frequency) of vocalizations, combined with factors influencing sound attenuation (temperature, humidity, and wind), thus play a crucial role in an animal's call transmission efficiency, and therefore in its efficient use of energy. Moreover, in this respect, studies on gibbon and bird songs showed that abiotic factors such as temperature do not only affect 'sec' sound transmission, but are also important factors influencing the behaviour of the sound transmitters in the first place (Whitten, 1982; Hutchinson, 2002). Calling after cold, wet, windy nights and/or on cold, wet, windy mornings were less frequent due to energy saving strategies in the subjects of these studies.

All these considerations seem especially important for Guereza colobus monkeys that are known for their energy-saving strategies in their everyday lives (Oates, 1977; Dasilva, 1992). These monkeys are known to use their roars in ritualized and stereotyped vocal morning exchanges that presumably function in group spacing (e.g. Marler, 1972; Oates, 1977). The chances of accidentally entering a stranger's territory during the course of the day, and therefore the chances of costly physical fights, are reduced by the information already shared in the morning chorus. Likewise, Harris (2006) and Harris et al. (2006) argued that these morning roars are used in ritualized 'vocal battles', because they are honest indicators of a male's fighting abilities, and therefore act as a competent and efficient tool in (long-distance) male-male competition. Based on the theory described above, these animals thus seem to have evolved a strategy that maximizes the benefits of accurately and efficiently communicating one's position or strength with a minimum of costs incurred, by producing their informative calls in the early morning.

The present chapter focuses on two separate aspects of the Guerezas' morning chorusing. First, the effects of two ecological circumstances (temperature and rainfall) on the occurrence of morning choruses were determined. Measurement of other parameters, such as background noise, were not taken into account, so they remain potentially interesting factors for future research (Egnor et al., 2007). Based on opportunistic observations made during the fieldwork periods, and following the studies of Whitten (1982) and Hutchinson (2002), the occurrence of morning chorusing was expected to be negatively influenced by high rainfall and low temperature.

Second, the chapter describes an experimental study in which morning chorus playback experiments were conducted in Sonso, to study the chorusing patterns in the forest. Because of the important spacing and male-male competition function of morning chorusing in Guerezas, it was hypothesised that these monkeys counter-roar if prompted with a conspecific morning roar. Based on response rates reported for predator playback studies with the related King colobus monkeys (Schel et al., 2009), it was predicted that Guerezas' morning calls (counter roaring) could be initiated by playbacks of conspecific morning choruses.

## **Part 1. Ecological factors influencing morning calling behaviour in Guerezas**

### **Methods**

The exact time of occurrence of morning choruses was recorded on 47 non-consecutive days over a period of approximately 5 months (April-August 2007; see Fig. 3.1) in Sonso. Data points refer to the exact time when a full chorus, i.e. a chorus that spread through the forest, was heard at camp. For this purpose, the observers determined the start of chorusing from 4h15 until 7h00 am. All choruses starting within this time period were noted down. Other days were spent in the vicinity of Guereza groups throughout the study area, to be able to record their occurring morning choruses for future acoustic analyses. In this case, the observers were present at the group at around 4h30, and all roars produced in a morning chorus by the focal group were noted down and recorded with a Sony TCD D8 DAT recorder connected to a Sennheiser K6/ME66 directional microphone. If other groups started chorusing earlier than the focus group, this was noted down as well.

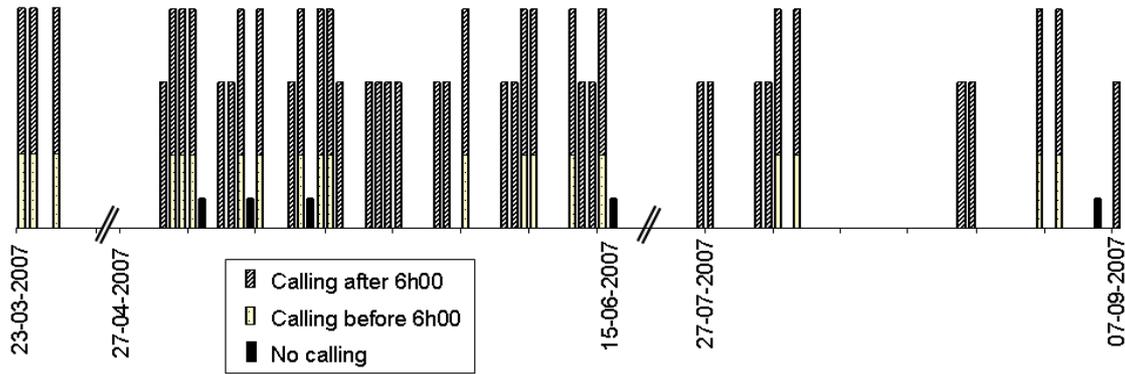
Rainfall data of the previous day and night (measured in mm on the morning of the experiment), and temperature data during the previous night (read on the morning of the experiment as the minimum temperature in °C on a minimum-maximum thermometer) were scored as abiotic factors possibly influencing the production of morning chorus calling (Fig. 3.2).

### **Statistics**

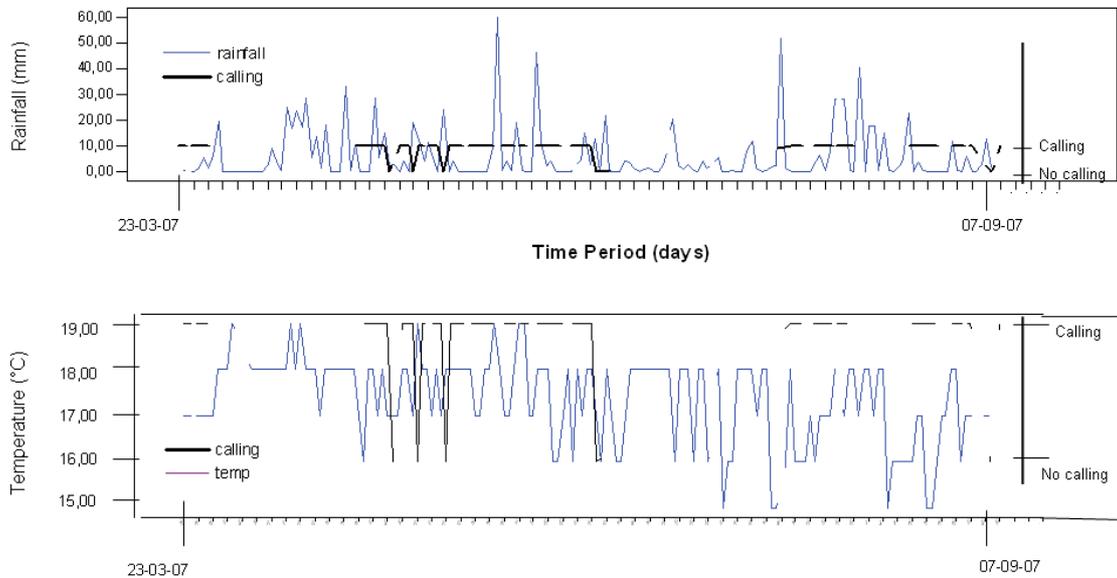
A binary logistic regression was run on the data to reveal if any of the two abiotic factors, or the interaction of both, influenced the calling pattern. This test generally predicts the probability of occurrence of a discrete outcome related to a set of 'predictor' variables (i.e. variables that might influence the outcome of classification). If the variables are strong enough predictors, the model gets more accurate if they are included, and will correctly classify a higher percentage of cases to a discrete outcome.

### **Results**

Morning chorus activity was collected on 47 days (Fig. 3.1). From these days, 5 days had to be discarded for further analyses because temperature and/or rainfall data were missing. Therefore, for the logistic regression, a total of N=42 sample days were used. On 37 of the 42 days the monkeys produced morning choruses, whereas on 5 days they remained silent. On 16 of the 37 chorus-days, the monkeys produced an early morning chorus, defined as a chorus produced before 6h00 am (data ranging from 4h06 to 5h54). On the other 21 days, they only produced morning choruses between 6h00 and 7h00 am (data ranging from 6h04 to 6h46).



**Figure 3.1.** Guereza morning chorus activity at Sonso, scored on 47 non-consecutive days over a time period of 5 months. Open bars indicate the occurrence of a chorus before 6h00 am, hatched bars indicate the occurrence of a chorus after 6h00 am, and filled bars indicate the occurrence of no chorus at all.



**Figure 3.2.** Rainfall (mm), temperature (°C), and occurrence of calling over a 5 month time period in Sonso. Markers on the x-axis represent time period intervals of 3 days. On the y-axes the respective values of rainfall (mm), temperature (°C), and the occurrence of calling.

Following Kinnear & Gray (2004), a logistic regression was applied as follows: the probability of ‘calling’ on a specific day for which all data were available was  $37/42 = 0.88$  (88%), and the probability of ‘no calling’ was  $5/42 = 0.12$  (12%). The best prediction of category membership for any given morning chorus day, therefore, would be to assign it to the ‘calling occurring’ category. This procedure would be correct in 100% of the cases in which calling indeed occurred, but false in the 12% in which

calling did not occur, resulting in a net success rate of 88% over all cases. Kinnear and Gray stated that ‘the purpose of the logistic regression is to improve on this success rate by exploiting any association between the dependent and independent variables to predict category membership [calling or no calling] with the greatest possible accuracy’. They also emphasized that, if certain variables do actually contribute to the occurrence/ non-occurrence of calling, this most probably does not happen in a linear, but rather in a logistic, manner, with the probability of calling/no calling likely to rise dependent on certain thresholds of, in this case, temperature and rainfall.

Using SPSS 12.0, a Forward Logistic Regression Test was performed. This type of logistic regression is recommended when data are explored, because it shows which variables are entered in the model and which ones are excluded. After running the test with temperature, rainfall, and the interaction of temperature \* rainfall as the independent variables, both rainfall and temperature could be discarded from the model as non-useful (non-reliable) predictors. However, the interaction of rainfall \* temperature was a useful, reliable indicator for category membership, i.e. to predict the occurrence of ‘calling’ or ‘no calling’ in the morning (Wald statistic= 4.991, df=1, p=0.025, n=42). This model did fit the data well ( $\chi^2=6.510$ , df=6, p=0.369, n=42), as 20% of the cases in which no calling occurred were now classified correctly, as well as 97.3% of the cases where calling occurred (as opposed to the incorrect and artificial initial 0% and 100% respectively when no co-variables were yet entered in the model). Finally, the test showed that if the interaction term were to be removed from the model, it would have a negative effect on the accuracy of the model (change in -2LL statistic=5.281, df=1, p=0.022, n=42).

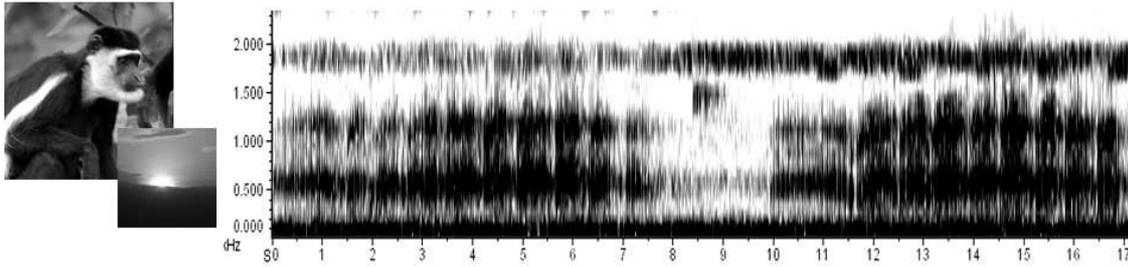
Hence, the results indicated that temperature and rainfall influenced the occurrence of dawn calling in *Guereza colobus* monkeys, but only if interacting with each other.

From the subset of ‘calling’, a similar regression test was conducted to find out whether the occurrence of calling before 6h00 (‘early calling’) could be explained by rainfall, temperature or the interaction of rainfall \* temperature as well, but in this case, none of the co-variables was able to explain the occurrence of ‘early calling’.

## **Part 2. Playback experiments with Morning Choruses**

### **Methods**

Because of the specific conditions in which the morning chorus experiments were conducted, some changes were made to the general experimental protocol described in chapter 2. Most importantly, the target group to be tested with a morning chorus playback was searched for in the evening before the experiment took place. The observers set out 90 minutes before dusk, to find an appropriate group and stay with it until the monkeys settled to sleep. During the twilight period, a tree at a distance of about 50-70m from the target group was selected, from which the conspecific morning roars could be played back the following morning. For this purpose, a rope that could carry the playback equipment the following morning was installed in the tree, using a catapult, fishing rod, spindle, and lead bullets. The following morning, the observers arrived silently at the tree between 4h00 and 4h30. The playback speaker was raised into the tree and positioned such that it aimed at the target group. After this procedure (usually around 4h45), the observers sat down in a hiding place and stayed quiet. Playback stimuli consisted of 5 minutes silence followed by a 15s recording of a morning chorus (N=3, Fig. 3.3) of an unfamiliar individual to the target group, broadcast between 5h00 and 5h30 am. However, if a natural chorus occurred during the set-up of the experiment, the observers waited until 6h00 before starting the trial, and it was clearly noted down that a chorus prior to the trial had already occurred. This procedure matched the natural condition, because there was a nearly 50% chance that morning choruses occurred as early as 5h00 am, and also a nearly 50% chance that a second chorus occurred later if they had already produced a chorus before 5h00 am (Fig. 3.1). Moreover, other studies had already shown that different monkey species reliably responded to playback stimuli of 15s of conspecific vocalizations (Zuberbühler, 2003; Arnold & Zuberbühler, 2006).



**Figure 3.3.** Spectrographic representation of Guereza morning chorus roars. The x-axis represents the time in seconds, the y-axis the frequency in kHz.

However, because it was not known which factors drive the morning choruses, several variants of the initial playback protocol were tested, as follows:

1. playing back a recording of a morning chorus similar to that used in the initial experimental setup, but lasting twice as long (30s; N=5)
2. playing back a 30s morning chorus from a familiar, neighbouring, individual (N=5)
3. playing back a continuous recording of morning chorusing from either a neighbouring or non-neighbouring individual (N=5)
4. playing back eagle shrieks (based on an observation of a natural initiation of chorusing following eagle alarms by a neighbouring blue monkey in the early morning; N=8)

## Results

Table 3.1 shows the different playback experiments that were conducted during this study and the monkeys' responses. Some additional data on the vocal behaviour of the animals before and after the trials and the more general conditions in which the trials were conducted are also reported.

The results showed that the monkeys did not respond as readily on the playback stimuli as expected. Only once did the monkeys respond to eagle shrieks played back to them around 6h15 am. However, on this occasion, the Guereza male produced roars right

before the playback was broadcast, possibly because he had seen the flashlight of the observer. Following the general protocol, the trial was classified as invalid.

Only trials, in which a continuous recording of morning chorusing of a neighbouring Guereza was played back to the monkeys, at the moment a distant chorus started, were successful in triggering calling from the target groups. During these two occasions, the monkeys responded after 75 s and 48 s of playback-chorusing by their neighbouring males. Unfortunately, these responses just happened in the last few days of the study, so no larger dataset could be collected.

**Table 3.1.** Responses of Guerezas on several different playback trials conducted in the early morning.

Playback Stimulus	Date	Time	Temp (°C)	Rain (mm)	Conditions before exp.	Vocal Response?	Chorus initiated?	Movement?	If chorus before: ♂ called?	If chorus after: ♂ called?
Morning Chorus (15s)	29-03-07	5:02	17	1.6	silent	no	no	yes	-	yes
Morning Chorus (15s)	30-03-07	5:03	18	6.4	silent	no	no	no	-	?
Morning Chorus (15s)	04-04-07	6:11	16.5	0	far chorus starts	no	no	no	?	-
Morning Chorus (15s)	05-04-07	5:02	16.5	0	far chorus starts	no	no	no	no	-
Morning Chorus (15s)	06-04-07	5:17	18	0	far chorus starts	no	no	no	no	-
Morning Chorus (30s)	12-04-07	5:03	18	3	early chorus before	no	no	no	yes	yes
Morning Chorus (30s)	13-04-07	5:01	18	0.4	rain	no	no	no	-	?
Morning Chorus (30s)	05-06-07	6:02	18	11.6	silent	no	no	no	-	yes
Morning Chorus (30s)	06-06-07	6:25	18	2.4	chorus before	no	no	no	yes	No
Morning Chorus (30s)	07-06-07	5:57	16	4.2	early chorus before	no	no	no	?	yes
Neighbour MC (30s)	26-07-07	4:52	18	0	silent	no	no	no	-	yes
Neighbour MC (30s)	27-07-07	5:21	16	0	silent	no	no	no	-	yes
Neighbour MC (30s)	28-07-07	5:45	16	0	silent	no	no	no	-	yes
Neighbour MC (30s)	02-08-07	5:40	17	0.4	chorus starts	no	no	no	no	yes
Neighbour MC (30s)	03-08-07	6:43	17	7.8	chorus before	no	no	no	?	Yes
Neighbour MC LOOP	23-08-07	5:20	15	0	Silent	no	no	no	-	yes
Neighbour MC LOOP	30-08-07	5:44	16	0	chorus starts	yes	no	no	-	yes
Neighbour MC LOOP	07-09-07	5:30	?	?	chorus starts	yes	no	no	-	no
Non-Neighb. LOOP	22-08-07	5:41	17	0.6	chorus starts	no	no	no	no	no
Non-Neighb. LOOP	01-09-07	5:31	?	0	chorus before	no	no	no	no	yes
Eagle shrieks (15s)	24-05-07	6:17	18	0	alarms before; for observers?	yes	no	yes	-	?
Eagle shrieks (15s)	29-05-07	6:30	17	4.2	chorus before	no	no	no	yes	yes
Eagle shrieks (15s)	08-06-07	6:15	16	0	chorus before	no	no	no	yes	yes
Eagle shrieks (15s)	12-06-07	6:20	18	?	chorus before	no	no	yes	yes	-
Eagle shrieks (15s)	13-06-07	6:04	17	4.8	silent	no	no	no	-	yes
Eagle shrieks (15s)	14-06-07	6:07	18	15	silent	no	no	no	-	yes
Eagle shrieks (15s)	15-06-07	6:01	18	2.8	chorus before	no	no	yes	yes	yes
Eagle shrieks (15s)	16-06-07	6:12	17	13	no choruses	no	no	yes	-	-

## **Discussion**

A variety of studies have investigated the factors influencing the occurrence and structure of dawn chorusing in different animal species (reviewed in Whitten, 1982; Hutchinson, 2002; Burt & Vehrencamp, 2005). Guereza colobus monkeys also produce low frequency roars in elaborate repetitive choruses, at specified times of the day, which most probably represent a time of day when auditory interference caused by background noise is lowest. Although these monkeys represent a valuable resource to get further insight in the factors underlying dawn chorusing, their morning choruses have not been studied in much detail with respect to the socio-ecological factors influencing this behaviour (Gautier & Gautier, 1977; Harris, 2006; Harris et al., 2006). The present study investigated the effects of two ecological factors on the occurrence of morning choruses of Guerezas, as well as some of the relevant social factors required for the initiation of morning choruses in this species.

Results showed that natural morning choruses were prevented by the interaction of low temperatures and high rainfall. If the animals spent a cold, wet night or morning, they were less likely to produce a chorus compared to when they spent a mild night and/or morning. This finding may be explained by the enhanced transmission circumstances on dry mornings, or by physiological differences caused by these external factors (e.g. Harris, 2006). The ambient noise levels were not measured in this study, but cicadas and hornbills start producing sound at dawn, which might interfere with transmission of monkey calls. Therefore, the early production of the roars might be a response to this factor as well.

The results of the playback experiments were somewhat at odds with the existing theory. The monkeys were expected to respond well to playback experiments conducted in the early morning, as predicted by the male-male competition- and spacing hypotheses (Marler, 1972; Oates, 1977; Harris et al. 2006), but this expectation was not confirmed with the present data. However, the fact that 2 out of 3 trials were successful if the choruses of a familiar neighbour were played over long durations at the moment a distant chorus started suggests that these monkeys integrate a range of variables before participating in chorusing behaviour. All the other experimental conditions failed to elicit a vocal response from the animals.

The fact that the animals remained silent in response to eagle vocalizations in the early morning, to which they respond fairly well in the daytime (see next chapters), could be explained by the fact that eagle shrieks do not normally occur this early. The animals might simply have been confused by this experiment, opting for cryptic behaviour to avoid detection, rather than to start roaring and giving away their position.

Results suggested that the conditions required for triggering morning chorusing entail many more complexities than initially thought. Guerezas might only be willing to participate in morning chorusing after particular individuals in their vicinity already had roared (cf. Snowdon & Cleveland, 1984). This hypothesis is supported by the response rate to the 'neighbour protocol', when morning choruses were played back in a loop for a prolonged period of time. Obviously, one individual will have to be the first one to start roaring in the morning, but why and how that individual is to be the first to call, is still unclear. Sometimes, roaring started somewhere in the forest but failed to spread, followed 5 minutes later by roaring from the same or a different direction, that did spread. Daily observations of directions from which chorusing started also did not yield any clear patterns (personal observation). Therefore, it is concluded that the conditions under which morning chorusing occurs need to be studied more extensively before conclusions can be made regarding this remarkable behaviour.

## Chapter 4

### Acoustic predator model experiments in Kaniyo Pabidi

Results of this chapter are published in the *Journal of Comparative Psychology*  
(Schel et al., 2009, *in press*)

#### Introduction

Many forest-living primates have evolved specialised vocal signals, the loud calls, which differ from the rest of the vocal repertoire in a number of ways (e.g. Gautier & Gautier, 1977; Whitehead, 1987; Delgado, 2006). These low-pitched, tonal signals are usually only produced by sexually mature males, have a high amplitude, and can carry over remarkably long distances (e.g. Waser & Waser, 1977; Henwood & Fabrick, 1979). The calls are often produced in a stereotyped and/or ritualized manner and appear to serve several functions, such as inter-group spacing, intra-group rallying and long range male-male competition (e.g. Gautier & Gautier, 1977; Delgado, 2006). For Guerezas, the proposed functions of the species-specific loud call, the roar, have been described in the previous chapters: in this species roars are thought to serve a role in intergroup interactions, male-male competition, and also in predatory contexts (Marler, 1972; Oates, 1977b; Oates, 1977a; Oates, 1994; Harris, 2006; Harris et al., 2006). Chapter three discussed the occurrence and use of highly contagious roars during the early morning, which seem to form an important aspect of the intergroup spacing- and male-male competitive strategies of Guerezas (Marler, 1972; Oates, 1977; Harris et al. 2006; Harris, 2006). Roaring during daytime seems more closely related to predatory situations, as described in almost all studies investigating the Guerezas' vocalizations (Hill & Booth, 1957; Marler, 1972; Oates, 1977a; Walek, 1978; Oates, 1994). To date, no study has investigated this behaviour systematically.

Like male-male competition, predation is an important evolutionary force, which has selected for a wide variety of highly specific anti-predator behaviours used by many different animal species (Lima & Dill, 1990; Stanford, 1998). One tactic that is regularly employed by primates is the production of vocal signals upon detecting a predator. As described in chapter one, this strategy has been described for many

primate species, and was also implicated for the Guerezas, who seem to use their loud roars and snorts for this purpose (Marler, 1972; Oates, 1977b; Oates, 1977a; Oates, 1994; Harris, 2006; Harris et al., 2006). However, not all species for which the use of vocal alarm signals has been reported make use of their loud calls in this context: some primates use barks, some use grunts and others may again use different vocal signals, such as coughs, for this purpose. All these different call types produced specifically in predatory situations are termed alarm calls. As described in chapter one, there are several different types of alarm call systems employed by different primate species (Table 1.1). These systems have been linked to the predator-specific escape techniques needed when confronted with specific predators, as well as the life-style of the monkeys themselves (Macedonia & Evans, 1993). To recapitulate, some primate species produce various types of acoustically discrete alarm calls in predator-specific ways, to which recipients typically respond as if they have witnessed the corresponding predator themselves (Seyfarth et al., 1980; Macedonia, 1990; Zuberbühler et al., 1999a; Zuberbühler, 2000; Zuberbühler, 2001; Kirchhof & Hammerschmidt, 2006; Papworth et al., 2008). The use of such functionally referential, or semantic, signals (Seyfarth et al., 1980) has mainly been found in arboreal primates that make use of highly distinct escape techniques when confronted with different predator types. In these species it is crucial for an individual's survival to be able to extract the highly specific information on whether the caller has identified an aerial or terrestrial predator, because these species' escape techniques are exclusively adapted to the predators' hunting techniques (Macedonia & Evans, 1993).

The call producers might not necessarily intend to communicate information to the listeners, but there seems to have evolved an evolutionary stable and highly efficient communication system between the call producers and call recipients (Seyfarth & Cheney, 2003). Callers produce discrete sounds potentially aimed at specific predators (Woodland et al., 1980; Zuberbühler et al., 1997; Zuberbühler et al., 1999b) or conspecifics (Cheney & Seyfarth, 1990), or, from a more conservative viewpoint, triggered by a particular inner state resulting from the presence of a predator (Owren & Rendall, 2001). However, in all cases the recipients have learned to efficiently associate these discrete calls with the presence of the corresponding predator.

Other work on this topic showed that some primate species produce alarm calls that are mainly associated with ‘response urgency’, i.e. the time constraints for escape behaviour that different predators impose on their prey (Robinson, 1980). The alarm calls of putty-nosed monkeys (Price, 2008), redfronted lemurs (Fichtel & Hammerschmidt, 2002) and ruffed lemurs (Macedonia, 1990) have been explained in this way.

Yet other primates make use of a mix of the two formerly mentioned systems, with some of their alarm calls being highly predator specific, and some others based on the response urgency in a variety of different situations (e.g. white faced capuchins: Digweed et al. 2005; lemurs: Fichtel & Kappeler, 2002; sifakas: Fichtel & van Schaik, 2006).

As mentioned, signal type used in alarm call systems can differ across species: chacma baboons and sooty mangabeys (Fischer et al., 2001; Range & Fischer, 2004), for example, use graded signals in the described systems, and more recently, it was shown that some primates, such as putty-nosed monkeys and white-handed gibbons, can encode predator information by assembling calls into unique call sequences (Zuberbühler, 2002; Arnold & Zuberbühler, 2006; Clarke et al., 2006; Schel et al., 2009). In these cases, individual calls do not necessarily carry any referential information, while the corresponding higher-order sequences might do. These last findings indicate that some primates make use of basic ‘syntactic’ rules to structure their anti-predator vocalisations (Marler, 1977).

This chapter will describe the Guerezas’ locomotor and vocal responses to acoustic predator models. The ultimate aim of this and the following chapters is to find out what alarm call system the Guerezas use. The present study tested responses to the vocalizations of three predator species: leopard growls, eagle shrieks, and chimpanzee vocalizations.

### ***Hypotheses and predictions***

It was hypothesised that that the Guerezas recognized the vocalizations of leopards, chimpanzees, and eagles as indicators of the presence of a specific predator. The

playback experiments were predicted to elicit behavioural responses adaptive to the different predator's hunting techniques. Another prediction was that, alongside the different behavioural responses, the monkeys produced distinct vocal responses to the different predator types as well.

## **Methods**

The study was conducted in Kaniyo Pabidi, where all three predator types occur naturally. The general characteristics of the study site are described in chapter 2, as are the general methods used for the playback experiments. In short, naïve monkey groups were searched for during daytime. If the animals remained unaware of the presence of the observers and no other disturbances had occurred, a predator playback experiment was conducted. A playback consisted of 5 minutes silence followed by 15 seconds of predator vocalizations: leopard growls, eagle shrieks or chimpanzee pant hoots. Around 3 minutes before the playback was broadcast to the monkeys, the observers would start recording the animals' vocal behaviour from a hiding place. The monkeys' responses were recorded for as long as the vocal response lasted, at least 15 minutes. These recordings were transferred onto a PC using Cool Edit 2000. To allow for systematic comparisons, only the first and last phrases of the first and last roaring sequences were analysed using the audio-software analysing programs Raven 1.2 and Praat. 4.3.12.

From the vocal responses produced in each trial, the following seven structural parameters were determined using spectrograms generated on RAVEN 1.2: (a) total duration of the vocal response (s), (b) total number of roaring sequences, (c) total number of roaring phrases, (d) mean number of roaring phrases per roaring sequence, (e) number of snorts, and (f) call delivery rate (phrases/s); cf. Oates & Trocco, 1983.

To compare the acoustic structure of individual roaring phrases given to the different acoustic predator model seven acoustic variables were measured: (a) phrase duration (ms) (b) number of pulses per roaring phrase, and (c) fundamental frequency (Hz) were measured using SPG's generated with Raven 1.2. The other 4 variables were extracted using PRAAT 4.3.12: (d) harmonics-to-noise ratio (HNR, dB), (e) first and (f) second formants (Hz), and (g) peak frequency (Hz). Additionally, the locomotor responses

elicited by the different playback stimuli were scored, using the protocol described in chapter 2.

### **Statistics**

As described in chapter 2, binomial tests were used to analyse the behavioural differences within a predatory context, with the test probability set at  $p=0.5$  and the critical significance level at  $\alpha=0.05$ . Comparisons between the contexts were made with a Fisher's Exact Test, with the test probability set at  $p=0.5$  and  $\alpha=0.05$ . The differences in acoustic measurements within and between the contexts were tested with non-parametric tests. For spectral comparison within the contexts, in order to test the differences between first and last phrases produced in a sequence, Wilcoxon matched pairs test were used (Bonferroni corrected  $\alpha=0.017$ ). For the comparison of spectral and temporal parameters between the predator contexts Mann Whitney U Tests were used (Bonferroni corrected  $\alpha=0.017$ ).

### **Results**

#### ***Leopard, eagle, and chimpanzee playback trials***

In 2006, 27 different Guereza groups were tested with playbacks of leopard growls and 31 different groups with playbacks of eagle shrieks. In 2007, an additional 9 groups were tested with leopard growls, an additional 9 groups with eagle shrieks and 18 groups were tested with chimpanzee pant hoots. One eagle trial was discounted as invalid because the monkeys saw the observers, one eagle trial was discounted as invalid due to equipment malfunctioning, and three leopard trials were discounted as invalid because the monkeys saw the equipment or the observer. Total numbers of valid playback experiments used for overall analyses thus were  $N_{\text{Leopard}}= 33$ ,  $N_{\text{Eagle}}= 38$ , and  $N_{\text{Chimpanzee}}=18$ .

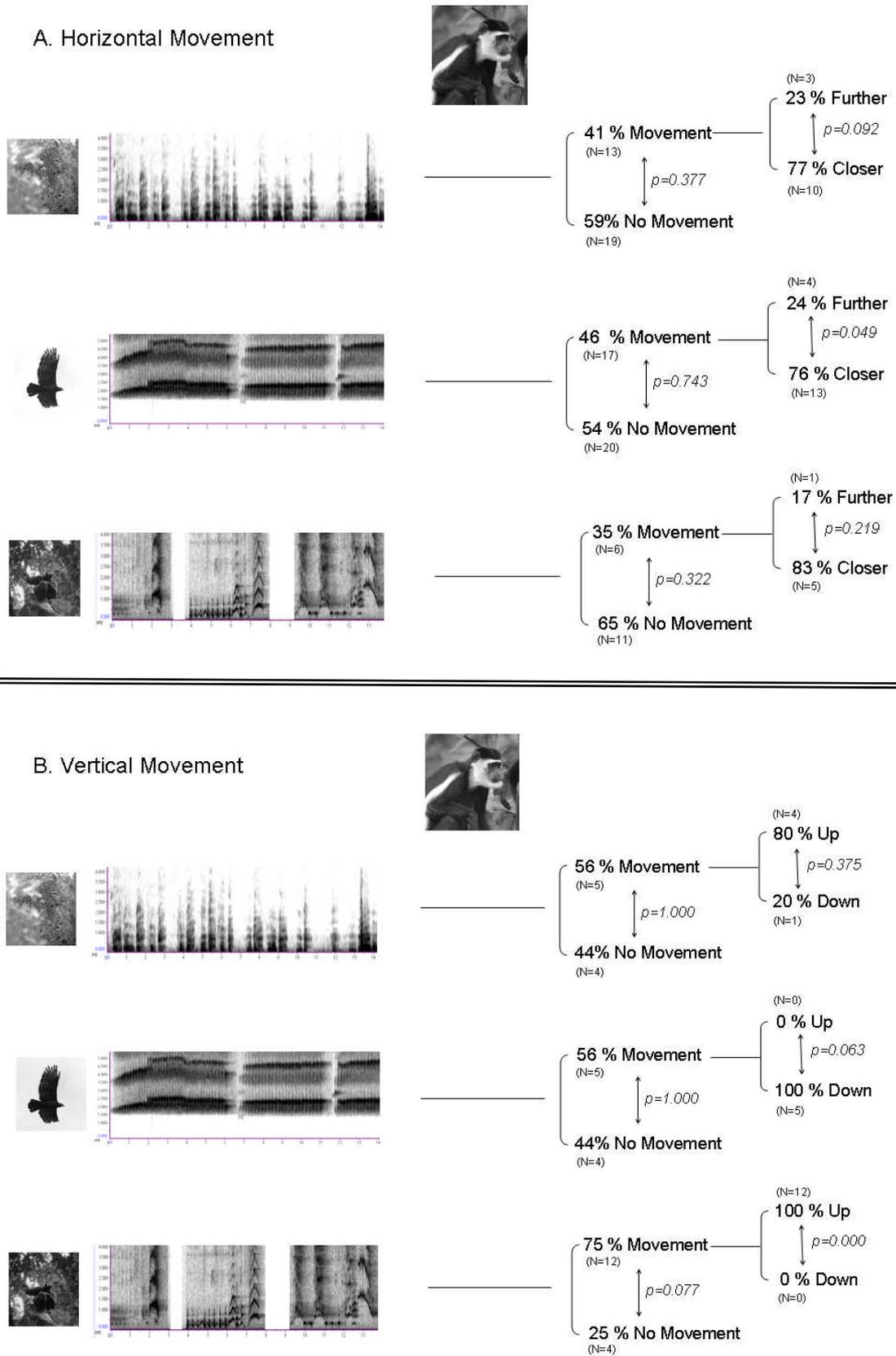
#### ***Behavioural response characteristics***

In 2006, locomotor responses during the experiments were only collected for the horizontal plane. In these trials, 'movement further', 'movement closer', or 'no movement' were scored during the leopard and eagle trials to find out if the monkeys approached the playback site. In 2007, data on the monkeys' movements in the vertical plane were also collected ('movement up', 'movement down', or 'no movement').

Sample sizes were as follows: vertical plane:  $N_{\text{Leopard}}=9$ ,  $N_{\text{Eagle}}=9$ , and  $N_{\text{Chimpanzee}}=16$  (in 2 chimpanzee trials it was not possible to see the monkeys' movements), horizontal plane:  $N_{\text{Leopard}}=32$  (in 1 trial it was not possible to see their movements),  $N_{\text{Eagle}}=37$  (in 1 trial it was not possible to see their movements), and  $N_{\text{Chimpanzee}}=17$  (in 1 trial it was not possible to see their movements).

### **Behavioural response characteristics compared within predator contexts**

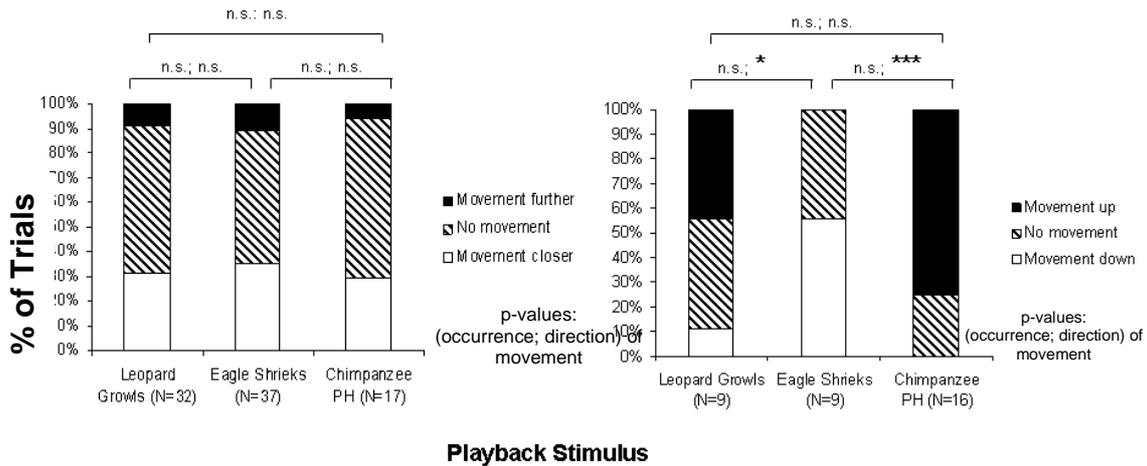
Binomial tests within the predator contexts and dimensional planes showed that, upon hearing leopard growls, the animals were equally likely to 'move' or 'not move', both in the horizontal plane ( $N_{\text{Move}}=13$ ;  $N_{\text{Not Move}}=19$ , exact  $p=0.377$ ) and in the vertical plane ( $N_{\text{Move}}=5$ ;  $N_{\text{Not Move}}=4$ , exact  $p=1.000$ ). From the subsets of trials in which the animals moved they were equally likely to move 'further' or 'closer' to the simulated leopard ( $N_{\text{Further}}=3$ ;  $N_{\text{Closer}}=10$ , exact  $p=0.092$ ), and also equally likely to move 'up' or 'down' ( $N_{\text{Up}}=4$ ;  $N_{\text{Down}}=1$ , exact  $p=0.375$ , Fig. 4.1). Upon hearing eagle shrieks, the animals were equally likely to 'move' or 'not move', both in the horizontal plane ( $N_{\text{Move}}=17$ ;  $N_{\text{Not Move}}=20$ , exact  $p=0.743$ ) and in the vertical plane ( $N_{\text{Move}}=5$ ;  $N_{\text{Not Move}}=4$ , exact  $p=1.000$ ). From the subsets of trials in which the animals moved the monkeys were more likely to move closer to the simulated eagles ( $N_{\text{Further}}=4$ ;  $N_{\text{Closer}}=13$ , exact  $p=0.049$ ), and there was a trend of them moving down ( $N_{\text{Up}}=0$ ;  $N_{\text{Down}}=5$ , exact  $p=0.063$ , Fig. 4.1). Upon hearing chimpanzee pant hoots, the animals were equally likely to 'move' or 'not move' in the horizontal plane ( $N_{\text{Move}}=6$ ;  $N_{\text{Not Move}}=11$ , exact  $p=0.332$ ). There was a trend towards 'movement' in the vertical plane ( $N_{\text{Move}}=12$ ;  $N_{\text{Not Move}}=4$ , exact  $p=0.077$ ). From the subsets of trials in which the animals moved they were equally likely to move 'further' or 'closer' ( $N_{\text{Further}}=1$ ;  $N_{\text{Closer}}=5$ , exact  $p=0.219$ ), and only moved up ( $N_{\text{Up}}=12$ ;  $N_{\text{Down}}=0$ , exact  $p=0.000$ ; Fig. 4.1).



**Figure 4.1.** Monkeys' locomotor behaviour in A. the horizontal plane and B. the vertical plane in response to the acoustic predator models, with corresponding percentages of movements and exact p-values of the differences between locomotor responses within predator contexts (Binomial tests,  $\alpha=0.05$ ).

**Behavioural response characteristics compared between predator contexts**

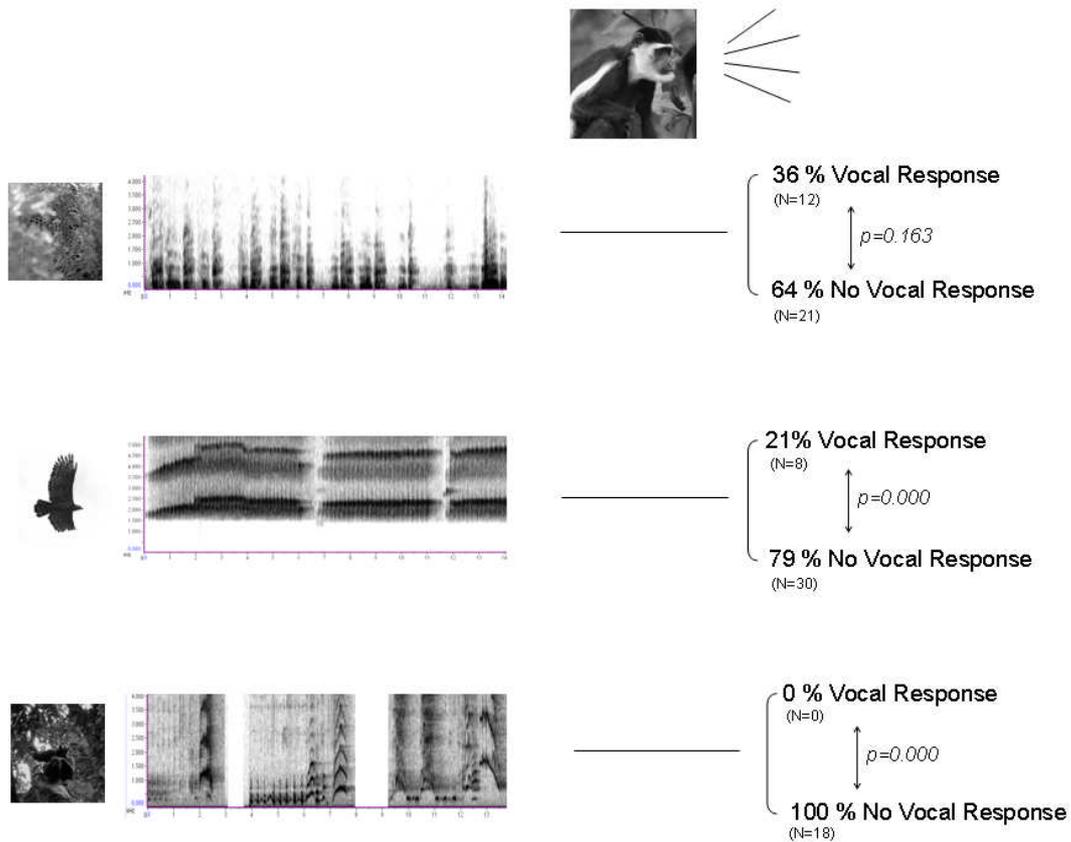
The Fisher's exact tests used to compare locomotor responses across predator contexts showed that the monkeys were equally likely to make movements or stay motionless in all three contexts, either in the horizontal (Leopard:  $N_{\text{Move}}=13$ ,  $N_{\text{NotMove}}=19$ , Eagle:  $N_{\text{Move}}=17$ ,  $N_{\text{NotMove}}=20$ ; Chimpanzee:  $N_{\text{Move}}=6$ ,  $N_{\text{NotMove}}=11$ : exact p L vs E=0.808; exact p L vs Ch= 0.767; exact p E vs Ch= 0.559) or the vertical planes (Leopard:  $N_{\text{Move}}=5$ ,  $N_{\text{NotMove}}=4$ , Eagle:  $N_{\text{Move}}=5$ ,  $N_{\text{NotMove}}=4$ ; Chimpanzee:  $N_{\text{Move}}=12$ ,  $N_{\text{NotMove}}=4$ : exact p L vs E=1.000; exact p L vs Ch=0.390; exact p E vs Ch=0.390, Fig. 4.2). If movement occurred, the monkeys behaved similarly in the horizontal plane (Leopard:  $N_{\text{Further}} = 3$ ,  $N_{\text{Closer}}=10$ , Eagle:  $N_{\text{Further}} = 4$ ,  $N_{\text{Closer}}=13$ , Chimpanzee:  $N_{\text{Further}} = 1$ ,  $N_{\text{Closer}}=5$ ; exact p L vs E=1.000; exact p L vs Ch=1.000; exact p E vs Ch=1.000), but differently in the vertical plane, depending on predator type: the monkeys moved down the trees more often in the eagle context than in the leopard context (Leopard:  $N_{\text{Up}} = 4$ ,  $N_{\text{Down}}=1$ , Eagle:  $N_{\text{Up}} = 0$ ,  $N_{\text{Down}}=5$ ; exact p L vs E=0.048, Fig. 4.2). In case of the chimpanzee context, if moving, the animals moved up in 100% of trials, whereas in the eagle context they moved down in 100% of trials: when comparing these two conditions, a highly significant p-value was found, indicating that there is a strong difference in vertical movements between these two conditions (Eagle:  $N_{\text{Up}}=0$ ,  $N_{\text{Down}}=5$ ; Chimpanzee:  $N_{\text{Up}} = 12$ ,  $N_{\text{Down}}=0$ ; E vs Ch=0.000, Fig. 4.2). Between the leopard and chimpanzee contexts, the exact p-value was high (exact p: L vs Ch=0.249, Fig. 4.2), indicating that the behaviour of the monkeys in these two contexts was similar.



**Figure 4.2.** Locomotor responses in the horizontal and vertical plane to the three different acoustic models. The first set of asterisks refers to the difference in occurrence of movement between the contexts; the second set to the difference in direction of movements between the contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < .05$ , \*\*  $p < .01$ , \*\*\*  $p = .000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

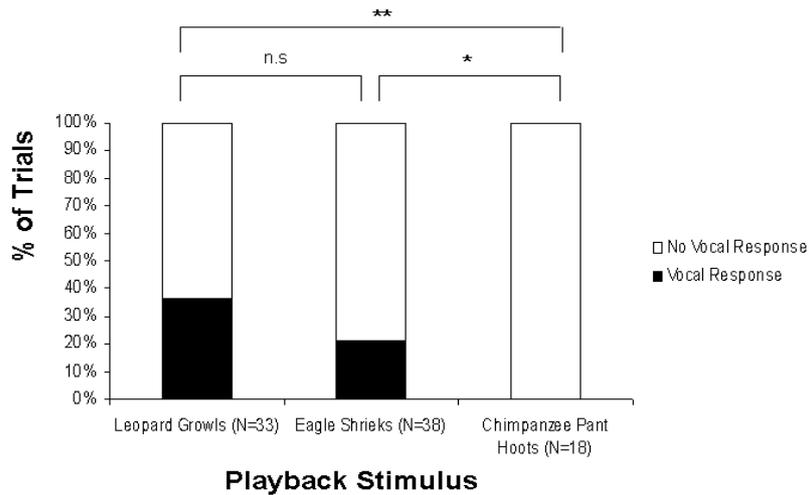
### ***Vocal response rates and response characteristics***

In 8 of 38 groups at least one individual responded with alarm vocalizations to the acoustic eagle model (response rate = 21%;  $N_{\text{Vocal Response (VR)}} = 8$ ,  $N_{\text{NoVR}} = 30$ ; exact p-value = 0.000). The response rate to the acoustic leopard model was higher, but still low: in 12 of 33 groups at least one monkey responded with alarm vocalizations (response rate = 36%;  $N_{\text{VR}} = 12$ ,  $N_{\text{NoVR}} = 21$ ; exact p-value = 0.163). In none of the 18 trials with chimpanzee pant hoots did the monkeys respond with vocalizations (response rate = 0%;  $N_{\text{VR}} = 0$ ,  $N_{\text{NoVR}} = 18$ ; exact p-value = 0.000).



**Figure 4.3.** Vocal response rates of the monkeys to the three different acoustic predator models, with corresponding exact p-values within contexts (Binomial test,  $\alpha=0.05$ ).

Comparing the vocal response rates between predator contexts showed that the response rates to leopard growls and eagle shrieks were similar (Leopards 36%, Eagle 21%, exact p: 0.19, Fisher’s Exact Test, two-tailed). However, compared to the responses to leopard growls and eagle shrieks, the monkeys responded significantly less to chimpanzee pant hoots (Chimpanzees 0%, Ch vs L: exact p-value: 0.004; Ch vs E: exact p-value: 0.044, Fig. 4.4).



**Figure 4.4.** Vocal response rates to the three different acoustic models, with exact p-values between contexts. n.s.: no significant difference between the contexts; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in vocal response rates between the contexts, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p = 0.000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

### ***Acoustic measurements of vocal responses***

In three of the twelve vocal responses to leopard growls, high levels of background noise made it impossible to code the complete vocal reaction. These recordings were excluded from acoustic analyses, generating a final sample size of  $N_{\text{Leopard}} = 9$  and  $N_{\text{Eagle}} = 8$  responses for which structural (temporal) measurements could be extracted. For the spectral measurements, the same dataset was used, but different trials were discarded because in this case the most important criterion was that the first two roaring sequences were of good enough quality for spectral measurements. One of the twelve vocal responses to leopard growls had to be discarded because of poor recording quality, two trials had to be discarded because the monkeys only produced snorts, and one trial had to be discarded because the monkeys only produced one-phrase sequences. It was therefore possible to obtain reliable spectral data for the analyses of the first roaring sequences from  $N = 8$  leopard and  $N = 8$  eagle responses. In one leopard response, the caller did not produce a second roaring sequence containing a first and last phrase; this individual just continued roaring with one phrase roaring sequences after the initial two phrase roaring sequence. This led to a final sample size of  $N = 7$  leopard responses and  $N = 8$  eagle responses for analyses of the second roaring sequences (summarized in Table 4.1). Acoustic analyses of the first and last roars of the

first two roaring sequences were made with PRAAT 4.3.12. Additional analyses were conducted with RAVEN 1.2.

**Table 4.1.** Number of trials conducted with the acoustic predator models in Kaniyo Pabidi, vocal response rates and number of trials used for subsequent acoustic analyses.

Stimulus	Nr valid trials	Vocal Response Rate		Suitable for Temporal Analyses	Suitable for Spectral Analyses	
		N	%		First RS	Second RS
Leopard growls	33	12	36	9	8	7
Eagle shrieks	38	8	21	8	8	8
Chimpanzee Pant Hoots	18	0	0	0	0	0

### ***Acoustic structure of individual roars***

Comparing the acoustic structure of first and last roaring phrases produced within either the leopard or the eagle contexts (chimpanzees were not considered because the monkeys did not respond vocally to them) revealed significant differences between the first and last roaring phrases in both sequences, for both the leopard and eagle contexts (Tables 4.2 and 4.3, and Fig. 4.5).

Comparing roaring phrases between the two predator types, no consistent significant differences were found in any of the spectral parameters, except for the harmonics-to-noise ratios (HNR), which were higher in response to leopards than eagles (Table 4.3 and Fig. 4.6).

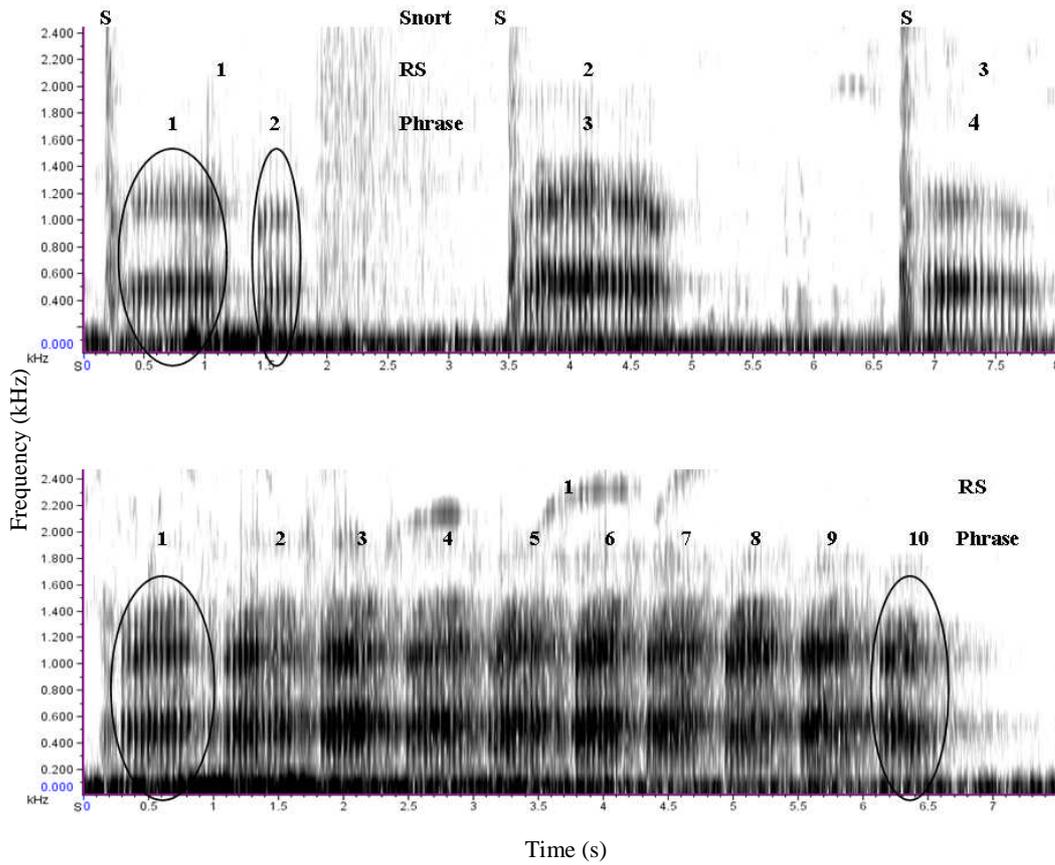
**Table 4.2.** Spectral measurements of first and last phrases produced in the first and second RS of vocal responses to acoustic leopard and eagle models.

Mdn= median value, M=mean value, and CI= 99% confidence interval.

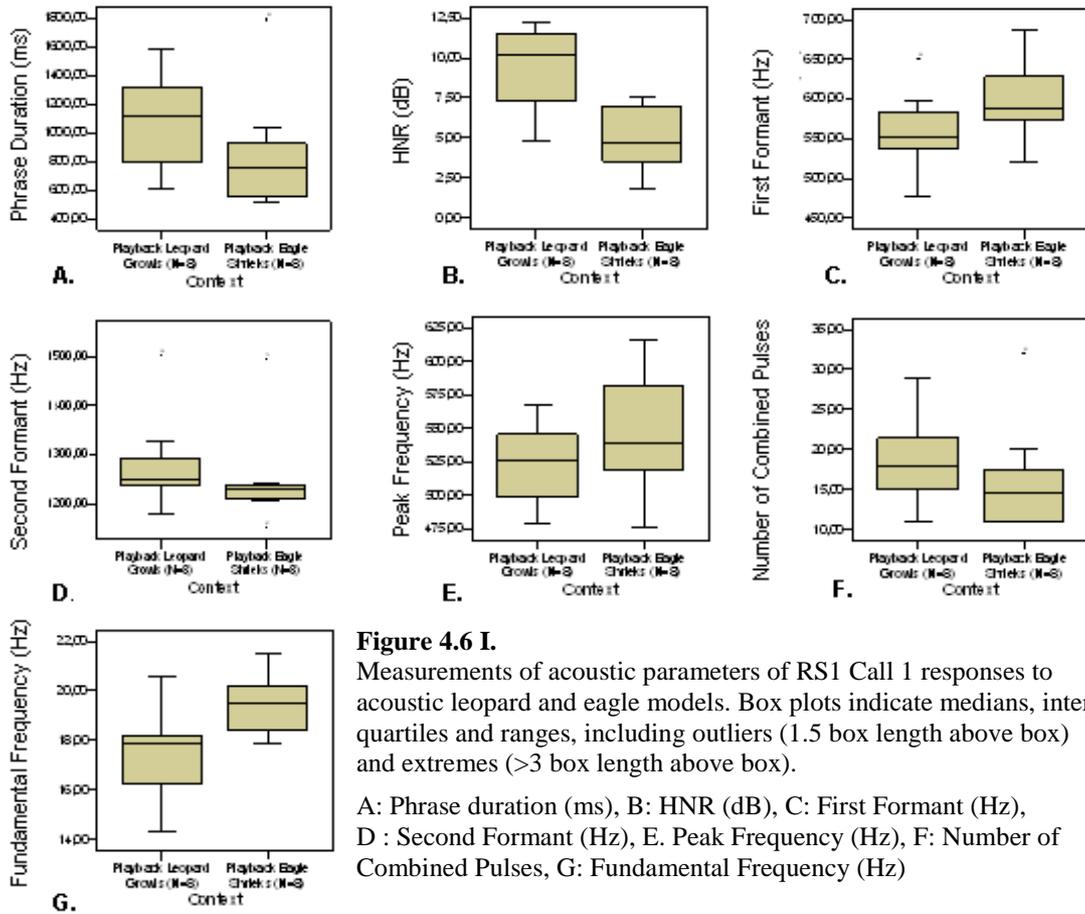
Acoustic variable		Acoustic Leopard Model			Acoustic Eagle Model		
		Mdn	M	CI	Mdn	M	CI
1 <sup>st</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	1110	1079	741 - 1417	755	845	423 - 1267
	HNR (dB)	10.14	9.36	7 - 12	4.64	4.98	3 - 7
	First Formant (Hz)	552	559	508 - 609	587	598	547 - 649
	Second Formant (Hz)	1248	1280	1180 - 1379	1229	1251	1147 - 1354
	Peak Frequency (Hz)	527	523	493 - 554	538	546	501 - 591
	Number of pulses	18	19	13 - 24	15	16	9 - 23
	Fundamental Freq (Hz)	18	17	15 - 19	20	19	18 - 21
1 <sup>st</sup> RS Last Phrase	Phrase Duration (ms)	371	292	129 - 455	324	354	281 - 427
	HNR (dB)	7.2	6.76	4 - 10	2.94	3.51	2 - 5
	First Formant (Hz)	586	635	441 - 830	540	619	435 - 803
	Second Formant (Hz)	1386	1416	1104 - 1727	1161	1282	996 - 1569
	Peak Frequency (Hz)	490	477	397 - 558	438	502	324 - 680
	Number of pulses	7	5	2 - 8	6	7	6 - 8
	Fundamental Freq (Hz)	18	18	15 - 20	20	20	18 - 21
2 <sup>nd</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	968	1068	719 - 1418	708	914	458 - 1371
	HNR (dB)	9.26	9.01	6 - 12	4.27	4.24	2 - 6
	First Formant (Hz)	572	603	471 - 734	589	602	543 - 661
	Second Formant (Hz)	1257	1299	1162 - 1437	1214	1290	1144 - 1436
	Peak Frequency (Hz)	544	623	346 - 900	568	628	405 - 852
	Number of pulses	18	18	13 - 24	14	16	10 - 23
	Fundamental Freq (Hz)	18	17	16 - 19	18	18	17 - 20
2 <sup>nd</sup> RS Last Phrase	Phrase Duration (ms)	295	335	112 - 559	359	353	217 - 488
	HNR (dB)	7.78	7.61	6 - 9	4.47	4.19	2 - 6
	First Formant (Hz)	520	607	371 - 843	595	601	544 - 659
	Second Formant (Hz)	1216	1320	986 - 1655	1225	1318	1104 - 1532
	Peak Frequency (Hz)	479	590	179 - 1002	468	479	414 - 543
	Number of pulses	5	6	2 - 10	7	7	4 - 9
	Fundamental Freq (Hz)	17	18	15 - 20	18	19	16 - 21

**Table 4.3.** Statistical output (exact p-values and effect sizes,  $r$ ) of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced within acoustic predator contexts (left hand side of the Table; Wilcoxon Signed Ranks Test,  $\alpha=.017$ ), followed by statistic output of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced across two different predator contexts (acoustic leopard and eagle models; right hand side of the Table; Man Whitney U test,  $\alpha=.017$ ).

Acoustic variable		Within Leopard (First vs Last phrase)		Within Eagle (First vs Last phrase)		Between Leopard and Eagle			
		Exact p	r	Exact p	r	First Phrase		Last Phrase	
						Exact p	r	Exact p	r
<b>1<sup>st</sup> RS</b>	Phrase Duration (ms)	<b>0.008</b>	0.63	<b>0.008</b>	0.63	<i>0.161</i>	0.37	<i>0.798</i>	0.08
	HNR (dB)	<i>0.195</i>	0.35	<i>0.250</i>	0.32	<b>0.003</b>	0.71	<i>0.038</i>	0.53
	First Formant (Hz)	<i>0.313</i>	0.28	<i>0.742</i>	0.11	<i>0.130</i>	0.39	<i>0.442</i>	0.21
	Second Formant (Hz)	<i>0.109</i>	0.42	<i>0.844</i>	0.07	<i>0.083</i>	0.45	<i>0.442</i>	0.21
	Peak Frequency (Hz)	<i>0.086</i>	0.46	<i>0.180</i>	0.35	<i>0.505</i>	0.18	<i>0.463</i>	0.20
	Number of pulses	<b>0.008</b>	0.63	<b>0.008</b>	0.63	<i>0.234</i>	0.31	<i>0.722</i>	0.09
	Fundamental Freq (Hz)	<i>0.945</i>	0.04	<i>0.383</i>	0.25	<i>0.028</i>	0.55	<i>0.077</i>	0.45
<b>2<sup>nd</sup> RS</b>	Phrase Duration (ms)	<b>0.016</b>	0.63	<b>0.008</b>	0.63	<i>0.189</i>	0.36	<i>0.694</i>	0.12
	HNR (dB)	<i>0.438</i>	0.27	<i>0.945</i>	0.04	<b>0.002</b>	0.75	<b>0.002</b>	0.77
	First Formant (Hz)	<i>0.938</i>	0.05	<i>0.844</i>	0.07	<i>0.694</i>	0.12	<i>0.189</i>	0.36
	Second Formant (Hz)	<i>0.938</i>	0.05	<i>0.945</i>	0.04	<i>0.463</i>	0.21	<i>0.867</i>	0.06
	Peak Frequency (Hz)	<i>0.297</i>	0.32	<b>0.008</b>	0.63	<i>0.554</i>	0.16	<i>0.930</i>	0.03
	Number of pulses	<b>0.016</b>	0.64	<b>0.008</b>	0.63	<i>0.29</i>	0.29	<i>0.710</i>	0.11
	Fundamental Freq (Hz)	<i>0.688</i>	0.14	<i>0.844</i>	0.07	<i>0.232</i>	0.3	<i>0.351</i>	0.25

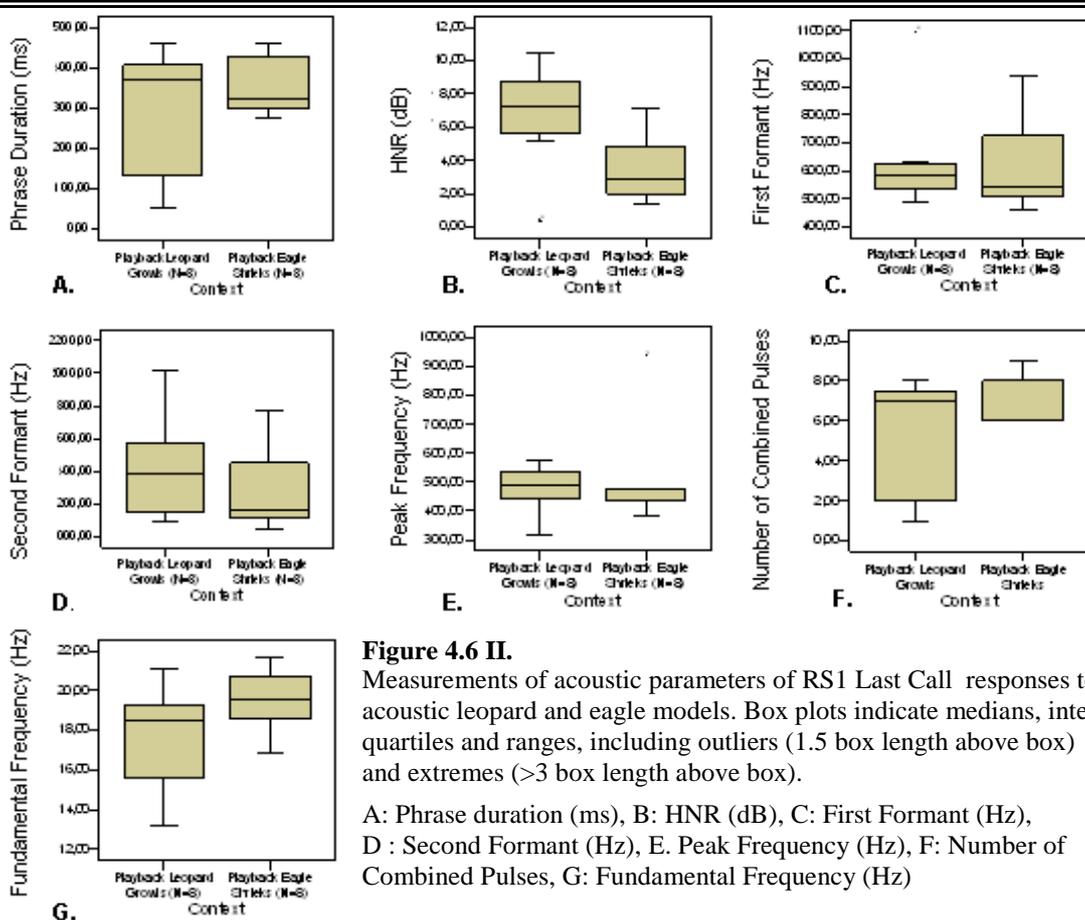


**Figure 4.5.** Spectrographic illustration of a Guereza's roaring, illustrating the significant differences in duration between first and last phrases within predator contexts and the non-significant differences in duration of first phrases and last phrases across predator responses. (A.) three Roaring Sequences given to an acoustic leopard model (8s), and (B.) one Roaring Sequence given to an acoustic eagle model (8s). Encircled are the first and last phrases measured from a RS. The x-axis represents the time in seconds, the y-axis represents the frequency in kHz.



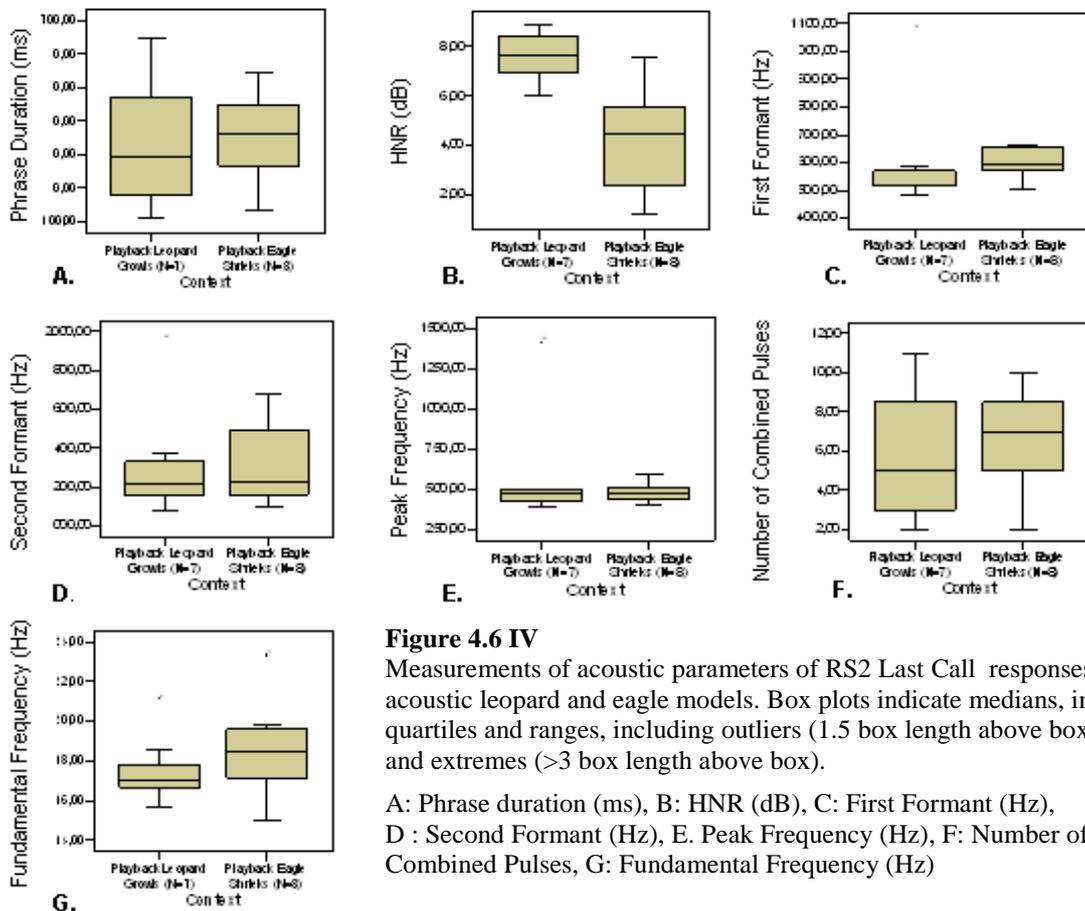
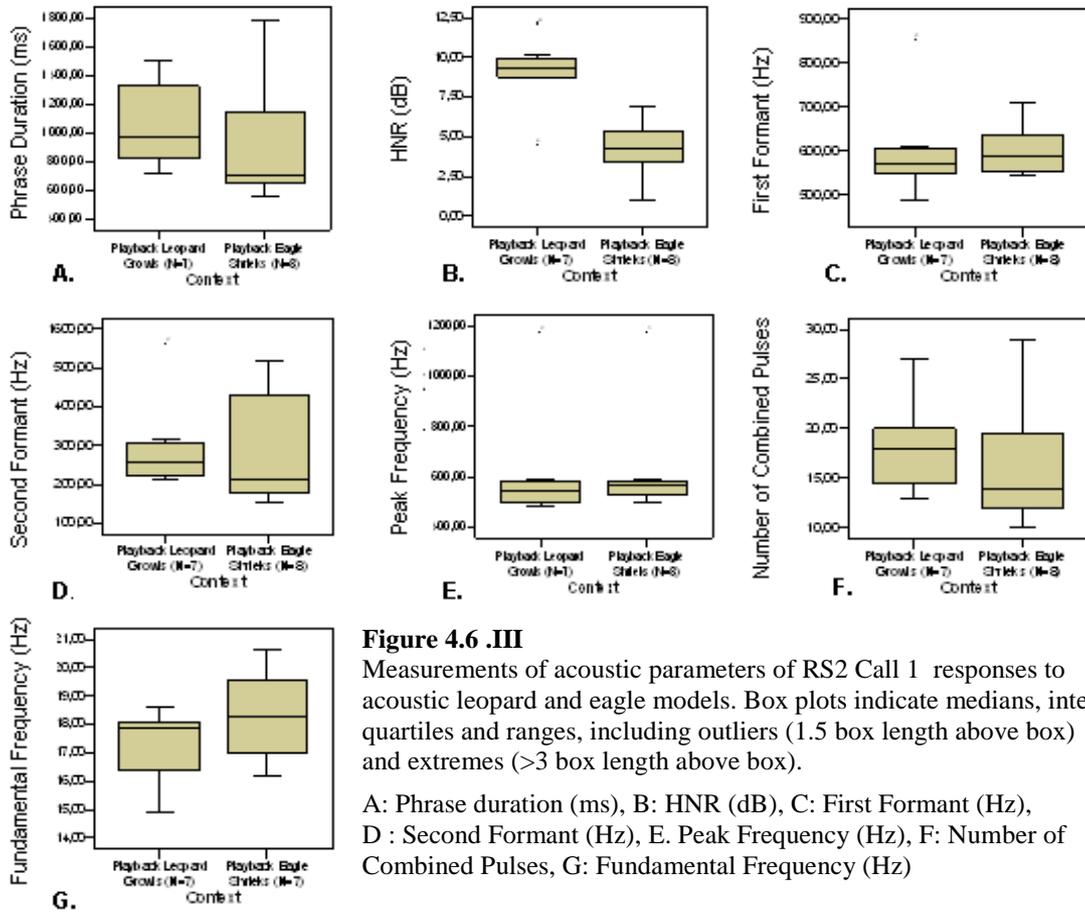
**Figure 4.6 I.** Measurements of acoustic parameters of RS1 Call 1 responses to acoustic leopard and eagle models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



**Figure 4.6 II.** Measurements of acoustic parameters of RS1 Last Call responses to acoustic leopard and eagle models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)

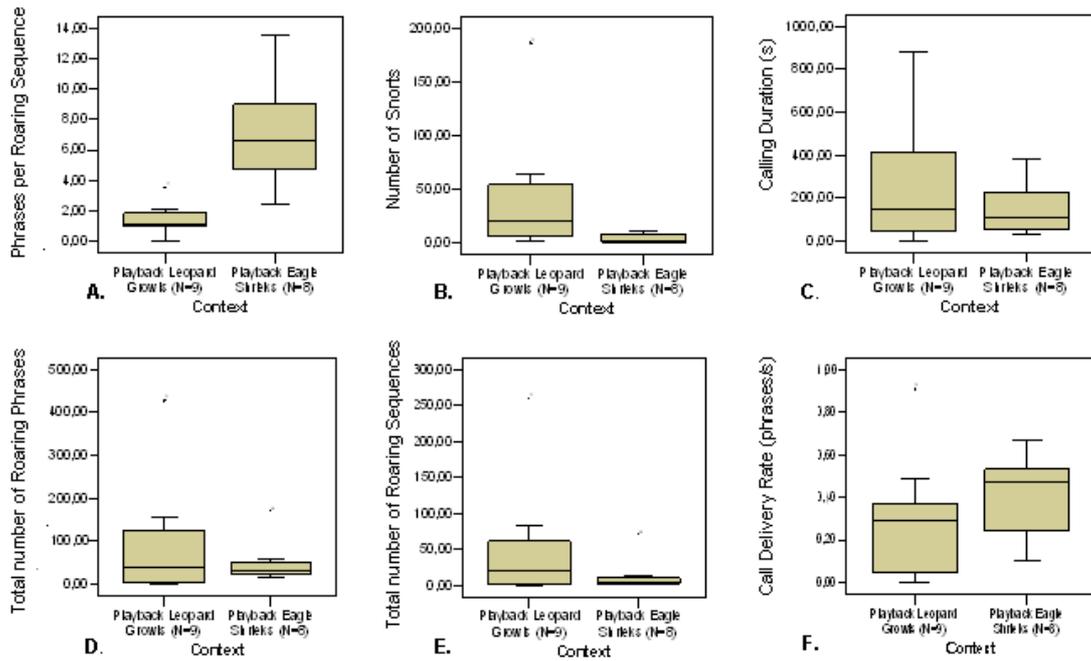


**Composition of Roaring Sequences**

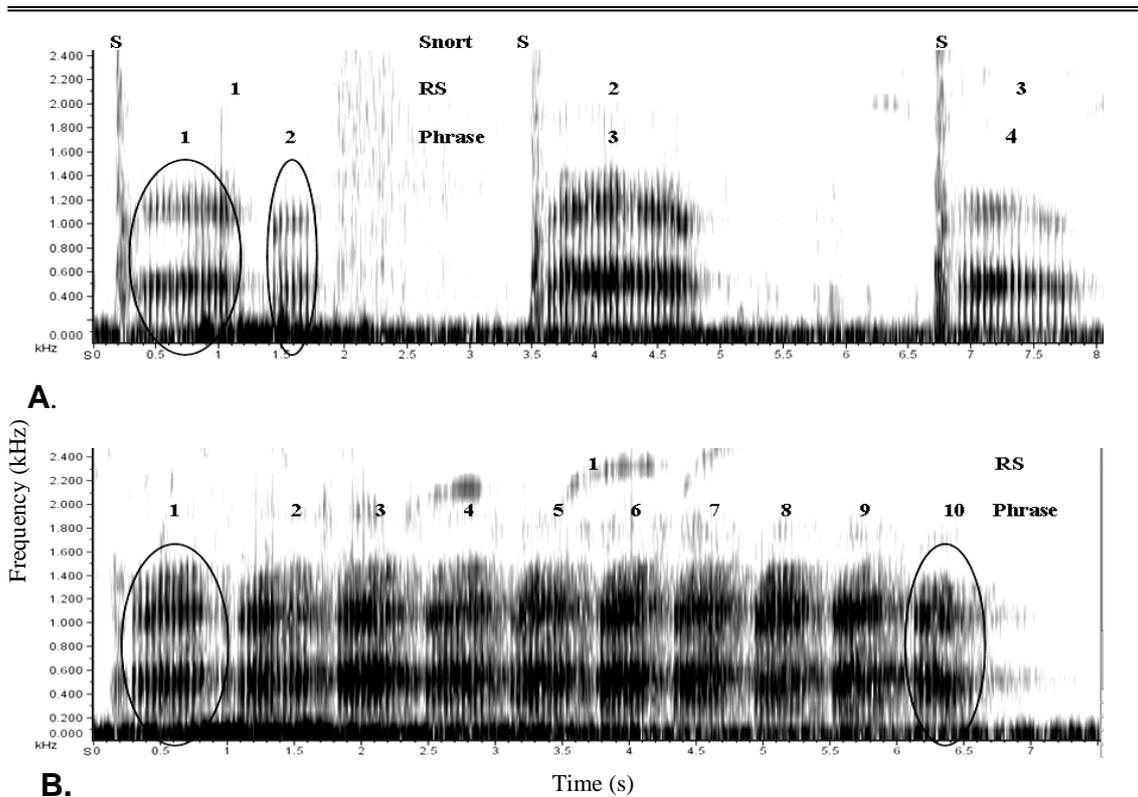
In contrast to the acoustic features, there were clear differences in the structural composition of the roaring sequences produced in response to eagles and leopards. Most importantly, the number of roaring phrases per sequence was significantly smaller in response to leopards than eagles ( $M_{\text{Leopard (L)}} = 1.4 \pm 1.1$ ;  $M_{\text{Eagle (E)}} = 7.1 \pm 3.5$ ;  $U = 1$ , exact  $p=0.000$ ,  $r=0.82$ ; U-test, two-tailed). Secondly, roaring sequences to leopards, but not eagles, were typically preceded by ‘snorts’ (9 of 9 leopard trials; 4 of 8 eagle trials, exact  $p=0.029$ ; Fisher’s Exact test, two-tailed). If the monkeys produced snorts in any of the two contexts, they produced a higher number of snorts in response to leopard growls than in response to eagle shrieks ( $M_L = 43.9 \pm 58.3$ ;  $M_E = 3.8 \pm 4.1$ ;  $U = 10.5$ , exact  $p=0.012$ ,  $r=0.60$ ; U-test, two-tailed). The total duration of calling ( $M_L = 248.7 \pm 284.7\text{s}$ ;  $M_E = 145.8 \pm 130.1\text{s}$ ;  $U = 30$ , exact  $p=0.587$ ,  $r = .14$ ; U-test, two-tailed), the total number of roaring phrases produced ( $M_L = 91.0 \pm 138.1$ ;  $M_E = 48.5 \pm 50.6$ ;  $U = 35$ , exact  $p=0.945$ ,  $r = .02$ ; U-test, two-tailed) and the total number of roaring sequences produced ( $M_L = 53.7 \pm 82.6$ ;  $M_E = 13.1 \pm 23.3$ ;  $U=28$ , exact  $p=0.465$ ,  $r=0.19$ ; U-test, two-tailed) did not differ between the two contexts. Finally, the call delivery rate between the two contexts was similar as well ( $M_L = 0.28 \pm 0.29$ ,  $M_E = 0.41 \pm 0.20$ ;  $U = 21$ , exact  $p=0.161$ ;  $r = 0.$ ; U test; two-tailed: Table 4.4 , Fig. 4.7, and Fig. 4.8).

**Table 4.4.** Temporal measurements of vocal response characteristics to acoustic leopard and eagle models. Mdn= median value, M= mean value and CI = 99% confidence interval. Statistical output (exact p-values and effect sizes,  $r$ ) of the Mann Whitney U Test to compare measurements across contexts are presented as well ( $\alpha=.017$ ). RS refers to roaring sequences.

Stimulus Type	Calling Duration (s)			Total Number RS			Total Number Phrases			Phrases per RS			Number of Snorts			Call Delivery Rate (phrases/second)		
	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI
<b>Leopard Growls</b>	149	248.7	-69.8 – 567.1	19	53.6	-38.7 - 146	39	90.9	-63.4 – 245.4	1.11	1.35	0.1 – 2.6	19	43.8	-21.3 – 109.1	0.29	0.28	-0.04 - 0.61
<b>Eagle Shrieks</b>	105.5	145.8	-15.2 – 306.7	3.5	13.1	-15.7 - 41.9	29	48.5	-14.1 – 111.1	6.56	7.06	2.8 – 11.4	2	3.8	-1.3 – 8.8	0.47	0.41	0.16 – 0.65
<b>Exact p value</b>	<i>0.587</i>			<i>0.465</i>			<i>0.945</i>			<i>0.000</i>			<i>0.012</i>			<i>0.161</i>		
<b>Effect size (r)</b>	0.14			0.19			0.02			0.82			0.60			0.35		



**Figure 4.7.** Measurements of temporal response characteristics to acoustic leopard and eagle models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box). A: Number of phrases/ RS, B: Number of snorts, C: Calling duration (s), D : Total number of phrases, E. Total number of RS (Hz), F: Call delivery rate (phrases/s).



**Figure 4.8** 8 Seconds continuous recording of a male producing A. three Roaring Sequences (RS) consisting of one snort-introduced 2-phrase RS, followed by two snort-introduced 1-phrase RS, to an acoustic leopard model, and B. one Roaring Sequences consisting of 10 phrases to an acoustic eagle model. Encircled are the first and last phrases that are produced in the first RS.

## Discussion

### ***Predator hunting techniques***

Concerning the monkeys' locomotor responses, some interesting patterns emerged. When the monkeys were confronted with leopard growls, eagle shrieks or chimpanzee pant hoots, they were equally likely to move either in the horizontal plane or the vertical plane in all three contexts. However, *if* they moved, this was clearly related to the predators' specific hunting techniques, and differed between the contexts. In response to leopards, the monkeys did not show a strong preference for movements in the vertical plane, nor for movements in the horizontal plane. Leopards probably pose a low threat to the monkeys, especially when vocalizing (and thus probably not hunting) and moreover because they can not promptly climb up a tree and follow the monkeys swiftly through the canopy. Therefore, it is not surprising that the monkeys responded somewhat ambiguously upon hearing the vocalizations of this predator. The Guerezas produced vocalizations in 36% of the leopard trials. This is a rather low response rate, which might reflect a low need to advertise perception to the predator and warn conspecifics, as it may have been considered as a non-dangerous threat in the vocalizing state. Alternatively, it may simply reflect a generally conservative nature of these monkeys when it comes to producing alarm calls.

Eagles theoretically pose a much higher threat to the monkeys. These predators normally sit silently on a branch and suddenly attack from within the canopy. They have also been observed to vocalize from within the canopy, e.g. when perched on a branch or sitting on or near the nest. Therefore, even when hearing this predator's vocalizations, an immediate attack may still be possible. Eagles are able to pursue monkeys through the canopy, and adult male monkeys have often been observed to chase and even fight an eagle trying to prey on his group. The behavioural responses found in the present study reflect this natural behaviour well: if the monkeys made movements after hearing eagle shriek playbacks, there was a trend to approach the simulated eagle, as well as moving downwards in the trees. The response rate, however, was relatively low (21%). Roaring in response to the presence of an eagle might therefore not be used in perception advertisement, but instead could be seen as an integrated part of the aggressive behaviour towards these predators, for example to signal aggressive intent while actively chasing and fighting an eagle. Costly roaring

might thus become more important and used in a higher proportion if the monkeys have actually spotted the eagle and can actively chase it.

Chimpanzees, finally, often hunt the monkeys in groups, and they can easily chase the monkeys through the canopy. They normally remain silent when hunting, but sometimes, when the actual hunt starts, produce vocalizations. Therefore, when hearing these predators' vocalizations, attack can follow, even if they have already given away their position. Normally, when the chimpanzees hunt in groups, the monkeys have a small chance of escaping. Therefore, perception advertisement seems an unproductive response. The most adaptive response seems to remain silent and cryptic to avoid detection, which is exactly what was found in the chimpanzee playback experiments. The Guerezas did not produce any vocalizations after hearing the chimpanzees' pant hoots, and if they moved, then they only moved up in the tree. The locomotor responses to chimpanzees, however, did not differ from the responses to leopard growls, which indicated that the animals used similar locomotor behaviour, but different vocal behaviour to both ground predator types.

### ***Predator specific acoustic structure?***

In contrast to other primate species in Budongo (e.g. blue monkeys; Papworth et al. 2008), there was no evidence that the Guerezas varied the acoustic structure of individual phrases according to the predator type that was encountered. Only one effect was found in the harmonics-to-noise ratio (HNR) of individual roaring phrases. This acoustic variable can be influenced by factors such as illness and age, and through an inadequate closure of the vocal folds, allowing excess airflow through the glottis, which can cause turbulence during phonation, a-periodic vocal fold vibration, and pitch perturbations (Riede et al., 2001; Ferrand, 2002; Shama et al., 2007). The HNR, amongst other acoustic variables, has been implicated as a useful tool in animal bioacoustics. It might possess some communicative meaning, for example in dogs, baboons and squirrel monkeys where it was suggested to be related to the animals' affective state (e.g. Fichtel et al., 2001; Riede et al., 2001; Rendall, 2003). Differences in HNR may be related to other aspects as well, as discussed below.

In this study, the phrases produced in response to acoustic leopard models were less noisy (i.e. had a higher HNR) than the phrases produced in response to acoustic eagle

models. This may theoretically be a by-product of the longer roaring sequences given to eagles. These roaring sequences may require the monkeys to take in more air before vocalizing compared to the shorter leopard sequences, perhaps causing subtle differences in vocal fold behaviour and turbulence when producing individual phrases. However, after careful inspection of the spectrogram and the recordings, there was an indication that the monkeys inhaled before producing individual phrases, both when producing the long eagle sequences and when producing the shorter leopard sequences, rejecting the posed hypothesis (cf. Harris, 2006).

Another interesting point related to this finding is that noisy sounds are generally better locatable than tonal sounds (Marler, 1967). Thus, if monkeys can use perception-advertisement as a strategy to repel predators, it might be beneficial to produce noisy alarm sequences that are easy to locate by both predators and conspecifics, whereas when confronted with pursuit hunters this may not be an efficient strategy. Both eagles and leopards rely on surprise and sit and wait in ambush until they can strike. Thus, monkeys may benefit by advertising detection, if this repels these predators. If anything, eagles seem less susceptible to such strategies and seem more adapted for a possible pursuit through the canopy once they have been discovered by the monkeys than leopards. Hence, Marler's (1967) localizability hypothesis is not supported by these data, because more locatable (noisy) sounds were produced to eagles and not leopards.

### ***Affect intensity?***

Another possible explanation is that the observed differences in HNR are the result of different levels of arousal (Fichtel et al., 2001; Rendall, 2003). Although no direct measurements of affect were taken in this study, following the rationale from these studies may imply that encountering an eagle may be more arousing than encountering a leopard, and this may affect HNR in the vocal responses. However, it seems unlikely that, especially over longer distances, this feature alone is conspicuous enough to effectively communicate predator information to conspecifics, although it may reveal something about the affective state of the signaller. If affect, as argued in some studies, is responsible for differences in HNR, then one should also observe differences in HNR of vocal responses produced within the same predator contexts, particularly if situations differ in response urgency. For example, a vocalizing leopard may not be perceived as

a major threat, whereas a silently hiding leopard may be perceived as highly dangerous, because it is likely to be hunting. If the HNR is reflecting the monkeys' affective state, then a difference in HNR is expected when comparing the monkeys' vocal responses to vocalizing leopards (acoustic model) vs silent leopards (visual model). This topic will be investigated, analysed and discussed in the next chapter.

### ***Predator-specific structural organisation***

Results were more clear-cut in terms of the structural organization of the responses at the level of call sequences. Responses to leopard growls consisted of a smaller number of roaring phrases per sequence than the responses to eagle shrieks. Furthermore, responses to leopard growls more frequently, but not exclusively, contained snorts than responses to eagle shrieks. A further striking effect concerned the acoustic difference of last calls when compared to the preceding calls in a sequence. Reliably, the last call in a sequence was lower pitched, which perceptually indicates the end of a roaring sequence. Whether this feature possesses any signal value or is just a mere by-product caused by relaxation of the animal's musculature at the end of a sequence, is an unresolved question.

Hence, Guerezas combined different call types ('first' and 'last' phrases and snorts) into context-specific alarm responses that relied primarily on the perceptual salience of 'few' versus 'many' in the number of roaring phrases produced before the last low-pitched phrase of a sequence. Snorts are more often produced in responses to leopards than in responses to eagles. Since Guerezas also produced snorts to humans and chimpanzees, the locatability hypothesis does not explain the production of this call type either.

The question whether these call sequences produced to the different predator types can be classified as referential signals or as mediated by motivational state or urgency response is not addressed here, but will be discussed in the next chapters, after having described the monkeys' responses to visual predator models.

## Chapter 5

### Visual predator model experiments in Kaniyo Pabidi

The previous chapter dealt with acoustic predator models, used to provoke predator-specific locomotor and vocal anti-predator responses from the Guereza colobus monkeys. The aim of the present chapter is to investigate the vocal and behavioural responses of Guerezas to the presentation of visual predator models and compare these to their responses to acoustic predator models as discussed in the previous chapter.

#### Introduction

Several studies have shown that many different primate species reliably respond with adaptive predator specific anti-predator behaviour to acoustic predator cues (e.g. ringtailed lemurs: Macedonia & Yount, 1991; Diana monkeys: Zuberbühler et al., 1997; redfronted lemurs and white sifakas: Fichtel & Kappeler, 2002; mantled howler monkeys: Gil-da-Costa et al., 2003; tamarins: Kirchhof & Hammerschmidt, 2006; reviewed in Blumstein et al. 2008). However, it could be argued that experimentally provoking anti-predator behaviour with acoustic predator models is flawed if the aim is to accurately describe a species' anti-predator behaviour (e.g. Arnold et al., 2008; Blumstein et al., 2008). First of all, at the proximate level, acoustic and visual models may influence a monkey's perceived threat. For example, a vocalizing leopard may be perceived as less dangerous than a silent leopard, simply because leopards normally do not vocalize while hunting (Jenny & Zuberbuhler, 2005). Furthermore, the different sensory modalities may employ different cognitive mechanisms, which may affect the type of anti-predator behaviour displayed (Blumstein et al., 2008). From an ultimate perspective, it has been argued that acoustic predator recognition requires more explicit cues, that often are highly species-specific, and thus may require more experience in evoking the proper anti-predator response than visual signals (Blumstein et al., 2000).

Moreover, acoustic predator models may be more sensitive to methodological flaws than, for example, the presentation of life-sized visual predator models (e.g. Arnold et al., 2008). For example, if playback stimuli are of a short duration, they may not

provide the subjects with sufficient evidence for the predator's presence. As a consequence, the animals might then first inspect the source of disturbance, before engaging in more specific anti-predator behaviour (Lima & Dill, 1990). Furthermore, when simulating predator presence with acoustic cues, the monkeys will never find the predator, which could affect their anti-predator behaviour. Another point is that warning signals become redundant after broadcasting a predator's vocalizations, because all group members will have heard the predator calls simultaneously. Visual detection will always be staggered and thus may elicit stronger responses from signallers, possibly also due to a naïve audience (Wich & Sterck, 2003).

Although previous playback studies have shown that some primate species are able to recognize the presence of a predator by its vocalizations alone and are able to reliably communicate this information to conspecifics and the predator itself (e.g. vervet monkeys (Seyfarth et al., 1980), ringtailed lemurs (Pereira & Macedonia, 1991), mustached tamarins (Kirchhof & Hammerschmidt, 2006), Diana monkeys (Zuberbühler et al., 1997; Zuberbühler, 2000), Campbell's monkeys (Zuberbühler, 2001), and blue monkeys (Papworth et al., 2008)), it is argued that, in order to obtain the most accurate description of an animals' anti-predator behaviour, visual predator models also need to be presented.

Therefore, the present study was designed to investigate the Guerezas' locomotor and vocal responses to visual predator models, to allow direct comparisons with the previous results from the playback studies. Comparing responses to both modalities is likely to reveal something about the underlying cognitive mechanisms that are involved in dealing with predators.

### ***Hypotheses and predictions***

It was hypothesised that the Guerezas recognized the leopard and chimpanzee models as relevant predator species by their visual characteristics. If correct, the prediction was that monkeys responded with anti-predator behaviour that was appropriate to the different predators' hunting techniques. Provided the monkeys responded vocally to the two models, a related question was whether they produced predator-specific vocal

alarms to the two predator types, and if these were similar to those produced to acoustic predator models.

## **Methods**

The study was conducted in the Kaniyo Pabidi area of the Budongo Forest Reserve, where all three major primate predators have been observed. The study site is described in chapter 2, as are the general methods used for the model experiments. In short, a naïve monkey group was searched along pre-cut trails between 8h00am and 18h00 pm. If the animals were unaware of the presence of the observers and no other disturbances occurred, a trial was conducted as follows: the experimenter, wearing either a fake leopard or fake chimpanzee fur draped over his head, shoulders and torso, started moving slowly towards the monkey group, while the observer recorded and observed the monkeys' vocal and locomotor behaviour from a hiding place. If the experimenter managed to approach the tree unnoticed, he shook some branches to grab their attention. After detection, he remained within sight of the group for about 15-20 minutes, before slowly moving back towards the observer's hiding place. The presentation of a visual eagle model to the Guerezas was considered impossible because of methodological impracticalities. Therefore, this study just dealt with the chimpanzee model and the leopard model experiments.

The monkeys' vocal responses were usually recorded for their entire duration, but for up to a maximum of 60 minutes total. Recordings were transferred onto a PC using Cool Edit 2000. To allow systematic comparisons, only the first and last phrases of the first and last roaring sequences produced were subjected to acoustic analyses with Raven 1.2 and Praat. 4.3.12.

The following six structural parameters were determined using spectrograms generated on RAVEN 1.2: (a) total duration of the vocal response (s), (b) total number of roaring sequences, (c) total number of roaring phrases, (d) mean number of roaring phrases per roaring sequence, (e) number of snorts, and (f) call delivery rate (phrases/s; cf. Oates & Trocco, 1983).

To compare the acoustic structure of individual roaring phrases given to the different predator models, 7 acoustic variables were measured: (a) phrase duration (ms) (b) number of pulses per roaring phrase, and (c) fundamental frequency (Hz) were measured using SPG's generated with Raven 1.2. The other 4 variables were extracted using PRAAT 4.3.12: (d) harmonics-to-noise ratio (HNR, dB, (e) first and (f) second formants (Hz), and (g) peak frequency (Hz). Additionally, the behavioural responses elicited by the different predator model stimuli were scored, using the protocol described in chapter 2.

### ***Statistics***

To analyse the behavioural differences within a predatory context, binomial tests were used, with the test probability set at  $p=0.5$ , and the critical significance level at  $\alpha=0.05$ . Comparisons between the contexts were made with Fisher's Exact Tests ( $\alpha=0.05$ ). The differences in acoustic measurements within and between contexts were tested with non-parametric tests. For spectral comparison within the contexts, in order to test the differences between first and last phrases produced in a sequence, a Wilcoxon matched pairs test was used (Bonferroni corrected  $\alpha=0.017$ ). For the comparison of spectral and temporal parameters between the predator contexts a Mann Whitney U Test was used (Bonferroni corrected  $\alpha=0.017$ ).

## **Part 1: Visual model experiments**

### **Results**

The predator model experiments were carried out between June and July 2007. 18 different Guereza groups were tested with a moving leopard model and 12 groups were tested with a moving chimpanzee model. None of the experiments had to be discounted as invalid.

### ***Behavioural response characteristics***

The monkeys' movements in the horizontal plane ('movement closer', 'movement further', and 'no movement') and vertical plane ('movement up', 'movement down', or

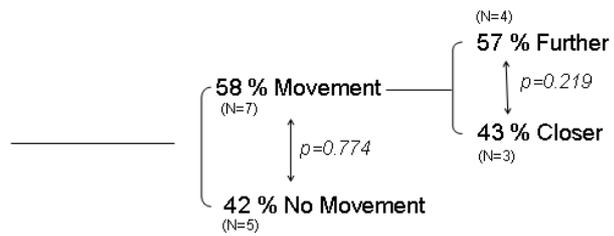
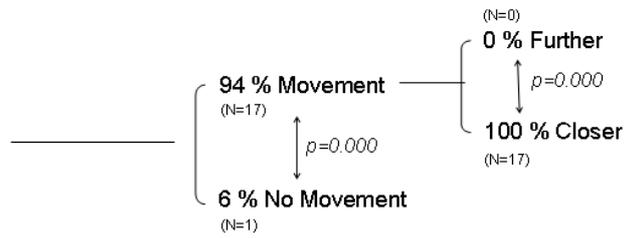
'no movement') were scored in all trials: horizontal and vertical:  $N_{\text{Leopard}}=18$ , and  $N_{\text{Chimpanzee}}=12$ .

### **Behavioural response characteristics compared within predator contexts**

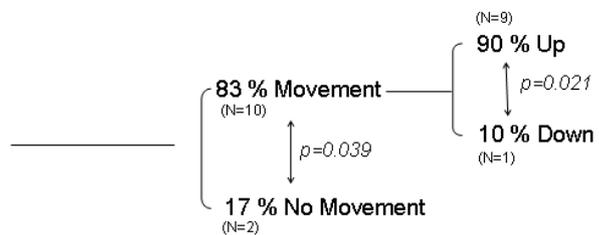
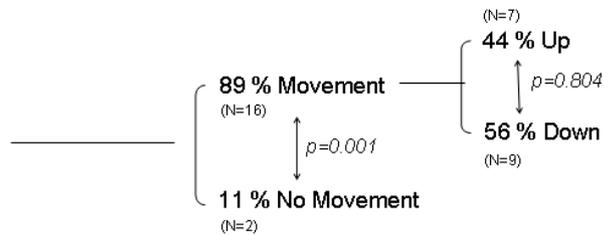
Results showed that the monkeys were significantly more likely to start moving than to remain still after detecting a leopard model, both in the horizontal ( $N_{\text{Move}}=17$ ;  $N_{\text{Not Move}}=1$ , exact  $p=0.000$ ) and in the vertical plane ( $N_{\text{Move}}=16$ ;  $N_{\text{Not Move}}=2$ , exact  $p=0.001$ ). Movement was always directed towards the model ( $N_{\text{Further}}=0$ ;  $N_{\text{Closer}}=17$ , exact  $p=0.000$ ), although equally likely to be directed 'up' or 'down' ( $N_{\text{Up}}=7$ ;  $N_{\text{Down}}=9$ , exact  $p=0.804$ , Binomial tests, Fig. 5.1).

After detection of the chimpanzee model, the monkeys were equally likely to move or stay still in the horizontal plane ( $N_{\text{Move}}=7$ ;  $N_{\text{Not Move}}=5$ , exact  $p=0.774$ ), but were significantly more likely to move in the vertical plane ( $N_{\text{Move}}=10$ ;  $N_{\text{Not Move}}=2$ , exact  $p=0.039$ ). If they moved in the horizontal plane, direction was random ( $N_{\text{Further}}=4$ ;  $N_{\text{Closer}}=3$ , exact  $p=1.000$ ). If they moved in the vertical plane, they were significantly more likely to move up in the trees ( $N_{\text{Up}}=9$ ;  $N_{\text{Down}}=1$ , exact  $p=0.021$ ; Fig. 5.1).

A. Horizontal Movement



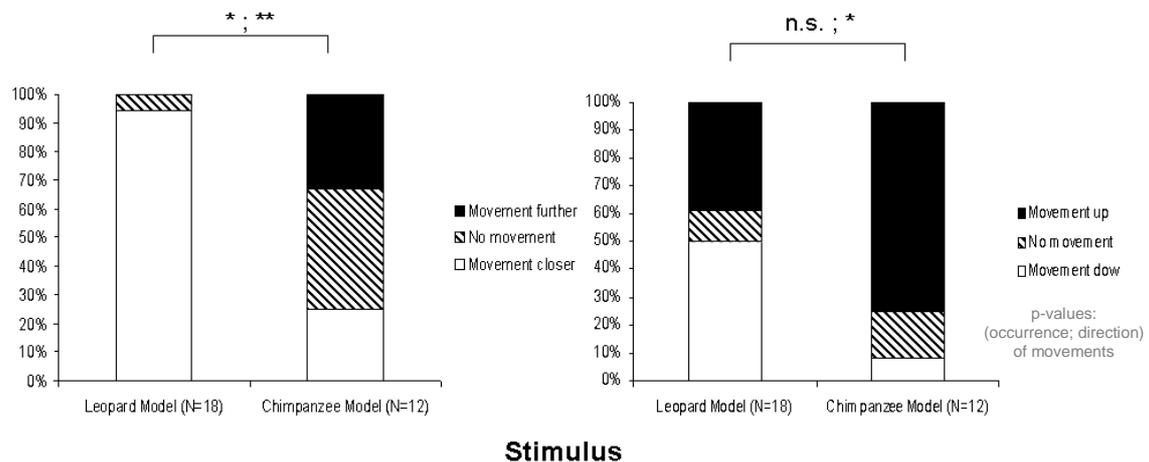
B. Vertical Movement



**Figure 5.1.** Monkeys' locomotor behaviour in A. the horizontal plane and B. the vertical plane in response to the visual predator models, with corresponding percentages of movements and exact p-values of the differences between locomotor responses within predator contexts (Binomial tests,  $\alpha=0.05$ ).

### Behavioural response characteristics compared between predator contexts

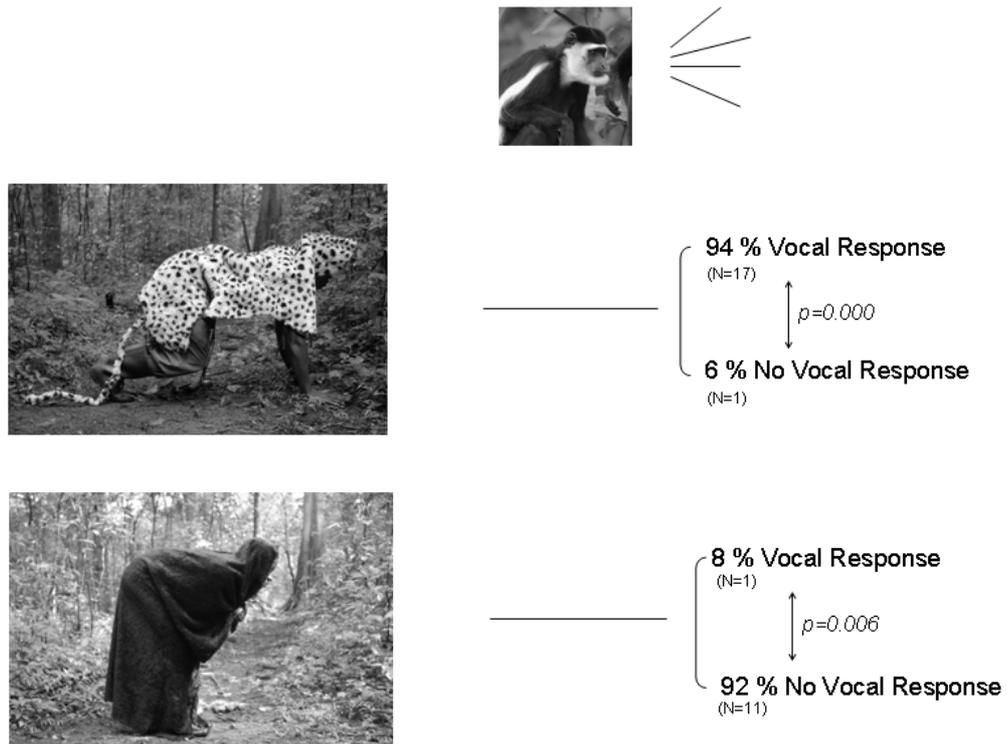
When comparing behavioural responses between the predator contexts the monkeys were more likely to start moving in the horizontal plane when detecting a leopard than a chimpanzee (Leopard:  $N_{\text{Move}}=17$ ,  $N_{\text{NotMove}}=1$ ; Chimpanzee:  $N_{\text{Move}}=7$ ,  $N_{\text{NotMove}}=5$ : exact p L vs Ch= 0.026), but equally likely to start moving in the vertical plane in both contexts (Leopard:  $N_{\text{Move}}=16$ ,  $N_{\text{NotMove}}=2$ ; Chimpanzee:  $N_{\text{Move}}=10$ ,  $N_{\text{NotMove}}=2$ : exact p L vs Ch=1.000). *If they moved, they were more likely to move closer to the leopards than to chimpanzees (Leopard:  $N_{\text{Further}} = 0$ ,  $N_{\text{Closer}}=17$ , Chimpanzee:  $N_{\text{Further}} =4$ ,  $N_{\text{Closer}}=3$ ; exact p L vs Ch=0.003), and more likely to move up in the presence of a chimpanzee than in the presence of a leopard (Leopard:  $N_{\text{Up}} = 7$ ,  $N_{\text{Down}}=9$ , Chimpanzee:  $N_{\text{Up}} = 9$ ,  $N_{\text{Down}}=1$ ; exact p L vs Ch=0.037; Fisher's Exact Tests, Fig. 5.2).*



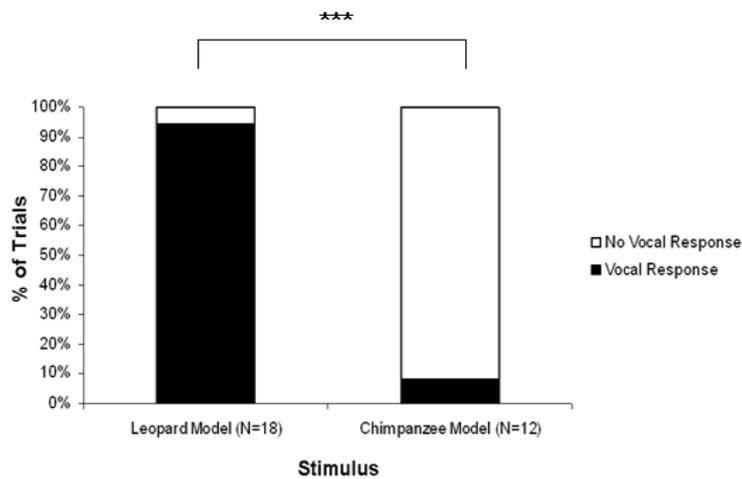
**Figure 5.2.** Locomotor responses in the horizontal and vertical plane to the two different visual models. The first set of asterisks refers to the difference in occurrence of movement between the contexts; the second set to the difference in direction of movements between the contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p = 0.000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

### Vocal response characteristics to model experiments

In 17 of the 18 groups that were tested with the leopard model, at least one individual responded with alarm vocalizations (response rate = 94%;  $N_{\text{Vocal Response (VR)}}=17$ ,  $N_{\text{NoVR}}=1$ ; exact p-value=0.000). The response rate to the chimpanzee model was much lower: in only 1 of 12 groups at least one monkey responded with alarm vocalizations (response rate = 8%;  $N_{\text{VR}}=1$ ,  $N_{\text{NoVR}}=11$ ; exact p-value=0.006, Fig. 5.3). These vocal response rates differed significantly between the two contexts (Leopards: 94%; Chimpanzees 8%, L vs Ch: exact p-value: 0.000; Fig. 5.4).



**Figure 5.3.** Vocal response rates of the monkeys to the two different visual predator models, with corresponding exact p-values within contexts (Binomial test,  $\alpha=0.05$ ).



**Figure 5.4.** Vocal response rates to the two different visual predator models, with exact p-values. n.s.: no significant difference between the contexts; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in vocal response rates between the contexts, \*  $p < .05$ , \*\*  $p < .01$ , \*\*\*  $p = .000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

**Acoustic measurements of vocal responses**

Of the 17 vocal responses to leopards, only N=7 were of sufficient quality for the structural measurements. In 11 of the 17 leopard responses, the roaring sequences of the first individual to call could be identified so that it was possible to measure the first two roaring sequences from these 11 individuals. One individual, however, produced roaring sequences composed of just one phrase, so this response had to be discarded from the final data set for the spectral analyses. The one vocal response given to the chimpanzee model was of very bad recording quality, making acoustic analyses difficult. Table 5.1 gives an overview of the number of trials conducted and responses suitable for further analyses.

**Table 5.1.** Number of trials conducted with the visual predator models, vocal response rates and number of trials used for subsequent acoustic analyses.

Stimulus	Nr valid trials	Response Rate		Suitable for Temporal Analyses	Suitable for Spectral Analyses	
		N	%		First RS	Second RS
Visual Leopard model	18	17	94.4	7	10	10
Visual Chimpanzee model	12	1	8.3	1	1	1

**Acoustic structure of individual roars**

Comparing the acoustic structure of first and last roaring phrases produced to the leopard model revealed significant differences between the first and last roaring phrases in both sequences, particularly in terms of phrase duration and number of pulses (Tables 5.2 and 5.3). Only one individual produced a vocal reaction to the chimpanzee model, which prevented further statistical analyses.

**Table 5.2.** Spectral measurements of first and last phrases produced in the first and second RS of vocal responses to visual leopard models. Mdn= median value, M=mean value, and CI= 99% confidence interval.

Acoustic variable		Response Visual Leopard Model		
		Mdn	M	CI
1 <sup>st</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	1112	1174	790 – 1558
	HNR (dB)	5.88	5.74	2.63 – 8.85
	First Formant (Hz)	569	570	511 – 630
	Second Formant (Hz)	1304	1307	1211 – 1404
	Peak Frequency (Hz)	509	516	476 – 557
	Number of pulses	20	20	13 – 26
	Fundamental Freq (Hz)	17	17	16 - 18
1 <sup>st</sup> RS Last Phrase	Phrase Duration (ms)	253	320	119 – 520
	HNR (dB)	4.55	3.97	1.20 – 6.75
	First Formant (Hz)	645	632	506 – 633
	Second Formant (Hz)	1393	1380	1155 – 1606
	Peak Frequency (Hz)	408	428	351 – 505
	Number of pulses	5	6	3 - 9
	Fundamental Freq (Hz)	20	19	17 - 21
2 <sup>nd</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	930	938	700 – 1176
	HNR (dB)	4.64	5.20	2.27 – 8.12
	First Formant (Hz)	559	570	531 – 608
	Second Formant (Hz)	1252	1260	1151 – 1370
	Peak Frequency (Hz)	534	529	502 – 557
	Number of pulses	17	16	13 – 20
	Fundamental Freq (Hz)	18	18	17 - 19
2 <sup>nd</sup> RS Last Phrase	Phrase Duration (ms)	260	263	117 – 409
	HNR (dB)	4.26	4.44	1.37 – 7.51
	First Formant (Hz)	549	553	457 – 649
	Second Formant (Hz)	1267	1287	1090 – 1484
	Peak Frequency (Hz)	420	451	368 – 534
	Number of pulses	5	5	2 - 7
	Fundamental Freq (Hz)	19	18	15 - 20

**Table 5.3.** Statistical output (exact p-values and effect sizes,  $r$ ) of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced within the visual leopard model context (Wilcoxon Signed Ranks Test,  $\alpha=.017$ ).

Acoustic variable		Within Visual Leopard Model (First vs Last phrase)	
		Exact p	r
<b>1<sup>st</sup> RS</b>	Phrase Duration (ms)	<b>0.002</b>	0.63
	HNR (dB)	0.131	0.35
	First Formant (Hz)	0.193	0.31
	Second Formant (Hz)	0.322	0.24
	Peak Frequency (Hz)	0.035	0.46
	Number of pulses	<b>0.002</b>	0.63
	Fundamental Freq (Hz)	<b>0.014</b>	0.54
<b>2<sup>nd</sup> RS</b>	Phrase Duration (ms)	<b>0.002</b>	0.63
	HNR (dB)	0.334	0.23
	First Formant (Hz)	0.375	0.22
	Second Formant (Hz)	0.492	0.17
	Peak Frequency (Hz)	0.021	0.50
	Number of pulses	<b>0.002</b>	0.63
	Fundamental Freq (Hz)	0.846	0.06

## Part 2: Visual model experiments vs acoustic model experiments

Besides monitoring the differences in response to the two different predator types, this chapter was concerned with assessing the possible differences in responses to the presentation of the two different predator modalities within a specific predator context. The results of these comparisons are given below.

### *Hypotheses and predictions*

It was hypothesised that that the monkeys recognised both the visual and acoustic models as their predators and responded in a modality-dependent way, either caused by different perception mechanisms or by differences in perceived dangerousness. If correct, in both cases the prediction was that monkeys should respond more strongly to the visual than to the acoustic models.

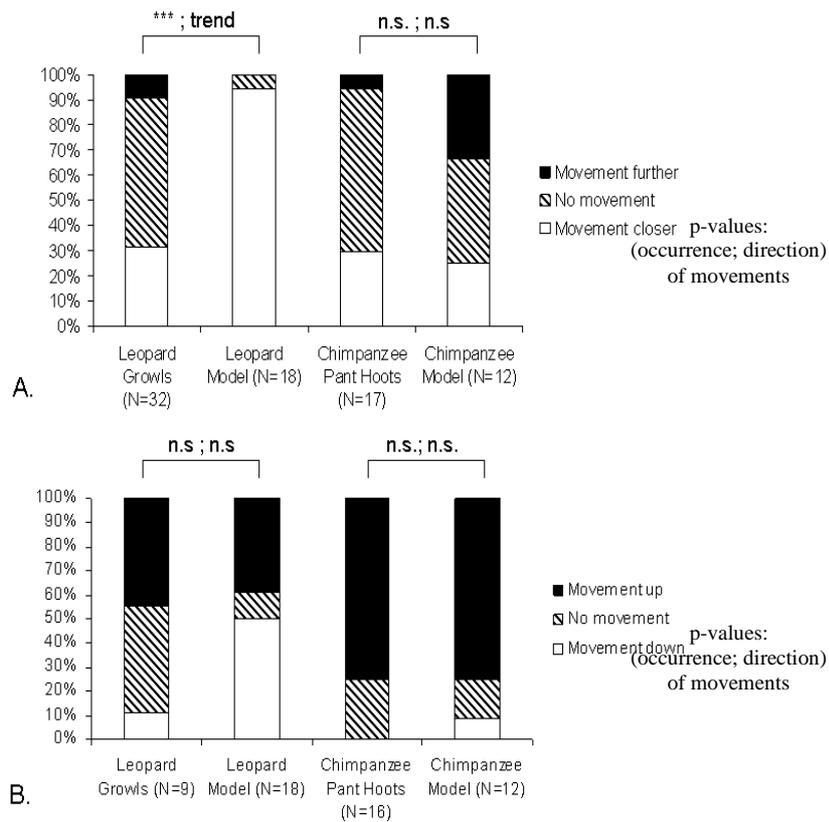
## Results

### ***Behavioural responses***

Comparing the locomotor response to leopard models, monkeys responded more strongly in the horizontal plane to visual than acoustic models (movement visual model: 94% (17/18), movement acoustic model: 41% (13/32), exact  $p=0.000$ , Fisher's Exact Test, two-tailed). No significant differences were found in the vertical plane (movement visual model: 89% (16/18), movement acoustic model: 56% (5/9): exact  $p=0.135$ , Fisher's Exact Test, two-tailed). If movement occurred in the horizontal plane, it was typically by approaching the model in both conditions (acoustic model:  $N_{\text{Further}} = 3$ ,  $N_{\text{Closer}}=10$ , visual model:  $N_{\text{Further}} =0$ ,  $N_{\text{Closer}}=17$ ; exact  $p$  acoustic vs visual  $=0.070$ , Fisher's Exact Test, two-tailed). No differences were found in the vertical movements either (acoustic model:  $N_{\text{Up}} = 4$ ,  $N_{\text{Down}}=1$ , visual model:  $N_{\text{Up}} =7$ ,  $N_{\text{Down}}=9$ ; exact  $p$  acoustic vs visual  $=0.313$ , Fisher's Exact Test, two-tailed, Fig. 5.5).

In response to chimpanzees the monkeys were equally likely to move in both planes in response to both model types (horizontal plane: visual model= 58% (7/12), acoustic model: 35% (6/17), exact  $p=0.274$ ; vertical plane: visual model=83% (10/12), acoustic model: 75% (12/16), exact  $p=0.673$ , Fisher's Exact Tests, two-tailed).

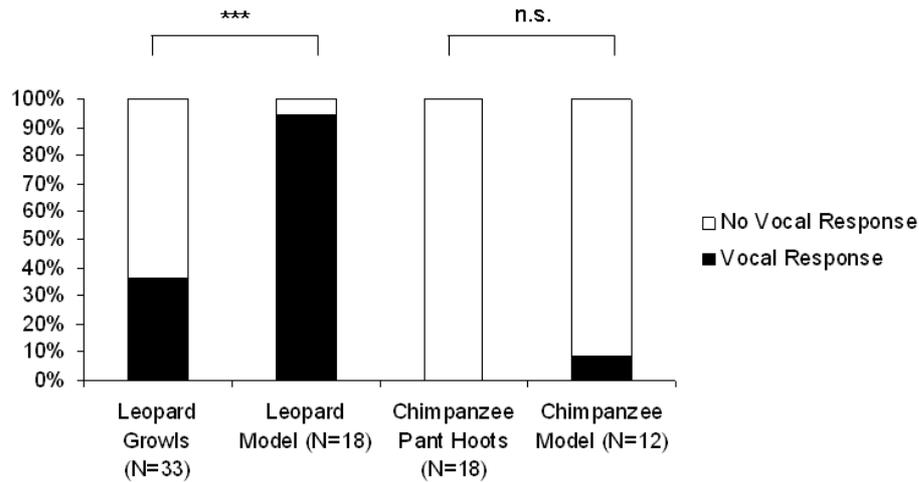
If monkeys moved there were no significant differences between model types in both horizontal and vertical plane (horizontal: acoustic model:  $N_{\text{Further}} = 1$ ,  $N_{\text{Closer}}=5$ , visual model:  $N_{\text{Further}} =4$ ,  $N_{\text{Closer}}=3$ ; exact  $p$  acoustic vs visual $=0.266$ ; vertical: acoustic model:  $N_{\text{Up}}= 12$  ,  $N_{\text{Down}}=0$ , visual model:  $N_{\text{Up}} =9$ ,  $N_{\text{Down}}=1$ ; exact  $p$  acoustic vs visual $=0.455$ , Fisher's Exact Test, two-tailed; Fig. 5.5).



**Figure 5.5.** Locomotor responses in (A.) the horizontal and (B.) vertical plane to the different predator models; acoustic and visual leopard and chimpanzee models. The first set of asterisks refers to the difference in occurrence of movement between the contexts; the second set to the difference in direction of movements between the contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < .05$ , \*\*  $p < .01$ , \*\*\*  $p = .000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

### Vocal response rates

The vocal response rates to visual models differed significantly from the vocal response rates to acoustic models, but only for leopards (response rate acoustic leopard model = 36.4% (12/33), visual leopard model = 94.4% (17/18), exact p-value = 0.000; response rate acoustic chimpanzee model = 0%, visual chimpanzee model = 8% (1/12), exact p-value = 0.4, Fisher's Exact tests, two-tailed: fig 5.6).



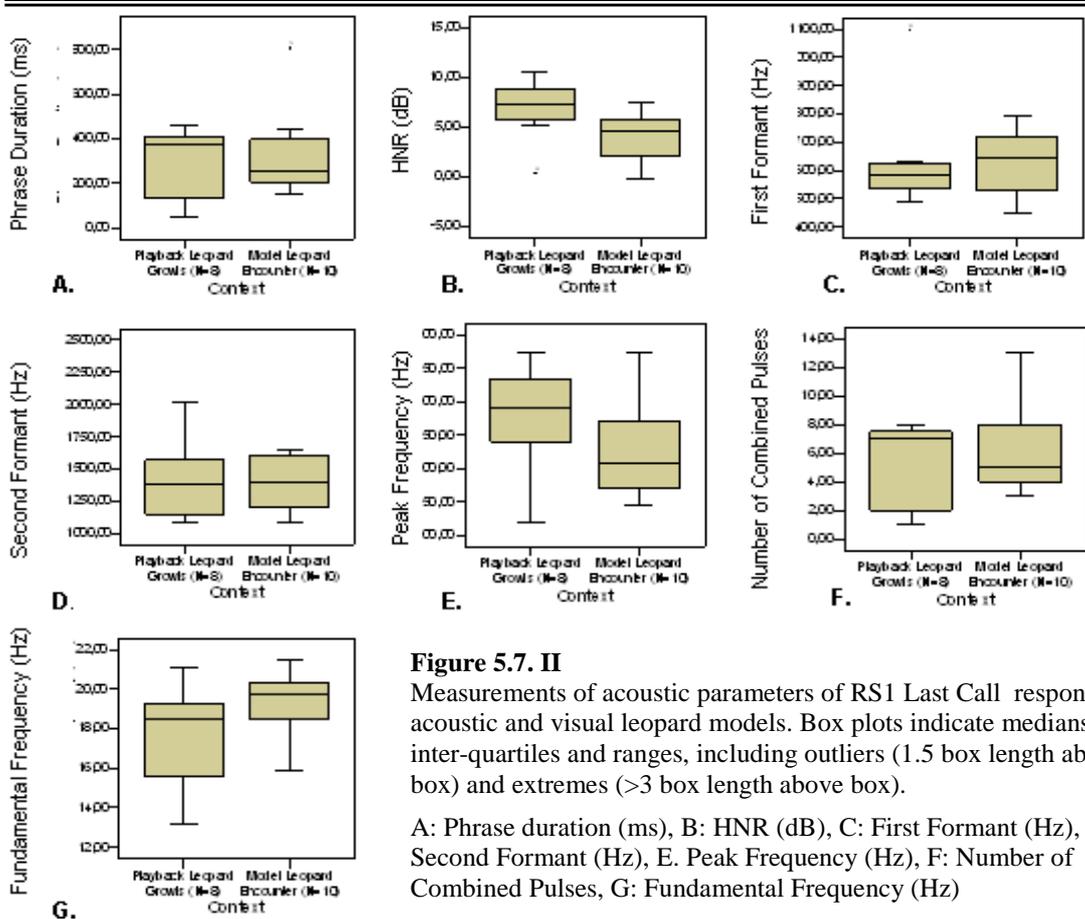
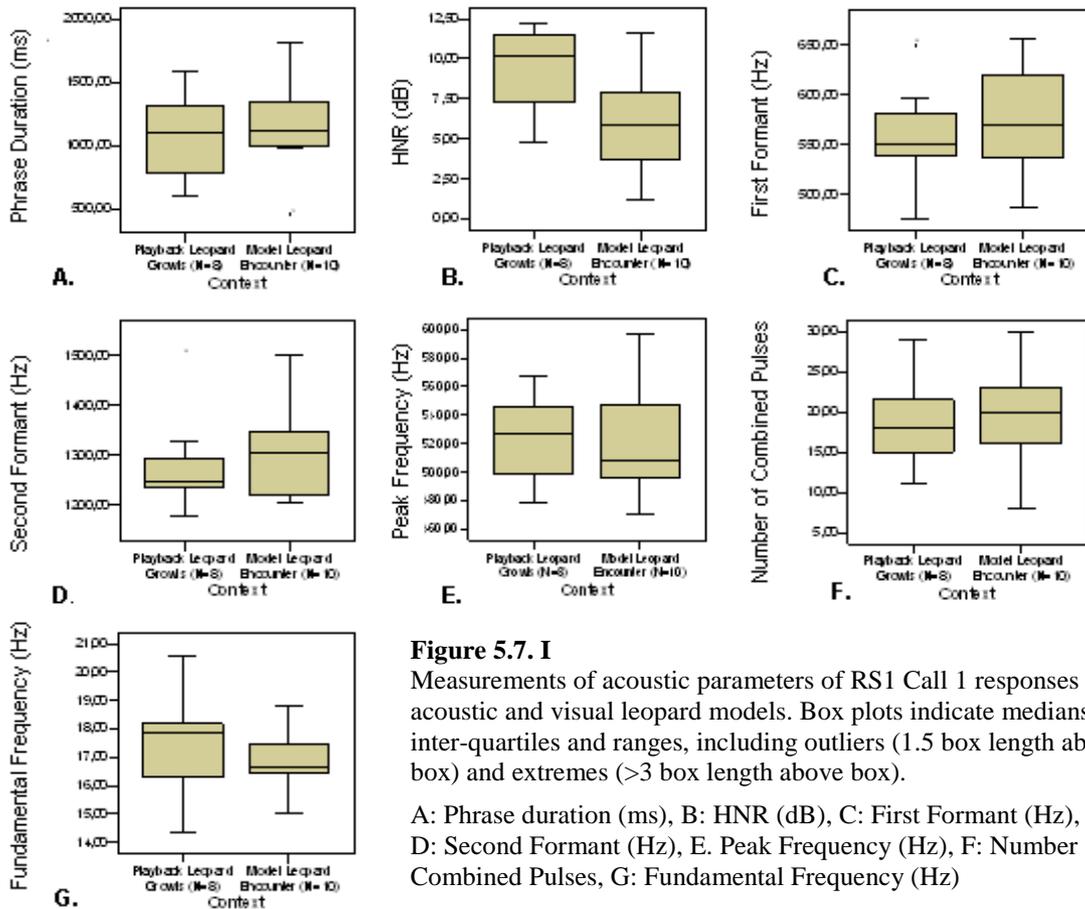
**Figure 5.6.** Vocal response rates compared between different predator modalities: acoustic and visual leopard and chimpanzee models. n.s.: no significant difference between contexts; \*, \*\*, \*\*\*: difference in vocal response rates between contexts, \*  $p < .05$ , \*\*  $p < .01$ , \*\*\*  $p = .000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

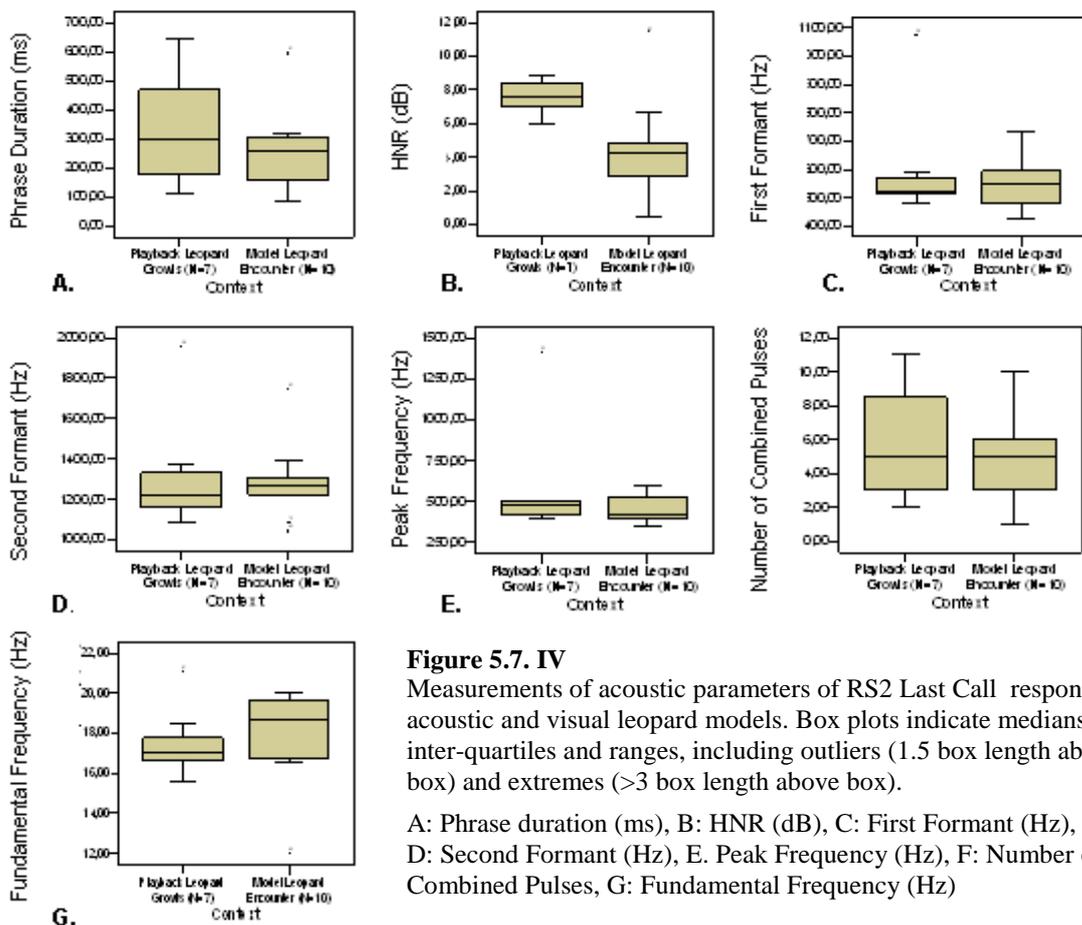
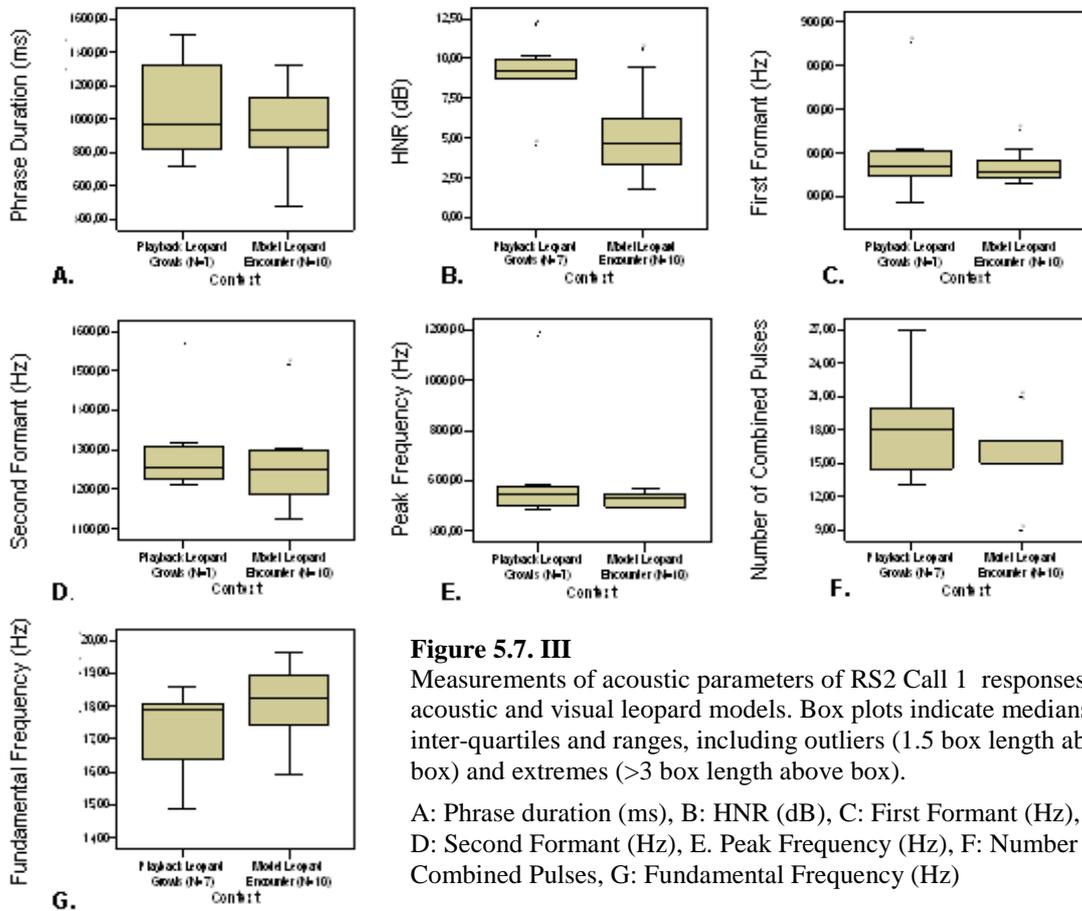
### ***Acoustic measurements***

Acoustic comparisons were only possible for leopard trials. For this purpose, data presented in Table 4.2 (acoustic leopard models) were compared with responses to visual leopard models (Table 5.2). Table 5.4 and fig 5.7 show results of the Mann Whitney U test. Results showed that callers tended to produce calls with higher HNR's to acoustic models than to visual models, i.e. calls to acoustic leopard models were less noisy than the calls to visual leopard models (Mann Whitney U test, all  $p$ -values  $< .033$ ; effect sizes ranging from 0.4-0.52). No further differences were found.

**Table 5.4.** Statistical output (exact p-values and effect sizes,  $r$ ) of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced across different predator modalities (acoustic and visual leopard models; Man Whitney U test,  $\alpha=.017$ ).

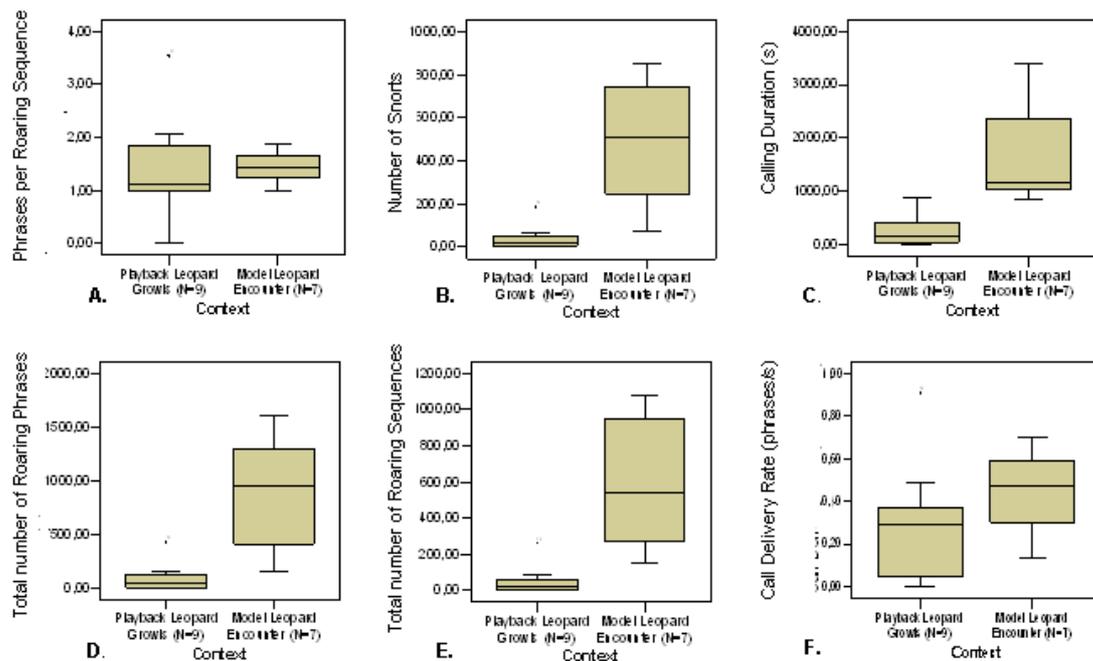
Acoustic variable		Between acoustic and visual Leopard model			
		First Phrase		Last Phrase	
		Exact p	$r$	Exact p	$r$
<b>1<sup>st</sup> RS</b>	Phrase Duration (ms)	0.696	0.10	1.000	0
	HNR (dB)	0.032	0.50	0.027	0.52
	First Formant (Hz)	0.633	0.13	0.633	0.13
	Second Formant (Hz)	0.573	0.15	1.000	0
	Peak Frequency (Hz)	0.586	0.14	0.164	0.34
	Number of pulses	0.467	0.18	0.812	0.06
	Fundamental Freq (Hz)	0.203	0.31	0.096	0.40
<b>2<sup>nd</sup> RS</b>	Phrase Duration (ms)	0.601	0.14	0.601	0.14
	HNR (dB)	0.033	0.40	<b>0.010</b>	0.60
	First Formant (Hz)	0.669	0.12	0.962	0.22
	Second Formant (Hz)	0.601	0.14	0.813	0.07
	Peak Frequency (Hz)	0.705	0.1	0.518	0.17
	Number of pulses	0.791	0.07	0.685	0.11
	Fundamental Freq (Hz)	0.230	0.31	0.376	0.23



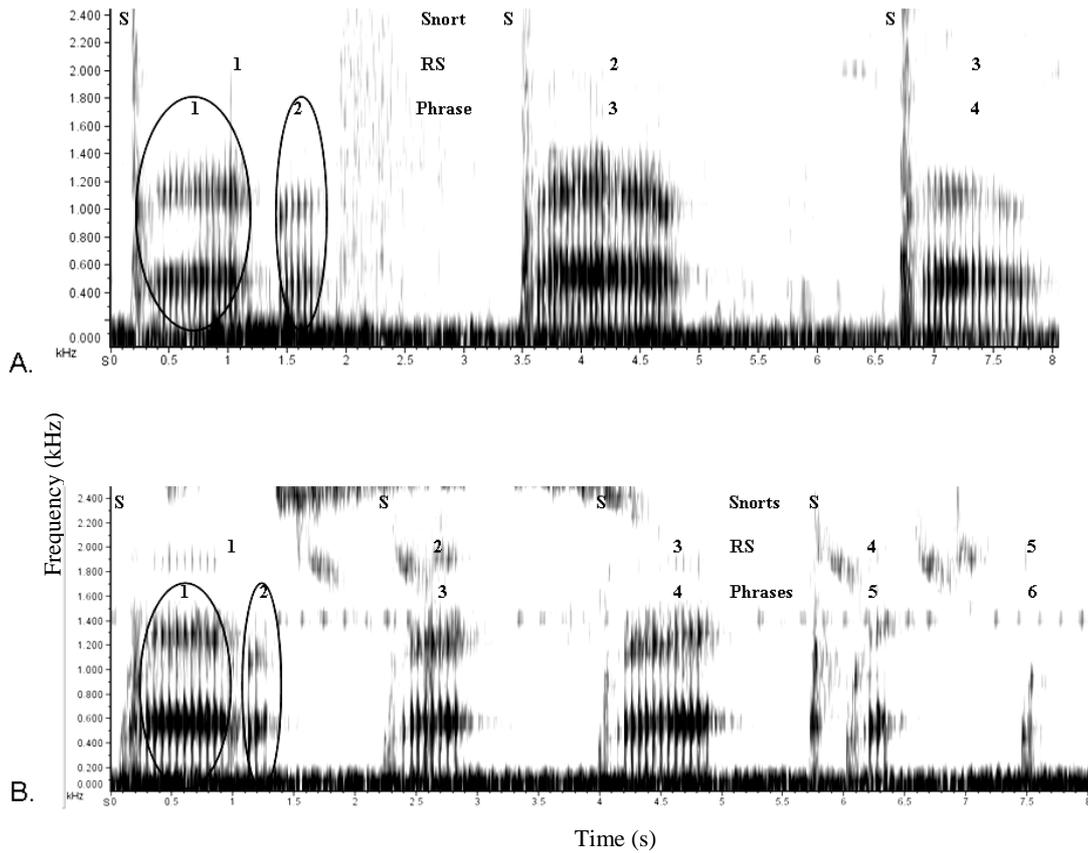


### Composition of Roaring Sequences

When comparing the structural characteristics of the vocalizations given to leopard models, vocal responses were significantly longer in duration to visual than to acoustic models (exact  $p=0.000$ , Mann Whitney U test, two-tailed). Related to this, the total number of phrases, the total number of roaring sequences and the total number of snorts differed significantly between the two contexts as well (all exact  $p$  values  $< .001$ , Mann Whitney U test, two-tailed). All responses to the leopard models were accompanied by snorts (visual model: 7 of 7; acoustic model: 9 of 9; Fisher's exact test: 1.000). No differences were found in the number of phrases per roaring sequence (exact  $p=0.733$ , Mann Whitney U test, two-tailed) and in call delivery rates (exact  $p=0.202$ , Mann Whitney U test, two-tailed, Fig. 5.8 and 5.9; Table 5.5).



**Figure 5.8.** Measurements of temporal response characteristics to visual and acoustic leopard models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes ( $>3$  box length above box). A: Number of phrases/ RS, B: Number of snorts, C: Calling duration (s), D: Total number of phrases, E: Total number of RS (Hz), F: Call delivery rate (phrases/s).



**Figure 5.9.** 8 Seconds continuous recording of a male producing (A.) three Roaring Sequences consisting of one snort-introduced 2-phrase RS, followed by two snort-introduced 1-phrase RS, to an acoustic leopard model, and (B) five Roaring Sequences consisting of one snort-introduced 2-phrase RS, followed by 3 snort-introduced one-phrase sequences and one single phrase to a visual leopard model. Encircled are the first and the last phrases that are produced in the first RS. The x-axis represents time in seconds, the y-axis frequency in kHz.

**Table 5.5.** Temporal measurements of vocal response characteristics to acoustic and visual leopard models. Mdn= median value, M= mean value and CI= 99% confidence interval. Statistical output (exact p-values and effect sizes, *r*) of the Mann Whitney U Test to compare measurements across contexts are presented as well ( $\alpha=.017$ ).

Leopard model type	Calling Duration (s)			Total Number RS			Total Number Phrases			Phrases per RS			Number of Snorts			Call Delivery Rate (Phrases/s)		
	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI
Acoustic	149	248.7	-69.8 - 567.1	19	53.6	-38.7 – 146	39	90.9	-63.4 – 245.4	1.11	1.35	0.13 – 2.58	19	43.8	-21.3 – 109.1	0.29	0.28	-0.04 - 0.61
Visual	1171	1737.9	221.6 - 3254.1	541	601	54 – 1148.6	952	874.6	75.8 – 1673.2	1.44	1.44	0.97 – 191	507	488.3	49.8 – 926.7	0.47	0.44	0.15 – 0.73
Exact p value	<b>0.000</b>			<b>0.001</b>			<b>0.001</b>			0.733			<b>0.001</b>			0.202		
Effect size ( <i>r</i> )	0.81			0.78			0.75			0.09			0.78			0.33		

## **Summary and discussion**

The first part of this chapter compared the monkeys' responses to visual leopard and chimpanzee models. The locomotor responses were extremely different between contexts, mirroring the different hunting techniques of these two predators. When confronted with a leopard, the monkeys were likely to move closer, whereas they mainly moved upward when confronted with a chimpanzee. Additionally, the monkeys behaved differently in the vocal domain: after detecting a leopard, they vocalized in a high proportion of trials (96%), whereas they typically remained silent to chimpanzees (92%). Acoustic comparisons were not made between the two contexts, due to small sample size.

When comparing the monkeys' responses to acoustic and visual predator models, differences emerged mainly in the leopard context. The animals moved more strongly in response to visual than acoustic models and produced vocalizations in a higher proportion of trials. No other differences were found. For the chimpanzees, modality of detection had no measurable effect: the monkeys behaved similar to both the acoustic and visual presence, i.e. they went up in the tree and remained silent.

When comparing the spectral characteristics of calls given to the different leopard models, only the HNR tended to differ. Even though differences were statistically significant in only 1 of the 4 measured phrases (after Bonferroni correction), similar trends were found in the other three phrases. Why callers produced noisier and longer roars to visual than acoustic models is not clear, but it is important to point out that the overall vocal response, in terms of how it was structured into sequences, was identical between both contexts.

### ***Predator hunting techniques and perception advertisement***

Results demonstrated that the monkeys recognized the two predator types visually and responded adaptively to their presence by taking into account their hunting techniques. To leopards, Guerezas made use of active detection advertisement, whereas to chimpanzees this strategy is not useful. Monkeys approached the leopard model in a high proportion of trials, simultaneously calling and following it until it had left the area. Direct visual contact appears to be important so that the predator can be

monitored, which decreases the monkeys' vulnerability, especially if they are at a safe height. This is different in the case of chimpanzees that can easily climb into a tree and catch a monkey. When detecting a silent chimpanzee but also when hearing chimpanzee vocalizations, the monkeys consistently and silently moved high up, possibly trying to hide. Calling to chimpanzees does occur sometimes, but appears to be restricted to cases when the monkeys are actually hunted and hiding is no longer an adaptive strategy. Impressive roaring accompanied by active fighting may then serve as a last resort strategy to escape from these predators. This was illustrated by a number of hunts that could be directly observed: in these cases, adult Guerezas actively fought the chimpanzees while producing their impressive roars (Cat Hobaiter, Zinta Zommers, L. Bates, Z. Machanda; personal communication, personal observation). In one case, a monkey lying injured on the forest floor, surrounded by a group of chimpanzees, still roared in an attempt to fight and escape.

### ***Calling effort as an indicator of stress***

One striking observation was that roaring responses could sometimes go on for a very long time, especially after detection of a visual leopard model. To what extent differences in calling effort are the direct result of differences in perceived threat is controversial. A study on captive marmosets found that producing alarm calls effectively lowers cortisol levels, a general direct measure of stress (Cross & Rogers, 2006; Clara et al., 2008). Other researchers have argued that calling effort is a consequence of arousal (e.g. Rendall, 2003). Whatever causal connection is more appropriate, higher calling rates appear to be linked with higher arousal. In the playback experiments conducted with the Guerezas, eagle shrieks tended to produce the highest calling effort, in terms of number of phrases in the first 30 seconds ( $19.1 \pm 9.4$  roaring phrases), followed by visual and acoustic leopard models ( $9.4 \pm 8.4$  and  $9.3 \pm 8.2$  roaring phrases, respectively). If the number of phrases per time is a reliable indicator of stress, then these results indicate that the monkeys are most affected when encountering an eagle, and less affected when encountering a chimpanzee or leopard, either visually or acoustically. If, however, the total number of calls produced was taken as an indicator of stress, then a different pattern emerged: the animals produced most roars to the visual leopard model, followed by an intermediate number produced to acoustic leopard models, followed by the smallest number of phrases to eagles,

indicating that eagles are the least arousing. Finally, if the call rate (phrases/s) was taken as a measure of affect, then all three predators appeared as equally stressful.

Of course, comparing responses to visual and acoustic predator models is problematic here. First of all, the visual stimuli are usually present for a much longer time period. Typically, the experimenter moved towards a group and stayed there for about 15 to 20 minutes, before moving back to the observers' hiding place. Often (in 53% of the trails [9/17]), the caller followed the model on its way back and only stopped calling after having lost track of it. Sometimes, the monkey kept on calling for more than an hour after the model disappeared. Hence, if calling duration is to be taken as a measure of affect, exposure time of visual and acoustic models needs to be standardised to allow a proper comparison. Secondly, different cognitive mechanisms may be at work when predators are encountered visually or acoustically, which may influence the monkeys' responses. Based on these points, it is thus proposed that arousal is best studied within predator type and within experimental modality (e.g. far visual leopard vs close visual leopard or far acoustic leopard vs close acoustic leopard).

One additional temporal vocal characteristic that probably could indicate something about the affective state of the caller is the intercall duration. A short intercall duration has been linked to high-arousal situations (Rendall, 2003). This parameter was not measured in the present study because of the specific (and restrictive) acoustical measurements taken in this study. It could be interesting to measure this in future studies on the Guerezas' alarm calling system. However, for Guerezas it probably would make more sense to look at the duration between roaring sequences instead of between separate roaring phrases.

The fact that visual leopard models generated noisier calls (in terms of HNR measures) is in line with the more general hypothesis that increased turbulence during phonation, a-periodic vocal fold vibration, and pitch perturbations (e.g. Ferrand, 2002; Shama et al., 2007) may be linked to an animals' motivational state (Fichtel et al., 2001; Riede et al., 2001; Rendall, 2003). In the previous chapter, more noisy roars were found in responses to eagles (consisting of roaring sequences containing many phrases). In the present study, the monkeys produced sequences that were structurally equal in both the visual and acoustic leopard contexts (short roaring sequences), but a higher noise level

was present in phrases produced to the visual leopard model. Thus, based on these findings, the first hypothesis posed in chapter 4 (HNR is influenced by the structure of roaring sequences) can be, once more, rejected. Another hypothesis offered in chapter 4 to explain the production of noisy calls concerned the locatability of the vocalizations by different predators in relation to their hunting techniques (Rundus et al., 2007). This hypothesis can also be rejected because the HNR should have been the same to both visual and acoustic leopard models. Hence, differences in HNR may be best explained in terms of differences in affective state of the callers, suggesting that detecting a silent visual leopard model causes higher levels of arousal in the monkeys than when hearing its vocalizations.

### ***Referential labelling***

Do these differences in HNR contain any communicative value, especially over long distances? As discussed, differences in the HNR could be interpreted as a mere by-product of the animals' arousal, indicating that this may not be an evolved feature of Guereza communication, especially also because it is unlikely to transmit over longer distances.

In sum, visual predator models seem to be perceived as more affective than acoustic predator models, as indicated by some indirect measures linked to affect. The overall composition of roaring sequences does not differ in situations supposedly modelling different affective situations within predator contexts, indicating that structural composition of roaring sequences seems only influenced by predator type and not by arousal. Thus, Guerezas seem able to communicate the type of predator encountered to conspecifics most efficiently by altering the structure of their alarm sequences, and by adding snorts. Affect does not appear to influence structural composition of the predator responses, indicating that these have the potential to function in reliable conspecific warning. To what extent this behaviour qualifies as referential signalling will be addressed in chapter 7.

## Chapter 6

### **Acoustic and visual predator model experiments in Sonso**

#### **Introduction**

In the previous two chapters, the alarm communication system of *Guereza colobus* monkeys of Kaniyo Pabidi was investigated and described based on experimental presentations of acoustic and visual predator models. One conclusion was that the observed response differences to the different modalities by which the predators were presented might have been caused by differences in affect. For example, the monkeys produced noisier phrases in response to visual than acoustic leopard models, simulated by playbacks, and vocal responses lasted much longer to the former. Furthermore, the monkeys were more likely to approach a visual than acoustic leopard models, while either moving up or down in the tree. No experiments were conducted with visual eagle models, but after playbacks of eagle shrieks, the monkeys often remained seated. If they moved, they approached the stimulus and typically moved down in the tree. The presence of chimpanzees was simulated with both visual and acoustic models, and here the monkeys reliably showed a strong preference to move up in their trees.

No differences were found in the vocal response rates to playbacks of leopard growls or eagle shrieks, in contrast to playbacks of chimpanzee calls, to which the monkeys mainly remained silent. These predator-specific behavioural and vocal responses indicated a perception advertisement function in the case of leopard presence, especially once the predator was visually detected by the monkeys. In response to eagles and chimpanzees, perception advertisement plays little role, although signalling of aggressive intent may be important once these predators are spotted or if there was a chase.

Another relevant finding was that the monkeys produced differently structured roaring sequences to acoustic leopard and eagle models, with sequences consisting of more phrases produced in the eagle context. Individual phrases to acoustic leopard and eagle models did not differ acoustically between the predator contexts in most relevant acoustic parameters, with exception of the HNR.

There were no differences in the organisational structure of sequences given to visual and acoustic leopard models, indicating that the observed differences in temporal structure of the roaring sequences were not caused by differences in perceived danger/affect. The number of phrases per roaring sequence thus could be a reliable indicator for the predator type encountered, functioning simultaneously in conspecific warning and perception advertisement in case of leopard presence. In the other two predator contexts, calling might primarily function in conspecific warning and to advertise aggressive intent to the predators, especially after detection.

### ***Objectives***

The overall aim of this chapter was to investigate the locomotor and vocal responses of the Guereza population at Sonso, where one of the key predators (the leopard) is absent, and to compare the results with those of Kaniyo Pabidi, which still has an intact predator fauna. Acoustic and visual predator model experiments were conducted, similar to those conducted at Kaniyo Pabidi as discussed in the previous chapters. A first analysis concerned the monkeys' responses to acoustic and visual predator models (section 1 and 2). A second analyses then concerned predator-specific comparisons between the two modalities (section 3). A third analysis, finally, focussed on the response differences between Sonso and Kaniyo Pabidi to determine to impact of predator experience on these monkeys' anti-predator behaviour (section 4).

### ***Predator experience***

In Kaniyo Pabidi, all three predators occur and pose a substantial threat to the monkeys. In Sonso, approximately 50km to the southwest, leopards have not been sighted for at least 40 years, whereas eagles occur at high densities, probably higher than at Kaniyo Pabidi. There are good reasons to assume that such differences in predation pressure are reflected in a prey species' anti-predator behaviour. Hauser (1988), for example, showed that the amount of exposure to a particular predator-related stimulus affected the acquisition rate of predator-specific anti-predator behaviour in vervet monkeys. Fichtel & van Schaik (2006) and Fichtel (2008) investigated the usage and comprehension of alarm calls in relation to differences in predator pressures in captive Coquerel sifakas and wild Verreaux sifakas. Under natural circumstances, the two

species are preyed upon by the same predators and produce similar alarm calls to these predators. Results showed that the captive Coquerels displayed weaker behavioural responses to the vocalizations of a relatively unfamiliar predator (e.g. a raptor) than the wild Verreaux sifakas that were familiar with it. Low exposure to this particular predator type appears to have been responsible for the weak association between its calls and its presence. Interestingly, the captive group of Coquerels responded equally strong as the wild Verreaux group to a silhouette of the raptor, confirming that recognition of predator vocalizations appears to be more experience dependent than recognition of physical appearance (cf. Blumstein et al., 2000). Additionally, the authors found a difference in comprehension of some of the conspecific alarm calls by the captive group compared to the wild group. The Coquerels associated alarm call types, used by wild Verreaux's to a range of disturbances, only to the presence of a raptor, probably because this was the predator that they had experienced the most. Of course, firm conclusions are difficult to make here because two different species were compared. Fichtel (2008) replicated the basic findings with a more suitable data set, in which two populations of Coquerel sifakas (one captive and one wild) and two wild populations of Verreaux sifakas were studied. Both populations of either species experienced different predation risks. It was found that Coquerel and Verreaux sifakas produced the same alarm call types in the same contexts, i.e. a specific call for aerial predators, and another call for other strong disturbances, including terrestrial predators. However, the comprehension of these calls differed remarkably between populations, and this could be explained by their different predator experiences. It appeared that both species had come to associate one call type, the growl, with the most relevant predator present in their home range, although the predator's biological class differed between the populations (see Coss, 1999 for a review). A related study by Kavanaugh (1980) showed that vervet monkeys who migrated into a new habitat started to produce a new alarm call type for one predator type that they were already familiar with from their former habitat. This seemed caused by the fact that the predator employed a different hunting technique in the new habitat that introduced different predation risks for the monkeys. The hunting behaviour of a predator, rather than its biological class, thus appears to be more important in shaping the alarm call behaviour of primates (cf. Macedonia & Evans, 1993).

Gradual decrease of a particular predator type, e.g. through its extermination by humans, may thus cause prey species to alter or lose their anti-predator behaviour to their natural predators (Coss, 1999; Yorzinski & Ziegler, 2007). Nevertheless, other studies have shown that, in some species, the basic knowledge of the predator-specific anti-predator behaviour could be rapidly re-acquired and accurately displayed when the prey animals are reconfronted with a predator, even after decades of its absence. This seems especially salient in those cases where prey species still are preyed upon by predator types other than the one that became absent. This so-called ‘multi-predator hypothesis’ introduced by Blumstein (2006) suggested that the presence of any predator is sufficient to maintain (or rapidly re-acquire) anti-predator responses for missing predators (e.g. Blumstein et al., 2000; Gil-da-Costa et al., 2003; Blumstein et al., 2008; Yorzinski & Vehrencamp, 2008). Even if prey animals do not encounter a specific predator anymore, they may still encounter other, similar, predators in their habitat. For example, monkeys previously hunted by leopards may still be vulnerable to predation by other felids that may be similar in body shape, size, eye positioning, or coat pattern. These felids could still elicit alarm vocalizations, that might be very similar or even identical to those produced to leopards (cf. Cheney & Seyfarth, 1990, discussed below; cf. Coss, 1999). Consequently, the appropriate vocal anti-predator response to re-introduced leopards may then readily be re-acquired, especially when visually confronted with this previously important predator (Cheney & Seyfarth, 1990; Evans, 1997; Blumstein et al., 2000; Gil-da-Costa et al., 2003; Blumstein et al., 2008; Yorzinski & Vehrencamp, 2008). An anecdotal observation of an encounter with a non-predatory species in Sonso illustrates the point (Monday Gideon, field assistant, personal communication):

*“It was a genet cat which is black and white in colour, the monkeys were calling [short sequences and snorts] and jumping from tree to tree through the branches while seeing or looking down to the ground. So what I did was that I looked exactly to where they were looking and saw something moving having a black and white colour exactly like that of a leopard. So I looked at it keenly and I realised it was a genet cat. This was in block a 4, southern part of the grid system.”*

Genet cats are indeed often described as ‘rat-like leopards’ (Kingdon, 2003), probably because several species have a blotched coat similar to that of a leopard. This simple

coat resemblance may have triggered the monkeys to start alarm calling to it, without first coming closer to inspect the 'predator'. If they had approached first, they probably would have identified the genet as a non-serious threat, and might not have started calling.

Moreover, predators might be more rapidly recognized by their physical appearance than by their vocalizations. Thus, when hearing potentially threatening calls, animals may first need to examine the source more closely before recognizing the sounds as given by a predator and engaging in energy consuming anti-predator behaviour (Lima & Dill, 1990).

The previous paragraphs suggest that monkeys are likely to respond to specific predator classes rather than particular predators, especially if they are not encountered very frequently. In fact, much of the current literature on functionally referential alarm calls in primates has acknowledged this fact. For example, in the studies on vervet monkeys, the term 'leopard alarm call' was used to refer to the majority of the cases in which this call was produced (i.e. in the presence of a leopard), although the animals produced the same call in the presence of some other felids, such as caracals and servals (Cheney & Seyfarth, 1990). Likewise, ringtailed lemurs were found to produce the same alarm call to several hawk species (Macedonia & Yount, 1991), and Guerezas have been observed to produce similar alarm sequences to crowned eagles and harrier hawks (personal observation).

An interesting situation arises when the same prey species lives in adjacent areas while experiencing different predation pressures. Genetic explanations will carry little weight in such situations and behavioural differences are more likely the result of differences in experience. Comparing the predator responses of monkeys in Sonso with those of Kaniyo Pabidi provides an opportunity to test the ideas discussed in the previous paragraphs. Although predator abundance might never have been completely equal between these two sites, the monkeys must have been subjected to the same predators over much of their evolutionary past. The fact that leopards in Sonso became locally extinct due to human interference, might have led to a higher eagle abundance because of the gap left by the leopards. Yet, it seems safe to assume that predation pressures exerted by these two predators were more or less equal until about 40-60 years ago,

when human interference became increasingly more important in the Sonso area. Interestingly, according to some studies, a time period of around 50 years is already long enough for animals, including primates, to ‘lose’ their specific anti-predator responses (e.g. Yorzinski & Ziegler, 2007; Blumstein et al., 2008).

### **Part 1. Acoustic model experiments**

The aim of this section was to describe the responses of monkeys at Sonso to acoustic models of the three main predators of Guerezas: leopards, eagles, and chimpanzees. As described before (p. 50), leopards are absent in Sonso, but eagles and chimpanzees occur regularly.

#### ***Hypotheses and predictions***

The hypothesis tested in this study was that the Guerezas at Sonso had retained their ability to recognize the vocalisations of their predators, including leopards. If correct, the responses to predators should be in line with their hunting techniques, and differ from those to control stimuli with novel non-predatory sounds (Appendix A). An alternative hypothesis was that the Guerezas recognized the vocalizations of chimpanzees and eagles, but not leopards. If correct, the playback experiments should elicit adaptive behavioural responses to eagles and chimpanzees, but not leopards. A last prediction was that the monkeys produced distinct vocal responses to the different predator types.

#### **Methods**

The general characteristics of the study site are described in chapter 2, as are the general methods used for the playback experiments. Playback experiments were conducted in Sonso, where eagles and chimpanzees are common natural predators to the Guereza colobus monkeys, while leopards are absent.

#### **Results**

##### **Leopard, eagle, and chimpanzee playback trials**

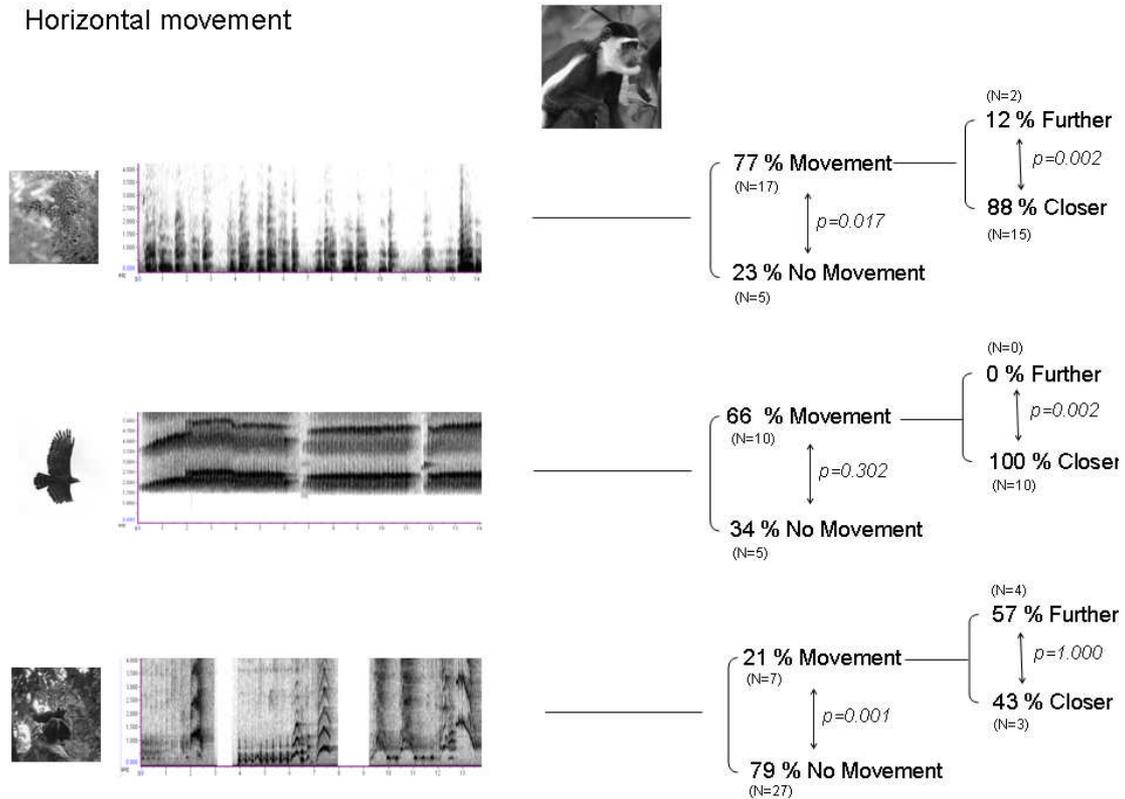
In 2005, 28 different colobus groups were tested with playbacks of leopard growls, 19 different groups with playbacks of eagle shrieks, and 23 different groups with

playbacks of chimpanzee pant hoots. In 2006, an additional 14 groups were tested with chimpanzee pant hoots. One eagle trial was discounted as invalid because it was conducted too close to a previous experiment, one eagle trial was discounted as invalid because the monkeys saw the equipment or the observer, two leopard trials were discounted as invalid because there appeared to be chimpanzees in the area, and one chimpanzee trial was discounted as invalid because of equipment malfunctioning. Sample sizes thus were as follows:  $N_{\text{Leopard}}=26$ ,  $N_{\text{Eagle}}=17$ , and  $N_{\text{Chimpanzee}}=36$ .

### **Behavioural response characteristics**

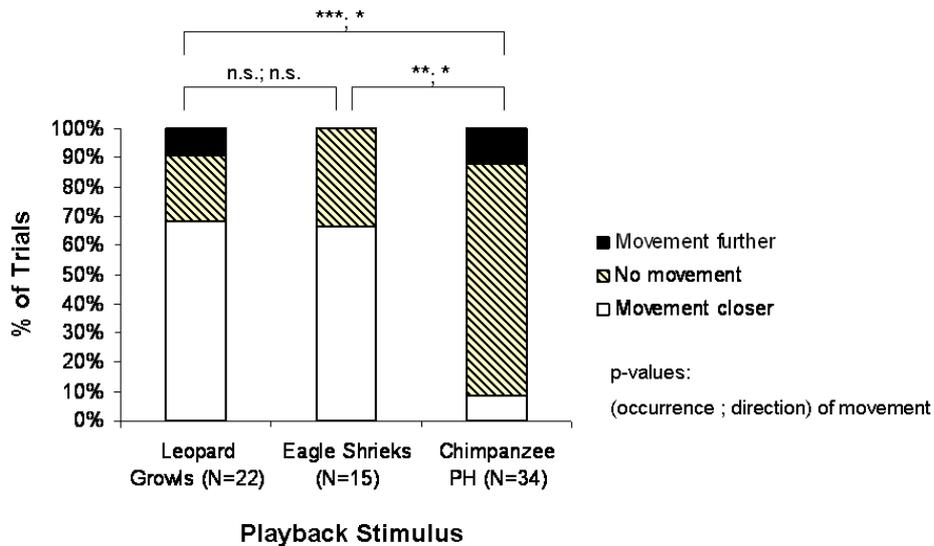
No systematic data concerning the monkeys' movements in the vertical plane were collected in 2005 and 2006. In four leopard trials, two eagle trials and two chimpanzee trials it was not possible to observe the animals. This led to a dataset of  $N_{\text{Leopard}}=22$ ,  $N_{\text{Eagle}}=15$ , and  $N_{\text{Chimpanzee}}=34$  to describe the monkeys' movements in the horizontal plane.

Binomial tests showed that upon hearing leopard growls, the animals were more likely to move than to stay seated ( $N_{\text{Move}}=17$ ;  $N_{\text{Not Move}}=5$ , exact  $p=0.017$ ). If movement occurred they were more likely to move closer than further ( $N_{\text{Further}}=2$   $N_{\text{Closer}}=15$ ; exact  $p=0.002$ , Binomial test,  $\alpha=0.05$ , Fig. 6.1). Upon hearing eagle shrieks, there was no difference between movement and staying seated ( $N_{\text{Move}}=10$ ;  $N_{\text{Not Move}}=5$ , exact  $p=0.302$ ), but if the monkeys moved, they were more likely to approach the simulated eagle ( $N_{\text{Further}}=0$ ;  $N_{\text{Closer}}=10$ , exact  $p=0.002$ , Binomial test,  $\alpha=0.05$ , Fig. 6.1). Upon hearing chimpanzee pant hoots, the monkeys were more likely to stay seated than to move ( $N_{\text{Move}}=7$ ;  $N_{\text{Not Move}}=27$ , exact  $p=0.001$ ). If they moved they were equally likely to move 'further' or 'closer' ( $N_{\text{Further}}=4$ ;  $N_{\text{Closer}}=3$ , exact  $p=1.000$ ; binomial test,  $\alpha=0.05$ , Fig. 6.1).



**Figure 6.1.** Monkeys' locomotor behaviour in the horizontal plane in response to the acoustic predator models, with corresponding percentages of movements and exact p-values of the differences between locomotor responses within predator contexts (Binomial tests,  $\alpha=0.05$ , two-tailed).

Across predator contexts, monkeys were equally likely to move in response to leopards and eagles, but significantly less likely to move in response to chimpanzees compared to the other two predators (Leopard:  $N_{\text{Move}}=17$ ,  $N_{\text{NotMove}}=5$ , Eagle:  $N_{\text{Move}}=10$ ,  $N_{\text{NotMove}}=5$ ; Chimpanzee:  $N_{\text{Move}}=7$ ,  $N_{\text{NotMove}}=27$ : exact p L vs E= 0.708; exact p L vs Ch= 0.000; exact p E vs Ch= 0.003). If they moved, they behaved similarly in the leopard and eagle contexts, i.e. they approached the speaker (Leopard:  $N_{\text{Further}}=2$ ,  $N_{\text{Closer}}=15$ , Eagle:  $N_{\text{Further}}=0$ ,  $N_{\text{Closer}}=10$ , Chimpanzee:  $N_{\text{Further}}=4$ ,  $N_{\text{Closer}}=3$ : exact p L vs E= 0.708). When compared with chimpanzees, they were more likely to move closer in both the eagle and leopard context (exact p L vs Ch= 0.000; exact p E vs Ch= 0.003; Fig. 6.2).

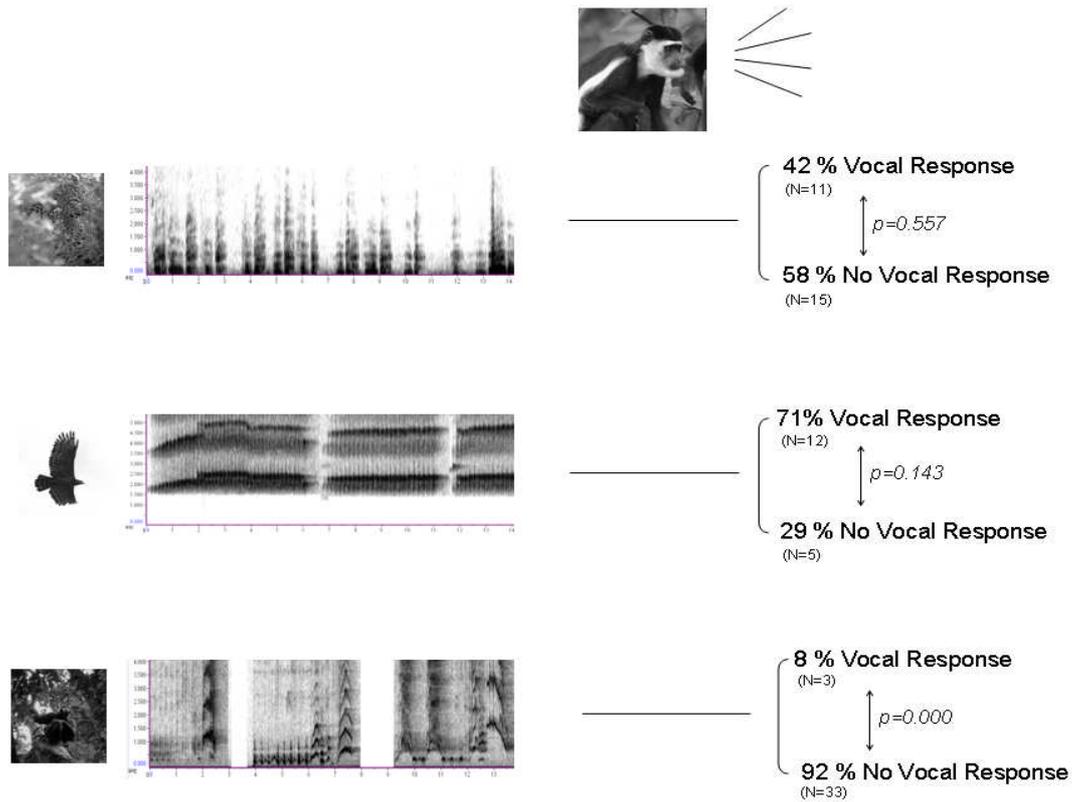


**Figure 6.2.** Locomotor responses in the horizontal plane to the three different acoustic models. The first set of asterisks refers to the difference in occurrence of movement between the contexts; the second set to the difference in direction of movements between the contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < .05$ , \*\*  $p < .01$ , \*\*\*  $p = .000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

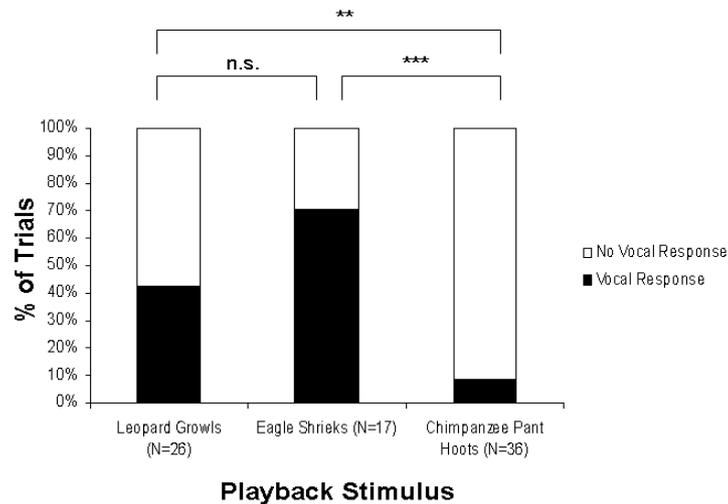
### Vocal response rates and response characteristics

The monkeys' vocal response rate to the chimpanzee playback stimuli was very low: in 3 of 36 trials did the monkeys respond with alarm calls (response rate = 8.3%;  $N_{VR} = 3$ ,  $N_{NoVR} = 33$ ; exact p-value = 0.000). In contrast, 12 of 17 trials with eagle shrieks triggered a vocal response (response rate = 70.6%;  $N_{VR} = 12$ ,  $N_{NoVR} = 5$ ; exact p-value = 0.143), whereas the response rate to leopard growls was intermediate: in 11 of 26 trials did the monkeys respond with vocalizations (response rate = 42.3%;  $N_{Vocal Response (VR)} = 11$ ,  $N_{NoVR} = 15$ ; exact p-value = 0.557; Binomial test,  $\alpha = 0.05$ , Fig. 6.3).

Across conditions, response rates to leopard growls and eagle shrieks were similar (Leopards 42%, Eagle 71%, exact p: 0.118, Fisher's Exact Test, two-tailed). However, compared to the responses to the acoustic leopard and eagle models, the monkeys responded significantly less to the acoustic chimpanzee model (Chimpanzees 8%, Ch vs L: exact p-value = 0.002; Ch vs E: exact p-value = 0.000, Fig. 6.4).



**Figure 6.3.** Vocal response rates of the monkeys to the three different acoustic predator models, with corresponding exact p-values within contexts (Binomial test,  $\alpha=0.05$ ).



**Figure 6.4.** Vocal response rates to the three different acoustic models, with exact p-values. n.s.: no significant difference between the contexts; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in vocal response rates between the contexts, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p = 0.000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

**Acoustic measurements of vocal responses**

Two vocal responses to leopard growls were excluded due to high levels of background noise or poor recording quality. One response to eagle trials was discarded because of high levels of noise produced by other calling individuals. None of the vocal responses to the chimpanzees was discarded, but due to small sample size (N=3) chimpanzee responses were excluded from this analysis. N=9 responses to leopard growls, and N=11 responses to eagle shrieks were submitted to acoustic analyses. For the spectral measurements, one eagle trial had to be excluded for analyses of the second roaring sequence because the caller produced only one roaring sequence, yielding a final sample size for the second roaring sequences of N=9 for leopard responses and N=10 for eagle responses (Table 6.1).

Acoustic analyses of the first and last roars of the first two roaring sequences were made with PRAAT 4.3.12. Additional analyses were conducted with RAVEN 1.2.

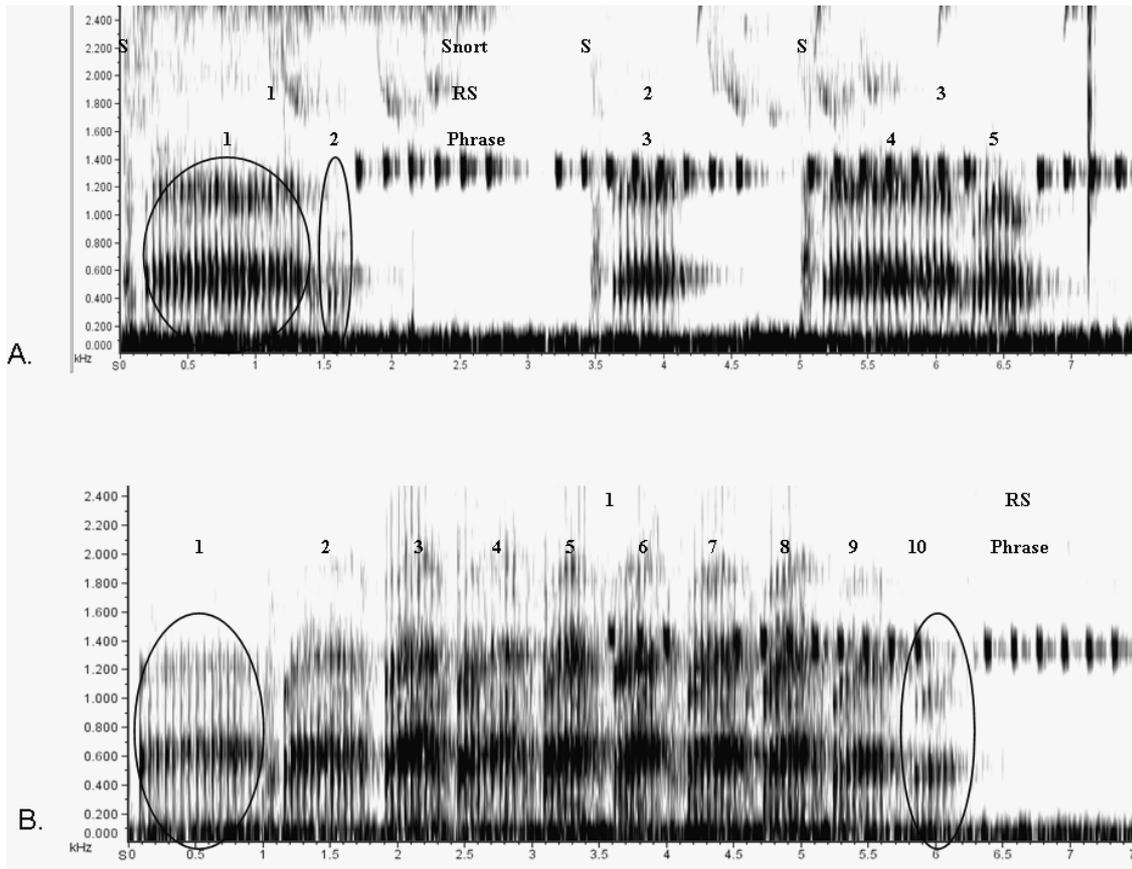
**Table 6.1.** Numbers of trials conducted with the acoustic predator models, vocal response rates and number trials used for subsequent acoustic analyses.

Stimulus type	Nr valid trials	Response Rate		Suitable for Temporal Analyses	Suitable for Spectral Analyses	
		N	%		First RS	Second RS
Leopard growls	26	11	42.3	9	9	9
Eagle shrieks	17	12	70.6	11	11	10
Chimpanzee screams	36	3	8.3	3	2	2

**Acoustic Structure of Individual Roars**

Within the leopard and eagle context, statistical comparisons revealed consistent significant differences between the first and final roaring phrases for both sequences (Fig. 6.5 and Tables 6.2 and 6.3).

When comparing roaring phrases between the two predator types, some differences were found, but there was no consistent pattern (Tables 6.2 and 6.3 and Fig. 6.6).



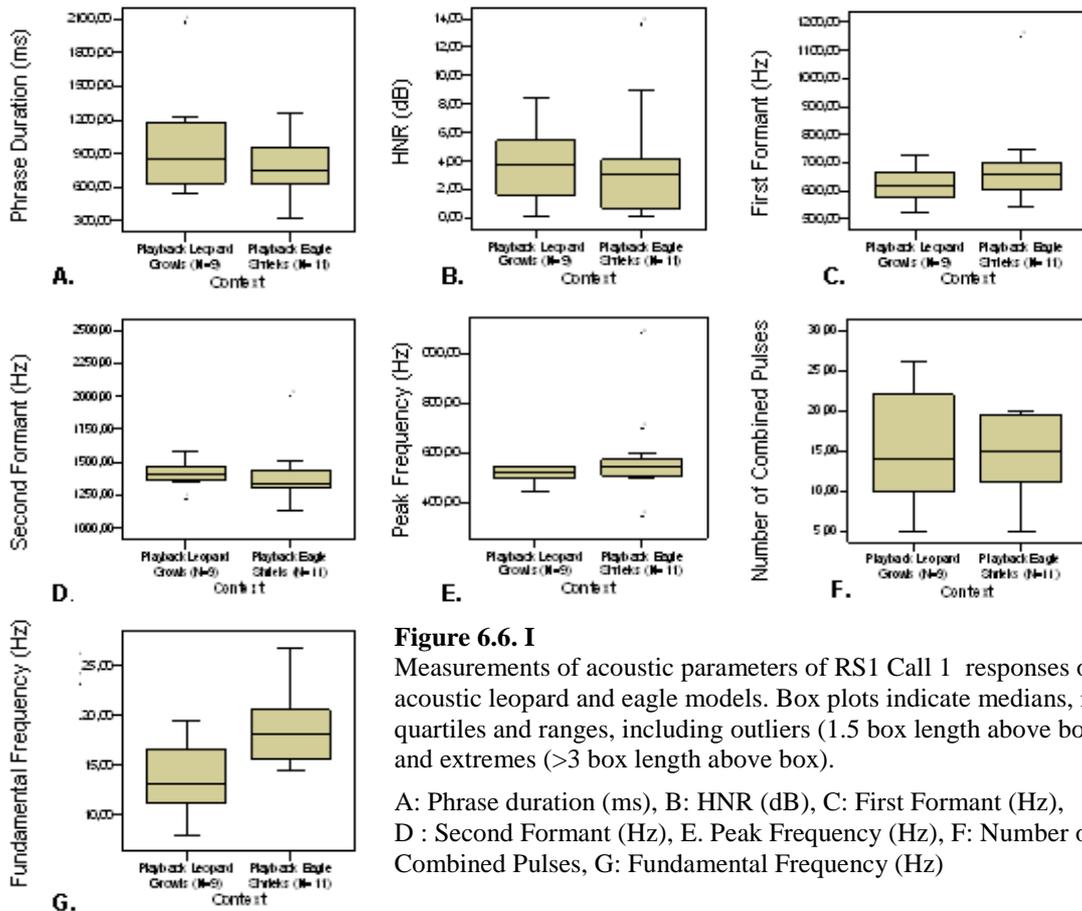
**Figure 6.5.** Illustrating the differences in duration of the First Calls and Last Calls in response to A. an acoustic leopard model, and B. an acoustic eagle model . Visible on the SPG are the separate combined pulses. On the x-axis the time in seconds, on the y-axis the frequency in Hz.

**Table 6.2.** Spectral measurements of first and last phrases produced in the first and second RS of vocal responses to acoustic leopard and eagle models. Mdn= median value, M=mean value, and CI= 99% confidence interval.

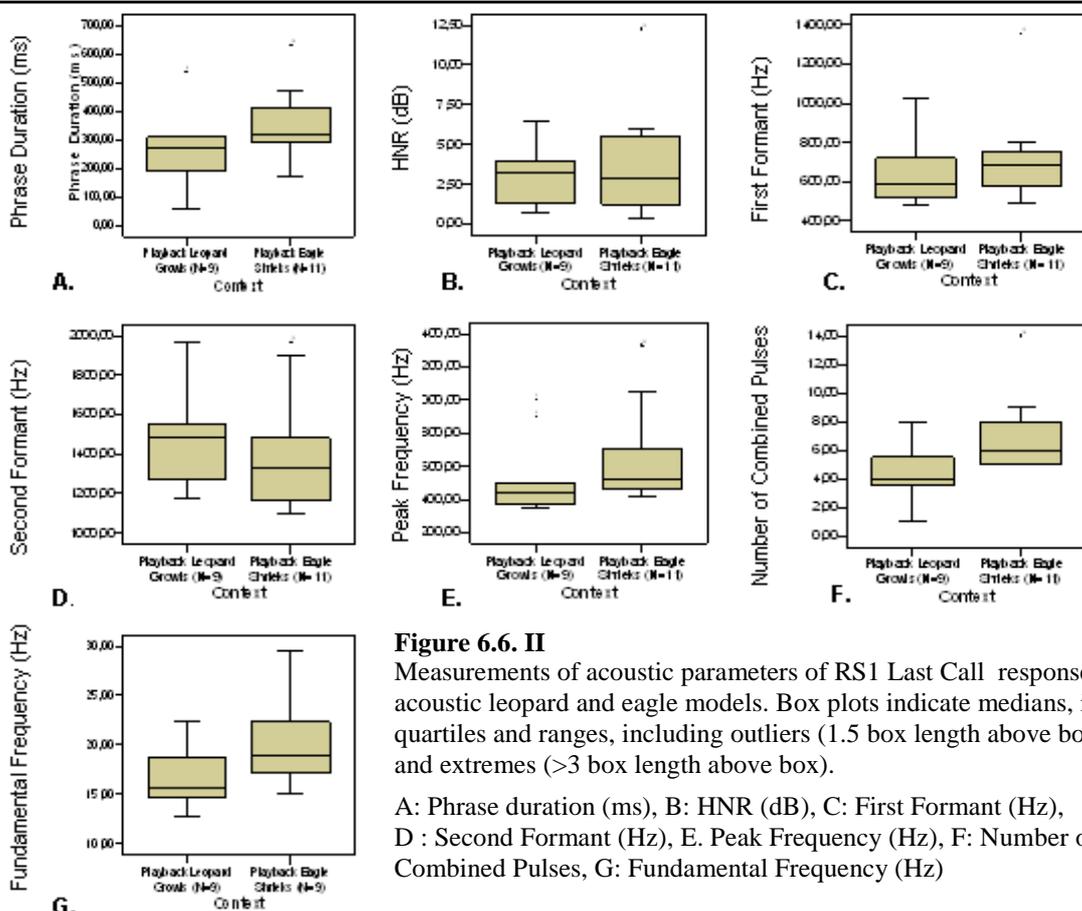
Acoustic variable		Acoustic Leopard Model			Acoustic Eagle Model		
		Mdn	M	CI	Mdn	M	CI
1 <sup>st</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	857	991.1	457.1 – 1515.1	757	788.9	539.1 - 1038.7
	HNR (dB)	3.74	3.75	0.68 – 6.81	3.13	3.85	-0.65 – 8.34
	First Formant (Hz)	621.1	617.2	540.0 – 694.4	658.5	691.2	535.8 - 846.6
	Second Formant (Hz)	1412.2	1411.1	1299.2 – 1523	1337.8	1398.5	1182 – 1615
	Peak Frequency (Hz)	521.6	515.9	479.1 – 552.7	546.8	581.3	404.7 – 757.9
	Number of pulses	14	16	5 – 27	15	15	10 – 20
	Fundamental Freq (Hz)	13	14	8 - 20	18	18	15 - 22
1 <sup>st</sup> RS Last Phrase	Phrase Duration (ms)	271	263.7	115.6 – 411.7	320	357.5	240.3 - 474.6
	HNR (dB)	3.19	3.16	1.01 – 5.31	2.85	3.79	0.15 – 7.43
	First Formant (Hz)	590.3	649.2	450.8 – 847.5	686.3	716.0	492.0 – 940.0
	Second Formant (Hz)	1487.2	1495.7	1199.9 – 1791.5	1327.4	1397.9	1110.5 – 1685.4
	Peak Frequency (Hz)	445.7	535.6	262.9 – 808.3	521.6	647.9	363.4 – 932.5
	Number of pulses	4	4	2 – 7	6	7	4 – 10
	Fundamental Freq (Hz)	16	17	13 - 21	19	20	16 - 24
2 <sup>nd</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	774	839	487.1 – 1190.4	766	790.4	628.9 – 951.9
	HNR (dB)	4.77	3.76	0.82 – 6.70	2.77	3.86	0.38 – 7.35
	First Formant (Hz)	581.4	617.5	496.5 – 738.5	658.3	696.5	552.5 – 840.6
	Second Formant (Hz)	1356.6	1390.6	1162.5 – 1618.7	1422.3	1441	1221.1 – 1659.9
	Peak Frequency (Hz)	521.6	504.7	460 – 549.4	572.1	658.1	443.1 – 873.1
	Number of pulses	13	13	8 – 19	13	13	11 – 16
	Fundamental Freq (Hz)	16	15	12 - 19	18	17	15 - 20
2 <sup>nd</sup> RS Last Phrase	Phrase Duration (ms)	358	370.8	180.1 – 561.4	416.5	396.2	265.4 - 527
	HNR (dB)	1.70	2.67	-1.01 – 6.36	3.7	4.0	0.55 - 7.56
	First Formant (Hz)	733.9	749.9	476.2 – 1023.7	727.1	705.5	587.6 – 823.4
	Second Formant (Hz)	1594	1520	1298.6 – 1831.6	1445.2	1471.6	1241.8 - 1701.5
	Peak Frequency (Hz)	471	546.8	247.3 – 846.4	496.3	574.6	370.3 – 779
	Number of pulses	6	6	3 – 9	8	7	4 - 10
	Fundamental Freq (Hz)	16	15	14 - 17	17	18	15 - 20

**Table 6.3.** Statistical output (exact p-values and effect sizes, *r*) of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced within predator contexts (left hand side of the Table; Wilcoxon Signed Ranks Test,  $\alpha=.017$ ), followed by statistic output of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced across two different predator contexts (acoustic leopard and eagle models; right hand side of the Table; Man Whitney U test,  $\alpha=.017$ ).

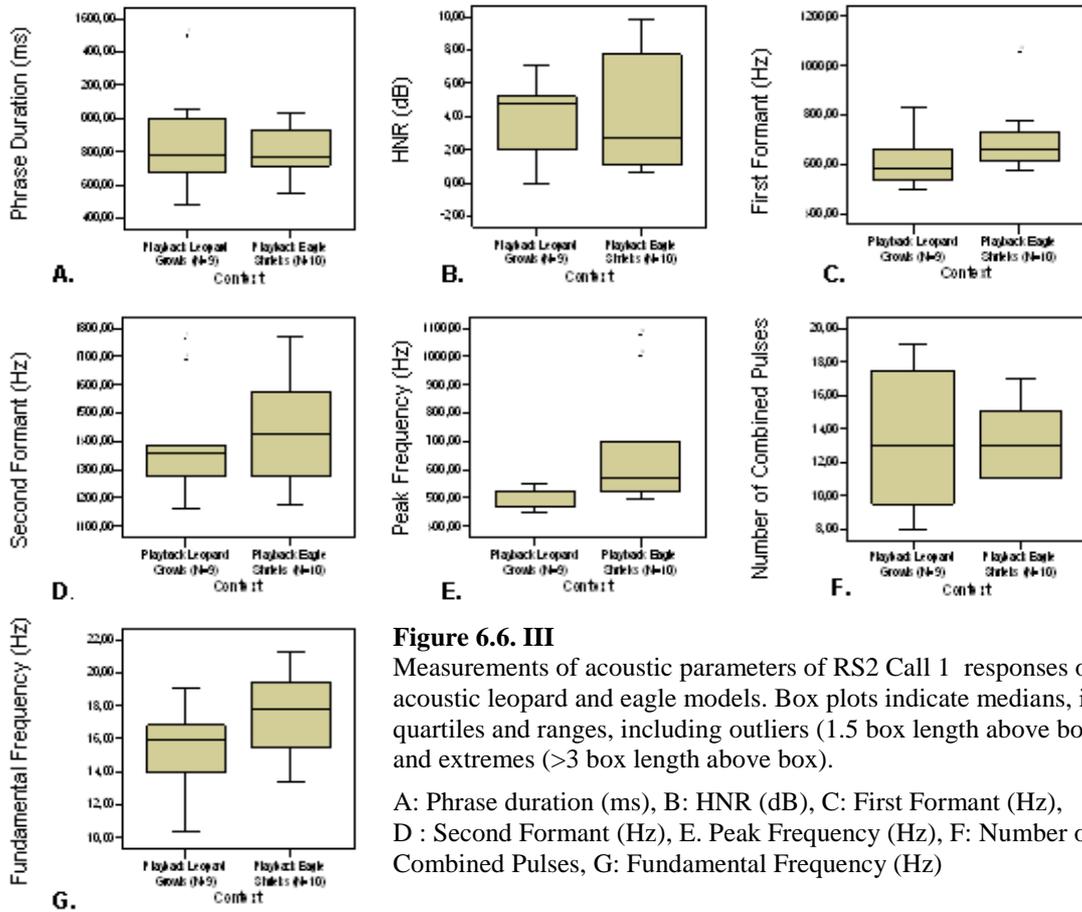
Acoustic variable		Within Leopard (First vs Last phrase)		Within Eagle (First vs Last phrase)		Between Leopard and Eagle			
		Exact p	r	Exact p	r	First Phrase		Last Phrase	
		Exact p	r	Exact p	r	Exact p	r	Exact p	r
<b>1<sup>st</sup> RS</b>	Phrase Duration (ms)	<b>0.004</b>	0.63	<b>0.001</b>	0.63	0.656	0.11	0.067	0.42
	HNR (dB)	0.176	0.34	0.820	0.07	0.645	0.11	1.000	0
	First Formant (Hz)	1.000	0.01	0.465	0.17	0.261	0.26	0.370	0.21
	Second Formant (Hz)	0.359	0.24	0.413	0.19	0.261	0.26	0.370	0.21
	Peak Frequency (Hz)	0.547	0.15	0.969	0.01	0.340	0.23	0.134	0.34
	Number of pulses	<b>0.016</b>	0.61	<b>0.002</b>	0.60	0.706	0.10	<b>0.016</b>	0.54
	Fundamental Freq (Hz)	0.297	0.31	0.320	0.23	0.047	0.47	0.051	0.45
<b>2<sup>nd</sup> RS</b>	Phrase Duration (ms)	<b>0.004</b>	0.63	<b>0.002</b>	0.63	0.968	0.02	0.780	0.08
	HNR (dB)	0.148	0.37	0.383	0.23	1.000	0	0.279	0.29
	First Formant (Hz)	0.203	0.32	0.770	0.08	0.113	0.37	0.720	0.09
	Second Formant (Hz)	0.109	0.41	0.557	0.15	0.497	0.17	0.515	0.17
	Peak Frequency (Hz)	0.438	0.22	0.098	0.38	<b>0.011</b>	0.57	0.388	0.21
	Number of pulses	<b>0.008</b>	0.61	<b>0.004</b>	0.61	0.943	0.02	0.385	0.21
	Fundamental Freq (Hz)	0.484	0.19	0.301	0.26	0.114	0.40	0.053	0.45



**Figure 6.6. I** Measurements of acoustic parameters of RS1 Call 1 responses on acoustic leopard and eagle models. Box plots indicate medians, interquartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).  
 A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



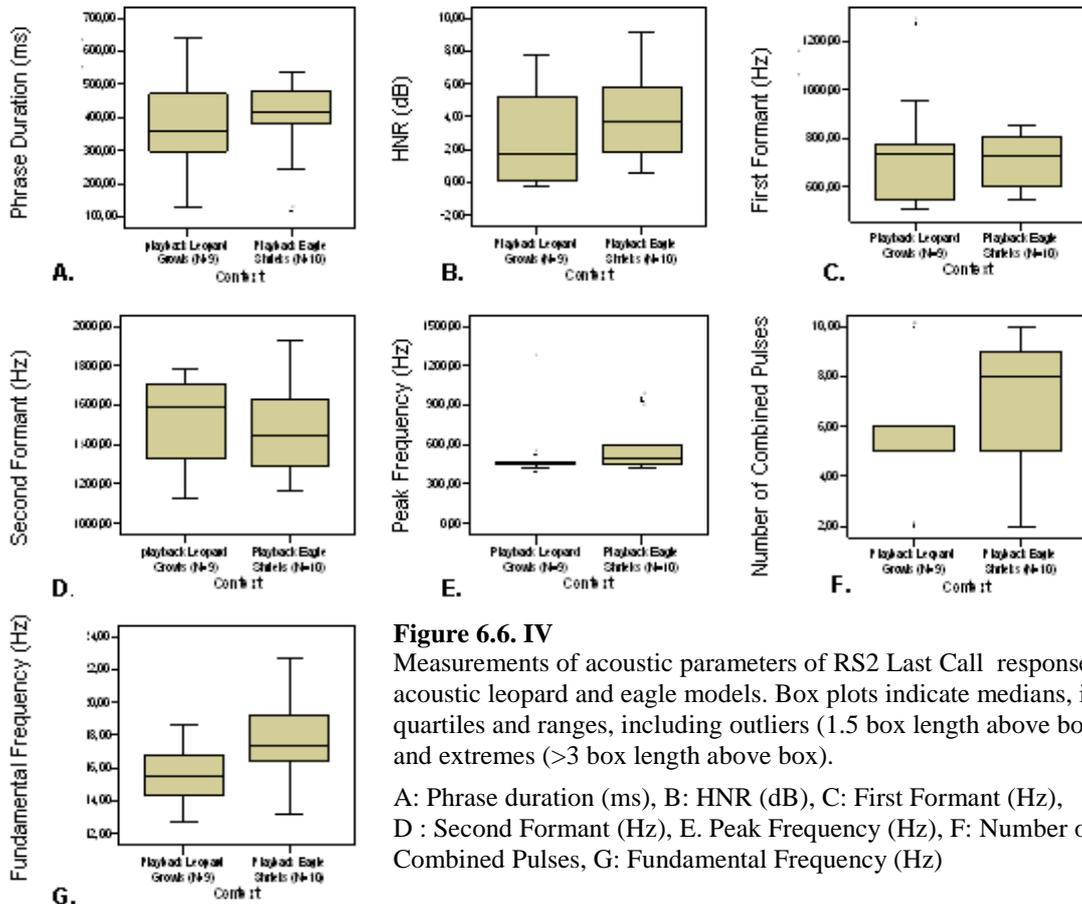
**Figure 6.6. II** Measurements of acoustic parameters of RS1 Last Call responses on acoustic leopard and eagle models. Box plots indicate medians, interquartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).  
 A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



**Figure 6.6. III**

Measurements of acoustic parameters of RS2 Call 1 responses on acoustic leopard and eagle models. Box plots indicate medians, interquartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D: Second Formant (Hz), E: Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



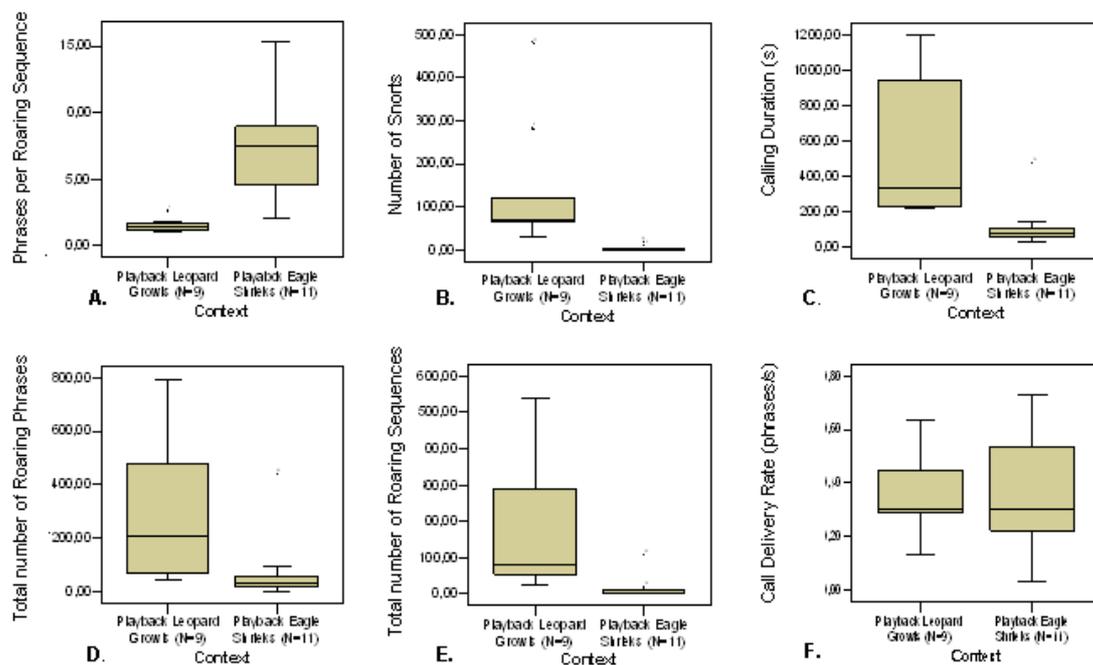
**Figure 6.6. IV**

Measurements of acoustic parameters of RS2 Last Call responses on acoustic leopard and eagle models. Box plots indicate medians, interquartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D: Second Formant (Hz), E: Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)

### Composition of Roaring Sequences

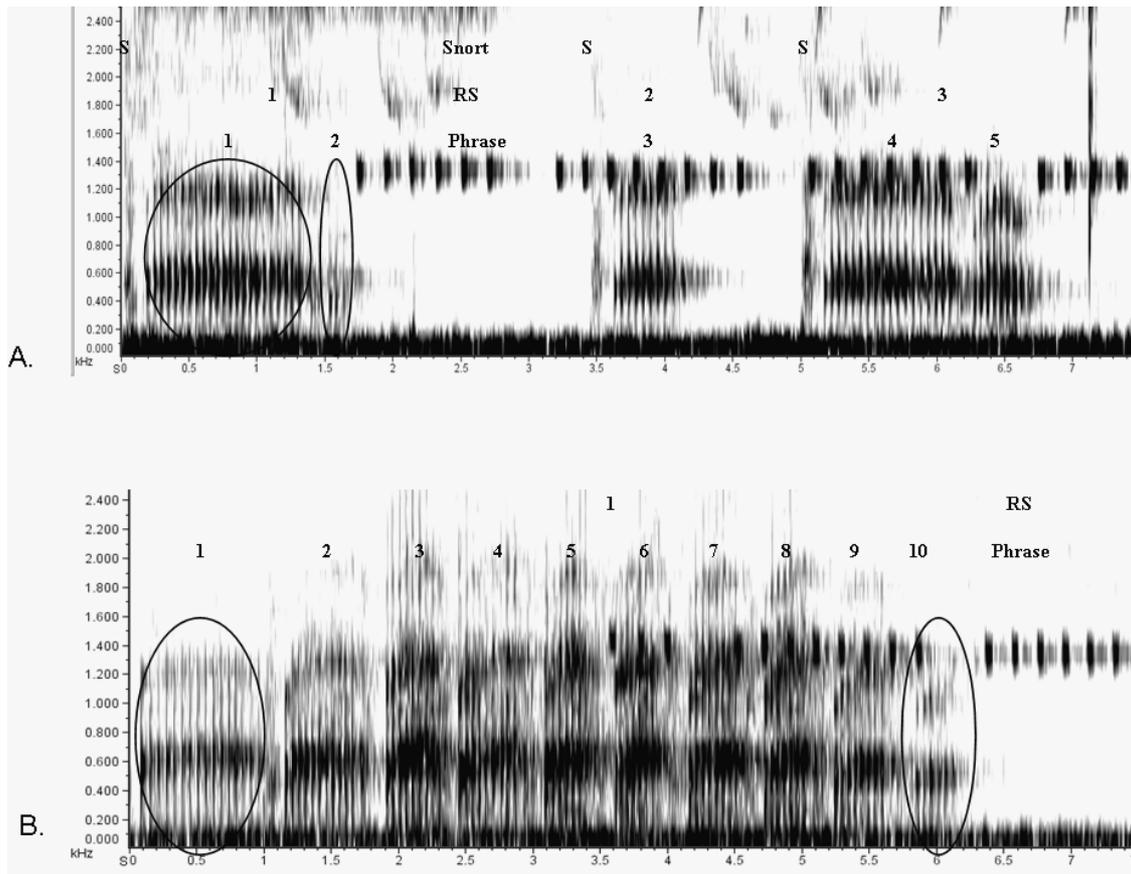
The composition of roaring sequences in response to eagle shrieks and leopard growls differed in a number of ways. Firstly, the number of roaring phrases per sequence was significantly smaller in response to leopard than eagle stimuli ( $U= 1.000$ , exact  $p= 0.000$ ,  $r= 0.82$ , Mann Whitney U test, two-tailed). Secondly, the roaring sequences to leopards, but not eagles, were typically preceded by snorts (9 of 9 leopard trials; 4 of 11 eagle trials, exact  $p= 0.005$ ; Fisher's Exact Test, two-tailed). If snorts were given in both contexts, the monkeys produced a higher number to leopard growls than to eagle shrieks ( $U= 0$ , exact  $p= 0.000$ ,  $r= 0.86$ , Mann-Whitney U test, two-tailed). Thirdly, the monkeys produced longer roars to leopards than to eagles, in terms of the total duration of calling ( $U= 5$ , exact  $p= 0.000$ ,  $r= 0.76$ ; Mann Whitney U-test, two-tailed), the total number of roaring phrases ( $U= 14$ , exact  $p= 0.006$ ,  $r= 0.60$ ; Mann Whitney U-test, two-tailed) and the total number of roaring sequences ( $U= 5$ , exact  $p= 0.000$ ,  $r= 0.76$ ; Mann Whitney U-test, two-tailed). The call delivery rate was similar between the two contexts ( $U= 47$ , exact  $p= 0.882$ ,  $r= 0.04$ ; Mann Whitney U test, two-tailed, Table 6.4 and Fig. 6.7).



**Figure 6.7.** Measurements of temporal response characteristics to acoustic leopard and eagle models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes ( $>3$  box length above box). A: Number of phrases/ RS, B: Number of snorts, C: Calling duration (s), D : Total number of phrases, E. Total number of RS (Hz), F: Call delivery rate (phrases/s).

**Table 6.4.** Temporal measurements of vocal response characteristics to acoustic leopard and eagle models. Mdn= median value, M= mean value and CI = 99% confidence interval. Statistical output (exact p-values and effect sizes,  $r$ ) of the Mann Whitney U Test to compare measurements across contexts are presented as well ( $\alpha=.017$ ).

Stimulus Type	Calling Duration (s)			Total Number RS			Total Number Phrases			Phrases per RS			Number of Snorts			Call Delivery Rate (phrases/s)		
	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI
<b>Leopard Growls</b>	330	595	133.2-1056.8	79	181	-11.2-372.5	210	279	-15.1-573.3	1.47	1.55	1.0-2.1	70	138	-28-304	0.30	0.37	0.18-0.56
<b>Eagle Shrieks</b>	75	116	-1.12-233.8	3	15	-15.3-44.6	32	73	-46.1-192.9	7.5	7.3	3.7-10.9	0	3	-2.58-7.86	0.30	0.36	0.13-0.58
<b>Exact p</b>	<i>0.000</i>			<i>0.000</i>			<i>0.006</i>			<i>0.000</i>			<i>0.000</i>			<i>0.882</i>		
<b>Effect size (r)</b>	0.76			0.76			0.60			0.82			0.86			0.04		



**Figure 6.8.** 8 Seconds continuous recording of a male producing A. three Roaring Sequences consisting of one snort-introduced 2-phrase RS, followed by a snort-introduced 1-phrase RS, followed by a snort-introduced two-phrase sequence to an acoustic leopard model, and B. one Roaring Sequences consisting of 10 phrases to an acoustic eagle model. Encircled are the first and last phrases that are produced in the first RS.

### Summary and discussion

The monkeys' locomotor responses showed that individuals approached the speaker in a high proportion of the leopard trials. Responses to eagle shrieks were more ambiguous, but if the monkeys moved, they usually approached as well. In response to chimpanzees, the animals mainly remained motionless, and in the few trials in which they moved, no clear pattern emerged. Both in the leopard and eagle contexts, the monkeys produced vocalizations in an equal proportion of the trials, which was in about half of all trials. To chimpanzees, they mainly remained silent. In the acoustic analyses of individual phrases given to leopards and eagles, vocalisations showed no consistent differences in spectral parameters. The structural composition of the calling response, however, differed strongly between the leopard and eagle contexts. Monkeys produced roaring sequences consisting of a smaller number of phrases per sequence to

leopards than to eagles, although these were given at the same rates. In response to leopard growls, the monkeys additionally produced roars for a longer period of time and these responses were more often accompanied by snorts.

Thus, the Guerezas at Sonso produced distinct anti-predator responses to the three different predator types, which seemed adaptive to their hunting techniques, despite the fact that these monkeys probably have never encountered a leopard before. The monkeys produced alarm vocalization in 42% of the leopard trials, and calling patterns were different from the ones given to eagles. Of course it is possible that the callers did not recognise this predator as such by its vocalizations, but that they just responded to the novelty of the sound (e.g. Yorzinski & Ziegler, 2007; Blumstein et al., 2008). Alternatively, they may have recognized the leopard, but not perceived it as a major threat (Jenny & Zuberbühler, 2005). The reason for why monkeys remained silent in a high proportion of trials may also be due to a motivation to postpone calling until the predator's physical presence, and therefore the predator type, was inspected and confirmed (e.g. Lima & Dill, 1990; Zuberbühler et al., 1997). The monkeys approached the site of playback in a high proportion of the leopard trials, which confirms that visual confirmation of the predator type is important, and a possible pre-condition to calling.

To investigate if the animals just responded to novelty in the leopard context, a series of control trials was conducted using hyena howls and elephant rumbles (Appendix A). Despite the fact that both control stimuli were acoustically loud, conspicuous and novel to the monkeys, the monkeys did not vocalise at all in response to both control stimuli, in contrast to the leopard stimuli. Furthermore, the monkeys approached leopard growls significantly more often than hyena howls or elephant rumbles.

In conclusion, the Guerezas at Sonso did not just call to leopard growls because of the novelty of the sound, but appeared to interpret these sounds as signs of a specific danger that was different from eagles, chimpanzees, and control stimuli, despite the fact that they had no prior experience with leopards.

As discussed previously, eagles pose a distinct threat to the monkeys due to their hunting style, and the behavioural responses of the monkeys reflect this well: they

either stayed motionless or approached after hearing eagle shrieks, presumably to find and chase it away. Roaring to eagles could be part of aggressive behaviour towards this predator, which would explain why it seems given at higher rates once the monkeys have spotted the eagle (personal observation).

Finally, chimpanzees are able to climb into the trees and capture monkeys at all heights. Perception advertisement and conspecific warning are thus especially risky strategies, and it may be more adaptive to hide and prepare for a potential physical fight if singled out by the chimpanzees. The most adaptive response to chimpanzees, therefore, is to remain cryptic (silent and motionless) until potential detection, which was indeed found in the chimpanzee playback experiments. Nevertheless, in 8% of the trials, at least one individual responded with vocalizations.

As predicted from earlier results (chapter 4), the Guerezas at Sonso produced roaring phrases that were acoustically similar in response to leopards and eagles. However, at the sequence level, roaring differed remarkably and consistently between the two contexts. In response to leopard growls, long alarm responses were produced, containing many roaring sequences composed of few phrases each, whereas in response to eagle shrieks short alarm responses were produced, containing few roaring sequences composed of many phrases. These differences are acoustically salient and sufficiently discriminate the two predators, so that conspecifics can infer the type of predator encountered by the caller (see chapter 7). The response rate to chimpanzees was unfortunately too low to make statements about the acoustic structure of these calls.

To conclude, the Guerezas at Sonso appeared to recognise the vocalizations of eagles and chimpanzees, but they also appeared to have retained the ability to recognise leopard vocalizations as a distinct sign of danger that is different from eagles and chimpanzees.

## **Part 2. Visual model experiments**

Following from the previous results, the question addressed in this section was whether monkeys showed any sign of being able to recognise a leopard as a dangerous predator by its visual appearance. The prediction was that monkeys should be able to do so, also because visual predator recognition has been argued to be less experience-dependent than acoustic predator recognition (Blumstein et al., 2000; Blumstein et al., 2008).

### ***Hypotheses and predictions***

The hypothesis tested with this study was that the Guerezas at Sonso had retained their ability to recognize leopards by their physical appearance, independent of individual experience. If correct, responses to visual leopard models should differ from those to control stimuli with novel visual non-predatory animals (Appendix B), and there should be signs of adaptation to the leopard's hunting technique. The second hypothesis stated that the Guerezas' recognition of predators was based on experience. If correct, monkeys should only exhibit adaptive anti-predator behaviour to chimpanzees, but not leopards.

### **Methods**

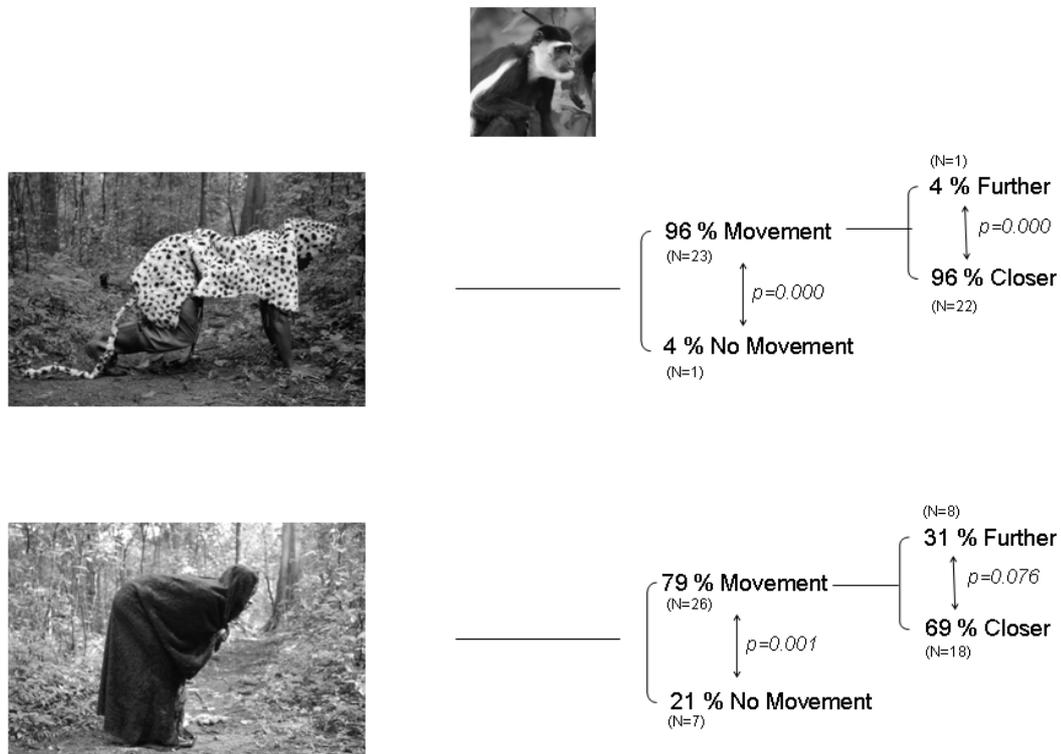
The basic methods of this study and the general characteristics of the study site are described in chapters 2 and 5. All data were collected in Sonso, where chimpanzees occur naturally, but leopards are absent.

### **Results**

In 2005, 11 different Guereza groups were tested with a moving leopard model. In 2006, another 19 groups were tested with the same stimulus, and 34 different groups were tested with a moving chimpanzee model. In the 2006 sample, groups previously exposed to the leopard model were not tested again, using a sampling method described in chapter 2. Of the 30 leopard trials, 6 trials were discounted: one because the monkeys saw the observer during the trial, two because chimpanzees were in the area, and three because of equipment malfunctioning. Of the 34 chimpanzee trials, one trial was discounted because the monkeys saw the observer. The final sample size for the visual model experiments was  $N_{\text{Leopard}} = 24$ , and  $N_{\text{Chimpanzee}} = 33$ .

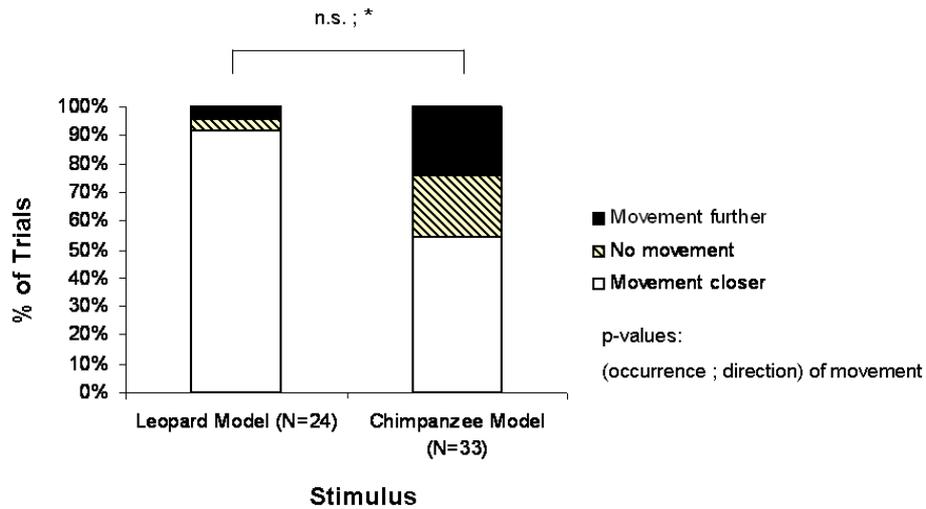
**Behavioural response characteristics**

The locomotor responses could be observed in all trials, leading to a final sample size of  $N_{\text{Leopard}}= 24$  and  $N_{\text{Chimpanzee}}= 33$ . Monkeys were very likely to start moving in the horizontal plane, both after detecting the leopard model ( $N_{\text{Move}}= 23$ ;  $N_{\text{Not Move}}= 1$ , exact  $p=0.000$ ) and the chimpanzee model ( $N_{\text{Move}}= 26$ ;  $N_{\text{Not Move}}= 7$ , exact  $p=0.001$ ). If they moved, they mostly approached the predator in the leopard context ( $N_{\text{Further}}= 1$ ;  $N_{\text{Closer}}= 22$ , exact  $p= 0.000$ ), and there was a trend to approach the chimpanzee as well ( $N_{\text{Further}}= 8$ ;  $N_{\text{Closer}}= 18$ , exact  $p= 0.076$ , Binomial test, Fig. 6.9).



**Figure 6.9.** Monkeys' locomotor behaviour in the horizontal plane in response to the visual predator models, with corresponding percentages of movements and exact p-values of the differences between locomotor responses within predator contexts (Binomial tests,  $\alpha=0.05$ , two-tailed).

Across predators, monkeys were equally likely to start moving in the horizontal plane (Leopard:  $N_{\text{Move}}= 23$ ,  $N_{\text{NotMove}}= 1$ ; Chimpanzee:  $N_{\text{Move}}= 26$ ,  $N_{\text{NotMove}}= 7$ : exact  $p \text{ L vs Ch}= 0.12$ ). However, they were significantly more likely to approach to the leopard model than the chimpanzee model (Leopard:  $N_{\text{Further}} = 1$ ,  $N_{\text{Closer}}= 22$ , Chimpanzee:  $N_{\text{Further}} = 8$ ,  $N_{\text{Closer}}= 18$ ; exact  $p \text{ L vs Ch}= 0.026$ , Fisher's Exact Test, Fig. 6.10).

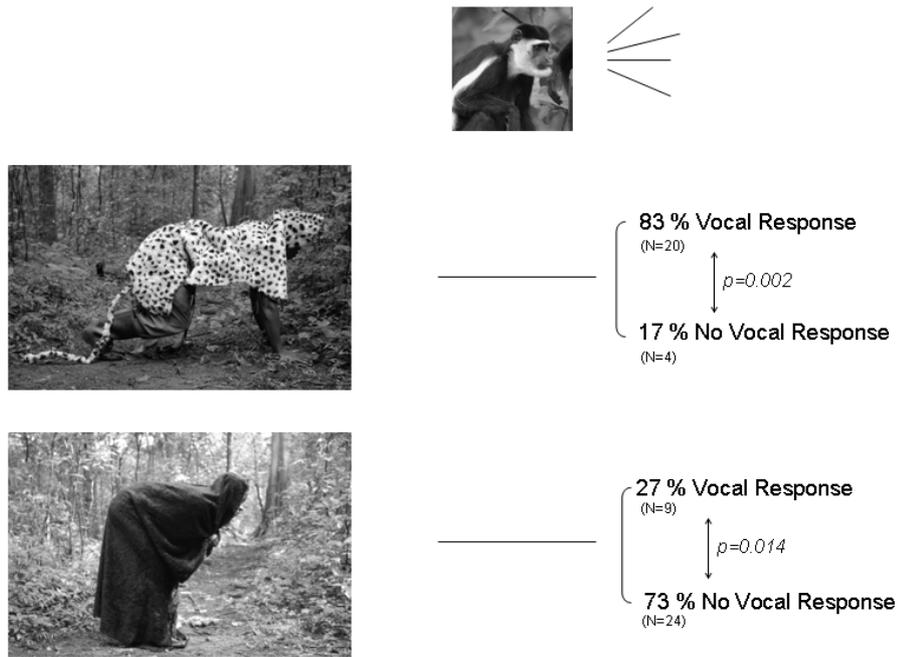


**Figure 6.10.** Locomotor responses in the horizontal and vertical plane to the two different visual models. The first set of asterisks refers to the difference in occurrence of movement between the contexts; the second set to the difference in direction of movements between the contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p = 0.000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

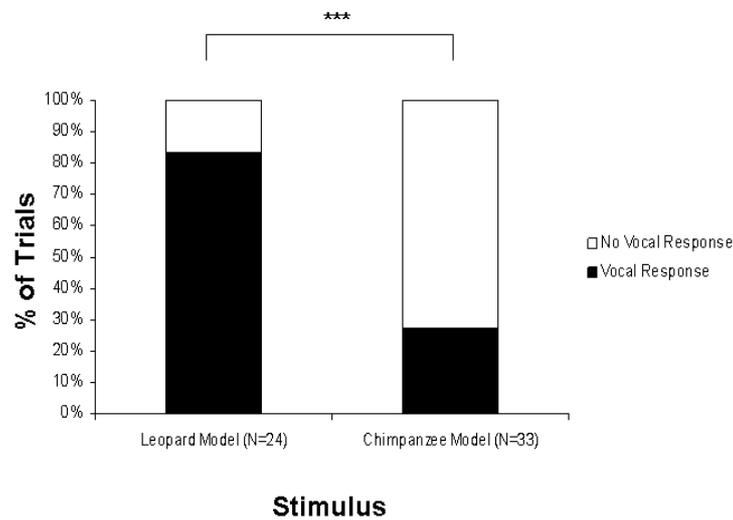
### **Vocal response characteristics to model experiments**

In 20 of the 24 groups tested with the leopard model, at least one individual responded with alarm vocalizations (response rate = 83%;  $N_{\text{Vocal Response (VR)}} = 20$ ,  $N_{\text{NoVR}} = 4$ ; exact  $p = 0.002$ ). The response rate to the chimpanzee model was much lower: in 9 of 33 groups at least one monkey responded with alarm vocalizations (response rate = 27%;  $N_{\text{VR}} = 9$ ,  $N_{\text{NoVR}} = 24$ ; exact  $p = 0.014$ ; Fig. 6.11).

Across predator types, monkeys responded much more likely with vocalizations to the leopard than to the chimpanzee model (Leopards: 83%; Chimpanzees 27%, L vs Ch: exact  $p = 0.000$ ; Fig. 6.12).



**Figure 6.11.** Vocal response rates of the monkeys to the two different visual predator models, with corresponding exact p-values (Binomial test,  $\alpha=0.05$ , two-tailed).



**Figure 6.12.** Vocal response rates to the two different visual predator models, with exact p. n.s.: no significant difference between the contexts; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in vocal response rates between the contexts, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p = 0.000$  (Fisher's Exact Test,  $\alpha=0.05$ , two-tailed).

**Acoustic measurements**

3 of the 20 vocal leopard responses could not be used for structural analyses due to noise produced by other individuals calling at the same time or bad recording quality, yielding a final dataset of N=17 responses. 12 of the 20 leopard responses were suitable for extracting spectral parameters of the individual phrases; the rest had to be discarded due to other individuals calling at the same time, bad recording quality, or the fact that callers did not produce at least 2 phrases in their vocal response.

Of the 9 vocal chimpanzee responses, 1 could not be used for the structural analysis due to other individuals calling at the same time. 6 of 9 responses were suitable to extract spectral parameters from; in two cases the monkeys only produced snorts, and in one case other calling individuals made it impossible to measure spectral parameters (Table 6.5).

Acoustic analyses of the first and last roars of the first two roaring sequences were made with PRAAT 4.3.12. Additional analyses were conducted with RAVEN 1.2.

**Table 6.5.** Number of trials conducted with the visual predator models, vocal response rates and number of trials used for subsequent acoustic analyses.

Stimulus	Nr valid trials	Response Rate		Suitable for Temporal Analyses	Suitable for Spectral Analyses	
		N	%		First RS	Second RS
Leopard model	24	20	83.3	17	12	12
Chimpanzee model	33	9	87.3	9	6	6

**Acoustic Structure of Individual Roars**

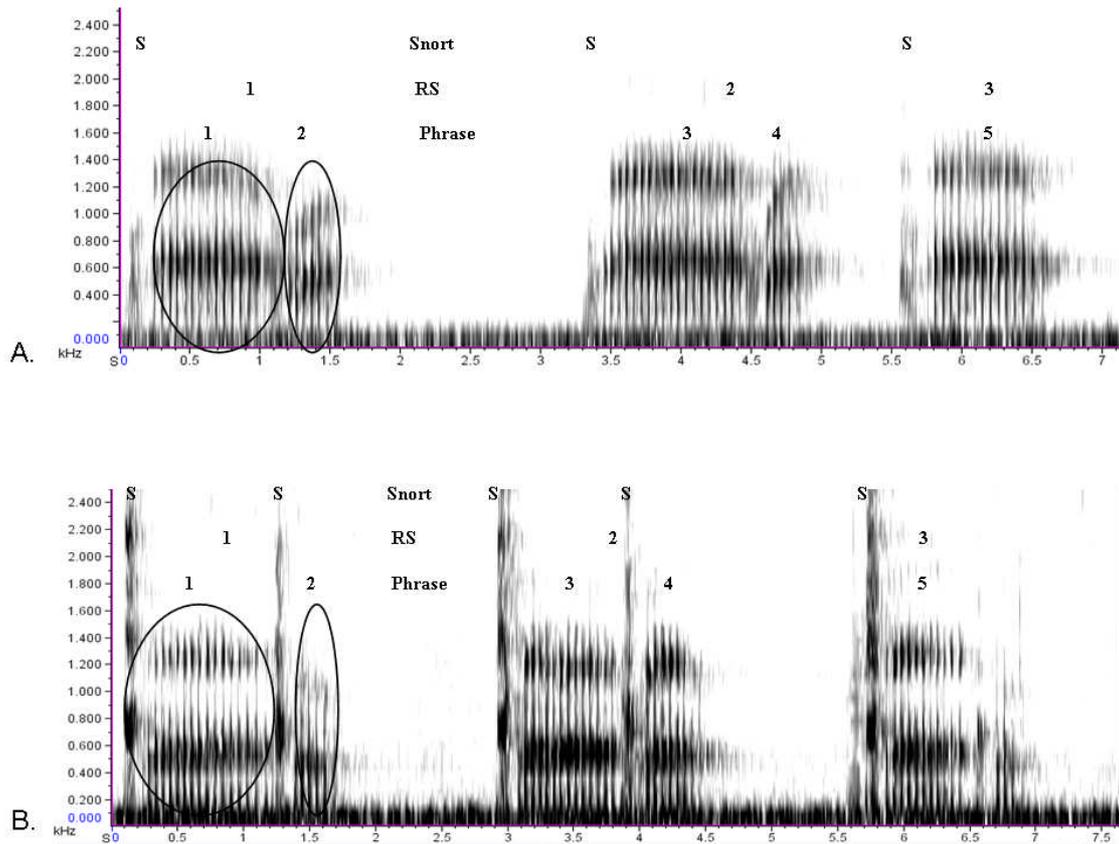
Within the leopard context, statistical comparisons revealed consistent significant differences between the first and final roaring phrases for both sequences. Although the results did not show any significant differences within the chimpanzee context, the findings were in the same direction (Tables 6.6 and 6.7; Fig. 6.13). Across contexts, there were no differences found in spectral measurements of individual phrases (Table 6.6 and 6.7, and Fig. 6.14).

**Table 6.6.** Spectral measurements of first and last phrases produced in the first and second RS of vocal responses to visual leopard and chimpanzee models. Mdn= median value, M=mean value, and CI= 99% confidence interval.

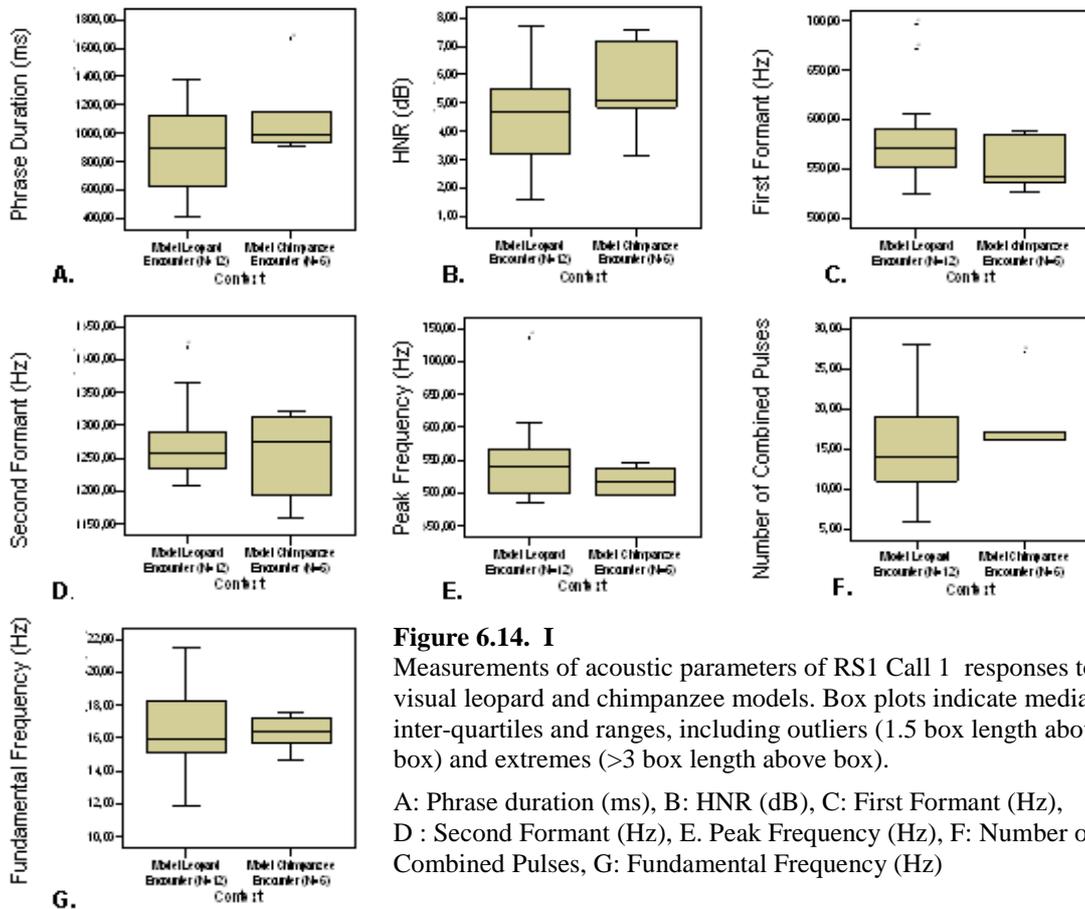
Acoustic variable		Leopard Model Alarm Response			Chimpanzee Model Alarm Response		
		Mdn	M	CI	Mdn	M	CI
1 <sup>st</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	893	897	630.8 – 1162.9	993	1108	635.2 – 1580.8
	HNR (dB)	4.68	4.57	3.04 – 6.1	5.08	5.49	2.8 – 8.2
	First Formant (Hz)	571	583	536.5 – 630	541	553	509.3 – 596.5
	Second Formant (Hz)	1258	1275	1219 – 1330	1276	1257	1146 – 1366
	Peak Frequency (Hz)	540	553	490.7 – 614.7	516	518	484.8 – 551.7
	Number of pulses	14	15	9 – 21	16	18	11 – 25
	Fundamental Freq (Hz)	16	16	14 - 19	16	16	15 - 18
1 <sup>st</sup> RS Last Phrase	Phrase Duration (ms)	284	310	199 – 421.7	315	306	108.5 – 503.1
	HNR (dB)	3.82	4.61	2.86 – 6.35	4.27	5.11	0.69 – 9.52
	First Formant (Hz)	568	569	499 – 639.7	532	557	435.5 – 678
	Second Formant (Hz)	1201	1248	1111 – 1383	1214	1245	964.8 – 1524.6
	Peak Frequency (Hz)	485	485	435.5 – 533.9	456	433	325 – 540.6
	Number of pulses	5	6	3 - 8	6	6	2 – 9
	Fundamental Freq (Hz)	17	17	15 - 19	18	18	15 - 21
2 <sup>nd</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	851	829	639.1 – 1019.1	1107	1189	489.1 – 1888.3
	HNR (dB)	4.61	5.16	2.81 – 7.50	4.49	4.87	0.92 – 8.82
	First Formant (Hz)	547	572	534.2 – 610.5	569	573	516 – 630.5
	Second Formant (Hz)	1241	1258	1201 – 1314	1245	1283	1145 – 1419
	Peak Frequency (Hz)	540	538	489.1 – 587.0	540	537	483.3 -591.7
	Number of pulses	14	14	10 – 19	17	18	11 – 25
	Fundamental Freq (Hz)	16	17	15 - 19	16	16	10 -21
2 <sup>nd</sup> RS Last Phrase	Phrase Duration (ms)	312	301	190.4 – 410.6	478	399	99.5 – 698.2
	HNR (dB)	5.79	6.05	2.45 – 9.64	3.83	3.99	1.04 – 6.94
	First Formant (Hz)	563	588	507.1 – 668.6	561	567	493.2 – 641.2
	Second Formant (Hz)	1198	1240	1118 – 1360	1271	1269	1046 – 1491
	Peak Frequency (Hz)	499	550	415.2 – 684.6	477	465	348.5 – 580.9
	Number of pulses	5	5	3 – 7	9	7	2 – 12
	Fundamental Freq (Hz)	18	17	15 - 20	16	17	13 - 21

**Table 6.7.** Statistical output (exact p-values and effect sizes, *r*) of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced within predator contexts (left hand side of the Table; Wilcoxon Signed Ranks Test,  $\alpha=.017$ ), followed by statistic output of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced across two different predator contexts (visual leopard and chimpanzee models; right hand side of the Table; Man Whitney U test,  $\alpha=.017$ ).

Acoustic variable		Within Leopard (First vs Last phrase)		Within Chimpanzee (First vs Last phrase)		Between Leopard and Chimpanzee			
						First Phrase		Last Phrase	
		Exact p	r	Exact p	r	Exact p	r	Exact p	r
<b>1<sup>st</sup> RS</b>	Phrase Duration (ms)	<b>0.000</b>	0.62	0.031	0.64	0.125	0.38	0.964	0.02
	HNR (dB)	0.791	0.06	0.563	0.21	0.221	0.30	0.837	0.06
	First Formant (Hz)	0.519	0.14	0.844	0.09	0.335	0.24	0.616	0.13
	Second Formant (Hz)	0.424	0.18	0.688	0.15	0.964	0.02	0.964	0.02
	Peak Frequency (Hz)	0.020	0.45	0.031	0.64	0.300	0.26	0.086	0.41
	Number of pulses	<b>0.000</b>	0.63	0.031	0.64	0.347	0.23	0.924	0.02
	Fundamental Freq (Hz)	0.129	0.32	0.156	0.45	0.982	0.01	0.494	0.18
<b>2<sup>nd</sup> RS</b>	Phrase Duration (ms)	<b>0.000</b>	0.62	0.031	0.64	0.067	0.44	0.157	0.34
	HNR (dB)	0.391	0.18	0.844	0.09	0.682	0.11	0.385	0.22
	First Formant (Hz)	0.791	0.06	0.844	0.09	0.820	0.07	0.892	0.04
	Second Formant (Hz)	0.380	0.16	0.844	0.09	0.437	0.20	0.616	0.13
	Peak Frequency (Hz)	0.490	0.16	0.031	0.64	0.945	0.02	0.236	0.29
	Number of pulses	<b>0.000</b>	0.63	0.031	0.64	0.096	0.40	0.155	0.35
	Fundamental Freq (Hz)	0.266	0.24	0.438	0.27	0.494	0.18	0.682	0.11

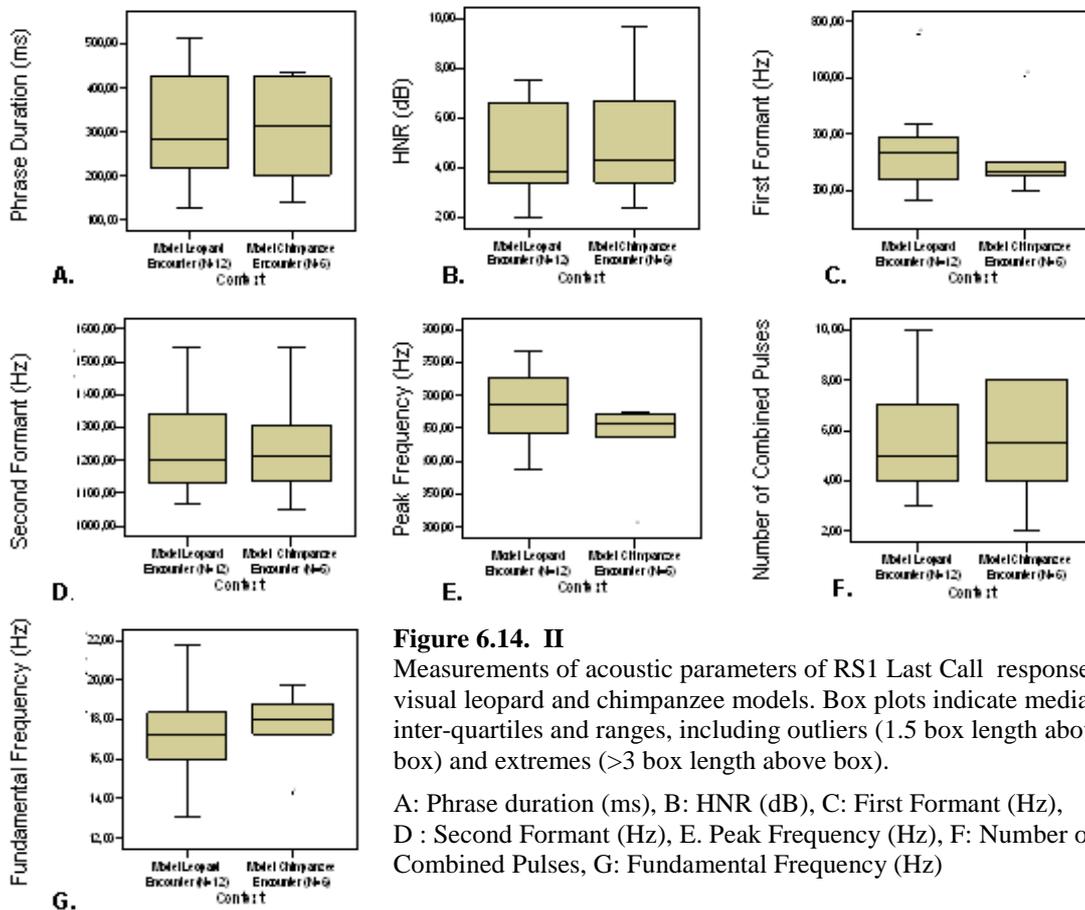


**Figure 6.13.** Spectrographic illustration of a Guereza's roaring, illustrating the significant differences in duration between first and last phrases within predator contexts and the non-significant differences in duration of first phrases and last phrases across predator responses. (A.) three Roaring Sequences given to a visual leopard model (8s), and (B.) one Roaring Sequence given to a visual chimpanzee model (8s). Encircled are the first and last phrases measured from a RS. The x-axis represents the time in seconds, the y-axis represents the frequency in kHz.



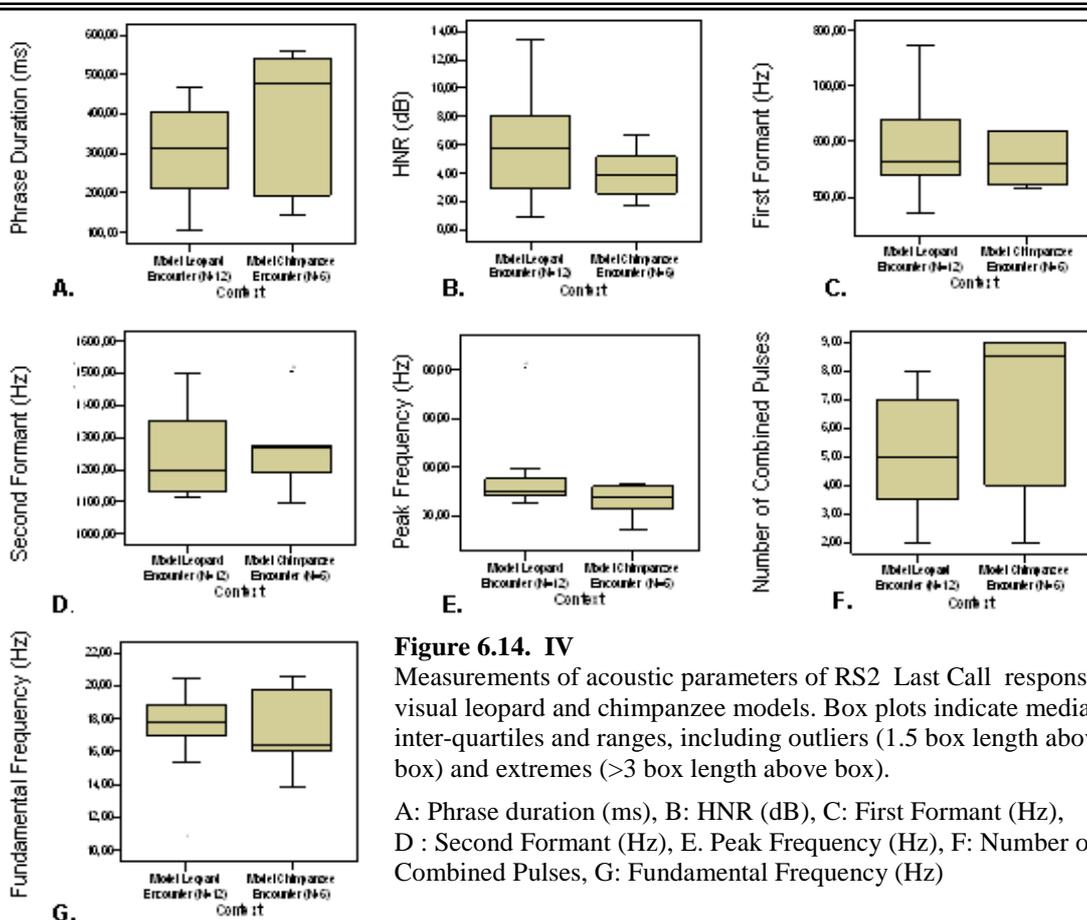
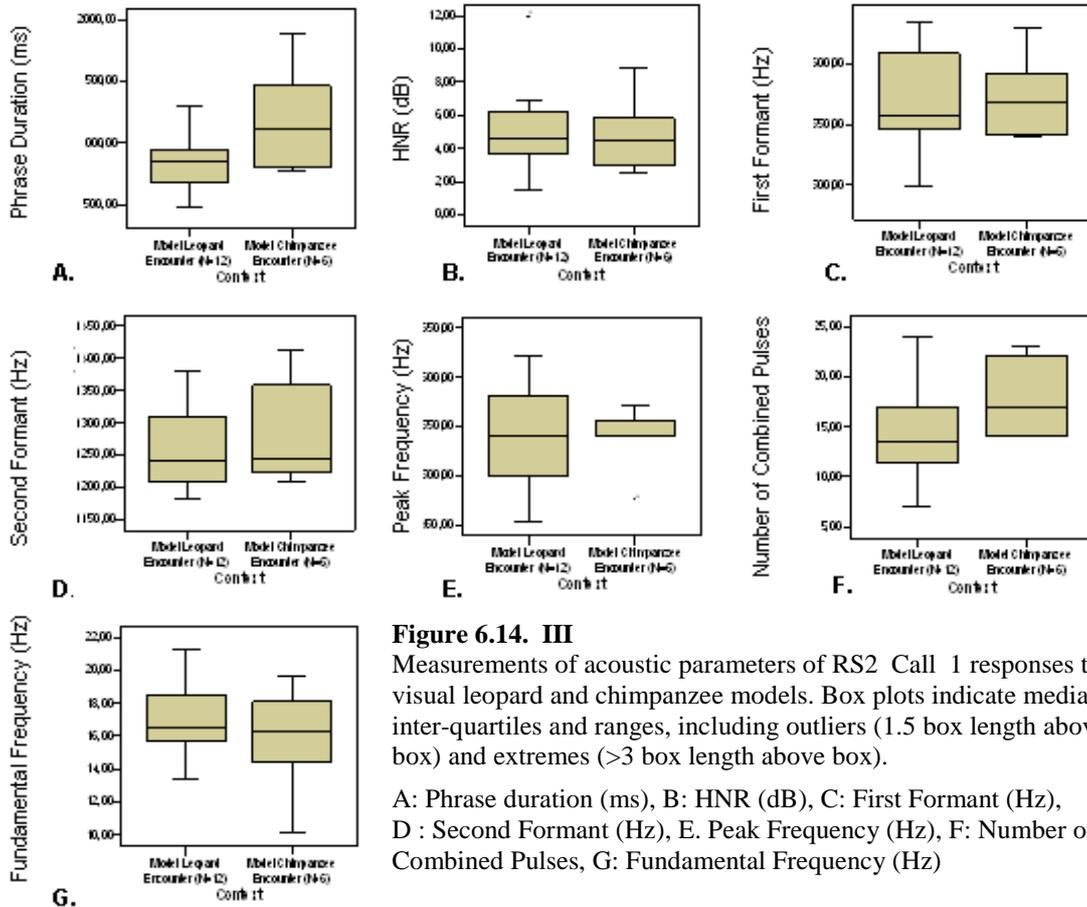
**Figure 6.14. I** Measurements of acoustic parameters of RS1 Call 1 responses to visual leopard and chimpanzee models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



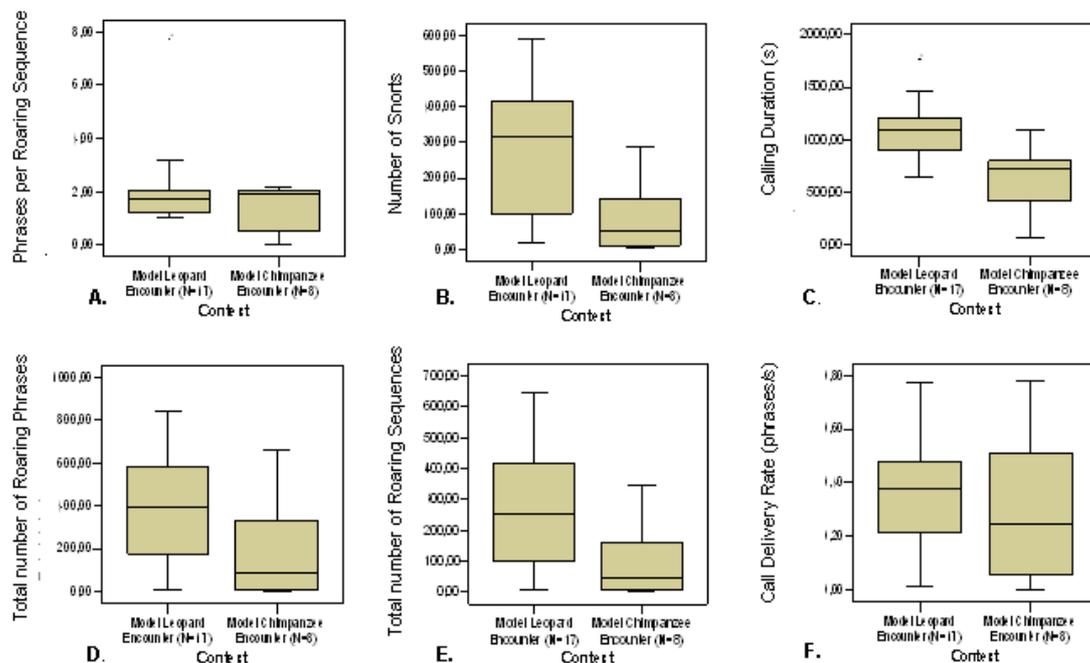
**Figure 6.14. II** Measurements of acoustic parameters of RS1 Last Call responses to visual leopard and chimpanzee models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



### Composition of Roaring Sequences

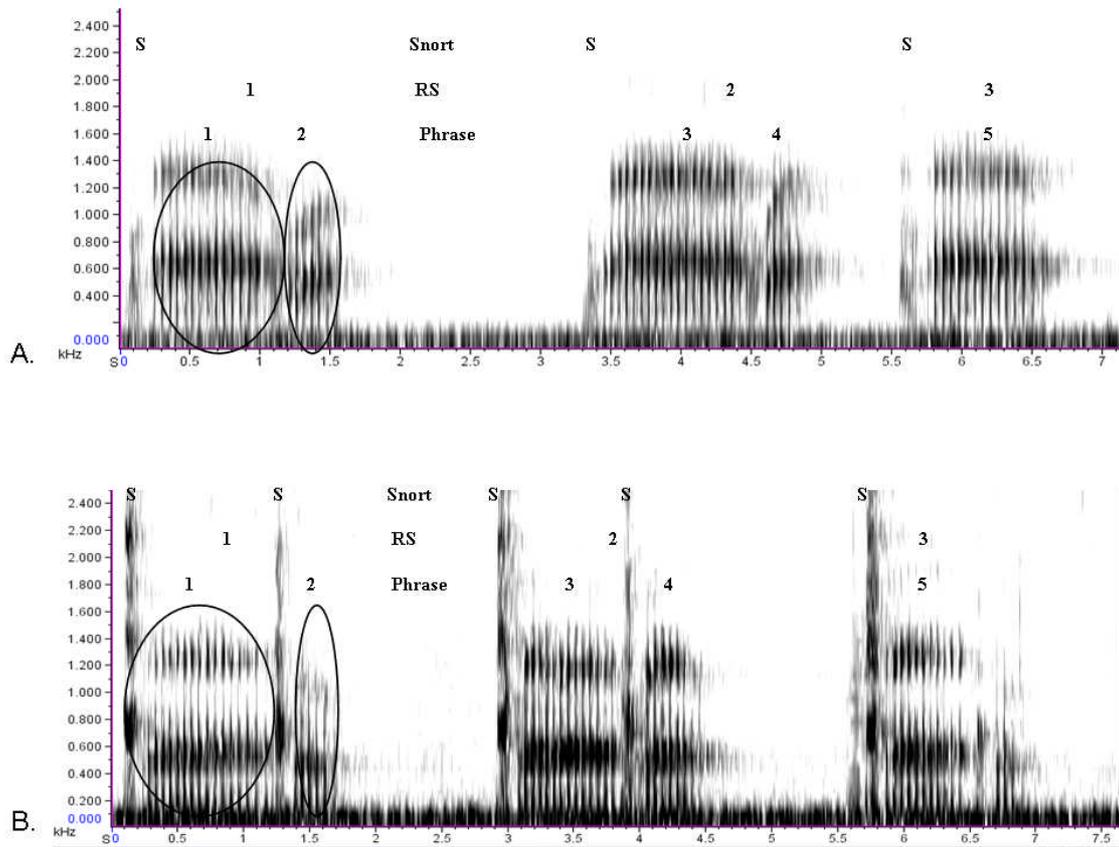
Across conditions, two differences were found in the temporal patterning of responses to leopard and chimpanzee models: first, the total calling duration was much longer in response to leopard than to chimpanzee models ( $U=17$ , exact-p value= 0.002,  $r=0.59$ , Mann Whitney U test, two-tailed). Second, although the responses to both predators were accompanied by snorts (17 of 17 leopard trials; 8 of 8 chimpanzee trials, exact  $p=1.000$ ; Fisher's Exact Test, two-tailed), the total number of snorts was higher in response to the leopard than to the chimpanzee model ( $U=24.5$ , exact p-value= 0.009,  $r=0.51$ , Mann Whitney U test, two-tailed). After Bonferroni corrections, there were trends in the same direction for two other parameters: the total number of roaring sequences ( $U=32.5$ , exact p-value=.038,  $r=0.41$ , Mann Whitney U test, two-tailed), and the total number of phrases ( $U=36$ , exact p-value= .064,  $r=0.37$ , Mann Whitney U test, two-tailed), which were both higher in the leopard than in the chimpanzee context. The number of roaring phrases per sequence did not differ between the contexts ( $U=60$ , exact p-value=0.659,  $r=0.09$ , Mann Whitney U test, two-tailed). Finally, the call delivery rate between the two contexts was similar as well ( $U=54$ , exact p-value=.432,  $r=0.16$ , Mann Whitney U test, two-tailed; Fig. 6.15 and 6.16; Table 6.8).



**Figure 6.15.** Measurements of temporal response characteristics to visual leopard and chimpanzee models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box). A: Number of phrases/ RS, B: Number of snorts, C: Calling duration (s), D: Total number of phrases, E: Total number of RS (Hz), F: Call delivery rate (phrases/s).

**Table 6.8.** Temporal measurements of vocal response characteristics to visual leopard and chimpanzee models. Mdn= median value, M= mean value and Conf. Int.= 99% confidence interval, including M in 99% of the samples. Statistical output (exact p-values and effect sizes,  $r$ ) of the Mann Whitney U Test to compare measurements across contexts are presented as well ( $\alpha=.017$ ).

	Calling Duration (s)			Total Number RS			Total Number Phrases			Phrases per RS			Number of Snorts			Call Delivery Rate (phrases/s)		
	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI
<b>Visual Leopard Model</b>	1093	1118	916 - 1320	252	262	120 - 403	394	404	212 - 596	1.7	2.1	0.99 - 3.21	315	274	143 - 405	0.38	0.35	0.20 - 0.51
<b>Visual Chimpanzee Model</b>	722	630	199 - 1060	45	97	-59 - 253	90	189	-114 - 492	1.9	1.3	0.25 - 2.54	53	88	-39 - 215	0.25	0.31	-0.06 - 0.66
<b>Exact p value</b>	<b>0.002</b>			0.038			0.064			0.659			<b>0.009</b>			0.432		
<b>Effect size (r)</b>	0.59			0.41			0.37			0.09			0.51			0.16		



**Figure 6.16.** 7 Seconds continuous recording of a male producing (A.) three Roaring Sequences consisting of two snort-introduced 2 phrase RS's, followed by a snort-introduced one phrase RS to a visual leopard model, and (B) three Roaring Sequences consisting of two snort-introduced 2 phrase RS's, followed by a snort-introduced one phrase RS to a visual chimpanzee model. Encircled are the first and the last phrases that are produced in the first RS. The x-axis represents time in seconds, the y-axis frequency in kHz.

Results thus suggested that there were no spectral differences in the acoustical parameters of individual phrases produced to leopards and chimpanzees. Furthermore, the Guerezas produced responses with similarly structured roaring sequences to both ground predators. The only difference was a longer total alarm reaction in response to the leopard models. Related to this, the monkeys produced more snorts in the leopard than in the chimpanzee context.

### Summary and discussion

Analyses of locomotor behaviour showed that the monkeys moved reliably in response to both the visual leopard and chimpanzee models. In response to the leopard model, they generally approached, whereas in response to the chimpanzee model, they behaved

more randomly (showing a trend to approach), but rates of movements were similar to both predators. To the leopard model, the monkeys vocalised in a high proportion of trials, whereas the opposite was the case for the chimpanzee model. There were no spectral differences between the two contexts in all four phrases from which acoustic measurements were taken. In the temporal domain, a longer total calling duration and more snorts were produced to the leopard than to the chimpanzee model. Strikingly, the Guerezas produced roaring sequences with a similar acoustic and temporal structure to both the leopard and the chimpanzee model.

The locomotor response to the leopard model is in line with a general perception advertisement strategy, as described in other animals, which consists of approach and conspicuous alarm calling upon detection (e.g. Woodland et al., 1980; Zuberbühler et al., 1997; Zuberbühler et al., 1999). The high vocal response rate to the visual leopard model (83%) further supports this general hypothesis.

Did the monkeys recognise the visual leopard model as a sign of a specific predator threat, despite their lack of experience, or can these results be explained with stimulus novelty (e.g. Yorzinski & Ziegler, 2007; Blumstein et al., 2008)? To address this hypothesis, a control experiment was conducted in which the Guerezas at Sonso were confronted with a moving model wearing a light green sheet with a flower pattern on it (Appendix B). In response to this stimulus, the monkeys consistently moved away, whereas they consistently approached the leopard model. These results demonstrated once more that the Guerezas' default response to novel visual stimuli is not necessarily approach and inspection, but that their locomotor response is based on more complex decisions. In these control trials, the monkeys also never vocalized, which contrasted strongly with the findings of the visual leopard model trials. These results thus suggested that the Guerezas interpreted the visual leopard model as a potentially dangerous predator that can be deterred by approaching and calling at it.

Occasionally, the monkeys produced alarm calls to visual chimpanzee models (27%; 9/33), although it was far more likely for them to remain silent. Calling in response to chimpanzees is generally not adaptive, and in naturally occurring situations was usually only observed when the monkeys had already been detected by the chimpanzees, perhaps as a way to communicate aggressive intent and readiness to fight (Harris et al.,

2006). At the time of this study, the chimpanzees in Sonso did not hunt frequently, and Guerezas were occasionally observed to chase them from trees and fighting them, sometimes accompanied by roaring.

Vocal responses to chimpanzees did not differ from those given to leopards in terms of acoustic structure, suggesting that the calls could function as general terrestrial predator alarms in Sonso. Whether or not these calls are specifically aimed at conspecifics is difficult to determine, although eavesdropping will always allow recipients to associate predator-specific alarms with the presence of a particular predator type (Owings & Morton, 1997; Rundus et al., 2007). At Sonso, over the last five decades, these terrestrial calls will have been produced primarily to the ground predator usually encountered on the ground, i.e. the chimpanzee. This may have led to highly specific associations in recipients (Fichtel & van Schaik, 2006; Fichtel, 2008), who may thus associate these vocalizations only with the presence of chimpanzees.

Nevertheless, the locomotor responses seemed fairly well-adapted to these predators' hunting techniques: if the leopard model was approached this was usually accompanied by strong vocal responses. The fact that the animals sometimes also approached the chimpanzees is at odds with the cryptic response observed during acoustic model experiments, and may be due to the fact that visual chimpanzee models could be less convincing than acoustic ones. Alternatively, the monkeys in Sonso may have learned that chimpanzees can be chased away, aided by aggressive roaring, since at the time of study the chimpanzees did not hunt very much. Interesting in this respect is the fact that general response rates in Sonso at present appear to be much lower (personal communication A. Candiotti) and chimpanzee hunting much higher.

The tentative conclusion is that the Guerezas have retained their ability to recognise leopards as dangerous predators, which can be repelled by calling at them. Chimpanzees do usually not evoke calls, unless individuals are forced or 'motivated' to fight and chase away this predator. The monkeys' vocalizations to chimpanzees and leopards do not appear to contain specific information about predator types, other than that a ground predator was encountered, although responses to leopards were longer in duration and contained more snorts than those to chimpanzees. It is unlikely, however,

that these calling features were sufficient to encode anything about the predator type encountered by the caller.

### **Part 3. Comparisons between visual and acoustic predator models**

Earlier, it was argued that seeing a predator may pose a different kind of threat than hearing its vocalizations, and that visual predator recognition is less experience dependent than acoustic predator recognition. In the previous two sections, the Guerezas' responses to visual and acoustic predator stimuli were compared within each predator modality. In the present section, the aim is to compare the monkeys' responses to visual and acoustic predator models to investigate whether visual and acoustic models evoked different responses from them.

#### ***Hypotheses and predictions***

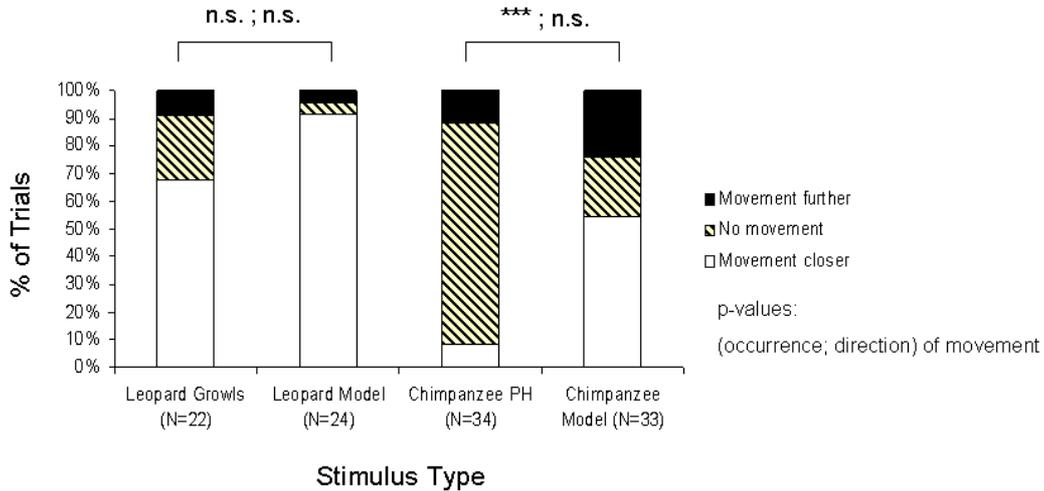
The hypothesis tested with this study was that the monkeys at Sonso recognized visual models with less effort than acoustic models, especially in the case of leopards (cf. Blumstein et al., 2000; Blumstein et al., 2008). If correct, then the animals were predicted to respond stronger to visual than acoustic presence of predators. Furthermore, visual leopards were predicted to elicit higher levels of perceived arousal in the monkeys (cf. chapter 5): this hypothesis also predicted stronger responses to visual than acoustic leopard presence, but additionally predicted the production of alarms containing arousal related acoustical characteristics that varied between contexts.

## **Results**

### ***Behavioural responses***

Monkeys were equally likely to move in the horizontal plane in response to the visual and acoustic leopard models (visual: 96% (23/24), acoustic: 77% (17/22), exact  $p=0.090$ , Fisher's Exact Test, two-tailed). If movements occurred, the monkeys approached the visual and acoustic leopard models at equal rates (acoustic:  $N_{\text{Further}}=2$ ,  $N_{\text{Closer}}=15$ , visual:  $N_{\text{Further}}=1$ ,  $N_{\text{Closer}}=22$ ; exact  $p$  acoustic vs visual = 0.565, Fisher's Exact Test, two-tailed, Fig. 6.17). However, monkeys moved significantly more often in response to the visual than the acoustic chimpanzee model (visual chimpanzee model = 79% (26/33); acoustic chimpanzee model: 21% (7/34), exact  $p=0.000$ , Fisher's

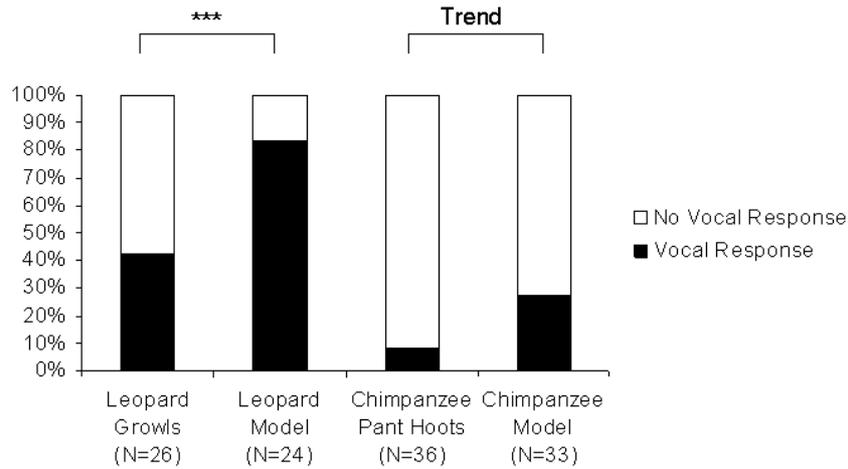
Exact Tests, two-tailed). If movements occurred, the Guerezas moved in random directions in both modalities (acoustic model:  $N_{\text{Further}}= 4$ ,  $N_{\text{Closer}}= 3$ , visual model:  $N_{\text{Further}} = 8$ ,  $N_{\text{Closer}}= 18$ ; exact p acoustic vs visual= 0.377, Fisher’s Exact Test, two-tailed, Fig. 6.17).



**Figure 6.17.** Locomotor responses in the horizontal plane to the different predator models; acoustic and visual leopard and chimpanzee models. The first set of asterisks refers to the difference in occurrence of movement between the contexts; the second set to the difference in direction of movements between the contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < .05$ , \*\* $p < .01$ , \*\*\* $p = .000$  (Fisher’s Exact Test,  $\alpha = 0.05$ , two-tailed).

**Vocal response rates**

Monkeys showed a strong difference in the vocal response rates to visual compared to acoustic leopard models (acoustic = 42% (11/26), visual = 83% (20/24), exact p= 0.003, Fisher’s Exact test, two-tailed; Fig. 6.18). A similar trend was found for the chimpanzee comparisons (response rate chimpanzee pant hoots= 8% (3/36), chimpanzee model= 27% (9/33), exact p= 0.056, Fisher’s Exact test, two-tailed; Fig. 6.18).



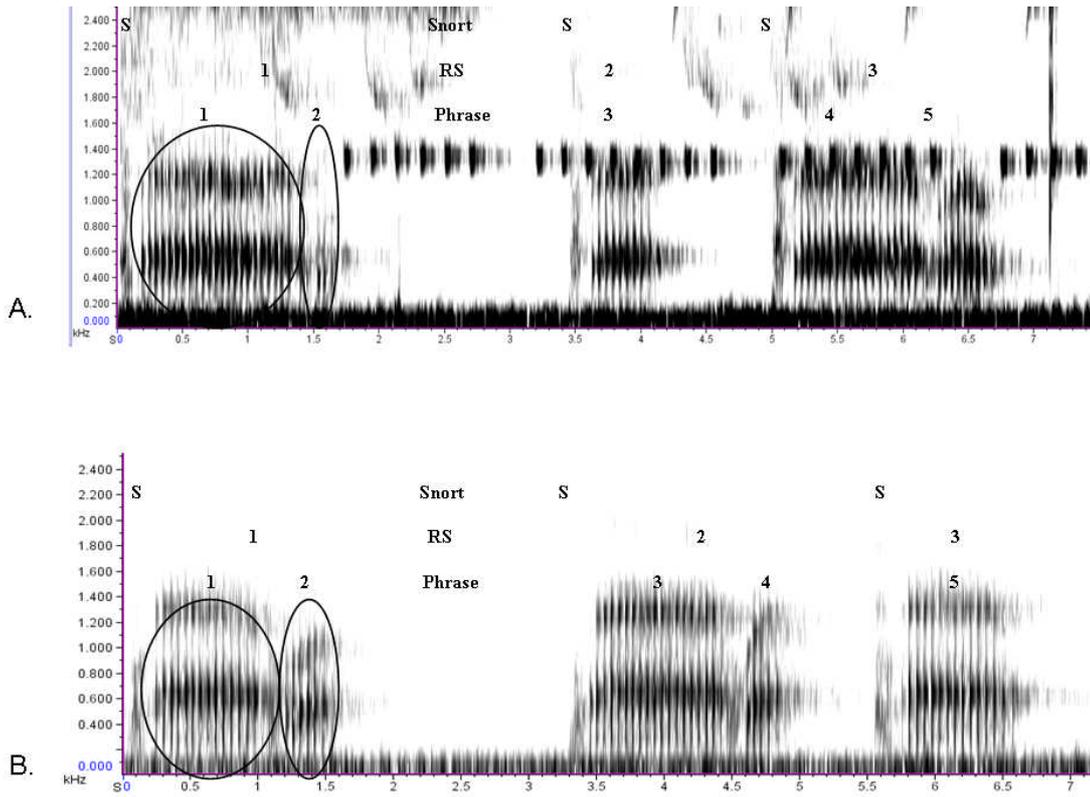
**Figure 6.18.** Vocal response rates compared between different predator modalities: acoustic and visual leopard and chimpanzee models. n.s.: no significant difference between contexts; \*, \*\*, \*\*\*: difference in vocal response rates between contexts, \*  $p < .05$ , \*\*  $p < .01$ , \*\*\*  $p = .000$  (Fisher's Exact Test,  $\alpha = 0.05$ , tw0-tailed).

### **Acoustic measurements**

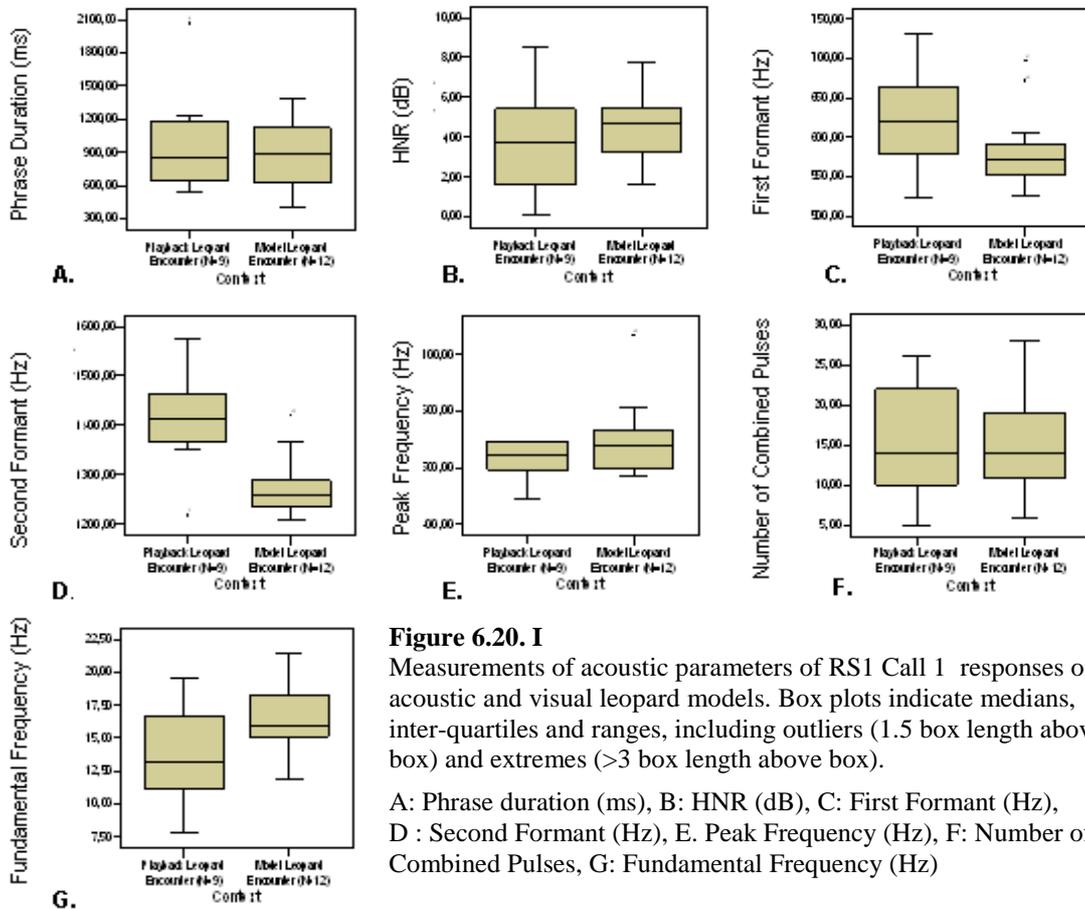
Acoustic comparisons were performed for the leopard trials only; the sample size for the chimpanzee trials was too small to conduct meaningful statistical tests. For this purpose, data presented in Table 6.2 (acoustic leopard model) and Table 6.6 (visual leopard model) were compared. Results showed some differences in spectral parameters, i.e. frequencies of the second formant (F2) of individual phrases tended to be lower in response to visual than acoustic leopard models (Mann Whitney U test, Bonferroni corrected  $\alpha = 0.017$ ; Fig. 6.19 and 6.20; Table 6.9).

**Table 6.9.** Statistical output (exact p-values and effect sizes,  $r$ ) of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced across different predator modalities (acoustic and visual leopard models; Mann Whitney U test,  $\alpha=.017$ ).

Acoustic variable		Within acoustic leopard model		Within visual leopard model		Between visual and acoustic leopard model			
		(First vs Last phrase)		(First vs Last phrase)		First Phrase		Last Phrase	
		Exact p	r	Exact p	r	Exact p	r	Exact p	r
<b>1<sup>st</sup> RS</b>	Phrase Duration (ms)	<b>0.004</b>	0.63	<b>0.000</b>	0.62	0.972	0.02	0.554	0.14
	HNR(dB)	0.176	0.34	0.791	0.06	0.554	0.14	0.153	0.32
	First Formant (Hz)	1.000	0.01	0.519	0.14	0.219	0.28	0.508	0.16
	Second Formant (Hz)	0.359	0.24	0.424	0.18	<b>0.004</b>	0.60	<b>0.015</b>	0.53
	Peak Frequency (Hz)	0.547	0.15	<b>0.020</b>	0.45	0.299	0.23	0.453	0.17
	Number of pulses	<b>0.016</b>	0.61	<b>0.000</b>	0.63	0.918	0.03	0.277	0.26
	FundamentalFreq (Hz)	0.297	0.31	0.129	0.32	0.261	0.27	0.343	0.22
<b>2<sup>nd</sup> RS</b>	Phrase Duration (ms)	<b>0.004</b>	0.63	<b>0.000</b>	0.62	0.931	0.02	0.310	0.23
	HNR(dB)	0.148	0.37	0.391	0.18	0.602	0.12	0.039	0.47
	First Formant (Hz)	0.203	0.32	0.791	0.06	0.554	0.14	0.129	0.34
	Second Formant (Hz)	0.109	0.41	0.380	0.16	0.082	0.39	0.020	0.52
	Peak Frequency (Hz)	0.438	0.22	0.490	0.16	0.210	0.28	0.065	0.41
	Number of pulses	<b>0.008</b>	0.61	<b>0.000</b>	0.63	0.778	0.07	0.711	0.09
	FundamentalFreq (Hz)	0.484	0.19	0.266	0.24	0.305	0.24	0.023	0.50



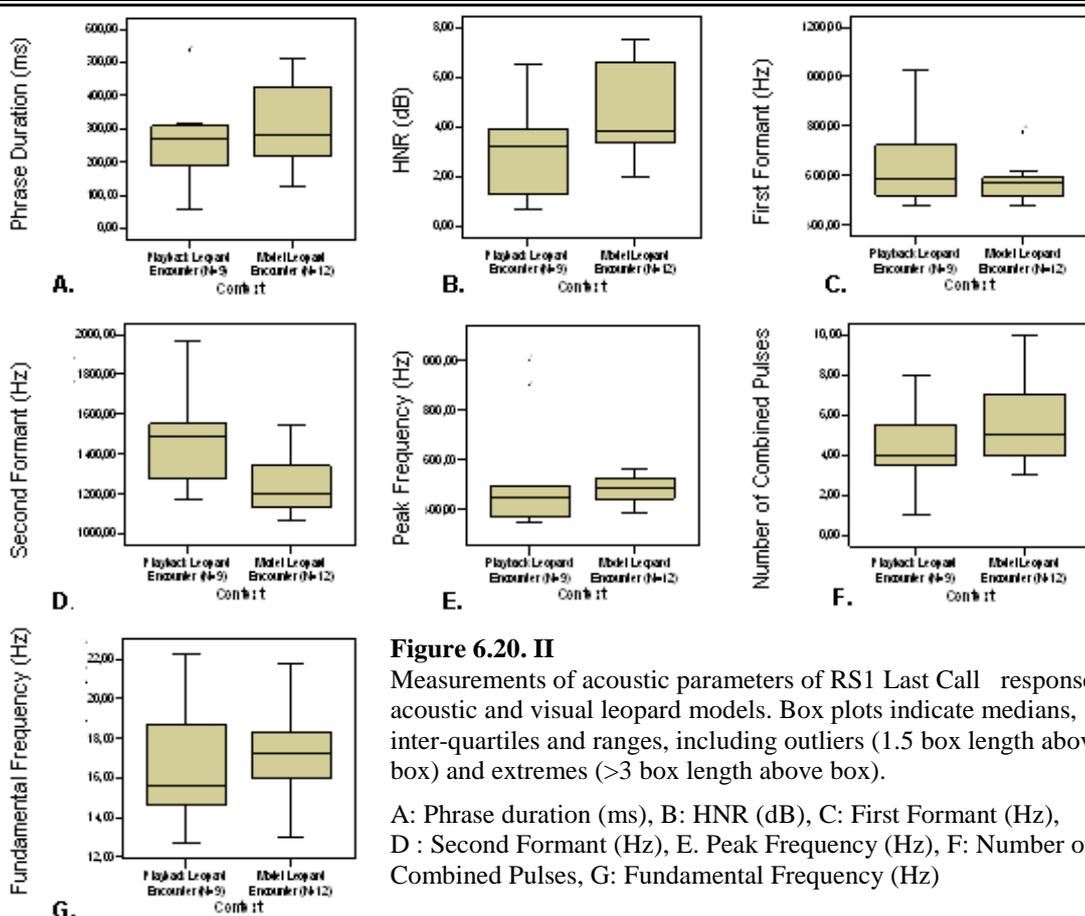
**Figure 6.19.** Spectrographic illustration of a Guereza's roaring, illustrating the non-significant differences between first and last phrases within and between (A.) acoustic and (B.) visual leopard models. Encircled are the first and last phrases measured from a RS. The x-axis represents the time in seconds, the y-axis represents the frequency in kHz.



**Figure 6.20. I**

Measurements of acoustic parameters of RS1 Call 1 responses on acoustic and visual leopard models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

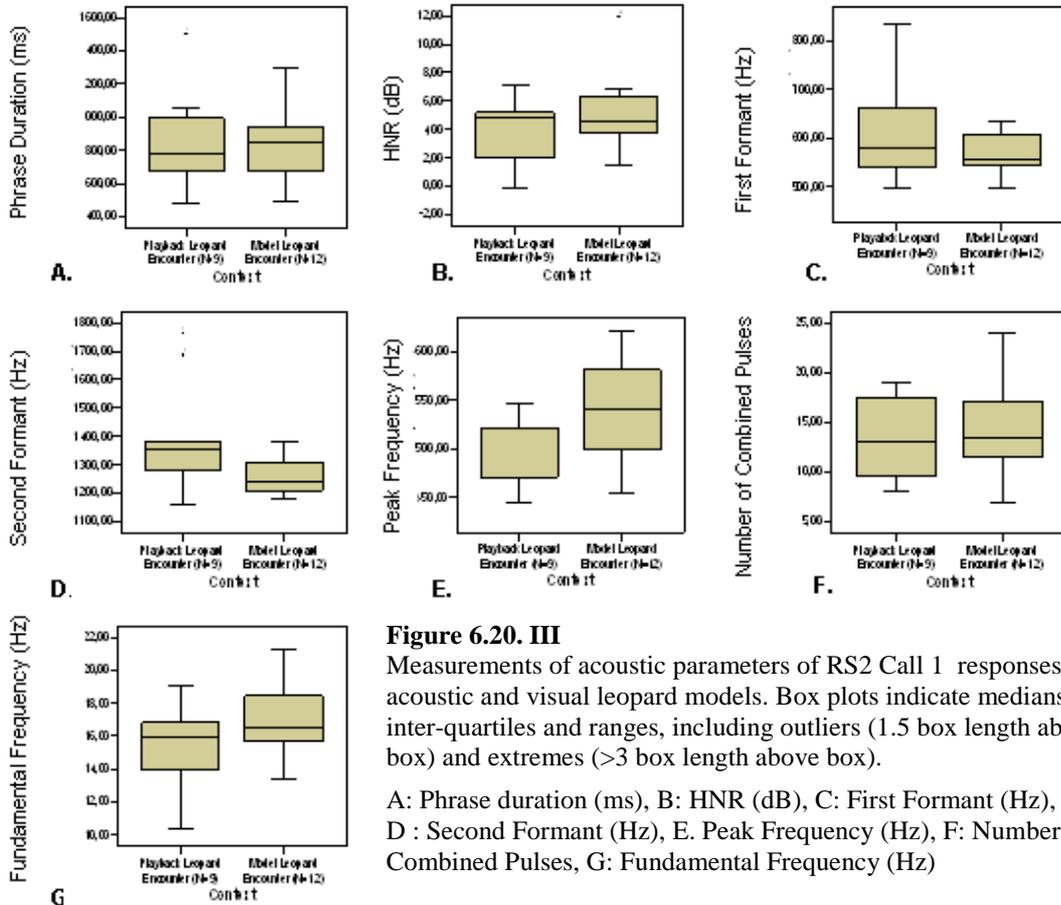
A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



**Figure 6.20. II**

Measurements of acoustic parameters of RS1 Last Call responses on acoustic and visual leopard models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

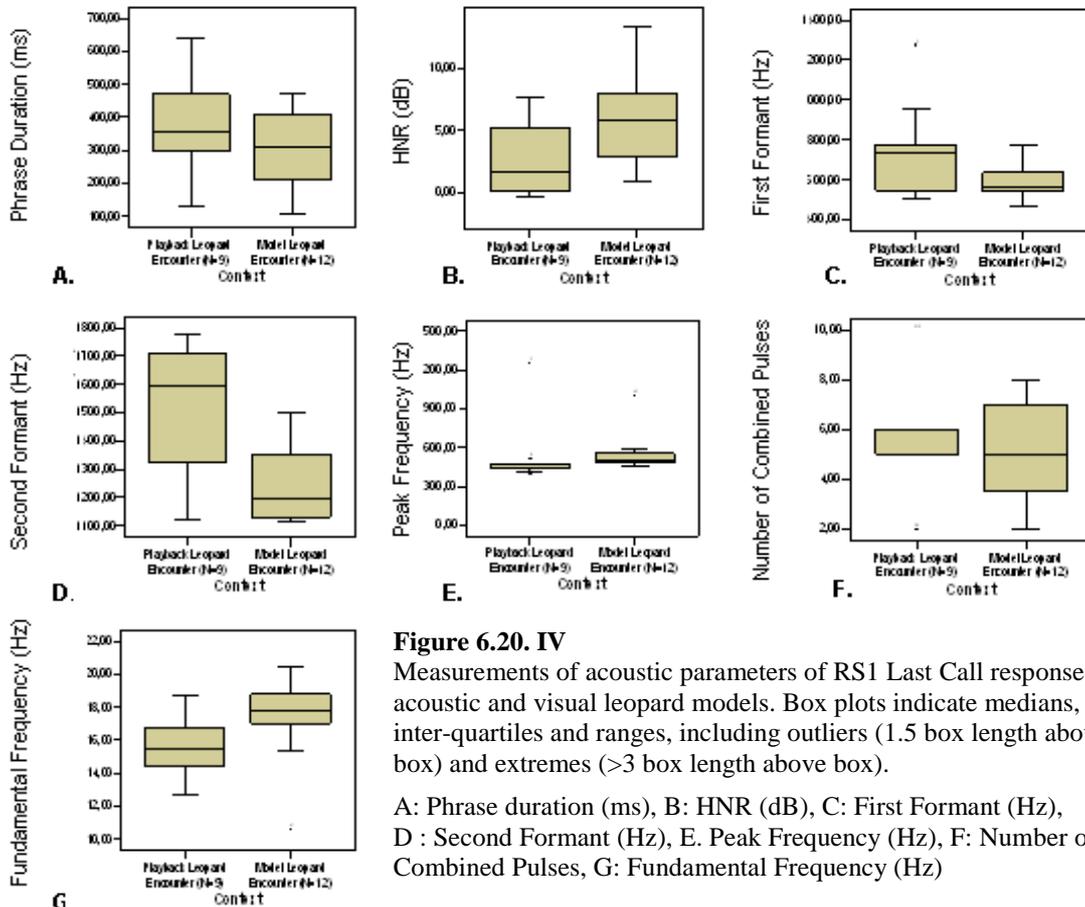
A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



**Figure 6.20. III**

Measurements of acoustic parameters of RS2 Call 1 responses on acoustic and visual leopard models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



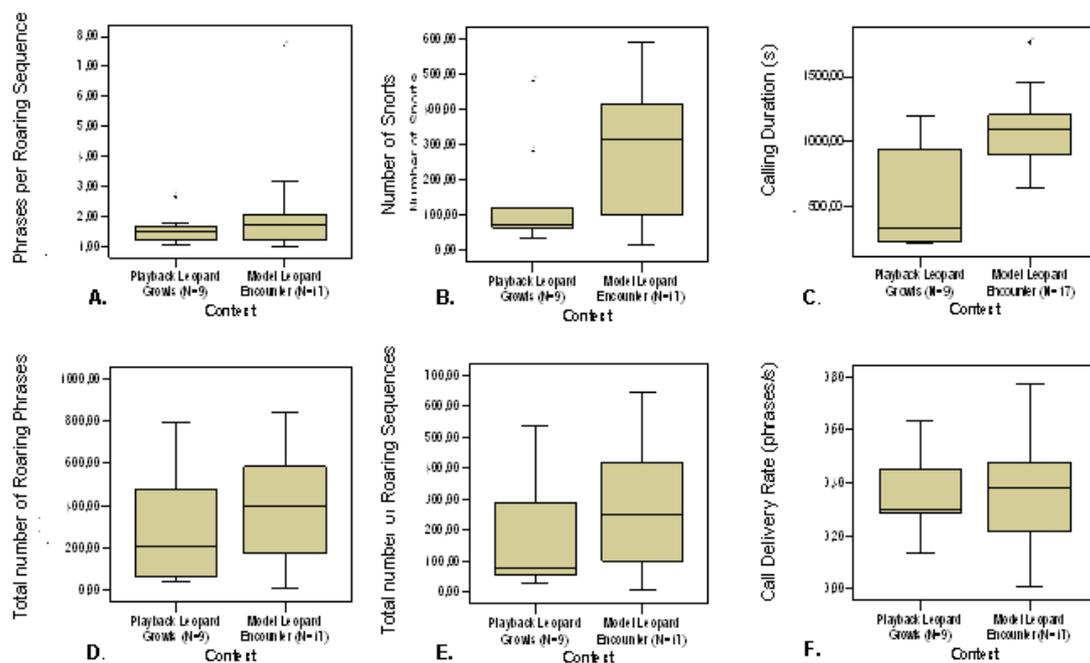
**Figure 6.20. IV**

Measurements of acoustic parameters of RS1 Last Call responses on acoustic and visual leopard models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box).

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz), D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)

### Composition of Roaring Sequences

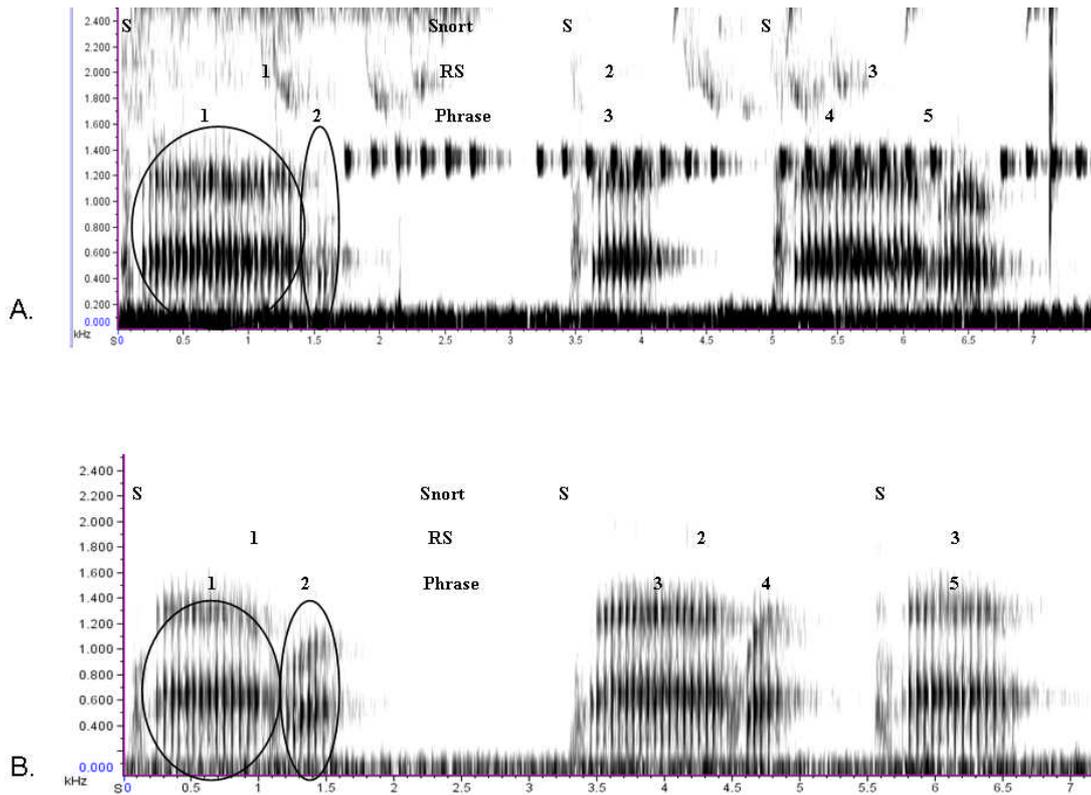
The only difference in the calling response to the two leopard models was in the total calling duration: Guerezas responded significantly longer to visual than acoustic leopard models ( $U=25$ , exact  $p=0.004$ ,  $r=0.54$ , Mann Whitney U test, two-tailed). In contrast, roaring sequences produced to both leopard models were always accompanied by snorts (9 of 9 leopard playback trials; 17 of 17 leopard model trials, exact  $p=1.000$ ; Fisher's Exact Test, two-tailed). Furthermore, the total number of roaring phrases, roaring sequences, and snorts did not differ between the two modalities (all exact  $p$ -values  $>.09$ ), nor did the call delivery rate ( $U=75$ , exact  $p$ -value= $0.958$ ,  $r=0.02$ , Mann Whitney U test, two-tailed), or the number of phrases per roaring sequence ( $U=59$ , exact  $p$ -value= $0.367$ ,  $r=0.18$ , Mann Whitney U test, two-tailed; Fig. 6.21; Table 6.10).



**Figure 6.21.** Measurements of temporal response characteristics to visual and acoustic leopard models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes ( $>3$  box length above box). A: Number of phrases/ RS, B: Number of snorts, C: Calling duration (s), D: Total number of phrases, E: Total number of RS (Hz), F: Call delivery rate (phrases/s).

**Table 6.10.** Temporal measurements of vocal response characteristics to acoustic and visual leopard models. Mdn= median value, M= mean value and CI= 99% confidence interval. Statistical output (exact p-values and effect sizes,  $r$ ) of the Mann Whitney U Test to compare measurements across contexts are presented as well ( $\alpha=.017$ ).

	Calling Duration (s)			Total Number RS			Total Number Phrases			Phrases per RS			Number of Snorts			Call Delivery Rate (phrases/s)		
	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI
<b>Acoustic leopard model</b>	330	595	133 - 1057	79	181	-11 - 373	210	279	-15 - 573	1.5	1.5	1.0 – 2.1	70	138	-28 - 304	0.30	0.37	0.18 – 0.56
<b>Visual leopard model</b>	1093	1118	916 - 1320	252	262	120 - 403	394	404	212 - 596	1.7	2.1	0.99 – 3.21	315	274	143 - 405	0.38	0.35	0.20 – 0.51
<b>Exact p value</b>	<b>0.004</b>			0.426			0.339			0.367			0.095			0.958		
<b>Effect size (<math>r</math>)</b>	0.54			0.16			0.20			0.18			0.33			0.02		



**Figure 6.22.** 7 Seconds continuous recording of a male producing (A.) three Roaring Sequences consisting of one snort-introduced 2 phrase RS, followed by a snort-introduced one phrase RS, followed by a snort-introduced 2 phrase RS to an acoustic leopard model, and (B) three Roaring Sequences (RS) consisting of two snort-introduced 2 phrase RS's, followed by a snort-introduced one phrase RS to a visual leopard encounter. Encircled are the first and the last phrases that are produced in the first RS. The x-axis represents time in seconds, the y-axis frequency in kHz.

### Summary and discussion

The monkeys' locomotor responses showed that they approached the visual and acoustic leopard models in equal proportions of trials. They responded with higher vocal response rates and responded for longer to visual than acoustic leopard models. Acoustic analyses revealed a lower second formant frequency (F2) in response to the visual than the acoustic leopard models. For chimpanzee models, results revealed a trend towards a higher response rate to the visual than the acoustic models. Also, the monkeys moved in higher proportions of visual than acoustic chimpanzee trials, but if they moved, they showed similar, random, behaviour.

### **Leopard responses**

The differences in vocal response rate to acoustic and visual leopard models may first of all indicate that localization and visual confirmation are preconditions for conspicuous calling in Guerezas. Secondly, it may indicate that the cognitive processes involved in visual recognition of predators are less dependent on experience than those involved in acoustic recognition (cf. Blumstein, 2000; Blumstein et al. 2008). Lastly, it may indicate that a silent leopard is perceived as more dangerous than a vocalizing one, leading to higher call rates. The differences in F2 frequencies and (arguably) response durations also support the latter hypothesis. Amongst others (e.g. Fichtel et al., 2001; Fischer et al., 2001; Clara et al., 2008; Yorzinski & Vehrencamp, 2008), a study on baboon vocalizations by Rendall (2003) has interpreted the total number of calls produced per bout, as well as the F2 frequency, as indicators of differences of arousal. Rendall (2003) argued that lower F2 frequencies were related to a higher affect intensity in the baboon study, which would suggest that visual leopard models cause a higher perceived affect intensity than acoustic ones. However, as discussed previously (chapter 5), the experimental protocol used in the different studies may be responsible for longer calling durations to the visual predator model. Therefore, this result can not be taken as an indicator of arousal in the present study.

### **Chimpanzee responses**

Monkeys tended to call in a higher proportion of trials to visual than acoustic chimpanzee models, although the default reaction to both was to remain silent. They also moved in a higher proportion of the visual than acoustic model trials; however, in both cases they moved in random directions. These results may suggest that visual chimpanzees are recognized more readily than acoustic chimpanzees. However, the chimpanzees at Sonso can be heard vocalizing very often, suggesting that the monkeys should be as familiar with their vocalizations as with their visual appearance. Therefore, it seems more likely that these results suggest that the animals felt more threatened after encountering a chimpanzee visually than acoustically. Unfortunately, no reliable acoustic data were available to check this possibility in more detail. Moreover, Guerezas seem to call to and approach chimpanzees as part of a specific strategy to advertise aggressive intent or fighting abilities (Chapter 5). Usually, however, this happened after the monkeys were detected by the chimpanzees (personal observation). The fact that the chimpanzees at Sonso did not hunt very much at the time

of the study, may have lead to the less strict display of cryptic behaviour in their presence.

One interpretation of these comparisons is that the Guerezas at Sonso were more aroused when encountering visual than acoustic predator models, although no other independent measures of arousal were available. Previous results have already shown that these monkeys have retained the ability to recognize acoustic and visual leopard models as dangerous predators, although recognition of this predator's physical forms may be less experience dependent than recognition of its calls. Therefore, another interpretation of these results is in terms of differences in predator recognition.

#### **Part 4. The anti-predator behaviour of the Sonso and Kaniyo Pabidi populations**

As described previously, a key difference between the Sonso and Kaniyo Pabidi study areas is that leopards have been absent in Sonso for decades, while eagle density is relatively high, and chimpanzee densities are more or less the same at both sites (Chapter 2). It is possible that the consequent differences in predation risks have lead to differences in locomotor and vocal anti-predator behaviour between the two sites (cf. Hauser, 1988; Fichtel & van Schaik, 2006; Fichtel, 2008). The question addressed in this section is, therefore, whether locomotor and vocal responses of the two Guereza populations differ as a result of the differences in predator abundance and predation risks between the two sites.

##### ***Hypotheses and predictions***

The hypothesis tested with this study was that the differences in predation risks caused differences in the locomotor and vocal behaviour between the two monkey populations. First and foremost, this could be caused by differences in experience. Recognition of predator models may require less effort if monkeys already have experience with a specific predator type. Additionally, differences in predator responses between sites could be caused by differences in perceived risks posed by different predator types, due to abundance. Under both hypotheses, it was predicted that the Guerezas at Sonso responded less strongly to leopards, more strongly to eagles, and equally strongly to

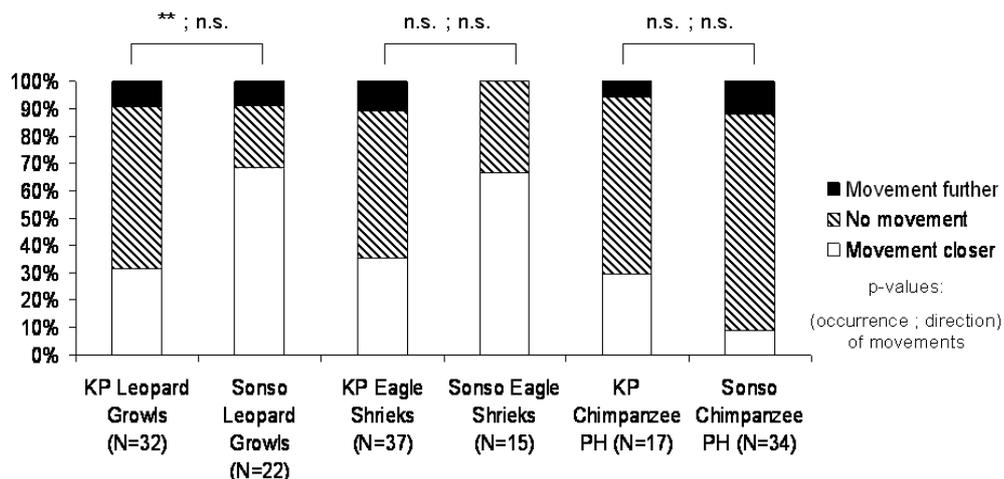
chimpanzees, compared to the ones at Kaniyo Pabidi, especially in the acoustic model conditions.

## Results

### Acoustic predator models

#### Locomotor responses

Comparisons between horizontal locomotor responses of the two monkey populations are shown in Fig. 6.23. In Sonso, the Guerezas were more likely to start moving in response to the acoustic leopard model (exact  $p = 0.012$ , Fisher's exact test, two-tailed). However, once the monkeys moved, they behaved similar at both sites, i.e. with approach (exact  $p = 0.63$ , Fisher's exact test, two-tailed).

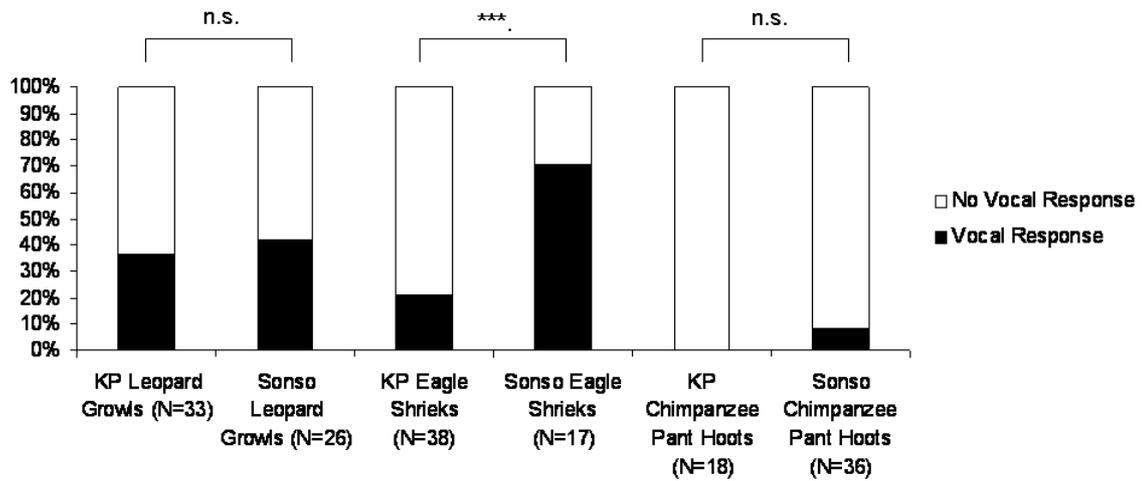


**Figure 6.23.** Locomotor responses in the horizontal plane to the three different acoustic predator models compared between Kaniyo Pabidi and Sonso. The first set of asterisks refers to the difference in occurrence of movement between the contexts; the second set to the difference in direction of movements between the contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < .05$ , \*\* $p < .01$ , \*\*\* $p = .000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

#### Vocal response rate

The results of comparisons between vocal response rates of both monkey populations are presented in Fig. 6.24. One strong difference was that in Sonso the Guerezas were

more likely to produce vocalizations in response to the acoustic eagle model than at Kaniyo Pabidi (exact  $p=0.000$ , Fisher's exact test, two-tailed).



**Figure 6.24.** Vocal response rates to the three different acoustic model trials compared between the two sites. n.s.: no significant difference between the contexts; \*, \*\*, \*\*\*: difference in vocal response rates between the contexts, \*:  $p<.05$ , \*\*:  $p<.01$ , \*\*\*:  $p=.000$  (Fisher's Exact Test,  $\alpha=0.05$ , two-tailed).

### ***Acoustic measurements of vocal response***

The raw data and boxplots of acoustic measurements from individual phrases produced in acoustic model trials in Kaniyo Pabidi are given in Table 4.2 and Fig. 4.6 (chapter 4). For Sonso, similar data are given in Table 6.2 and Fig. 6.6 (present chapter). Table 6.11 presents the results of acoustic comparisons between both sites in responses to the acoustic leopard and eagle models. Results showed that Guerezas at Sonso, compared to Kaniyo Pabidi, produced phrases with lower HNR's in response to acoustic leopard models (all exact  $p$ -values  $<0.015$ , Mann Whitney U test, two tailed, Bonferroni corrected  $\alpha=0.017$ ). Phrases produced in response to acoustic eagle models were identical between the two sites (all exact  $p$ -values  $> 0.043$ , Mann Whitney U test, two-tailed, Bonferroni corrected  $\alpha=0.017$ ).

**Table 6.11.** Statistical output (exact p-values and effect sizes,  $r$ ) of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced within predator modality across sites (within acoustic leopard and eagle contexts, between KP and Sonso; Mann Whitney U test,  $\alpha=0.017$ ).

Acoustic variable		Acoustic leopard model				Acoustic eagle model			
		Between KP and Sonso				Between KP and Sonso			
		First Phrase		Last Phrase		First Phrase		Last Phrase	
		Exact p	r	Exact p	r	Exact p	r	Exact p	r
<b>1<sup>st</sup> RS</b>	Phrase Duration (ms)	0.423	0.21	0.541	0.16	0.904	0.04	0.840	0.06
	HNR(dB)	<b>0.002</b>	0.70	<b>0.015</b>	0.58	0.140	0.36	0.762	0.08
	First Formant (Hz)	0.114	0.40	0.963	0.02	0.075	0.42	0.177	0.32
	Second Formant (Hz)	0.036	0.51	0.423	0.21	0.075	0.42	0.272	0.27
	Peak Frequency (Hz)	0.905	0.04	0.621	0.13	0.888	0.04	0.122	0.36
	Number of pulses	0.410	0.23	0.533	0.17	0.820	0.06	0.466	0.18
	Fundamental Freq (Hz)	0.054	0.51	0.425	0.21	0.310	0.25	0.778	0.08
<b>2<sup>nd</sup> RS</b>	Phrase Duration (ms)	0.174	0.36	0.758	0.09	0.762	0.08	0.515	0.17
	HNR(dB)	<b>0.003</b>	0.70	<b>0.004</b>	0.72	0.474	0.18	0.959	0.03
	First Formant (Hz)	0.918	0.04	0.142	0.38	0.043	0.48	0.083	0.42
	Second Formant (Hz)	0.299	0.28	0.189	0.36	0.122	0.38	0.146	0.36
	Peak Frequency (Hz)	0.236	0.31	0.851	0.05	1.000	0	0.348	0.23
	Number of pulses	0.077	0.46	0.982	0.01	0.493	0.18	0.679	0.11
	Fundamental Freq (Hz)	0.189	0.36	0.025	0.56	0.481	0.19	0.360	0.23

### Composition of Roaring Sequences

The raw data and boxplots of temporal measurements from responses to acoustic leopard and eagle models in Kaniyo Pabidi are given in Table 4.4 and Fig. 4.7 (Chapter 4), and in Table 6.4 and Fig. 6.7 for Sonso (present chapter). Comparisons showed that the structural features of acoustic eagle model responses were identical at both sites (all exact p-values  $>.19$ , Mann Whitney U test, two tailed). However, responses to the acoustic leopard model differed: in Sonso, Guerezas produced significantly more snorts ( $U=12.5$ ,  $p_{\text{exact}} = 0.011$ ,  $r=0.58$ ). Effect sizes for total calling duration ( $U=16$ ,  $p_{\text{exact}}=0.030$ ,  $r=0.51$ ), number of RS ( $U=15$ ,  $p_{\text{exact}}=0.024$ ,  $r=0.53$ ), and number of roaring phrases ( $U=15$ ,  $p_{\text{exact}} = 0.024$ ,  $r=0.53$ ) were strong, even though not significant after a Bonferroni correction. However, the call delivery rate ( $U=31$ ,  $p_{\text{exact}} = 0.422$ ,  $r=0.20$ ) and number of phrases per roaring sequence did not differ between the sites ( $U=33$ ,  $p_{\text{exact}} = 0.532$ ,  $r=0.16$ ; Table 6.12).

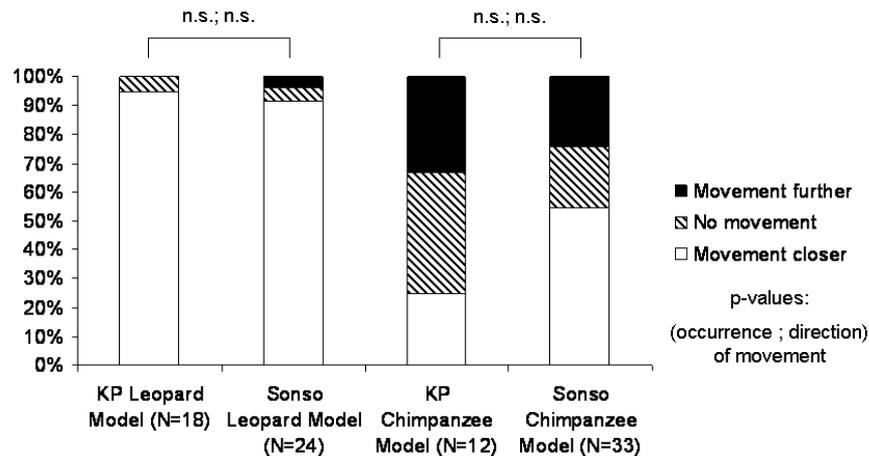
**Table 6.12.** Statistical output (exact p-values and effect sizes,  $r$ ) of the Mann Whitney U Test to compare temporal measurements within acoustic predator model context across sites ( $\alpha=.017$ ).

Predator model	Acoustic leopard model between KP and Sonso		Acoustic eagle model between KP and Sonso	
	Exact p	$r$	Exact p	$r$
Calling duration (s)	0.030	0.51	0.840	0.06
Total number of RS	0.024	0.53	0.887	0.04
Total number of Phrases	0.024	0.53	0.920	0.03
Phrases per RS	0.532	0.16	0.984	0.01
Snorts	<b>0.011</b>	0.58	0.183	0.31
Call delivery Rate	0.422	0.20	0.545	0.15

### Visual Model experiments

#### Locomotor responses

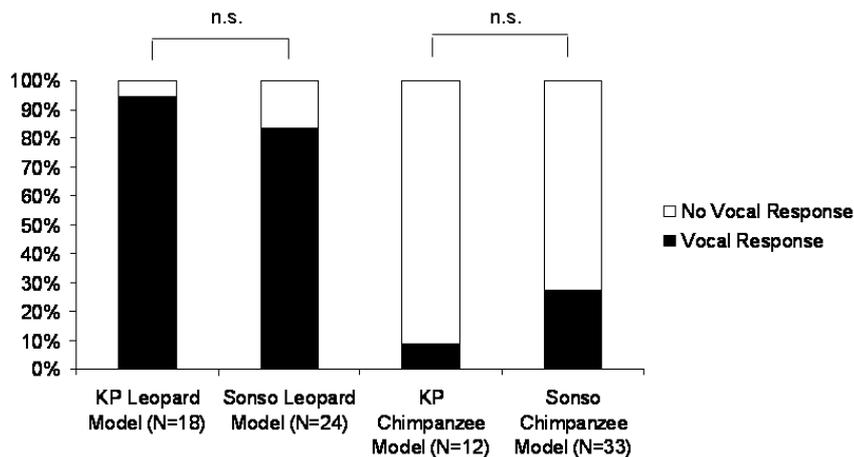
Comparisons between horizontal locomotor responses of the two monkey populations are presented in Fig. 6.25. No differences were found in any of the contexts: the monkeys behaved similar in Kaniyo Pabidi and Sonso after encountering visual leopard and chimpanzee models.



**Figure 6.25.** Locomotor responses in the horizontal plane in response to the two different visual predator models, compared between Kaniyo Pabidi and Sonso. The first set of asterisks refers to the difference in occurrence of movement between the contexts; the second set to the difference in direction of movements between the contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p = 0.000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

### Vocal responses

Results of comparisons between vocal response rates of both monkey populations are presented in Fig. 6.26. No differences were found in any of the contexts: the monkeys showed similar response rates in Kaniyo Pabidi and Sonso after encountering visual leopard and chimpanzee models.



**Figure 6.26.** Vocal response rates to the two different visual model trials compared between the two sites.

n.s.: no significant difference between the contexts; \*, \*\*, \*\*\*: difference in vocal response rates between the contexts, \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p = 0.000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

### Acoustic measurements of vocal response

The raw data and boxplots of acoustic measurements from individual phrases produced in visual model trials in Kaniyo Pabidi are given in Table 5.2 and Fig. 5.7 (chapter 5), and in Table 6.6 and Fig. 6.14 for Sonso (present chapter). Table 6.13 shows the results of acoustic comparisons between both sites in response to the visual leopard and chimpanzee models. There was a trend towards a higher peak frequency in individual 'last' roaring phrases in response to visual leopard model in Sonso compared to Kaniyo Pabidi (all exact  $p$ -values  $< 0.059$ , Mann Whitney U test, two-tailed, Bonferroni corrected  $\alpha = 0.017$ ). Statistical comparison of vocal responses to chimpanzee models could not be made due to small sample size.

**Table 6.13.** Statistical output (exact p-values and effect sizes,  $r$ ) of comparisons between acoustic measurements of first and last phrases of the first and second Roaring Sequences produced within predator modality across sites (within visual leopard context, between KP and Sonso; Mann Whitney U test,  $\alpha=.017$ ).

Acoustic variable		Visual leopard model			
		Between KP and Sonso			
		First Phrase		Last Phrase	
		Exact p	r	Exact p	r
<b>1<sup>st</sup> RS</b>	Phrase Duration (ms)	0.080	0.38	0.771	0.07
	HNR (dB)	0.305	0.22	0.872	0.04
	First Formant (Hz)	0.722	0.08	0.228	0.27
	Second Formant (Hz)	0.628	0.11	0.140	0.32
	Peak Frequency (Hz)	0.219	0.27	0.059	0.41
	Number of pulses	0.082	0.37	0.931	0.02
	Fundamental Freq (Hz)	0.456	0.17	0.037	0.44
<b>2<sup>nd</sup> RS</b>	Phrase Duration (ms)	0.261	0.25	0.418	0.18
	HNR (dB)	0.872	0.04	0.346	0.21
	First Formant (Hz)	0.821	0.06	0.381	0.20
	Second Formant (Hz)	0.923	0.03	0.539	0.14
	Peak Frequency (Hz)	0.808	0.06	0.047	0.42
	Number of pulses	0.152	0.31	0.634	0.11
	Fundamental Freq (Hz)	0.203	0.28	0.593	0.12

### **Composition of Roaring Sequences**

The raw data and boxplots of temporal measurements from visual leopard and chimpanzee model responses produced in Kaniyo Pabidi are given in Table 5.5 and Fig. 5.8 (Chapter 5), and in Table 6.8 and Fig. 6.15 for Sonso (present chapter). Comparisons of temporal characteristics of vocal responses to visual leopard models across sites revealed no differences; Guerezas at both sites responded with a large number of roaring sequences consisting of a few phrases each (Table 6.14).

**Table 6.14.** Statistical output (exact p-values and effect sizes, *r*) of the Mann Whitney U Test to compare temporal measurements within the visual leopard model context across sites ( $\alpha=.017$ ).

Temporal parameter	Visual Leopard model between KP and Sonso	
	Exact p	r
Calling duration (s)	0.288	0.23
Total number of RS	0.065	0.38
Total number of Phrases	0.075	0.37
Phrases per RS	0.151	0.30
Snorts	0.087	0.36
Call delivery Rate	0.418	0.17

## Summary and discussion

### *Summary acoustic model experiments*

#### **Leopards**

Locomotor responses to acoustic leopard models differed across sites: at Sonso, the Guerezas approached the leopard growls in a higher proportion of trials than at Kaniyo Pabidi. Vocal response rates to acoustic leopard models were similar between the sites, but if the monkeys called, individual roaring phrases produced at Sonso were noisier than in Kaniyo Pabidi. Furthermore, Guerezas at Sonso responded with alarms containing more snorts than those produced by their relatives in Kaniyo Pabidi. The temporal patterning of roaring sequences was similar across sites.

#### **Eagles**

Locomotor responses to acoustic eagle models were similar across sites; occurrence of movement was random, and if movement occurred the monkeys approached the stimulus. The vocal response rates to acoustic eagle models, however, differed strikingly between the two sites: at Sonso, compared to Kaniyo Pabidi, the monkeys responded much more strongly. Acoustic measurements of individual roaring phrases produced to acoustic eagle models at both sites did not differ, and temporal patterning of roaring was similar at both sites as well.

#### **Chimpanzees**

Within site comparisons of locomotor responses to acoustic chimpanzee models showed a random response in the occurrence of movements by Guerezas at Kaniyo

Pabidi, and a preference to move at Sonso. Statistical tests across sites, however, showed no differences. Vocal response rates to acoustic chimpanzee models were similar: Guerezas were most likely to remain silent at both sites. In Kaniyo Pabidi, the animals did not respond vocally at all in response to the acoustic chimpanzee model, whereas in Sonso they produced a few vocal responses. No acoustic comparisons between the sites were possible because of the lack of response in Kaniyo Pabidi.

### ***Summary visual model experiments***

#### **Leopards**

Locomotor responses to visual leopard models were similar at Kaniyo Pabidi and Sonso: the monkeys moved closer to the model. Vocal response rates to this stimulus were also similar: at both sites, the Guerezas responded strongly after detecting the visual leopard model. Furthermore, temporal patterning of roaring in response to visual leopard models was similar at both sites as well.

#### **Chimpanzees**

Although within site comparisons of locomotor responses showed a random response by Guerezas at Kaniyo Pabidi, and a preference to move in response to the visual chimpanzee model in Sonso, the statistical test comparing locomotor responses across sites showed no differences in occurrence of movement. The direction of movements was random at both sites. The vocal response rates to this stimulus were also similar at both sites: the animals were most likely to remain silent to visual chimpanzee models. Chimpanzee responses in Kaniyo Pabidi were not sufficient to conduct reliable acoustic comparisons between the sites for the chimpanzee context.

Hence, the results of this study showed some differences between study sites in the Guerezas' locomotor and vocal predator responses, that may be related to the different predation risks present at the two sites (discussed below).

### ***Discussion***

#### **Leopard presence: experience**

One relevant finding was that the Guerezas at Sonso approached the acoustic leopard model more frequently than the Guerezas at Kaniyo Pabidi. At Sonso, the Guerezas

most likely had no experience with this predator's vocalizations, but still seemed to interpret leopard vocalizations as something dangerous, despite their lack of experience. In contrast, leopards are present in Kaniyo Pabidi, indicating that Guerezas at this site have more experience, and consequently may have formed associations between a leopard's vocalizations and its physical appearance. Thus, approaches to inspect the source of disturbance may be less urgent. Strikingly, the presentation of visual leopard models did not lead to any differences in locomotor responses across sites. This overall pattern is consistent with the hypothesis that visual predator recognition is less experience dependent than acoustic predator recognition (Blumstein et al., 2000; Blumstein et al., 2008).

Nevertheless, in previous chapters, it was argued that approaching a predator can also be part of a 'perception advertisement' anti-predator strategy, which is useful against stalking predators, such as leopards. The fact that there was a difference in approach rates between sites, but not in vocal response rates, suggests that the monkeys at Sonso approached in order to inspect the source, whereas the Guerezas at Kaniyo Pabidi already recognized the vocalizations, and thus started calling right away, as part of their general perception advertisement strategy to leopards. Apart from these differences in approach rates, no other differences were found in relation to leopard presence.

### **Leopard presence: arousal**

Arousal is often invoked as an explanatory variable in animal behaviour. Although no specific data were collected to measure arousal independently in this study, it may be that the differences in the vocal characteristics between sites are the product of different affective states. For example, animals experiencing a negative affective state and/or higher affect intensity tend to produce noisy and high pitched calls, with a greater number of calls produced per response or time period (e.g. Fichtel et al. 2001; Rendall, 2003; Clara et al. 2008). Following this logic, the monkeys at Sonso experienced a more intense affective state (higher arousal) than the animals in Kaniyo Pabidi when confronted with an acoustic (but not a visual) leopard model. This is because acoustic analyses of their roars revealed that they were noisier than those in Kaniyo Pabidi. The monkeys at Sonso also produced more snorts in response to this stimulus. Hence, despite their lack of experience with leopard vocalizations, the Guerezas at Sonso responded strongly to leopard-related stimuli, especially the acoustic ones. Of course,

one could now argue that the monkeys at Sonso experienced higher arousal because they perceived the sounds as disturbing and potentially dangerous but then did not have the means to directly associate the sounds with a particular predator type. Guerezas, in other words, may experience decreased levels of arousal when knowing a predator than when having to deal with uncertain situations or unknown dangers.

#### **Eagle presence: experience**

Calling in response to eagles appears to be used as an aggressive display, most importantly during direct encounters. However, although the Guerezas at both sites did not encounter the eagle directly (because of the experimental setup), they called in response to its vocalizations occasionally, and in a higher proportion at Sonso than at Kaniyo Pabidi. Differences in predator recognition at the two sites are probably irrelevant. Even though eagle abundance is lower in Kaniyo Pabidi, the monkeys showed adaptive locomotor behaviour in response to the vocalizations of this predator, indicating that they recognised this predator by acoustic cues. The differences in response rates may be a sign of differences in experience in how to best deal with this predator. Due to the high eagle abundance at Sonso, the Guerezas at this site are frequently observed chasing away eagles while roaring fiercely. Because of these frequent interactions, the monkeys at Sonso may have learned to use their calling preemptively, i.e. before any physical interaction has taken place.

#### **Eagle presence: arousal**

Another hypothesis was that higher eagle abundance at Sonso had led to higher affect intensity perceived by the monkeys. The acoustic features of individual phrases thought to relate to affect intensity (e.g. HNR) did, however, not differ between the sites in the present study. Thus, following the earlier argument made for leopards, affect intensity can probably not explain the occurrence of higher call rates to acoustic eagle models in Sonso than Kaniyo Pabidi, because the Sonso individuals are more familiar with crowned eagles.

#### **Chimpanzee presence: experience**

The responses to chimpanzees did not differ between the two sites. Chimpanzee abundance is more or less equal at both sites, although hunting pressures may differ slightly. Guerezas at both sites, however, seemed to recognize the acoustic and visual

models of these predators as something that is best avoided by remaining cryptic, which probably is the most adaptive strategy to adopt in the presence of chimpanzees. However, occasional calling was observed in response to chimpanzees, most importantly to the visual model in Sonso. Although this was not the default response, and the monkeys preferred to remain silent, the occurrence of calling may be explained by differences in experience. The monkeys in Sonso may have learned through their many encounters with chimpanzees, that they can fight them successfully. This experience may have relaxed and adapted their strictly cryptic responses.

### **Chimpanzee presence: arousal**

Most likely, the appearance of a silent chimpanzee will be more arousing than hearing a chimpanzee's vocalizations. Normally, when chimpanzees are hunting, they do this silently, and may just emit calls just before or during the actual hunt. Nevertheless, no differences were found in the responses to the acoustic and visual chimpanzee model. This can be explained by the fact that the default response to a chimpanzee is to remain cryptic, especially when at great risk. It thus appears counter-intuitive to try and assess arousal solely from the monkeys' behavioural responses, because they will probably be even less responsive to visual chimpanzees than to acoustic chimpanzees.

Hence, the overall conclusion of the present chapter is that Guerezas at both sites recognise predators by visual and acoustic cues. The Guerezas at Sonso have retained this ability in the case of leopards, which are recognised as dangerous even in the absence of individual experience. Recognition was more accurate in the visual than in the acoustic domain, supporting the hypothesis that visual predator recognition is less experience dependent than acoustic predator recognition (Blumstein, 2000; Blumstein et al., 2008). Although the arousal hypothesis is difficult to test with these data, it appeared that, within sites, visual predator models caused higher arousal in Guerezas than acoustic models, represented by differences in acoustic parameters such as HNR and F2. Between sites, differences in experience seem to have led to site specific adaptive behaviour with respect to the predator specific anti-leopard and – eagle responses, especially in response to their vocalizations. Finally, it is argued that less experience with predators may lead to higher levels of arousal in Guerezas.

## Chapter 7

### **Responses to conspecific alarm vocalisations in Kaniyo Pabidi and Sonso**

#### **Introduction**

In the previous experiments the Guereza monkeys responded with adaptive responses to the hunting techniques used by their predators. In response to leopard growls, there was a tendency to approach the stimulus, to eagle shrieks the monkeys consistently moved down and approached the stimulus, while to chimpanzee pant hoots, they generally moved up. Guereza monkeys responded stronger to visual than acoustic models of a leopard, suggesting that perception advertisement is an important way of dealing with this predator. Such a difference was not found in the chimpanzee context where visual and acoustic models triggered the same cryptic response. Calling to chimpanzees may be used as a last resort after detection. Natural observations of eagle encounters confirmed that the monkeys chase eagles out of their territory, while roaring fiercely, which could be replicated by playback experiments. These observations suggested that the calls in this context display aggressive intent.

Experiments conducted at Sonso suggested that monkeys still recognized leopards as a dangerous source, although this predator has been locally extinct for several decades. When comparing responses to eagles and leopards, the monkeys produced roaring sequences with differing structures suggesting that the calls have the potential to convey information about predator type. The acoustic responses to leopard and chimpanzee models at Sonso did however not show any acoustic differences between them, suggesting that it may be used as a general ground predator alarm at this site.

To determine whether the Guerezas' alarm sequences appear meaningful to conspecific receivers, in this chapter the results of a playback study are presented, in which the different predator alarm vocalizations were played back to nearby monkeys. Locomotor and vocal responses were recorded and compared with the responses to acoustic and visual predator models.

Several studies have shown that some primates can produce discrete acoustic signals in response to different predator types, which appear meaningful to recipients (e.g. Seyfarth et al., 1980; Macedonia, 1990; Zuberbühler et al., 1997; Zuberbühler, 2000; Zuberbühler, 2001; Fichtel & Kappeler, 2002; Kirchhof & Hammerschmidt, 2006). These signals can function in conspecific warning, because group members seem to infer the nature of the eliciting stimulus and respond with specific anti-predator behaviour adapted to the predator type; Cheney and Seyfarth (1990), Marler et al. (1992), Seyfarth and Cheney (2003).

Other studies have argued that conspecific warning may not be the only evolved function of predator alarm calling. Signallers may be targeting the predator (Woodland et al., 1980; Zuberbühler et al., 1997) while conspecifics are mere eavesdropping (Owings, 1994). However, such signals can still be meaningful to receivers, if they manage to learn the relationship between event and call type. A predator's sensory and psychological specializations, rather than those of the conspecific receiver, could then have acted as the main selection pressure in the evolution of form and patterning of alarm signals (e.g. Owings & Morton, 1997; Rundus et al., 2007).

The aim of the present study was to determine whether the Guerezas' alarm sequences are meaningful to conspecific receivers. As the vocal responses to the different predator types showed strong context related differences in the temporal structure and differences in the number of snorts it is likely that nearby monkeys are able to make inferences about the type of predator encountered by the caller.

### ***Hypotheses and predictions***

The hypothesis tested with this study was that the alarm sequences contained information about the predator type encountered by the caller. The prediction was that recipients would respond with the anti-predator behaviour already described in response to the predator model experiments (chapters 4, 5 and 6). The alternative was that the alarm sequences produced in response to the different predator types did not contain any information about the predator or type of threat encountered by the signaller, but merely indicated the presence of a conspecific stranger. Guerezas usually do not roar in intergroup encounters, but they may produce tongue clicks and grunts

while jumping around noisily and conspicuously (Marler, 1972, Harris, personal communication, personal observation). Hence, under this hypothesis the prediction was that the recipients would start conspicuous behavioural displays, as described by Marler (1972), but not produce roars.

Not all primate species reliably respond to conspecifics alarm calls with their own alarm calls, but they usually do respond with their predator-specific anti-predator behaviour (e.g. Cheney & Seyfarth, 1990; Zuberbühler et al., 1997; Zuberbühler, 2001; Fichtel et al., 2005). However, if counter-calling occurs, then it is usually similar to those calls just heard. In chapter 3, playbacks of conspecific morning choruses yielded only a very low response rate from the neighbouring Guerezas, suggesting that the recipients' locomotor responses in the present study provide an equally important set of dependent variables.

A second aim of this chapter was to test whether the alarm calls given to leopards and chimpanzees are general ground predator alarms (cf. section 2 'visual models', chapter 6) or whether they conveyed more detailed information about the predator type present. In the latter case, the monkeys were predicted to respond with predator-specific anti-predator behaviour, i.e. move up silently in response to chimpanzee-elicited roars and respond with roars and approach to leopard-elicited roars.

## **Part 1: Playback of conspecific alarms in Kaniyo Pabidi**

### **Methods**

#### ***Playback stimuli***

Playback stimuli of conspecific alarm responses were edited from vocal responses on acoustic predator models recorded in Sonso. In Sonso, no acoustic differences were found in the vocal responses to visual leopard and chimpanzee models, but it is of course possible that some subtle features were not measured. Hence, leopard and chimpanzee responses recorded in Sonso were played back to different groups in Sonso and Kaniyo Pabidi as well, to test whether the two responses were perceived differently.

### ***Playback protocol, data collection, and analyses***

The general methods used in the playback experiments were described in chapter 2. In short, naïve monkey groups were located during daytime. If the animals remained unaware of the presence of the observers, and no other disturbances had occurred, a playback experiment was conducted. Stimuli consisted of 5 minutes silence followed by 15 seconds of alarm vocalizations, either leopard, eagle or chimpanzee responses. Around 3 minutes before the playback was broadcast to the monkeys, the observers started to record the animals' vocal behaviour from a hiding place. Recordings lasted for the entire duration of the vocal response lasted, at least 15 minutes. Recordings were then transferred onto a PC using Cool Edit 2000. The first and last phrases of the first and last roaring sequences produced were then subjected to acoustic analyses using Raven 1.2 and Praat. 4.3.12.

The following six structural parameters were determined using spectrograms generated on RAVEN 1.2: **(a)** total duration of the vocal response (s), **(b)** total number of roaring sequences, **(c)** total number of roaring phrases, **(d)** mean number of roaring phrases per roaring sequence, **(e)** number of snorts, and **(f)** call delivery rate (phrases/s; cf. Oates & Trocco, 1983).

To compare the acoustic structure of individual roaring phrases given to the different playbacks, seven acoustic variables were measured: **(a)** phrase duration (ms) **(b)** number of pulses per roaring phrase, and **(c)** fundamental frequency (Hz) were measured using SPG's generated with Raven 1.2. The remaining four variables were extracted using PRAAT 4.3.12: **(d)** harmonics-to-noise ratio (HNR, dB), **(e)** first and **(f)** second formants (Hz), and **(g)** peak frequency (Hz).

Finally, the locomotor responses elicited by the different playback stimuli were scored, using a protocol described in chapter 2.

### **Results**

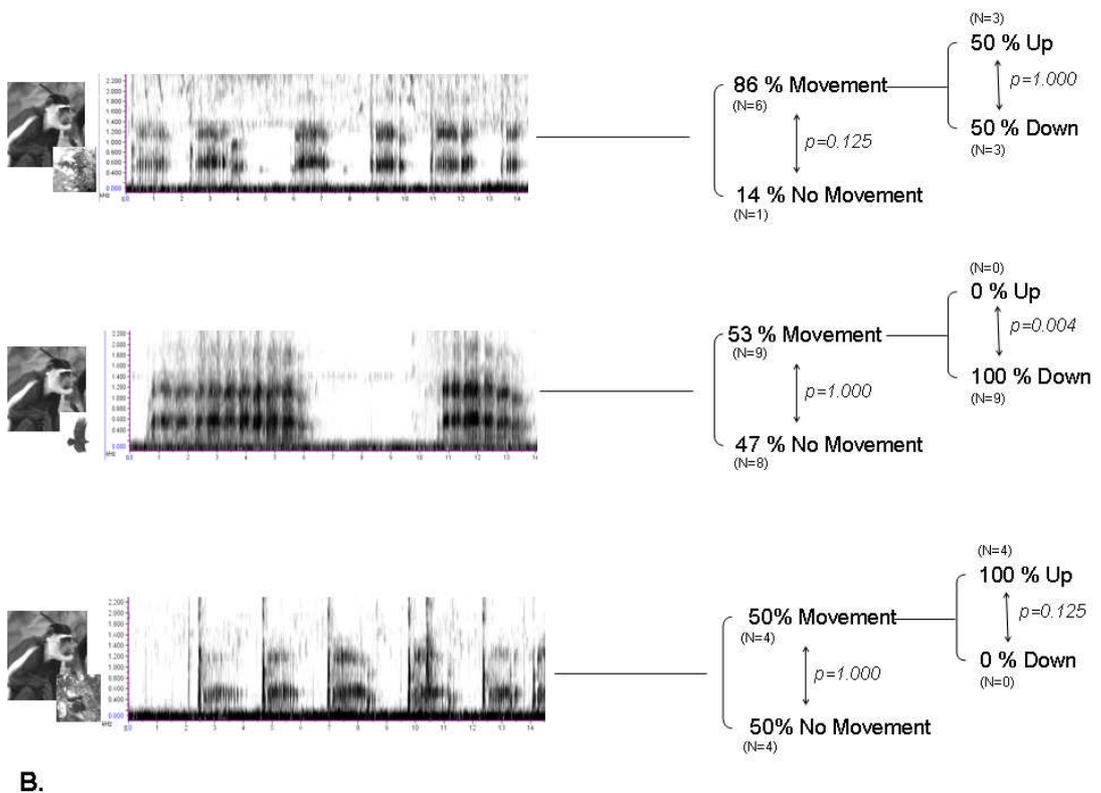
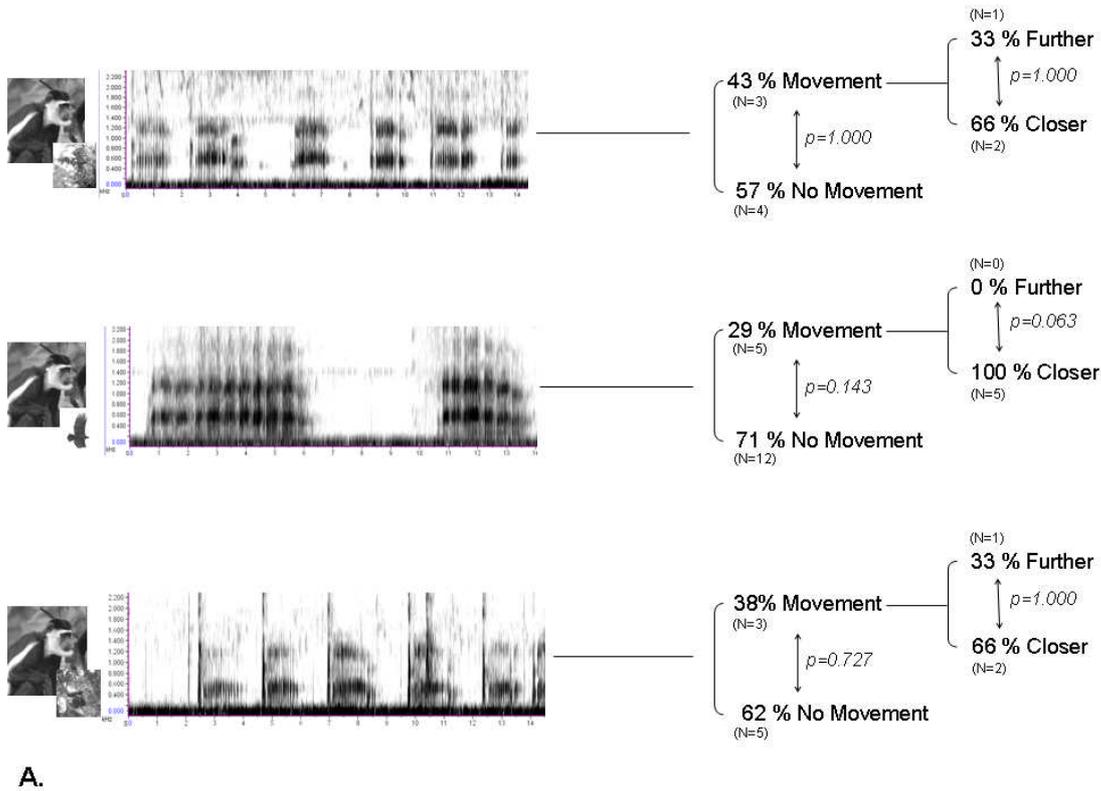
Leopard alarms were played back to N= 7 different groups, eagle alarms to N= 17 different groups, and chimpanzee alarms to N= 8 different groups. No trial had to be discounted, and in all cases it was possible to observe the animals' movements in both the horizontal and vertical planes.

**Behavioural response characteristics**

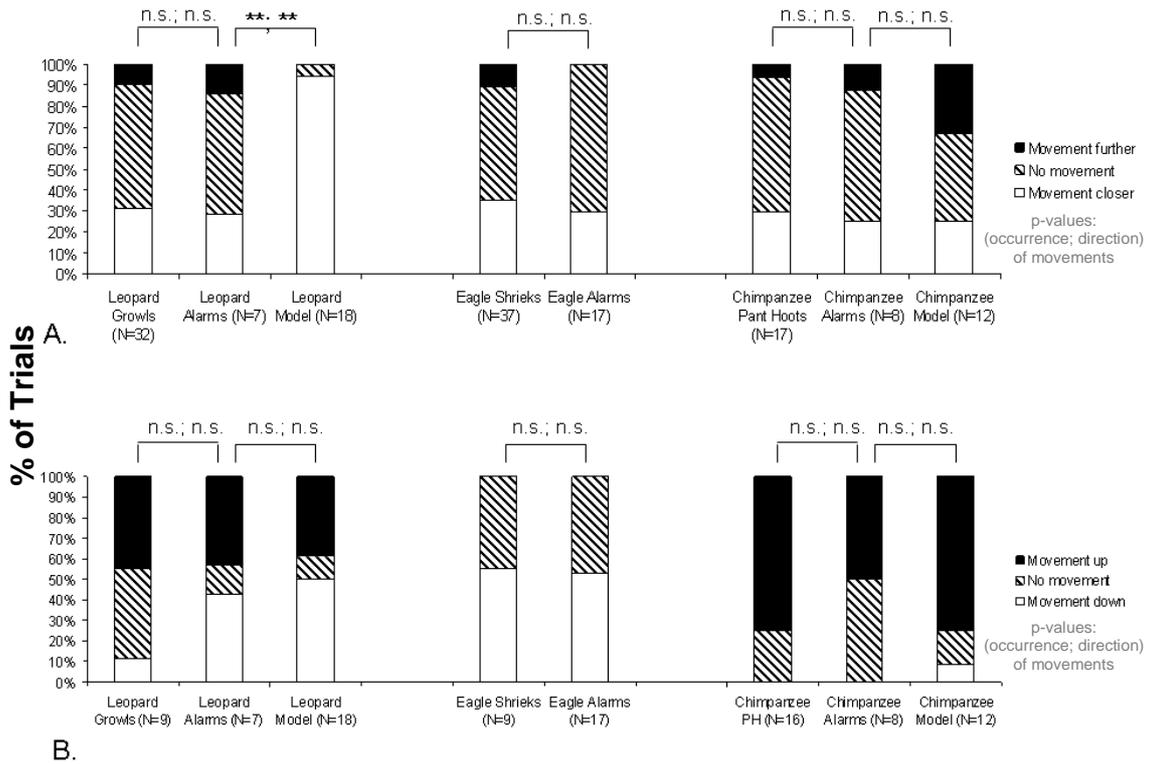
Monkeys were equally likely to move or remain where they were after hearing leopard alarms, both in the horizontal and vertical plane (horizontal:  $N_{\text{Move}}=3$ ;  $N_{\text{Not Move}}=4$ , exact  $p=1.000$ ; vertical:  $N_{\text{Move}}=6$ ;  $N_{\text{Not Move}}=1$ , exact  $p=0.125$ , binomial test). If they moved, they did not do so consistently in a particular direction in either of the planes (horizontal:  $N_{\text{Further}}=1$ ;  $N_{\text{Closer}}=2$ , exact  $p=1.000$ ; vertical:  $N_{\text{Up}}=3$ ;  $N_{\text{Down}}=3$ , exact  $p=1.000$ , Fig. 7.1). These behavioural responses resembled those to the leopard growls (all exact  $p$ -values  $>0.26$ , Fisher's Exact tests, two-tailed), but differed from the response to the visual leopard model (visual leopard:  $N_{\text{Move}}=17$ ;  $N_{\text{Not Move}}=1$ ; leopard alarms:  $N_{\text{Move}}=3$ ;  $N_{\text{Not Move}}=4$ , exact  $p=0.012$ , Fisher's Exact Test, two-tailed, Fig. 7.2). If the monkeys moved in the latter contexts, they approached more often in response to the visual leopard model than in response to the leopard alarms (visual leopard model:  $N_{\text{Further}}=0$ ;  $N_{\text{Closer}}=17$ ; conspecific leopard alarms:  $N_{\text{Further}}=1$ ;  $N_{\text{Closer}}=2$ , exact  $p=0.002$ , Fisher's Exact Test, two-tailed; figure 7.2).

In response to eagle alarms, the monkeys were equally likely to move or stay where they were in both the horizontal and vertical plane (horizontal:  $N_{\text{Move}}=5$ ;  $N_{\text{Not Move}}=12$ , exact  $p=0.143$ ; vertical:  $N_{\text{Move}}=9$ ;  $N_{\text{Not Move}}=8$ , exact  $p=1.000$ , binomial test). If they moved, they tended to approach the stimulus (horizontal:  $N_{\text{Further}}=0$ ;  $N_{\text{Closer}}=5$ , exact  $p=0.063$ , binomial test) and moved down in the tree (vertical:  $N_{\text{Up}}=0$ ;  $N_{\text{Down}}=9$ , exact  $p=0.004$ , binomial test; Fig. 7.1). These behavioural responses were similar to those in response to the playbacks of eagle shrieks (all exact  $p$ -values  $>0.29$ , Fisher's Exact tests, two-tailed, Fig. 7.2).

In response to the chimpanzee alarms, the monkeys were equally likely to move or stay where they were in both the horizontal plane and vertical plane (horizontal:  $N_{\text{Move}}=3$ ;  $N_{\text{Not Move}}=5$ , exact  $p=0.727$ ; vertical:  $N_{\text{Move}}=4$ ;  $N_{\text{Not Move}}=4$ , exact  $p=1.000$ , binomial test). If they moved, they moved up on all occasions, although sample sizes were too small to reveal this as a significant effect (horizontal:  $N_{\text{Further}}=1$ ;  $N_{\text{Closer}}=2$ , exact  $p=1.000$ ; vertical:  $N_{\text{Up}}=4$ ;  $N_{\text{Down}}=0$ , exact  $p=0.125$ , binomial test; Fig. 7.1). These behavioural responses were similar to those in response to acoustic and visual chimpanzee models (all exact  $p$ -values  $>0.16$ , Fisher's Exact tests, two-tailed, Fig. 7.2).



**Figure 7.1.** Monkeys' locomotor behaviour in A. the horizontal plane and B. the vertical plane in response to the acoustic models, with corresponding percentages of movements and exact p-values of the differences between locomotor responses within contexts (Binomial tests,  $\alpha=0.05$ , two-tailed).

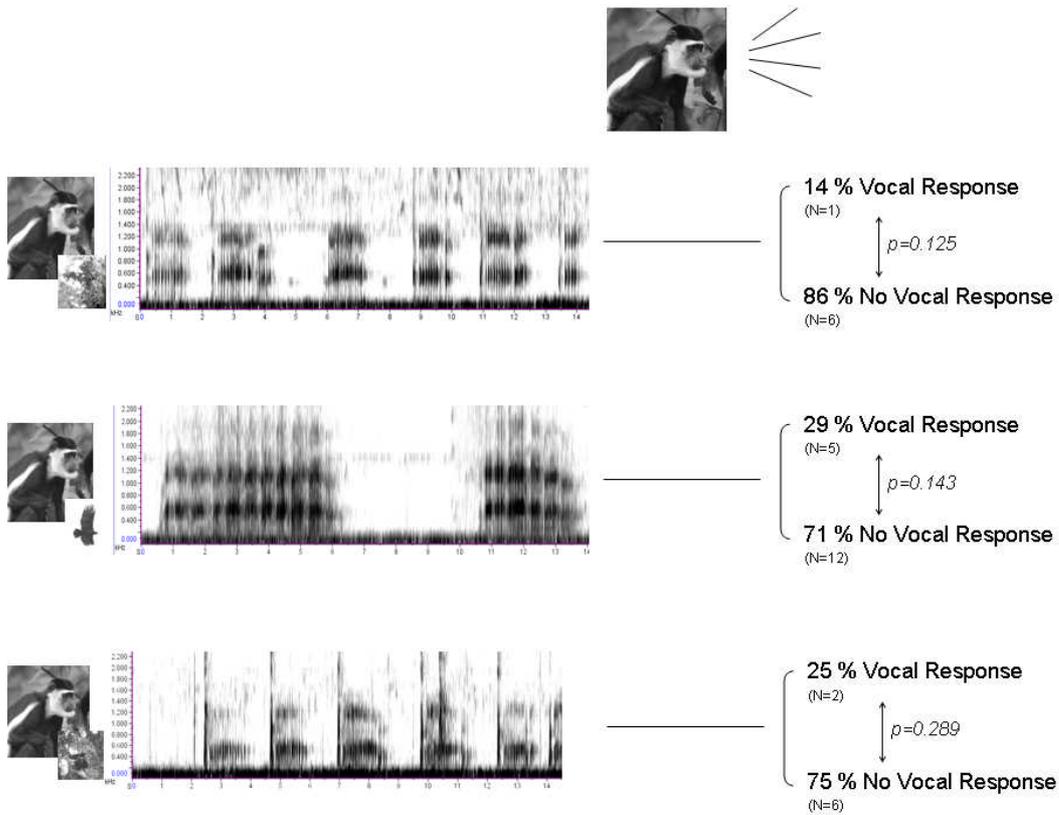


**Figure 7.2.** Locomotor responses in the horizontal and vertical plane to the different stimulus types. The first set of asterisks in any graph refers to the difference in occurrence of movement between two contexts; the second set to the difference in direction of movements between two contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < .05$ , \*\*  $p < .01$ , \*\*\*  $p = .000$  (Fisher’s Exact Test,  $\alpha = 0.05$ , two-tailed).

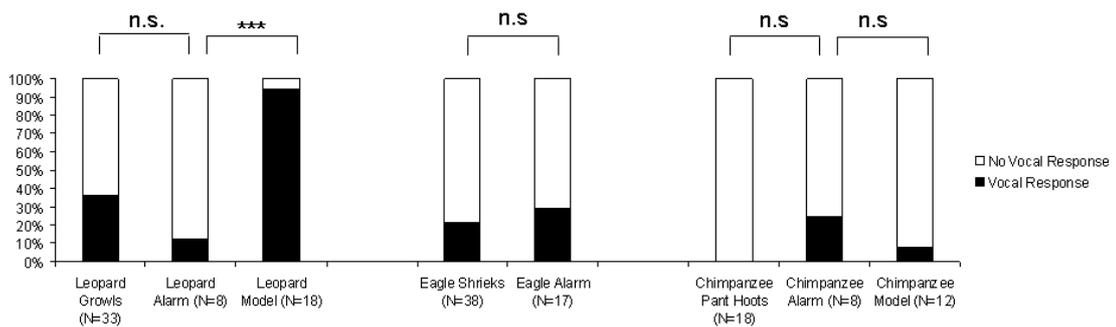
**Vocal Response characteristics to conspecific alarm responses**

In 1 of 7 trials with leopard alarms the monkeys responded with vocalizations (response rate=14.3%; binomial test: exact  $p = 0.125$ , Fig. 7.3). This response rate did not differ from the one to the acoustic leopard model (response rate: 36.4%; exact  $p = 0.39$ , Fisher’s Exact Test, two-tailed), but it differed from the one to visual leopard models (response rate: 94%; exact  $p = 0.000$ , Fisher’s Exact Test, two-tailed, Fig. 7.4). In 5 of 17 trials with eagle alarms the animals responded with vocalisations (response rate=29.4%; binomial test: exact  $p = 0.143$ , Fig. 7.3). This response rate did not differ from that given to eagle shrieks (response rate: 21%;  $p_{\text{exact}} = 0.31$ , Fisher’s Exact Test, two-tailed, Fig. 7.4). Finally, in 2 of 8 trials with chimpanzee alarms the animals responded with vocalizations (response rate = 25%; binomial test: exact  $p = 0.289$ , Fig. 7.3). This response rate did not differ from that given to either the acoustic and visual

chimpanzee models (0 %; 0/18: exact  $p=0.09$ ; 8%; 1/12: exact  $p=0.54$  respectively; Fig. 7.4).



**Figure 7.3** Vocal response rates of the monkeys to the three different acoustic models in Kaniyo Pabidi, with corresponding exact p-values (Binomial test,  $\alpha=0.05$ , two-tailed).



**Figure 7.4.** Vocal response rates to the different model types in Kaniyo Pabidi, with exact p-values. n.s.: no significant difference between the contexts; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in vocal response rates between the contexts, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p = 0.000$  (Fisher's Exact Test,  $\alpha = 0.05$ , two-tailed).

**Acoustic measurements of vocal responses**

As predicted, the number of vocal responses to the conspecific alarm sequences was low, and not sufficient to conduct meaningful acoustic comparisons (Table 7.1). However, preliminary inspection of the few vocal responses indicated that the structure of roaring sequences produced in response to the different conspecific alarm sequences was generally similar to those produced in the corresponding predator contexts. Most importantly, the number of roaring phrases per sequence corresponded well with that found in the actual predator contexts, indicating that the monkeys produced identical sequences either when confronted with the predators themselves or with corresponding conspecific predator alarms: long roaring sequences after hearing a conspecific eagle alarm, and short roaring sequences after hearing a conspecific leopard alarm.

**Table 7.1.** Number of trials conducted with conspecific alarms, vocal response rates and number of trials used for subsequent acoustic analyses.

	Nr valid trials	Response Rate		Suitable for Temporal Analyses	Suitable for Spectral Analyses	
		N	%		First RS	Second RS
<b>Leopard growls</b>	33	12	36.4	9	8	7
<b>Leopard Alarms</b>	7	1	14.3	1	1	1
<b>Leopard Model</b>	18	17	94.4	7	10	10
<b>Eagle Shrieks</b>	38	8	21	8	8	8
<b>Eagle Alarms</b>	17	5	29.4	5	4	4
<b>Chimpanzee PH</b>	18	0	0	0	0	0
<b>Chimpanzee Alarm</b>	8	2	25	2	2	2
<b>Chimpanzee Model</b>	12	1	8.3	1	1	1

Thus, both the locomotor and (preliminary) vocal responses to the conspecific alarms produced in response to the leopards, eagles and chimpanzees seemed identical to the responses on the corresponding acoustic predator models (leopard growls, eagle shrieks or chimpanzee pant hoots). Although the data set is fairly small, in response to leopard alarms, the Guerezas moved either up or down the tree, and were equally likely to

move further or closer to the stimulus. In response to eagle alarms, they moved down and approached the stimulus. In response to the chimpanzee alarms they did not show a strong preference for horizontal movement in a specific direction, and all vertical movements were directed upwards.

## **Part 2: Playback of conspecific alarms in Sonso**

### ***Methods***

In Sonso, leopard alarms were played back from the forest floor to 22 different groups and from within the canopy at 12-15m to 10 additional groups. Of these, 3 trials were discounted due to equipment malfunctioning or detection by the monkeys. Eagle alarms were played back from the forest floor to 23 different groups, and from within the canopy to 10 additional groups. None of the eagle alarm trials had to be discarded. Chimpanzee alarms were played back from within the canopy to 10 different monkey groups. None of these trials had to be discarded. Sample sizes thus were  $N= 29$  for leopard alarms,  $N= 33$  for eagle alarms, and  $N= 10$  for chimpanzee alarms. In all cases it was possible to observe the animals' movements. For the trials conducted from within the canopy the locomotor responses in both the horizontal and vertical planes were recorded. For the remaining trials, behavioural responses were only recorded for the horizontal plane.

### ***Results***

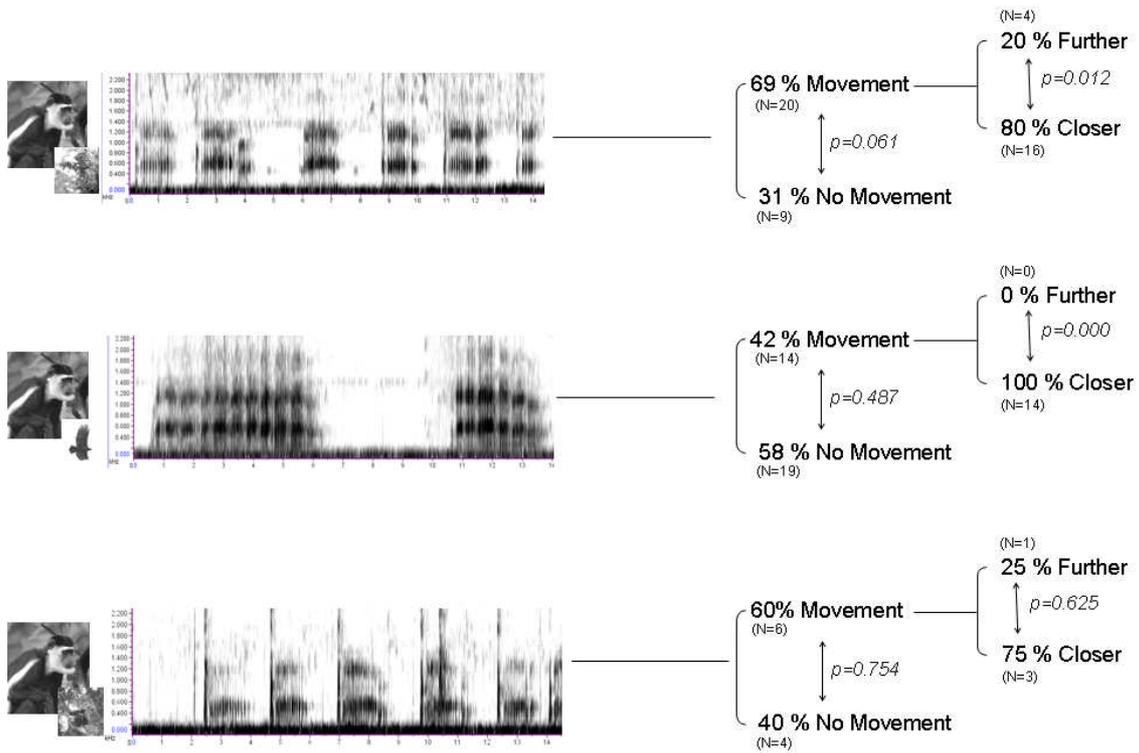
#### ***Behavioural response characteristics***

The monkeys were equally likely to start moving or stay seated after hearing leopard alarms in both dimensional planes, although there was a tendency to start moving in the horizontal plane (horizontal:  $N_{\text{Move}}= 20$ ;  $N_{\text{Not Move}}= 9$ , exact  $p= 0.061$ ; vertical:  $N_{\text{Move}}= 6$ ;  $N_{\text{Not Move}}= 4$ , exact  $p= 0.754$ , binomial tests). If the monkeys moved, they showed no preference in the vertical plane ( $N_{\text{Up}}= 2$ ;  $N_{\text{Down}}= 4$ , exact  $p= 0.687$ ), but a strong preference to approach the stimulus in the horizontal plane ( $N_{\text{Further}}= 4$ ;  $N_{\text{Closer}}= 16$ , exact  $p= 0.012$ , binomial test, Fig. 7.5). The locomotor responses in the horizontal plane were similar to those in response to the acoustic leopard model (all exact  $p$ -values  $>0.55$ , Fisher's Exact tests, two-tailed, Fig. 7.6), but different from the responses to the visual leopard model: the monkeys moved in a higher proportion of the trials conducted

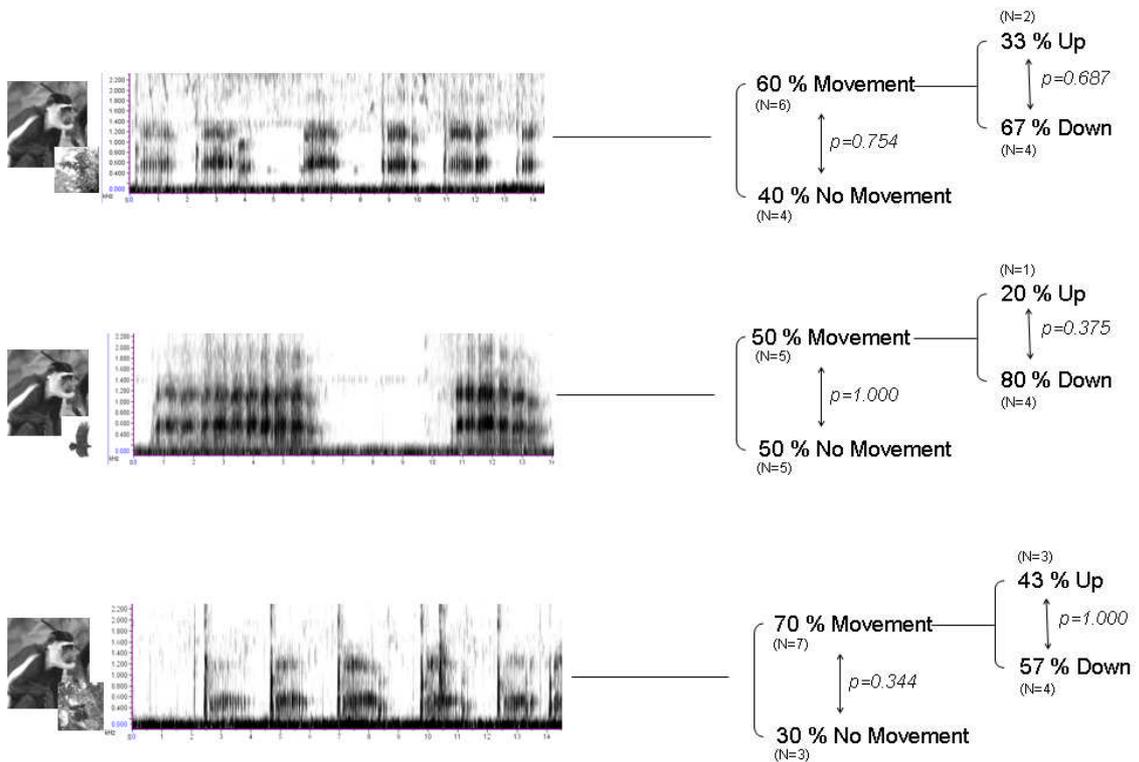
with the visual leopard model than in the trials conducted with leopard alarms (leopard model:  $N_{\text{Move}} = 23$  ;  $N_{\text{Not Move}} = 1$ ; leopard alarms:  $N_{\text{Move}} = 20$ ;  $N_{\text{Not Move}} = 9$ , exact  $p = 0.015$ , Fisher's Exact Test, two-tailed). However, in the subsets of trials in which the animals moved, there was no difference in the direction of movements (visual leopard model:  $N_{\text{Further}} = 1$ ;  $N_{\text{Closer}} = 22$ ; leopard alarms:  $N_{\text{Further}} = 4$ ;  $N_{\text{Closer}} = 16$ , exact  $p = 0.17$ ; Fisher's Exact Test, two-tailed; Fig. 7.6). Locomotor responses in the vertical plane could not be compared because they were not recorded in the acoustic and visual model experiments.

In response to the eagle alarms, the monkeys were equally likely to move or stay seated in both planes (horizontal:  $N_{\text{Move}} = 14$ ;  $N_{\text{Not Move}} = 19$ , exact  $p = 0.487$ ; vertical:  $N_{\text{Move}} = 5$ ;  $N_{\text{Not Move}} = 5$ , exact  $p = 1.000$ , binomial tests, Fig. 7.5). However, if they moved, the monkeys consistently approached the stimulus (horizontal:  $N_{\text{Further}} = 0$ ;  $N_{\text{Closer}} = 14$ , exact  $p = 0.000$ , binomial test), but moved randomly in the vertical plane ( $N_{\text{Up}} = 1$ ;  $N_{\text{Down}} = 4$ , binomial test, exact  $p = 0.375$ ; Fig. 7.5). The locomotor responses in the horizontal plane were similar to those in response to the acoustic eagle model (all exact  $p$ -values  $> 0.27$ , Fisher's Exact tests, two-tailed). Locomotor responses in the vertical plane could not be compared because they were not recorded in the acoustic and visual model experiments.

In response to the chimpanzee alarms, the monkeys were equally likely to move or stay seated (horizontal:  $N_{\text{Move}} = 4$ ;  $N_{\text{Not Move}} = 6$ , exact  $p = 0.754$ ; vertical:  $N_{\text{Move}} = 7$ ;  $N_{\text{Not Move}} = 3$ , exact  $p = 0.344$ , binomial tests, Fig. 7.5). If they moved, directions were random (horizontal:  $N_{\text{Further}} = 1$ ;  $N_{\text{Closer}} = 3$ , exact  $p = 0.625$ ; vertical:  $N_{\text{Up}} = 3$ ;  $N_{\text{Down}} = 4$ , exact  $p = 1.000$ , binomial tests; Fig. 7.5). The locomotor responses in the horizontal plane were similar to those in response to the playbacks of chimpanzee pant hoots (all exact  $p$ -values  $> 0.24$ , Fisher's Exact tests, two-tailed, Fig. 7.6), but different from those in the chimpanzee model context, in which the animals consistently moved (exact  $p = 0.04$ ) either closer or further (exact  $p = 1.000$ ). Locomotor responses in the vertical plane could not be compared between the contexts because these were not scored in the playback experiments.

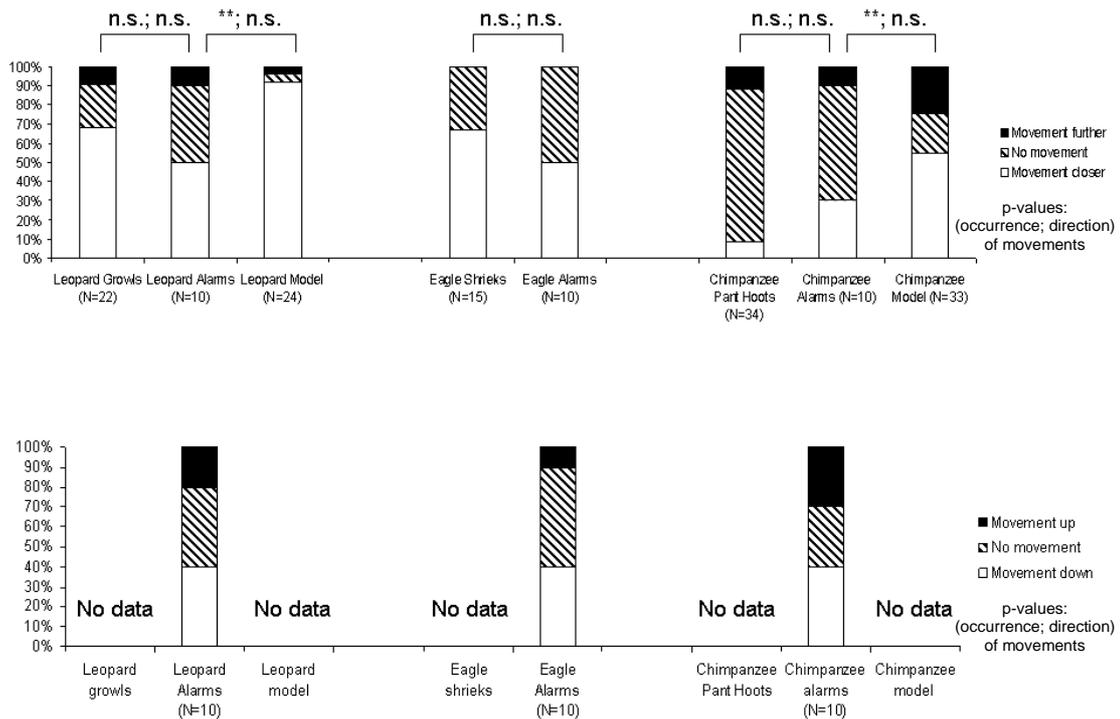


A.



B.

**Figure 7.5.** Monkeys' locomotor behaviour in A. the horizontal plane and B. the vertical plane in response to the acoustic models in Sonso, with corresponding percentages of movements and exact p-values of the differences between locomotor responses within predator contexts (Binomial tests,  $\alpha=0.05$ , two-tailed).



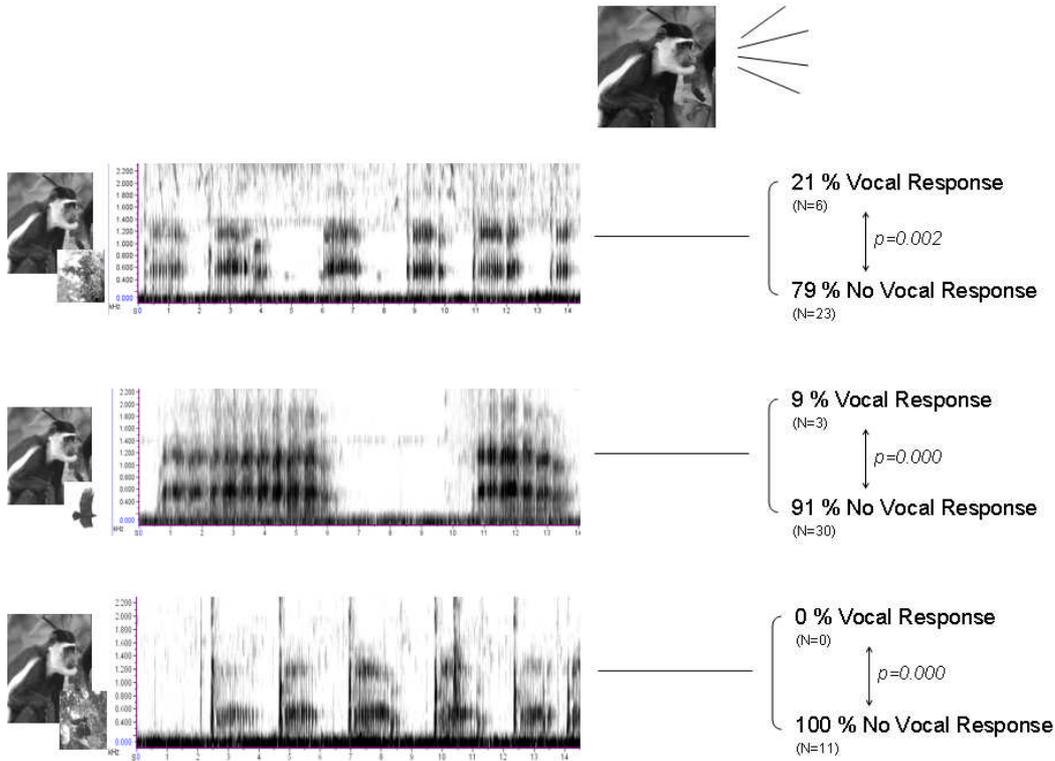
**Figure 7.6.** Locomotor responses in the horizontal and vertical plane to the different model types in Sonso. The first set of asterisks in any graph refers to the difference in occurrence of movement between two contexts; the second set to the difference in direction of movements between two contexts, as follows: n.s.: no significance; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in the occurrence or direction of movements \*  $p < .05$ , \*\* $p < .01$ , \*\*\* $p = .000$  (Fisher’s Exact Test,  $\alpha = 0.05$ , two-tailed).

### Vocal responses to conspecific alarms

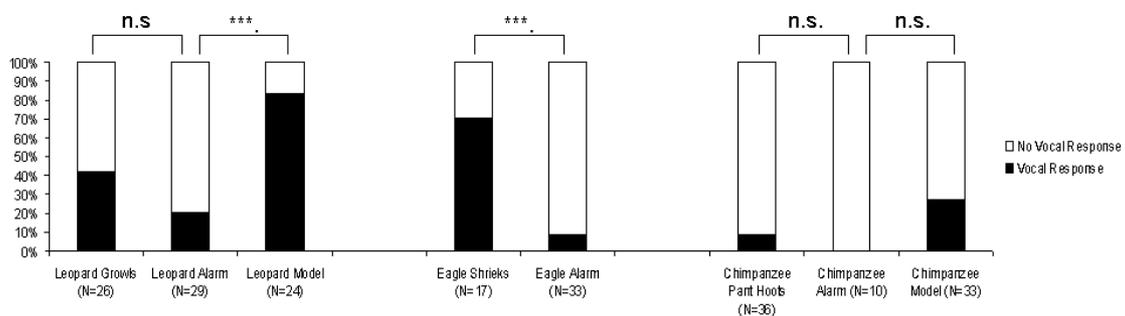
In 6 of 29 trials with leopard alarms the monkeys responded with their own alarm calls (response rate= 21%). The animals were more likely to remain silent than to call in response to this stimulus (binomial test: exact  $p = 0.002$ , Fig. 7.7). This response rate did not differ from that to acoustic leopard models (response rate: 42%; exact  $p = 0.14$ , Fisher’s Exact Test, two-tailed, Fig. 7.8), but differed from the response rate to visual leopard models (response rate: 83%; exact  $p = 0.000$ , Fisher’s Exact Test, two-tailed, Fig. 7.8).

In 3 of 33 trials with eagle alarms the animals responded with vocalizations (response rate= 9%). The monkeys were more likely to remain silent than to call in response to this stimulus (binomial test, exact  $p = 0.00$ , Fig. 7.7). Interestingly, the response rate differed from that given to the acoustic eagle model (response rate: 71%; exact  $p = 0.000$ , Fisher’s Exact Test, two-tailed, Fig. 7.8).

In none of the 11 trials with chimpanzee alarms the animals responded with vocalizations (response rate=0%). The response rate did not differ from that to the acoustic chimpanzee models and visual chimpanzee models (response rate: 8%; exact  $p=1.000$ , response rate: 27%; exact  $p=0.09$ , Fisher's Exact Test, two-tailed, respectively, Fig. 7.8).



**Figure 7.7.** Vocal response rates of the monkeys to the three different acoustic models in Sonso, with corresponding exact p-values (Binomial test,  $\alpha=0.05$ , two-tailed).



**Figure 7.8.** Vocal response rates to the different model types in Sonso, with exact p-values. n.s.: no significant difference between the contexts; trend:  $0.05 < p < 0.08$ , \*, \*\*, \*\*\*: difference in vocal response rates between the contexts, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p = 0.000$  (Fisher's Exact Test,  $\alpha=0.05$ , two-tailed).

**Acoustic measurements of vocal responses**

The number of recorded vocal responses to conspecific alarm sequences were not sufficient in Sonso to conduct meaningful acoustic comparisons (Table 7.2). However, preliminary inspection indicated that the structure of roaring sequences produced to the different alarm call sequences resembled those produced to the corresponding predator. Most importantly, the number of roaring phrases per sequence corresponded well with those found in the actual predator contexts, indicating that the monkeys produced identical sequences either when confronted with the predators themselves or with the corresponding predator alarms: long roaring sequences after hearing eagle alarms, and short roaring sequences after hearing leopard alarms. One difference, however, was that the monkeys responded in a much smaller proportion of trials to eagle alarms than to the corresponding eagle model.

**Table 7.2.** Number of trials conducted, vocal response rates and number of trials used for subsequent acoustic analyses.

	Nr valid trials	Response Rate		Suitable for Temporal Analyses	Suitable for Spectral Analyses	
		N	%		First RS	Second RS
<b>Leopard growls</b>	26	11	42.3	9	9	9
<b>Leopard Alarms</b>	29	6	20.7	6	3	3
<b>Leopard model</b>	24	20	83.3	17	12	12
<b>Eagle Shrieks</b>	17	12	70.6	11	11	10
<b>Eagle Alarms</b>	33	3	9.1	3	3	3
<b>Chimpanzee PH</b>	36	3	8.3	3	2	2
<b>Chimpanzee Alarm</b>	10	0	0	0	0	0
<b>Chimpanzee Model</b>	33	9	87.3	12	6	6

**Discussion**

Most studies investigating the functionally referential capacities of primate alarm calls compared the monkeys' behavioural responses to conspecific predator alarms to their responses to the corresponding predator, sometimes simulated by predator vocalizations, and typically found identical behaviours in both conditions. The

Guerezas are no exception; their locomotor responses to predator alarms matched those displayed in response to the corresponding acoustic predator models. As predicted, the vocal response rates to conspecific alarms were low, but if recipients produced vocalizations, a preliminary inspection indicated that temporal structures of roaring sequences were similar to those produced in response to the corresponding predator stimuli. The alarm sequences of Guerezas therefore seem to be meaningful to recipients, i.e. they denote the type of predator experienced by the signaller.

One interesting finding of this study concerned the low response rate to eagle alarms in Sonso, compared to the response rate to the acoustic eagle model. One explanation for this is that if eagle alarms are an indication of aggressive intent accompanying approach and chasing behaviour (see chapter 4), then they should be produced more often if the eagle can be located than if its presence is merely indicated by a conspecific's alarm calls. Another possibility is that the animals were confused about the identity of the caller and did not respond because of this. In chapter three, counter-roaring in dawn chorus experiments was only elicited by playback of roars of neighbouring individuals. This factor was not controlled for in this study, although for certain trials it could be deduced that the target group was confronted with neighbouring individuals. A preliminary analysis revealed, however, that this did not seem to lead to more vocal responses.

The locomotor responses to leopard alarms generally resembled the responses to acoustic leopard models. As argued earlier, acoustic models might be perceived as less dangerous than silent, visual models. Once a leopard had been detected visually, the monkeys consistently started roaring and snorting, and approached the predator while either moving up or down the tree. The consistent differences in behaviour to direct visual and indirect acoustic or communicated leopard presence became clear from the comparisons between visual and acoustic predator models, as well as those between the visual model and the corresponding alarm calls, confirming that seeing the leopard was an important precondition for calling.

The responses to chimpanzee alarms did not differ from the responses to the acoustic and visual models. The general patterns in the locomotor responses to conspecific chimpanzee alarms were similar to those of the acoustic and visual model experiments.

When preliminary comparing the monkeys' locomotor responses to chimpanzee and leopard alarms at Kanyio Pabidi with each other, no significant differences in movement emerged (vertical: leopard alarms:  $N_{Up}=3$ ,  $N_{Down}=3$ ; chimpanzee alarms:  $N_{Up}=4$ ,  $N_{Down}=0$ : exact  $p=0.19$ ; horizontal: leopard alarms:  $N_{Further}=1$ ,  $N_{Closer}=2$ ; chimpanzee alarms:  $N_{Further}=1$ ,  $N_{Closer}=2$  exact  $p=1.000$ , Fisher's exact test, two-tailed). This finding was similar to that of the study with acoustic predator models in Kanyio Pabidi (chapter 4); the locomotor responses to acoustic chimpanzee models were significantly directed upwards in that study, as seems to be the case in this study, although not significant. Vocal response rate, the only behavioural characteristic differing between the two ground predators in the acoustic model contexts, did also not differ in this study (exact  $p=0.16$ , Fisher's exact test).

The data of the present chapter thus indicated that the monkeys behaved similarly in both the leopard and chimpanzee contexts: there was no preferred direction of movements, and vocal response rates were equal. Based on these results, it is concluded that the monkeys behaved adaptively to the eagle related stimuli (acoustic eagle model and eagle alarms), but more ambiguously to the chimpanzee and leopard stimuli. This possibly means that the responses to chimpanzees and leopards were general ground predator responses, and, correspondingly, that the 'leopard' and 'chimpanzee' alarms conveyed only general 'ground predator' information. This is in line with the findings of chapter 6, where no acoustic differences were found between the vocal responses to visual leopard and chimpanzee models that were later used to edit the conspecific alarm playback stimuli. However, sample sizes were small in this study, and adding more data may reveal a different story.

One other issue concerns the fact that two different protocols were used in Sonso, but not Kanyio Pabidi. A proportion of the conspecific alarms were broadcast from a height of 12-15m and it may be that this variable had an effect on the monkeys' responses. However, calling from the ground can occur, for example if a captured *Guereza*, surrounded by chimpanzees, produces alarms from the forest floor. Correspondingly, statistical comparisons between the responses to alarm calls from the forest floor and trees did not reveal any significant differences (all exact  $p$ -values  $>0.253$ , Fisher's Exact Test, two-tailed), suggesting that it did not matter from which direction the conspecific alarms were played back.

## Chapter 8

### Concluding remarks and future directions

#### Aim of the study

Although Guereza colobus monkeys have been renowned for their extra-ordinary vocal capacities, there have been very few systematic efforts in studying these. Probably because their roars can transmit over long distances, the assumption has been that these vocalizations function in inter-group spacing and male-male competition, while not much attention has been given to a possible function as predator alarm calls.

A first aim of this thesis was to present a detailed description of the form and function of anti-predator behaviour of Guereza colobus monkeys, with a special focus on their alarm call behaviour. A second aim was to determine the effects of predator experience on the anti-predator behaviour of these monkeys, with a focus on the production and comprehension of alarm vocalizations. These questions were addressed by studying Guereza monkeys' anti-predator responses within two populations that differed in predator densities and predation risks. Studying the Guerezas' anti-predator behaviour at Kaniyo Pabidi, an undisturbed forest patch with an intact predator fauna, provided an opportunity to collect data on the 'normal' anti-predator behaviour of the monkeys. Collecting comparable data at Sonso, a forest patch where the predator fauna has been altered due to human interference (no leopard presence and high eagle presence), provided the ideal comparison concerning the influence of predator experience on the monkeys' anti-predator behaviour.

With this thesis, a detailed description of the locomotor and vocal behaviour of the two Guereza populations in response to acoustic and visual predator models, as well as to acoustic alarm responses of conspecifics, was presented. To this end, both established and new protocols were used to increase our understanding of the vocal and physical anti-predator behaviour and associated cognitive capacities of this species in particular, and, by extension, those of the primate lineage in general. In the following, a summary of the key empirical results is presented, before drawing some general conclusions

concerning the Guerezas' anti-predator behaviour and its wider relevance for the study of human language evolution.

## **Summary of key empirical findings**

### ***Which factors influence morning chorusing?***

Guerezas are well known for their roaring before sunset, the so-called dawn choruses, and chapter 3 aimed to investigate the socio-ecological factors that influence this behaviour. Previous studies have argued that this behaviour plays an important role in long-distance male-male competition and group spacing, also because it usually elicits counter-roaring from conspecifics in natural situations. Data indicated that the interaction of two ecological parameters, temperature and rainfall, influenced the occurrence of dawn chorusing, with morning chorusing less likely to occur on cold, wet mornings. On moderately cold mornings, dawn chorusing occurred either once (between 6h00 and 7h00 am) or twice (between 4h00 and 6h00 am, and between 6h00 and 7h00 am). The number of roaring choruses per morning was not influenced by rainfall and temperature, and may be dependent on other external factors, such as ambient noise or illumination. Enhanced sound transmission or physiological circumstances caused by external factors, such as temperature and rainfall, may play crucial roles in explaining the findings of this study.

Playback experiments with recordings of roaring sequences conducted in the early morning hours aimed to trigger the start of the dawn chorusing event, by eliciting counter-roaring from conspecifics. Preliminary data indicated that only playback of (a) a continuous and prolonged recording sequence, (b) from a neighbouring individual, (c) at the moment a distant chorus started, was a powerful enough stimulus to trigger counter-calling from the focal group. Thus, Guerezas appear to integrate a range of variables, before participating in chorusing behaviour. Identity of the caller, timing, and length of calling represent three variables that are likely to be important, but most likely there are other external factors that play a role in the occurrence of this remarkable behaviour.

***Do Guerezas respond to acoustic predator models with predator-specific behaviour?***

Another important context in which roaring is produced, is in response to predators and their vocalisations, including leopard growls, eagle shrieks, and chimpanzee pant hoots. Results of playback experiments (chapter 4) showed that the monkeys' locomotor response was adapted to the hunting techniques of the three predators. Movements in response to eagle models were downwards and closer, movements to chimpanzee models tended to go up, and movements in response to leopard models triggered approach, while either moving up or down.

The vocal response rates to the acoustic leopard model suggested that Guerezas might have considered vocalizing leopards as posing a low threat. Conspicuous perception advertisement, a usually effective strategy used by different monkey species in the presence of leopards, was only used hesitantly. Calling to leopards was more common in the presence of visual, silent, leopards (chapter 5). In the presence of eagles, roaring was an integrated part of aggressive anti-predator behaviour, also used during direct physical encounters. In Kaniyo Pabidi, no roars were produced in response to chimpanzees, which typically caused cryptic behaviour.

Highly significant acoustic differences were found between the vocal responses to leopard and eagle models. However, in contrast to other monkey species, these differences were not at the level of individual calls, but in terms of differently structured alarm sequences in response to the different predator types. Roaring sequences composed of snorts followed by few roaring phrases were usually produced to leopards, whereas roaring sequences composed of many phrases without preceding snorts were usually produced to eagles.

Some attempts were made to link the monkeys' vocal behaviour to underlying psychological factors, such as arousal. One acoustic variable, HNR, linked to arousal in other studies, was lower in phrases produced to eagles than to leopards. Although no independent data were collected to measure arousal, these findings were consistent with the interpretation that the monkeys were more aroused when encountering an eagle than a leopard.

***Do Guerezas' responses to visual and acoustic predator models differ?***

Acoustic predator models alone may be insufficient to accurately describe a species' natural anti-predator behaviour. Thus, visual predator models (a leopard and a chimpanzee) were also presented to the monkeys at Kaniyo Pabidi (chapter 5). Results showed that the monkeys behaved with similar adaptive behaviour to the visual leopard model as in response to the acoustic leopard model. However, even though the basic locomotor responses were similar, the visual models consistently caused stronger responses. Similarly, the monkeys' vocal response rate was higher to visual than acoustic leopard models, most likely a reflection of a perception advertisement strategy. Direct visual contact thus seems to be an important pre-condition for calling.

Roaring as a predator deterrence strategy is maladaptive in response to chimpanzees and was not usually observed in response to the visual chimpanzee model. Occasional roaring in response to this predator may function as a last resort strategy, to intimidate and fight an aggressor while trying to escape from it. Locomotor responses to acoustic and visual chimpanzee models were similar.

Concerning the arousal hypothesis, acoustic analyses revealed that roaring phrases produced to visual leopard models had lower HNR's than phrases to acoustic leopard models, suggesting that Guerezas perceived encounters with visual leopards as more threatening. Apart from this, the overall structural composition of roaring sequences was similar in response to visual and acoustic leopards (short roaring sequences composed of a few phrases each, introduced by snorts), suggesting that, if the arousal hypothesis applies, it does not impact on the structural composition of vocal responses.

***How is Guereza anti-predator behaviour determined by predation risk?***

A second question of this thesis was whether differences in predator experience are reflected in anti-predator behaviour of Guerezas. This was addressed by investigating Guereza anti-predator responses at a second study site, deprived of leopards, Sonso, and by comparing the monkeys' responses with those of the Guereza population at Kaniyo Pabidi (chapter 6). Results showed that the monkeys' overall anti-predator behaviour at both sites was similar, especially in response to visual predator models.

Anti-predator responses to acoustic leopard and eagle models were generally stronger in Sonso than in Kaniyo Pabidi; the Sonso monkeys approached the acoustic leopard model more frequently, and produced more snorts than their relatives at Kaniyo Pabidi. They showed a higher vocal response rate to the acoustic eagle model as well. A series of control experiments suggested that the monkeys at Sonso had retained their ability to recognize leopard cues as dangerous, and that their higher approach rate was caused by a stronger motivation to locate and inspect the disturbance, most likely to identify the exact source of the vocalizations. Visual leopard models elicited locomotor and vocal responses that were similar at both sites, suggesting that the monkeys at Sonso had retained the ability to accurately recognize a leopard by its physical appearance.

The higher vocal response rate to acoustic eagle models in Sonso compared to Kaniyo Pabidi seemed to reflect the fact that eagle predation was higher at Sonso. However, at both sites there was no strong preference to call in response to eagles' vocalizations, again suggesting that a visual confrontation is an important precondition to calling. In response to both acoustic and visual chimpanzee models, the monkeys at Sonso mainly remained silent, similar to findings in Kaniyo Pabidi, where chimpanzee predation pressures were comparable. If vocalizations were produced to chimpanzees in Sonso they were identical to the ones given to leopards, suggesting that the monkeys use one general ground predator alarm.

Measurements of HNR of individual phrases produced to leopards were higher at Kaniyo Pabidi than Sonso, suggesting that Sonso individuals were more aroused when encountering a leopard, especially the acoustic model. Lack of experience with a predator's vocalizations may thus be more arousing than recognising a known dangerous source. The overall basic structural composition of the different predator-specific alarm sequences was similar between the two sites, once more suggesting that the basic features of predator-specific vocal responses were not affected by arousal, provided this psychological variable bears any relevance in explaining the behaviour of these monkeys (see final discussion).

***Are Guerezas' alarm calls meaningful to conspecific recipients?***

In a final study (chapter 7) it was assessed whether the alarm vocalizations produced in response to the predator models are meaningful to recipients. Conspecific alarm sequences were played back to monkey groups in Kaniyo Pabidi and Sonso. Results showed that the monkeys behaved with locomotor behaviour adapted to the predators' hunting techniques, similar to their behaviour in response to acoustic predator cues, suggesting that the calls were meaningful. One further result was that the alarm responses produced to leopard and chimpanzee models elicited similar behaviour in the Guerezas. Since previously it was found that the acoustic characteristics of the responses to leopard and chimpanzee models in Sonso were similar, it was concluded that the Sonso Guerezas produced a general alarm for disturbances on the ground.

**Table 8.1.** Overview of the most important empirical results of this thesis.

	Site	Acoustic Leopard Model	Visual Leopard Model	Conspecific Leopard Alarm	Acoustic Chimp Model	Visual Chimp Model	Conspecific Chimp Alarm	Acoustic Eagle Model	Conspecific Eagle Alarm
<b>Vertical Plane: Movement ? Direction ?</b>	<b>KP</b>	random random	yes random	random random	yes (trend) up	yes up	random random/ up	random down (trend)	random down
	<b>Sonso</b>	-	-	random random	-	-	random random	-	random random
<b>Horizontal Plane: Movement ? Direction ?</b>	<b>KP</b>	random approach (trend)	yes approach	random random	random random	random random	random random	random approach	random approach (trend)
	<b>Sonso</b>	yes approach	yes approach	yes (trend) approach	no random	yes approach (trend)	random random	random approach	random approach
<b>Vocal response rate</b>	<b>KP</b>	intermediate (36%)	high (94%)	low (14%)	low (0%)	low (8%)	intermediate (25%)	low (21%)	intermediate random (29%)
	<b>Sonso</b>	intermediate (42%)	high (83%)	low (21%)	low (8%)	low (27%)	low (0%)	intermediate (71%)	low (9%)
<b>Structural response characteristics</b>	<b>KP</b>	- Roaring Sequences (RS) M= 54 - Phrases M= 91 - Phrases /RS M= 1.4 - Snorts M= 44 - Duration M= 249s - Call delivery rate (CDR) M= 0.28	- RS M= 601 - Phrases M= 875 - Phrases /RS M= 1.4 - Snorts M= 488 - Duration M= 1738s - CDR M= 0.44	-	-	-	-	- RS M= 13 - Phrases M= 49 - Phrases /RS M= 7 - Snorts M= 4 - Duration M=146s - CDR M= 0.41	-
	<b>Sonso</b>	- RS M= 181 - Phrases M= 279 - Phrases /RS M= 1.6 - Snorts M=138 - Duration M= 595 - CDR M= 0.37	-RS M= 262 - Phrases M= 404 - Phrases /RS M= 2.1 - Snorts M= 274 - Duration M= 1118s - CDR M= 0.35	-	-	- RS M= 97 - Phrases M= 189 - Phrases /RS M=1.3 - Snorts M= 88 - Duration M= 630s - CDR M= 0.31	-	- RS M= 15 - Phrases M= 73 - Phrases /RS M= 7 - Snorts M=3 - Duration M=116s - CDR M= 0.36	-

## **General discussion of the results**

In the following, results obtained in Kaniyo Pabidi will be treated as the Guerezas' default responses to their predators, on which discussion points will be based. This is because the forest has never been subjected to logging and the predator fauna is still largely intact, suggesting that Kaniyo Pabidi most likely exemplifies the evolutionary stable predator-prey equilibrium present in undisturbed areas of the Budongo Forest Reserve.

### **Arousal and affect Intensity**

One persistent result throughout this thesis was the presence of specific acoustic differences between certain contexts, that may be indicative of the affective state of the animals, especially the noisiness of the calls (as measured by HNR) and the overall calling effort (as measured by duration and response rate). As described earlier, several studies have proposed that noisiness of calls is an indicator of arousal (or affect intensity), with sounds produced in situations with high affect intensity being noisier ('harsher') than sounds in situations related to lower affect intensity (e.g. Compton et al., 2001; Fichtel et al., 2001; Riede et al., 2001; Rendall, 2003; Feighny et al., 2006; Theis et al., 2007; Clara et al., 2008). In some cases, pitch, calling duration, call rate, amplitude, and formant frequencies were also interpreted as the product of changes in affective states. Most of these studies analysed close-range social signals, but more recently, the hypothesis has been applied to long-distance (social) vocalizations as well (e.g. Feighny et al. 2006; Theis et al. 2007).

### ***Measuring affect***

Judging from HNR measures, the Guerezas have been most aroused in the presence of a vocalizing eagle, and a visual, silent leopard (chapter 4 and 5). However, as mentioned previously, no direct measurements of arousal (e.g. cortisol levels, heart rate) were taken. Cross & Rogers (2006), Clara et al. (2008) and Rendall (2003) further argued that high calling effort (in terms of calls per time unit) also reflects high affect based on the relation between call rates and cortisol (Cross & Rogers 2006; Clara et al. 2008). However, in Clara et al. 's (2008) study, cortisol levels were determined from hair samples, which made their claims controversial (e.g. Davenport et al., 2006; Accorsi et al., 2008), because acute stress can be more accurately determined from

cortisol levels in saliva (Cross & Rogers, 2006). Provided the link between calling duration and affect is meaningful, then Guerezas seemed to experience leopards in general, and visual silent leopards in particular, as more affective than eagles.

Until it becomes possible to explain emotional states in animals in terms other than e.g. physiological responses, such as release of hormones (Cross & Rogers, 2006) and brain activation (Fichtel et al. 2001)), analogies to human physiology and psychology seem to be the only ways to study affect in animals. However, as the example given above illustrates, post-hoc interpretations of results based on such proxies are somehow arbitrary and should be interpreted with great care. One important point seems to be that the influence of affect on vocalizations can only be studied using highly specific data sets, collected under controlled circumstances, in which the influences of affect were determined beforehand, e.g. by measuring physiological stress responses, and by using proxies for affect that fit the proposed study well. In the present study, this was not possible.

### ***Affective vs semantic signalling***

Acoustically distinct calls produced in specific predator contexts may function in conspecific warning. Affect and other factors (e.g. socio-ecological ones, see chapter 3) may however have acted as selective forces determining the form and function of such vocalizations. Yet, it seems reasonable to suggest that even if their original structures have originated from differences in affect, calls should not be influenced by rapidly changing motivational states if they are to function in conspecific warning. It is also conceivable that semantic and affective information co-exist within the same signal (Cheney & Seyfarth, 2003). In this respect, HNR is interesting because it is variable, in the sense that it can for example also be influenced by illness or age and other factors causing turbulence through inadequate closure of the vocal folds (Riede et al., 2001; Ferrand, 2002; Shama et al., 2007), but it probably does not provide the listener with semantic information about the nature of external events. Duration of vocal responses is equally unsuitable as a vehicle of semantic content of predator types: by the time an animal will have learned that a specific predator is present, solely based on the length of a response, it may already have been attacked. In accordance with this latter notion, playback stimuli of conspecific alarms produced to eagles and leopard both consisted

of 15 s recordings, which elicited anti-predator behaviour from recipients similar to that displayed to the predator type it was originally produced for. Calling duration and HNR thus appear to inform listeners more about the affective state of the signaller, without transmitting any semantic information to conspecifics about the nature of the danger.

In the present study, the basic structural composition of the roaring sequences reliably distinguished between alarm responses to leopards and eagles, while HNR and call duration were better explained by differences in affect. Roaring sequence composition thus appears to be a relatively stable feature that appears not very susceptible to influences of affect. Rather, it appears to reliably indicate to recipients the predator type encountered by signallers. An anecdotal observation illustrates this point:

*“On July 4<sup>th</sup> 2006, an acoustic eagle model trial was conducted in Kaniyo Pabidi. The monkeys were located to the north, the playback equipment was positioned around 20m from the group to the south, and the researchers hid out of sight, again 10m south from the speaker. After the playback of eagle shrieks, the male started roaring, producing two long roaring sequences typical of eagle responses, and rushed to the location of the speaker. He moved over it, and sat silently at around 3m from the researchers, to the south of the speaker. He was looking up and around, as if scanning the surroundings for the presence of an eagle, and made one more relatively long roaring sequence. This is when he also looked down and saw the researchers hidden in the bush. First, he looked away, then looked again, peering more intensely. He then instantly started tongue clicking and producing pronounced snorts followed by one-phrase roaring sequences, while moving around a lot; the response typically produced in the presence of ground predators. He continued tongue clicking and calling until the observers got up and left the area.”*

A proper way of studying the influence of affect on primate vocalizations may thus be to make comparisons within a particular predator class, by studying receivers' responses to vocalizations produced in different situations (e.g. eagle vocalizations played back from far vs eagle vocalizations played back from close). A similar comparison may involve visual and acoustic predator models of the same predator type. This showed (chapter 5) that visual models generally triggered higher HNR measurements than acoustic models, as well as longer responses and higher response

rates. This finding was consistent with the arousal hypothesis, while the structure of roaring sequences remained stable. However, a major problem with this approach was that exposure times were unequal. Exposure to visual models was usually much longer than to acoustic ones, which could have influenced the calling duration of the monkeys. One other finding was that the response rate to visual and acoustic leopard models differed remarkably. Again, these differences may seem to reflect differences in affect or general arousal causing the animal to respond promptly, but they may also be explained as mediated by differences in cognitive capacities concerning the adaptations to specific anti-predator techniques or recognition of visual and acoustic patterns.

Concerning the locomotor responses, movements seemed to be highly adapted to the different predators' hunting techniques, rather than being mediated by arousal. Accordingly, locomotor responses to unknown control stimuli, that generated a certain degree of uncertainty in the monkeys, differed significantly from the responses to the different predator types.

In sum, in this section it was tried to highlight the difficulties caused by the relationship between (1.) the (theoretical or inferred) affect intensity caused by different predator types, (2.) the animals' (theoretical or inferred) affective state related to this, and (3.) the influence of all this on their vocalizations. Since this was not the main topic of this research but a mere post-hoc explanation of the datasets, no further progress was made (Scherer, 2003). Affect may influence some acoustic variables in the responses of the animals, most notably the HNR, but it is not clear whether this has an evolved communicative function, especially over long distances. To conclude, it may not be possible to classify animal signalling according to a motivational-referential continuum, as proposed by Marler et al. (1992), with purely referential signals at one end and purely affective signals at the other, because most likely there will always be an interplay between these two (Seyfarth & Cheney, 2003).

### **The impact of predator experience**

A major aim of this thesis was to investigate the effects of differences in predation pressures and predator experience on Guerezas' anti-predator behaviour. Previous studies have shown that higher predator abundance can lead to faster acquisition of the appropriate anti-predator response (Hauser, 1988) and that primates can flexibly alter

their vocal responses according to changes in hunting techniques of key predators (Kavanaugh, 1980). It has also been documented that flexible alarm call usage and comprehension is influenced by the predator types present in a particular habitat (e.g. Fichtel & van Schaik, 2006; Fichtel, 2008) and that high predator pressure leads to increased complexity in primates' vocal and cognitive capacities (Zuberbühler, 2000a; Zuberbühler & Jenny, 2002; Isbell, 2006). Some basic aspects of the vocal and behavioural responses to predators may be relatively hard-wired (e.g. Winter et al., 1973; Newman & Symmes, 1982; Cheney & Seyfarth, 1990; Hammerschmidt et al., 2000; Mineka & Öhman, 2002), but other, more specialised, aspects of anti-predator behaviour, such as usage and comprehension of predator-specific alarm calls, may be subject to significant learning (e.g. Cheney & Seyfarth, 1990; Fischer et al., 2000; Janik & Slater, 2000). Furthermore, predator recognition in different sensory modalities may depend on different cognitive processes that are more or less experience dependent (cf. Blumstein et al., 2000). Specifically, visual recognition may benefit from visual cues shared with other predators still in the area. Along these lines, it was argued that “relatively hard-wired traits will have evolutionary responses, while relatively experience-dependent traits will have an immediate response to the predator loss” (Blumstein et al., 2000).

The Guerezas' anti-predator behaviour differed between the two sites corresponding to relative predation pressures. Although at both sites the monkeys responded with similar predator-specific alarm sequences, there were some differences in locomotor responses: acoustic leopard models caused more approach in Sonso, where leopards are absent, than in Kaniyo Pabidi, where leopards still occur. The visual leopard model caused similar behaviour at both sites. These results are consistent with Blumstein et al.'s (2000) theory, suggesting that recognition of visual models, as well as the production of alarm calls, are 'evolutionary' responses, not influenced by the absence of leopards, whereas recognition of acoustic leopard cues, and the usage and comprehension of alarm calls are more experience dependent.

In Sonso, eagle density is higher than in Kaniyo Pabidi, and Guerezas use their roars as an integrated part of aggressive behaviour to chase away eagles, usually triggered after visual detection of an eagle. Nevertheless, the monkeys sometimes responded with roars to acoustic eagle presence at both sites, but vocal response rates in Sonso were

much higher than in Kaniyo Pabidi. It is possible that the Sonso monkeys have learned to respond aggressively in the absence of direct contact with this predator, not only because of high eagle densities, but also because of high primate densities, which may have increased the number of learning opportunities.

In sum, the data of this thesis reconfirmed Blumstein et al.'s (2000) hypothesis that visual predator recognition is less experience dependent, and more hard-wired and evolutionarily stable, leading to accurate anti-predator responses in areas where specific predators are absent. Acoustic predator recognition is more affected by predator loss, more experience dependent, and less hard wired.

### ***Are there predator specific ground alarms?***

The monkeys at Sonso produced vocal responses to chimpanzees and leopards that did not differ from each other, but it is not clear whether this is because of their lack of experience with leopards or because they only produce one general ground alarm. In order to discriminate between the two hypotheses, the monkeys' responses to chimpanzees at Kaniyo Pabidi are needed. From a functional perspective, it would seem useful for Guerezas at this site to discriminate between the two ground predators, simply because they require extremely differing anti-predator responses. Preliminary data suggested that the fundamental frequency, the number of phrases per RS and the phrase duration of last phrases in chimpanzee responses differed from responses to leopards, suggesting that Kaniyo Pabidi monkeys may discriminate vocally between the two ground predators, potentially based on a different parameter than number of roaring phrases per sequence (see Appendix C).

### ***Morning chorus roars and eagle roars***

Related to the previous, structurally and acoustically, the morning and eagle roars resembled each other closely, apart from the duration of the first phrase produced. All other parameters were equal (Appendix D), indicating that receivers need to rely on one acoustic parameter in deciding whether the roars in the early morning were given to an eagle or not.

In sum, the Guerezas appear to produce a general ground predator alarm consisting of short roaring sequences introduced by snorts, but within these sequences they can possibly modify phrases that differ acoustically in structure to further narrow down which ground predator was encountered. Likewise, they discriminate long roaring sequences produced in the morning to either eagles or by chorusing neighbours based on the difference in the first phrase.

### **Advertisement of male quality**

Harris (2006) in her study on Guereza morning chorusing introduced the idea of a group dominance rank, which was based on the outcome of intergroup encounters. Interestingly, she also showed that group rank (i.e. effectively male rank) predicted and varied negatively with a male's calling efforts. In her study, low ranking males refrained more often from morning chorusing. A similar finding was reported by Sicotte et al. (2007), who found that for one group, a group take-over took place after the resident male's roaring rates had dropped dramatically, possibly advertising that he was weakened at that moment. Thus, it seems likely that overall calling duration will be affected by male quality and ecological effects on this. Roaring duration may be useless for conspecific warning but it may reveal something about the caller's fitness, with a possible additional function in predator deterrence.

Guerezas sometimes already start roaring before they even have directly seen an eagle, but just heard their shrieks. This could inform the predator about the general quality and fighting abilities of the signaller, which may cause it to single out a weaker, non-roaring, monkey. If correct, it then is predicted that higher quality males will start roaring more often in response to acoustic models of predators than weaker males, which is an interesting matter for future studies.

### **Caller identity and individual variation in call characteristics**

In the morning chorus experiments (chapter 3), the monkeys seemed more likely to respond to neighbouring individuals, leading to the hypothesis that Guerezas may be able to recognize individuals by their vocal characteristics. Although a similar suggestion has been made by Harris (2006) she did not compare acoustic parameters of individual roaring phrases between males. Spectral acoustic parameters need to be

compared between individuals; these could allow Guerezas to recognize others in terms of individual call characteristics, an aspect that the results of chapter 3 seem to point to.

## **Guerezas' vocal alarm responses**

### ***Conspecific warning and predator deterrence***

Probably the most salient findings of this thesis concerned the Guerezas' structural vocal response differences to the different predator types. In contrast to other primate species, no evidence was found that individual roaring phrases of Guereza colobus monkeys varied in their basic acoustic structure depending on the predator type encountered. Instead, analyses revealed consistent differences in the structural organisation at the level of roaring sequences and the use of snorts. The fact that the listeners responded adaptively to hearing these responses led to the conclusion that Guerezas provide nearby listeners with information about the type of predator or threat spotted by the caller, a conspecific warning function.

However, predator-specific alarm calls can also benefit the signaller directly (Cheney & Seyfarth, 1981). Predators often differ with regard to sensory and psychological specializations, which is likely to act as a direct selection factor in the evolution of form and patterning of alarm signals. Following this rationale, signallers will then evolve specific anti-predator signals to repel the predator from their direct surroundings (e.g., Owings & Morton, 1997; Rundus et al., 2007). Thus, predator-specific vocal behaviour allows receivers to make inferences about predator type based on signalling alone, although this may not be the evolved function of predator specific signalling. In line with this, eavesdropping is increasingly recognized as an important mechanism in animal communication (McGregor & Dabelsteen, 1996; Peake et al., 2005) and it is entirely conceivable that callers are targeting the predator while conspecifics are merely eavesdropping, suggesting that there is not necessarily symmetry in the mechanisms and functions of signaller and receiver behaviour (Owings, 1994; Cheney & Seyfarth, 2003).

In line with this, results of this thesis showed that the overall response rates to the different predator types were relatively low. Colobus monkeys generally lead a relatively cryptic life (chapter 1 and 3) and may thus often be reluctant to engage in

conspicuous calling behaviour, unless they are in direct visual contact with a predator, much in contrast to other primates such as Diana monkeys or blue monkeys (Zuberbühler, 2000b; Papworth et al., 2008). In general, conspicuous calling may be a more effective strategy to leopards than to eagles. Forest leopards are surprise hunters that lose much of their dangerousness once detected. A radio-tracking study has shown that leopards move on and leave the area once detected by a group of alarm calling monkeys, suggesting that conspicuous alarm calling has direct benefits for the caller (Zuberbühler et al., 1999). Crowned eagles might be less affected by such behaviour, although it was suggested that monkeys start calling at this predator as part of aggressive chasing behaviour. Calling in response to chimpanzees may have a similar function: usually, this is not observed, but may occur when monkeys are detected by this predator and fighting it may be their last chance of impressing and escaping from this predator.

### **Classification of the Guereza alarm call system**

#### ***Predator labelling***

For vervet monkeys and some other primates, it has been argued that individuals use their alarm calls to refer to, or ‘label’, specific external events, such as the presence of a leopard. Although Guerezas produced at least two acoustically distinguishable call types (two types of roaring phrases, snorts), none of them was given exclusively to one predator type (chapter 4 and 6). Instead, the monkeys assembled roaring phrases and snorts into longer sequences that differed between predator contexts. These predator-specific sequences appeared meaningful to conspecific receivers, at least at the level of general predator class.

#### ***Urgency response***

As discussed before, results might be interpreted as mediated by basic differences in arousal or response urgency, rather than as the product of cognitively more complex mental representations of different predator types. Predator class may only be relevant insofar as they indicate different levels of threat. According to this hypothesis, a predator’s biological class is only one of several variables that feed into the caller’s computations about a predator’s degree of threat. However, as argued earlier, this did not seem to be the case in Guerezas’ alarm call responses that reliably differed in

structural composition between predator types, and only differed in acoustic features that did not seem to carry semantic, but rather affective, meaning (e.g. HNR which could reveal something about the caller's emotions, but probably does not carry any specific signal meaning, especially over longer distances).

In sum, it was shown in this thesis that Guerezas combine different call types in context-specific vocal responses, relying primarily on perceptual salience of 'few' versus 'many' in the number of roaring phrases produced before the last low-pitched phrase of a sequence. These differences in call sequencing seemed to reliably encode predator type, because recipients responded to them as if they had witnessed the predator themselves. Furthermore, although some acoustic parameters may be influenced by affect intensity, the predator specific sequences remained stable across contexts that (theoretically) differed in affect intensity.

### **Call combinations and its implications for the theory of language evolution**

The fact that Guerezas organised their call responses into sequences, by combining one or more vocal signals, is not a novel finding (e.g. Marler, 1972; Robinson, 1984). However, very few systematic studies have been conducted to examine the communicative significance or meaning of such vocal sequencing, which have been referred to as instances of 'zoo-syntax' (Marler, 1977; Zuberbühler, 2002; Arnold & Zuberbühler, 2006a; Arnold & Zuberbühler, 2006b; Clarke et al., 2006).

'Syntax' in human language is a '...generative system, which allows the parsing and production of hierarchical structures in language' (Fitch, 2005). Together with semantics and vocal learning, it constitutes one of the crucial components of human language, responsible for its limitless expressive power (Hauser, 1996; Tomasello, 2003; Fitch & Hauser, 2004; Fitch, 2005). According to Nowak et al. (2000), animal communication is typically regarded as non-syntactic, based on single signals referring to whole situations. In contrast, human language is syntactic, based on signals consisting of discrete components that have their own meaning (but see e.g. Robinson, 1984; Marler, 1977). Despite this traditional view and in accordance with earlier reports, recent research suggests that several primate species produce call sequences,

and that receivers attend to them (Zuberbühler, 2002; Arnold & Zuberbühler, 2006b; Clarke et al., 2006; Arnold & Zuberbühler, 2008). However, in non-human primates, these capacities usually do not go beyond ‘concatenation’ processes, which suggests an understanding of the transitional probabilities between a finite number of calls situated close together in a sequence (Fitch & Hauser, 2004), or a simple addition of meaning (Byrne, 1982; Robinson, 1984). Similarly, Marler (1977) distinguished two types of ‘zoo-syntax’: phonological syntax, referring to the rules governing the sequencing of meaningless units into higher-order structures, and lexical syntax, referring to the rules governing the sequencing of meaningful units into higher order structures that derive their meaning from the combined meaning of the components.

In the following, an attempt is made to classify the sequencing of Guerezas’ calls based on these different concepts.

Structural analyses of Guerezas’ call sequences revealed the following rules:

- Sequences usually contain two acoustically distinct types of roaring phrases (P), with the ‘last’ (L) phrases usually being lower-pitched than the rest
- The number of phrases can be characterised as ‘few’ or ‘many’, depending on the context, that is **PPPPPL** for eagle or during morning choruses, and **PPL** for leopards and other disturbances on the ground
- Sequences can be preceded by snorts (S): e.g. (**S\_PPL**) or (**S\_PPPPPPL**)
- Snorts are usually not produced directly after a ‘last’ phrase
- Snorts can occur alone or in snort sequences, usually in the presence of humans, chimpanzees or leopards (**S\_\_S\_S\_\_S\_S\_\_\_\_\_S**)
- Single phrases do not occur
- Single phrases, accompanied but not necessarily preceded by snorts do occur, although they are usually produced as part of longer calling bouts produced to ground predators (**S\_\_SP\_S\_\_S\_P\_S\_\_P**)
- All sequences produced to leopards contain snorts
- Some sequences to eagles contain snorts

In early reports it was suggested that snorts function as an alarm call in response to ground predators (e.g. Hill & Booth, 1957; Marler, 1972). Although generally correct, in this study it was found that snorts were also produced in other contexts, particularly

to e.g. eagles and as part of morning choruses. In any one of these two additional contexts, snorts always precede roaring sequences and are never produced as single units. Therefore, the pattern is that snorts, if produced singly, indicate the presence of a disturbance on the ground, but if they are part of a roaring sequence, they appear in other contexts as well. Phrases, in contrast, appear to serve as units that obtain their meaning once they are combined into higher-order sequences.

As mentioned, roaring phrases and snorts are used in contexts other than predation, most evidently during dawn chorusing. These sequences are structurally similar to eagle responses. Acoustic comparisons of individual phrases, however, revealed that one acoustic parameter, the duration of the first phrase produced in the first roaring sequence differed between these two contexts (Appendix D) and playback experiments will now be necessary to investigate if receivers attend to these acoustic differences.

Thus, Guerezas possess a form of ‘zoo-syntax’, but it is not directly obvious whether this represents an example of lexical or phonological syntax. Individual phrases appear to have little or no meaning and obtain their meaning only once combined into sequences. Snorts can be given alone, but only in response to a danger on the ground, indicating that they carry independent meaning. They seem to lose this specific meaning when combined with roaring sequences, but only if the sequences consist of ‘many’ phrases, but not when combined with sequences that consist of ‘few’ phrases.

A salient finding of this study concerned the perceptual salience of the ‘few’ versus ‘many’ differences in the number of phrases in roaring sequences, produced in predator-specific ways. ‘Few’ sequences reliably indicated the presence of a ground predator, and it is currently not clear whether the acoustic structure of individual phrases and the temporal structure of sequences reveal further acoustic cues that would allow receivers to discriminate between leopards and chimpanzees. Sequences in response to eagles are more context-specific, although two observations in Sonso showed that Guerezas can produce the same roaring sequences to raptors that are probably not dangerous, such as the harrier hawk, although no recordings were made. The monkeys’ alarm calling behaviour was not simply a reflection of different response urgencies, and probably cannot be termed as ‘mixed’ either.

## **Conclusion**

To conclude, the Guerezas have evolved a complex vocal alarm calling system that has the capacity to reliably communicate predator class to conspecifics, by the use of predator-specific call sequences. The acoustic features of individual phrases (or calls) did not differ from each other in meaningful ways, which indicates that individual phrases do not function as vehicles of semantic content. The Guerezas' vocal system thus provides another example of zoo-syntax, in which specific units of a vocal repertoire are combined into sequences that are meaningful to recipients, suggesting that it is functionally referential, at least at the level of the general predator class.

According to a definition by Macedonia & Evans (1993) this alarm call system does not qualify as functionally referential, because the sequences do not denote individual predator types, but broad classes. However, another view is that this definition distorts the meaning of the term 'referential' as used by linguists and philosophers. Future work may be able to address the intriguing possibility whether roaring responses to chimpanzee are acoustically different from those to leopards, in areas where both predators are common. In Sonso, where only chimpanzees are present, no differences were found, but in Kaniyo Pabidi, where both predators are present, this may be the case (Appendix C). If this were the case, the Guerezas' call system would be able to convey narrow reference (chimpanzee, leopard) by altering acoustic cues within broad reference (ground predator, aerial predator), a phenomenon that has not been found in many other primate species (see e.g. Templeton et al., 2005; Slobodchikoff et al. 1991).

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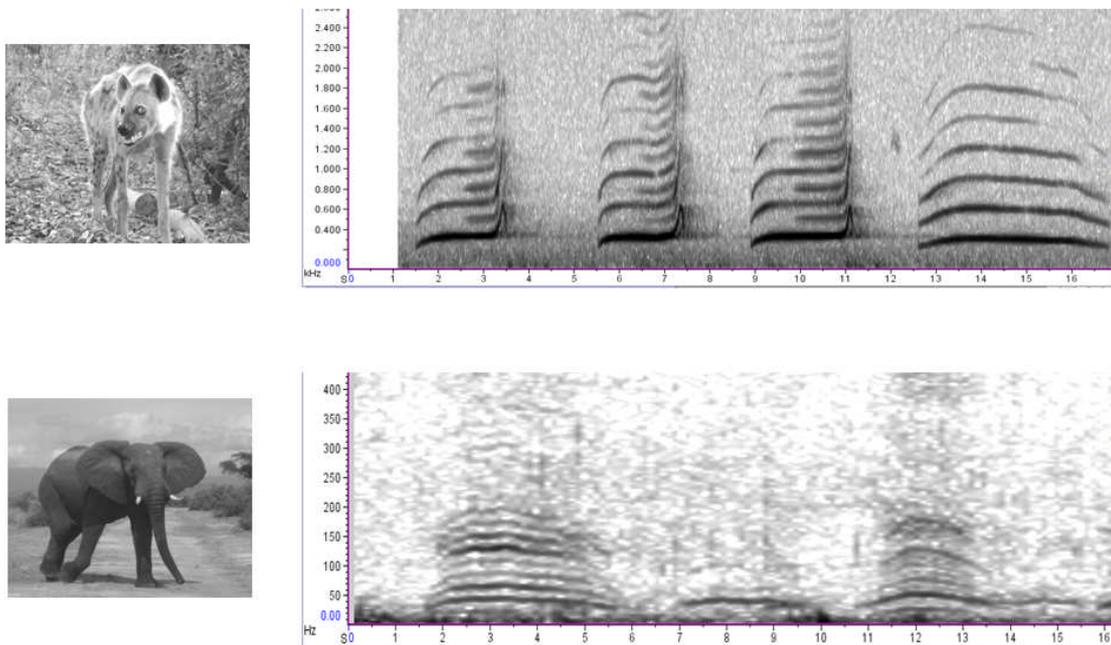
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## Appendix A

### Guerezas' responses to hyena howls and elephant rumbles

To investigate whether Guerezas at Sonso just responded to novelty in the acoustic leopard context, a series of control trials was conducted using hyena howls and elephant rumbles. Hyena howls and elephant rumbles were extracted from pre-recorded sounds available through the Raven 1.2 software package (Cornell Laboratory of Ornithology, Ithaca, New York; Fig. A.1.).

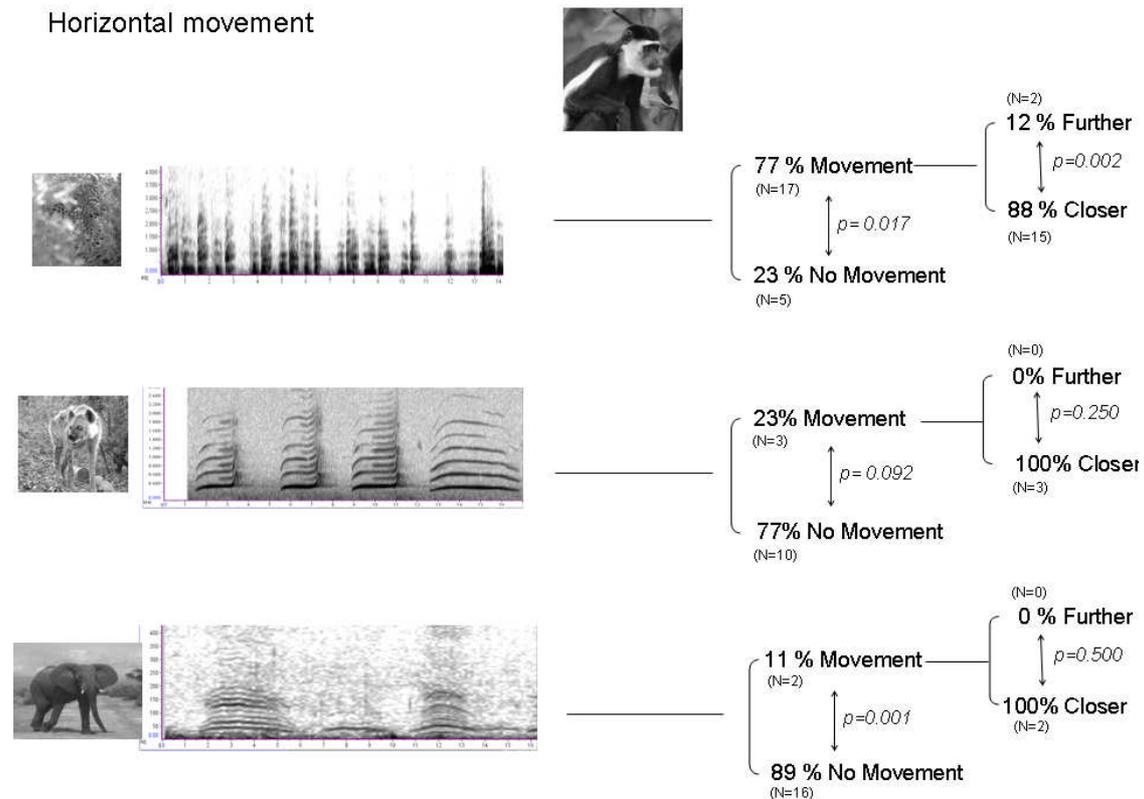


**Figure A.1.** Spectrographic representation of control vocalizations used as playback stimuli: A. hyena howls (17s), and B. elephant rumbles (16 s). The x-axes in the figures represent the time in seconds, the y-axis in part A represents the frequency in kHz; in B the frequency in Hz. Photo hyena © R. Wittig & C. Crockford, printed with permission; elephant: A.M. Schel.

### Methods and Results

Following the general playback protocol described in chapter 2, a total of N=13 hyena and N=18 elephant trials were conducted with the Guerezas in Sonso. Locomotor responses in the horizontal plane (Fig. A.2.) and vocal response rates (Table A.1) were compared with those to the acoustic leopard model.

## Locomotor responses



**Figure A.2.** Monkeys' locomotor responses in the horizontal plane in response to the acoustic controls, with corresponding percentages of movements and exact p-values of the differences between locomotor responses within contexts (Binomial test,  $\alpha = 0.05$ ).

Fisher's Exact tests conducted between contexts revealed that locomotor responses elicited by the control stimuli differed significantly from those to the leopard growls. The monkeys approached leopard growls significantly more often than hyena howls or elephant rumbles: (hyena howls:  $N_{\text{movement}} = 3$ ,  $N_{\text{no movement}} = 10$ ; elephant rumbles:  $N_{\text{movement}} = 2$ ,  $N_{\text{no movement}} = 16$ ; leopard growls:  $N_{\text{movement}} = 17$ ,  $N_{\text{no movement}} = 5$  exact p-value hyena-leopard: 0.004, exact p-value elephant-leopard: 0.000).

## Vocal Responses

Vocal response characteristics are summarized in Table A.1. In response to hyena howls and elephant rumbles, the monkeys consistently remained silent. Response rates differed significantly from those to the leopard growls: vocal response rate hyena howls: 0% (0/13); vocal response rate elephant rumbles: 0% (0/18); vocal response rate leopard growls: 42% (11/26) (exact p-value hyena-leopard: 0.007; exact p-value

elephant-leopard: 0.001, Fisher's exact test, two-tailed). No acoustic measurements could be taken.

**Table A.1.** Numbers of trials conducted with hyena howls and elephant rumbles, vocal response rates and number trials used for subsequent acoustic analyses.

<b>Stimulus type</b>	<b>Nr valid trials</b>	<b>Response Rate</b>		<b>Suitable for Temporal Analyses</b>	<b>Suitable for Spectral Analyses</b>	
		<b>N</b>	<b>%</b>		<b>First RS</b>	<b>Second RS</b>
<b>Leopard growls</b>	26	11	42	9	9	9
<b>Hyena howls</b>	13	0	0	0	0	0
<b>Elephant rumbles</b>	18	0	0	0	0	0

## Appendix B

### Guerezas' responses to 'moving flower sheet'

To investigate whether Guerezas at Sonso just responded to novelty in the visual leopard context, a series of control trials was conducted using a moving model of a light green flower sheet (Fig. B.1.)

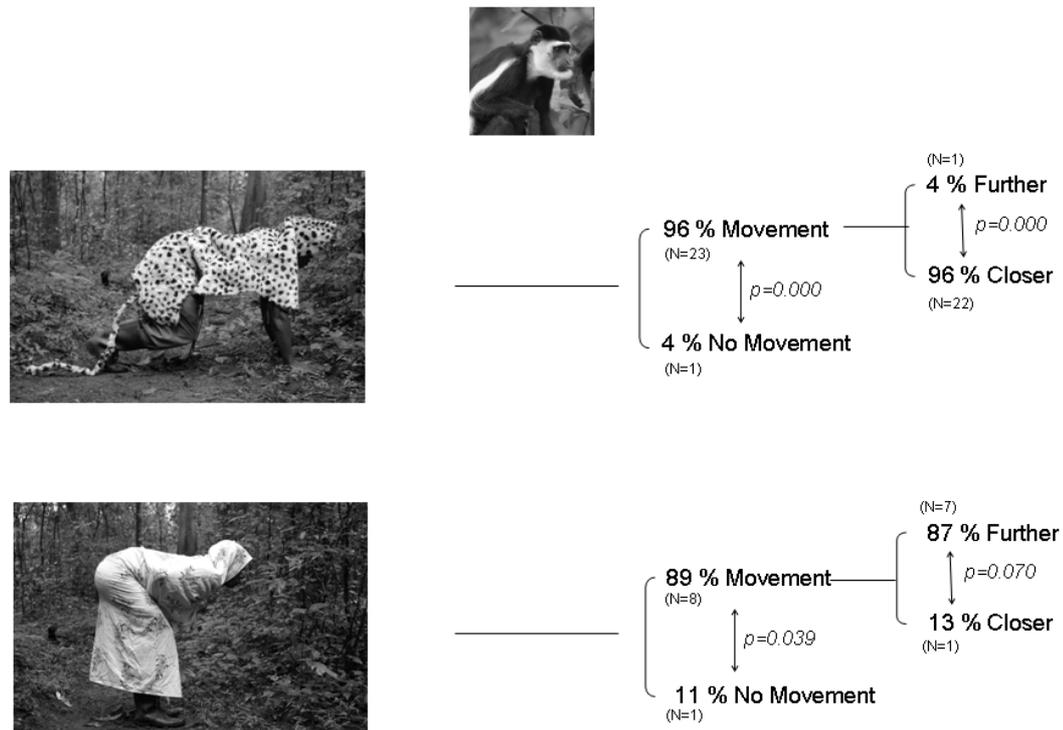


**Figure B.1.** The 'moving flower sheet' model.

### Methods and Results

Following the general experimental protocol described in chapter 2, a total of N= 9 flower sheet experiments were conducted with the Guerezas in Sonso. Locomotor responses in the horizontal plane (Fig. B.2.) and vocal response rates (Table B.1.) were compared with those to the visual leopard model.

### Locomotor responses



**Figure B.2.** Monkeys' locomotor responses in the horizontal plane in response to the moving flower sheet model, with corresponding percentages of movements and exact p-values of the differences between locomotor responses within contexts (Binomial test,  $\alpha = 0.05$ ).

Fisher's Exact tests conducted between contexts revealed that locomotor responses elicited by the control stimulus differed significantly from those to the visual leopard model. Even though the monkeys started moving in a similar proportion of trials (flower sheet:  $N_{\text{movement}} = 8$ ,  $N_{\text{no movement}} = 1$ ; leopard model:  $N_{\text{movement}} = 23$ ,  $N_{\text{no movement}} = 1$ ; exact p sheet-leopard = 0.48, Fisher's Exact test, two-tailed), they moved in opposite directions (flower sheet:  $N_{\text{Further}} = 7$ ,  $N_{\text{Closer}} = 1$ ; leopard model:  $N_{\text{Further}} = 1$ ,  $N_{\text{Closer}} = 22$ ; exact p sheet-leopard = 0.000, Fisher's exact test, two-tailed).

### Vocal Responses

Vocal response characteristics are summarized in Table B.2. In response to the moving flower sheet, the monkeys consistently remained silent, which contrasted significantly with the high vocal response rate to visual leopards (vocal response rate flower sheet: 0% (0/9); vocal response rate leopard model: 83% (20/24); exact p sheet-leopard = 0.000, Fisher's exact test, two-tailed).

**Table B.1.** Numbers of trials conducted with visual leopard models and the flower sheet, vocal response rates and number trials used for subsequent acoustic analyses.

<b>Stimulus type</b>	<b>Nr valid trials</b>	<b>Response Rate</b>		<b>Suitable for Temporal Analyses</b>	<b>Suitable for Spectral Analyses</b>	
		<b>N</b>	<b>%</b>		<b>First RS</b>	<b>Second RS</b>
<b>Leopard model</b>	26	11	42	9	9	9
<b>Flower sheet</b>	9	0	0	0	0	0

## APPENDIX C

### Chimpanzee Model experiments in Kaniyo Pabidi Preliminary Comparisons

#### Acoustic Structure of Individual Roars

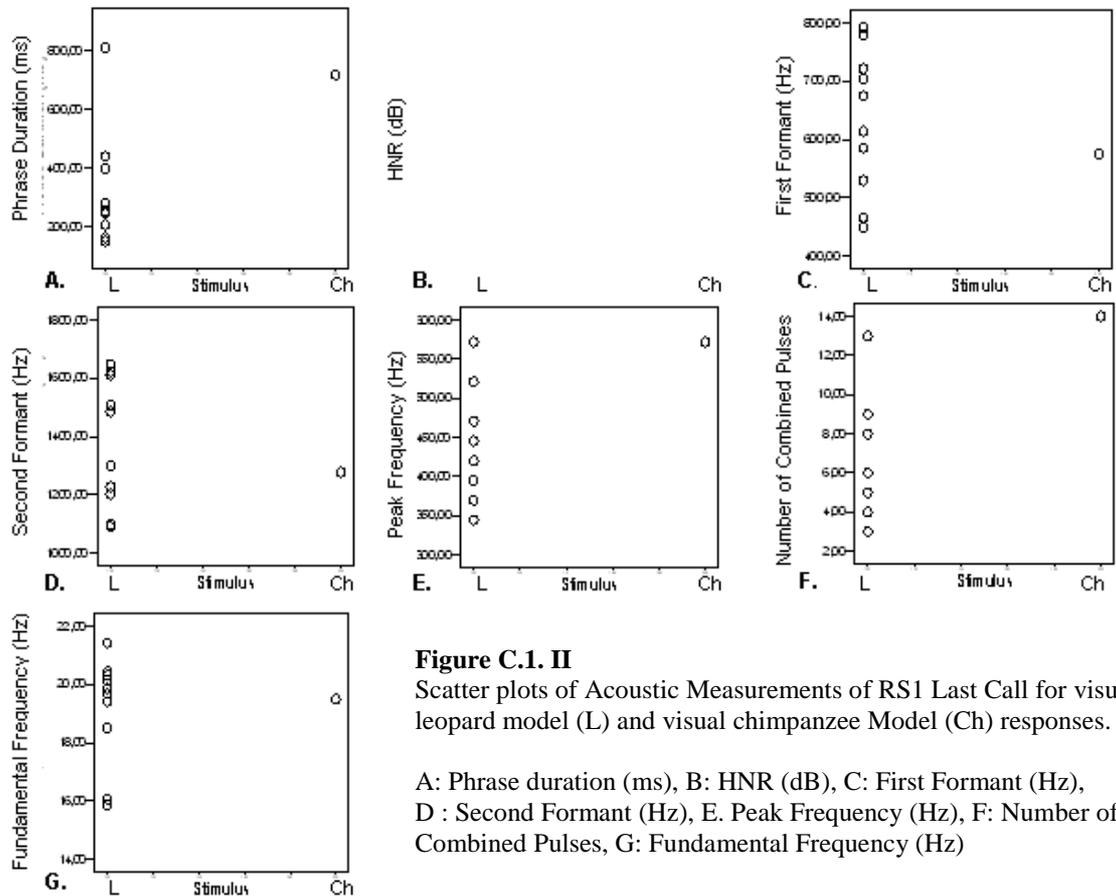
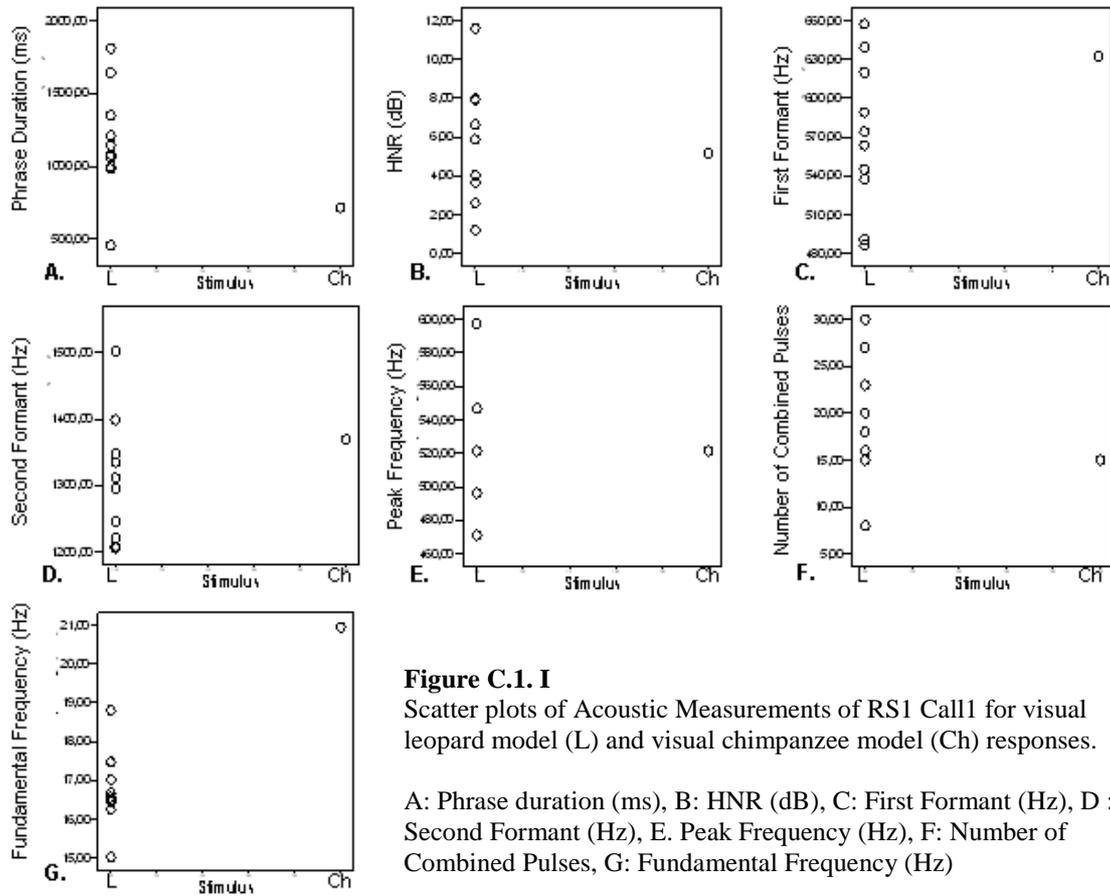
Because only one vocal reaction in response to the appearance of the chimpanzee model was collected in Kaniyo Pabidi, it was not possible to reliably test the differences between the vocal alarms produced in leopard and chimpanzee contexts statistically. To get an impression of how the monkeys responded to chimpanzee models compared to leopard models, z-scores for the individual measurements of this one trial were calculated using the mean and corresponding SD's of the leopard group. From these z-scores, the p-values could be derived from a z-score table, which are one tailed (Field, 2005), and therefore were multiplied by two, to get the two tailed p-values (Table C.1.).

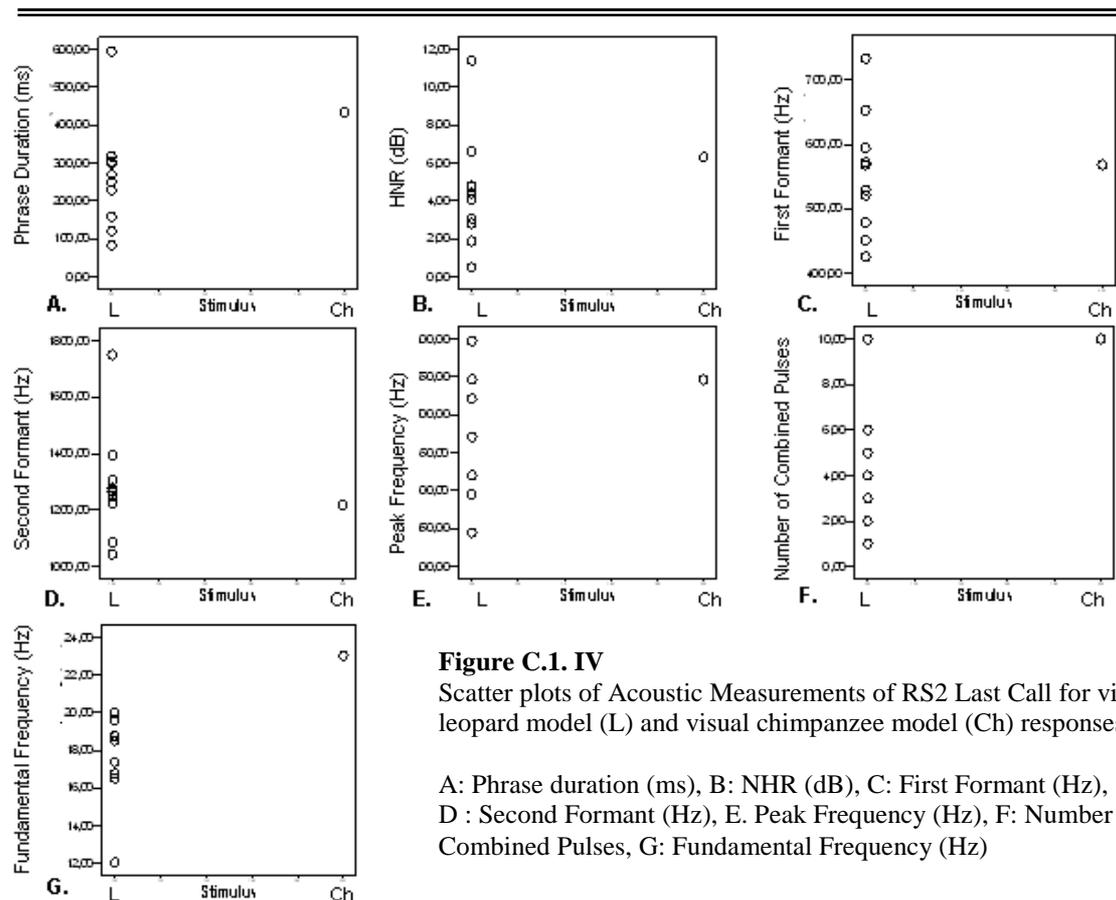
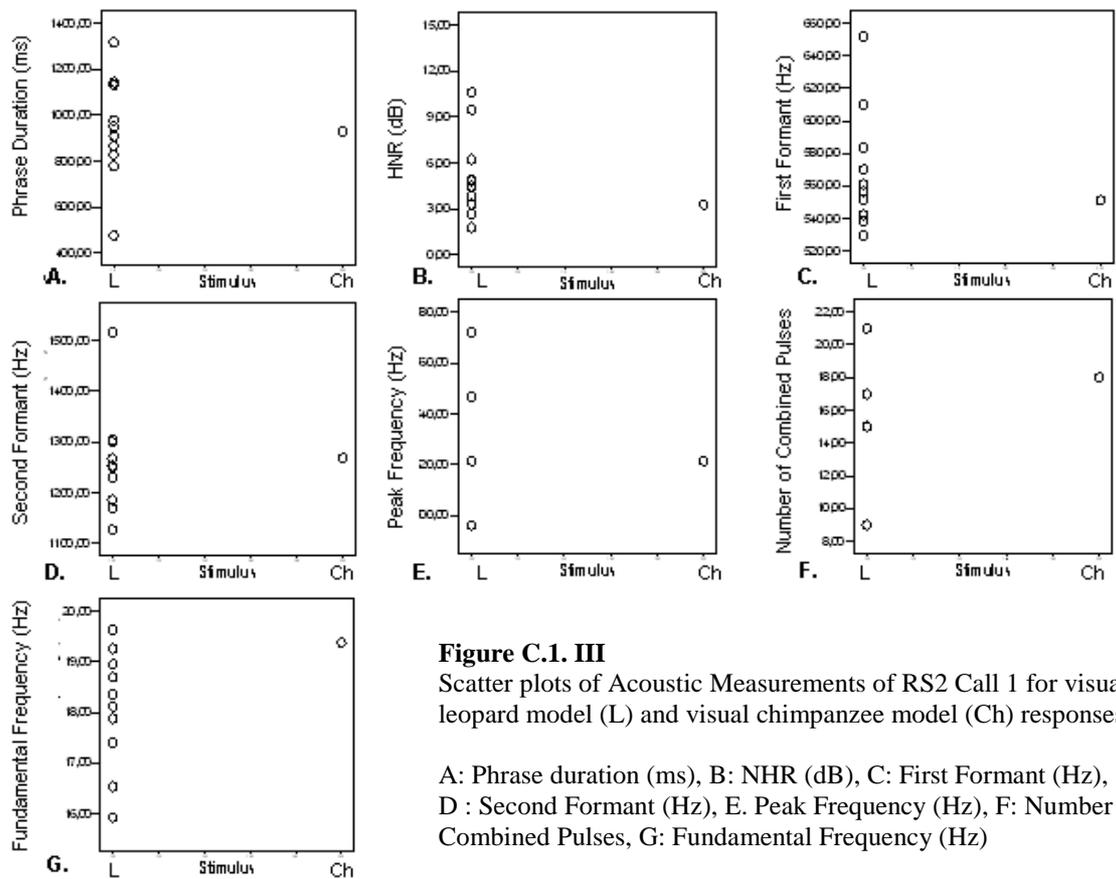
Furthermore, the raw data of this one, noisy, response are plotted in Figure C.1., next to the measurements of the responses to the leopard model. Using this strategy, it was at least possible to get an impression, for every parameter, of the degree of similarity or difference from those found in the leopard population.

**Table C.1.** Measurements, z-scores and corresponding p-values of the preliminary comparison of acoustic measurements of leopard and chimpanzee responses in Kaniyo Pabidi. Mdn= median value, M=mean value, and CI= 99% confidence interval.

Acoustic variable		Leopard Model Alarm Response			Chimp Model Alarm Response	Compared with L values	
		Mdn	M	CI		z-score	p
1 <sup>st</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	1112	1174	790 – 1558	716	-1.225	0.218
	HNR (dB)	5.88	5.74	2.63 – 8.85	5.16	-0.191	0.848
	First Formant (Hz)	569	570	511 – 630	633	1.086	0.276
	Second Formant (Hz)	1304	1307	1211 - 1404	1370	0.670	0.502
	Peak Frequency (Hz)	509	516	476 – 557	522	0.146	0.880
	Number of pulses	20	20	13 – 26	15	-0.833	0.406
	Fundamental Freq (Hz)	17	17	16 - 18	21	4.000	<b>0.000</b>
1 <sup>st</sup> RS Last Phrase	Phrase Duration (ms)	253	320	119 – 520	718	2.041	<b>0.042</b>
	HNR (dB)	4.55	3.97	1.20 – 6.75	-	-	-
	First Formant (Hz)	645	632	506 – 633	575	-0.463	0.646
	Second Formant (Hz)	1393	1380	1155 – 1606	1278	-0.464	0.646
	Peak Frequency (Hz)	408	428	351 – 505	572	1.946	0.052
	Number of pulses	5	6	3 - 9	14	2.667	<b>0.008</b>
	Fundamental Freq (Hz)	20	19	17 - 21	20	0.500	0.618
2 <sup>nd</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	930	938	700 – 1176	929	-0.034	0.976
	HNR (dB)	4.64	5.20	2.27 – 8.12	3.25	-0.687	0.490
	First Formant (Hz)	559	570	531 – 608	551	-0.514	0.610
	Second Formant (Hz)	1252	1260	1151 – 1370	1269	0.084	0.936
	Peak Frequency (Hz)	534	529	502 – 557	522	-0.259	0.794
	Number of pulses	17	16	13 – 20	18	0.667	0.502
	Fundamental Freq (Hz)	18	18	17 - 19	19	1.000	0.318
2 <sup>nd</sup> RS Last Phrase	Phrase Duration (ms)	260	263	117 – 409	434	1.204	0.230
	HNR (dB)	4.26	4.44	1.37 – 7.51	6.33	0.632	0.528
	First Formant (Hz)	549	553	457 – 649	569	0.172	0.866
	Second Formant (Hz)	1267	1287	1090 – 1484	1219	-0.354	0.726
	Peak Frequency (Hz)	420	451	368 – 534	547	1.185	0.234
	Number of pulses	5	5	2 - 7	10	1.667	0.950
	Fundamental Freq (Hz)	19	18	15 - 20	23	2.500	<b>0.012</b>

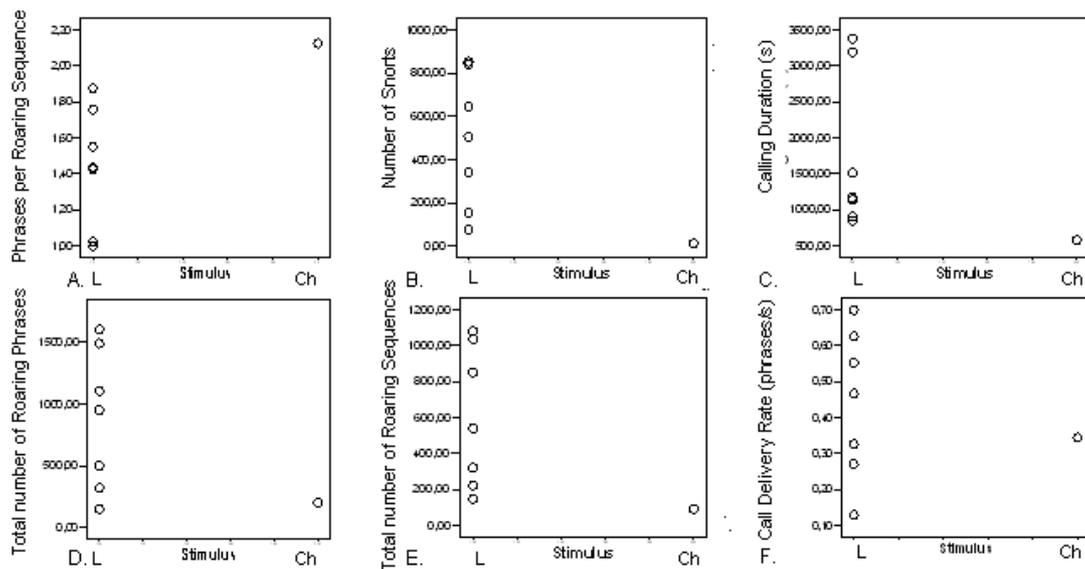
Exploring the responses to this one chimpanzee trial with the responses to the leopard model, a few potential differences in acoustic parameters showed between the leopard model and chimpanzee model responses. The phrase duration of the last phrase produced in the first roaring sequence was longer in chimpanzee responses than in leopard responses (with a similar, but non significant, finding for the second roaring sequence). The fundamental frequency differed between the contexts for the first phrase of the first RS and the last phrase of the second RS (Table C.1.). Scatter plots indicating where the data points of the chimpanzee trial fall in the range of leopard measurements are given in Fig. C.1.





### Composition of Roaring Sequences

By comparing the structural data from the one chimpanzee trial with the population mean of the leopard model responses (Table C.2.), one interesting difference between the contexts showed, that may or may not hold when collecting more data on this topic in the future. In response to the chimpanzees, the monkey produced more phrases per roaring sequence than in response to the leopard model. All other parameters fell within the range found for the leopard model responses (Figure C2 and Table C.2).



**Figure C. 2.** Scatterplots of temporal characteristics for Leopards (L) and Chimpanzees (Ch).

**Table C.2.** Measurements, z-scores and corresponding p-value of the preliminary comparisons of temporal characteristics in leopard and chimpanzee responses in Kaniyo Pabidi. Mdn= median value, M=mean value, and CI= 99% confidence interval.

	Calling Duration (s)			Total Number RS			Total Number Phrases			Phrases per RS			Number of Snorts			Call Delivery Rate (Phrases/s)		
	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI
<b>Leopard Model</b>	1171	1737.9	221.6-3254.1	541	601	54-1148.6	952	874.6	75.8-1673.2	1.44	1.44	0.97-1.91	507	488.3	49.8-926.7	0.47	0.44	-
<b>Chimpanzee Model</b>	580	580	-	94	94	-	200	200	-	2.13	2.13	-	11	11	-	0.34	0.34	-
<b>z-score</b>	1.07			-1.298			-1.184			2.060			-1.525			-0.488		
<b>p-value</b>	0.285			0.194			0.238			0.039			0.126			0.624		

## Appendix D

### **Acoustic comparison of vocalizations during natural eagle encounters, presentation of acoustic eagle models, and morning choruses**

Morning chorus roars are perceptively very similar to eagle alarm responses. To investigate whether there was a difference in acoustic parameters between contexts, or whether the animals may have some other, basic knowledge about the circumstances and timing at which identical sequences that fulfill different functions are produced, eagle responses recorded in Sonso were compared to the morning roars recorded in Sonso.

Furthermore, this appendix is interesting with respect to the question how the Guerezas' natural predator responses compare with responses on acoustic models. The Guerezas' roars produced in natural eagle encounters were compared with those produced in acoustic eagle model experiments conducted in Sonso.

#### **Methods**

##### ***Collection of naturally occurring eagle responses***

In 2005, Guerezas' responses to natural eagle encounters were recorded from 4 different groups in Sonso. In 2007, two additional responses to natural eagle encounters were recorded. On four of the recordings, the first few roaring sequences produced in response to the eagle presence are not present, but the number of roaring sequences and number of phrases per absent roaring sequence was noted down. The other two recordings contained all the roaring sequences produced in response to the eagle encounters.

Temporal measurements were complicated by these circumstances: the total duration of the vocal responses could not be determined accurately in the cases where the complete vocal response were not recorded. Nevertheless, it was still possible to measure the total number of roaring sequences, the total number of roars, the number of roars per roaring sequence and the total number of snorts by using the information noted down

during the eagle encounters. The call delivery rate could be calculated using the recorded sections.

Also, spectral measurements were complicated because of this. Where normally the first and last roars of the very first and second roaring sequence produced in a specific context would be measured acoustically, in the cases of missing recordings of first and second roaring sequences it was only possible to measure the first and last roars of the first two sequences that were recorded.

### **Collection of morning chorus roars**

Morning chorus roars were recorded in 2007, as an integrated part of the protocol used in the morning chorus experiments described in chapter 3. ‘Un-contaminated’ first morning choruses of 8 different groups in Sonso were recorded successfully. As described in chapter 3, the monkeys often produced two bouts of morning choruses: a first chorus between 5h00 and 6h00 am and a second chorus around 7h00. On some days a playback experiment was conducted just before the first natural chorus started. Since it is possible that choruses recorded after an attempted playback experiment were contaminated (i.e. possibly modified by the monkey having just heard a playback stimulus), these choruses were not considered in any analyses on the naturally occurring morning choruses. From the 8 remaining morning choruses, it was possible to measure the temporal and spectral characteristics without any constraints.

### **Collection of responses on eagle shriek playbacks**

Chapter 6 has described the collection of responses to experimentally induced eagle responses in Sonso. N=11 responses were used for spectral measurements on the first sequence and N=10 for the spectral measurements on the last sequence.

### ***Acoustic analyses and statistics***

Acoustic analyses and statistics followed those described in Chapter 2 and used in all other chapters.

### **Results**

Although the raw data for the acoustic measurements of the first and last phrases of the first and second recorded roaring sequences produced in response to the eagle playback

stimuli were already given earlier (Table 6.2), they are repeated in Table D.1, where the raw data for the other vocal responses are also reported.

Comparisons within the contexts showed that the animals produced differently structured first and last phrases in the morning chorus context and in the playback eagle context, but that they produced similarly structured first and last phrases in the natural eagle context (Table D.2).

Comparison between the acoustic parameters measured in the three contexts revealed that there were consistent differences in the phrase duration and number of pulses for the first phrases produced in the first and second roaring sequences in the vocal responses (all p-values < .04, Table B.2, Kruskal-Wallis Test,  $\alpha=0.05$ , two-tailed). The last phrases produced in all three contexts were acoustically identical. Post Hoc testing revealed that the monkeys responded with identical phrases in natural eagle encounters and the acoustic eagle model encounters, but that there was a big difference in phrase duration of first phrases produced in the morning chorus context, compared to both eagle contexts (Table D.3 and Figure D1).

**Table D.1.** Spectral measurements of the first and last phrases produced in the first and second roaring sequences in the three different eagle contexts. Mdn= median value, M=mean value, and CI= 99% confidence interval.

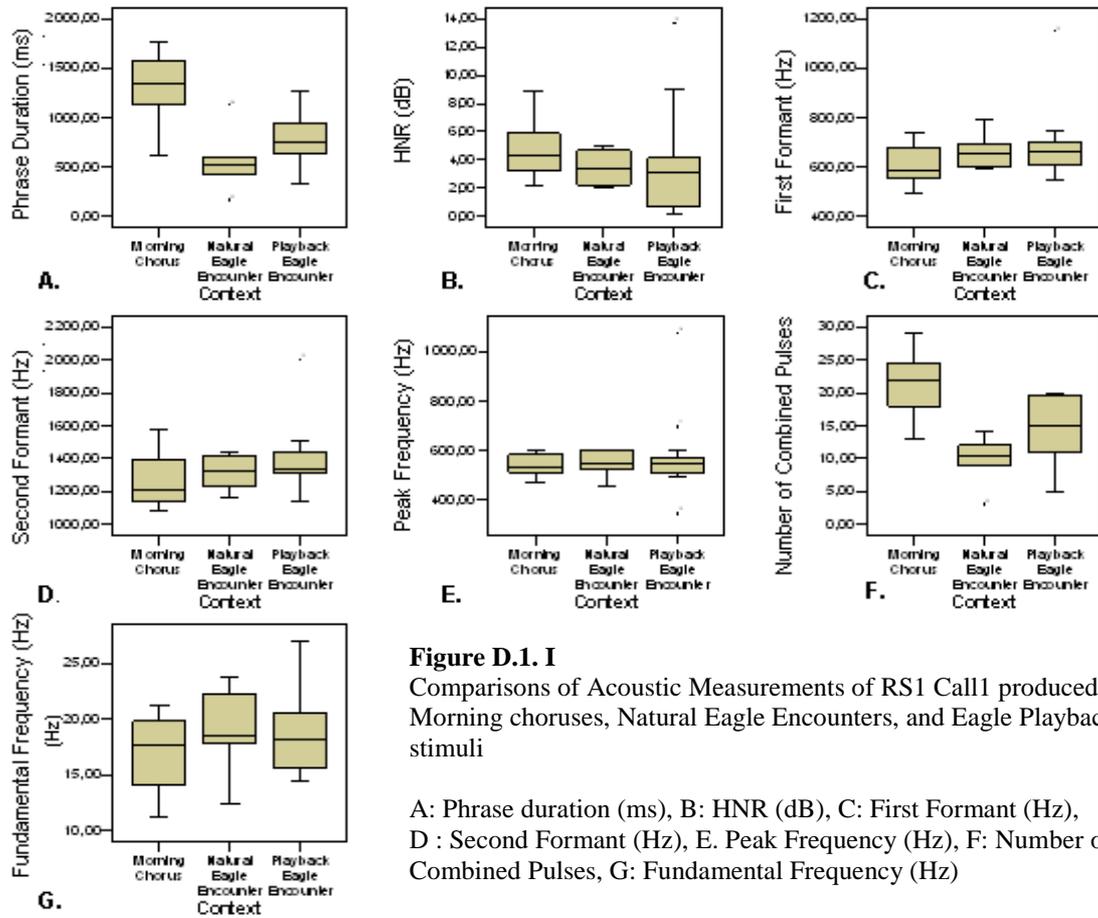
Acoustic variable		Morning Chorus (MC)			Natural Eagle Encounter (NEE)			Playback Eagle Encounter (PBE)		
		Mdn	M	CI	Mdn	M	CI	Mdn	M	CI
1 <sup>st</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	1346	1311	859 – 1763	522	558	37 – 1079	757	789	539.1 - 1038.7
	HNR (dB)	4.31	4.74	2.07 – 7.41	3.34	3.43	-0.88 – 7.73	3.13	3.85	-0.65 – 8.34
	First Formant (Hz)	585	607	499 – 715	657	664	543 – 784	659	691	535.8 - 846.6
	Second Formant (Hz)	1207	1266	1048 – 1485	1319	1314	1129 – 1498	1338	1399	1182 – 1615
	Peak Frequency (Hz)	531	540	483 – 596	547	545	458 – 631	547	581	404.7 – 757.9
	Number of pulses	22	21	15 – 28	11	10	4 – 16	15	15	10 – 20
	Fundamental Freq (Hz)	18	17	12 - 21	19	19	12 - 25	18	18	15 - 22
1 <sup>st</sup> RS Last Phrase	Phrase Duration (ms)	379	343	137 – 549	340	311	26 – 597	320	357	240.3 - 474.6
	HNR (dB)	3.43	3.86	1.18 – 6.54	7.55	5.59	-13.9 – 25.07	2.85	3.79	0.15 – 7.43
	First Formant (Hz)	563	582	492 – 671	647	658	559 – 756	686	716	492.0 – 940.0
	Second Formant (Hz)	1211	1247	1056 – 1438	1288	1347	1119 – 1574	1327	1398	1110.5 – 1685.4
	Peak Frequency (Hz)	446	460	356 – 563	484	476	395 – 558	522	648	363.4 – 932.5
	Number of pulses	6	6	2 – 10	5	5	1 - 10	6	7	4 – 10
	Fundamental Freq (Hz)	18	18	14 - 22	19	18	9 -26	19	20	16 - 24
2 <sup>nd</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	1444	1322	705 – 1940	638	674	299 – 1049	766	790	628.9 – 951.9
	HNR (dB)	3.66	4.23	1.28 – 7.17	5.19	5.18	-2.17- 12.53	2.77	3.86	0.38 – 7.35
	First Formant (Hz)	578	608	504 – 713	585	610	531 – 690	658	697	552.5 – 840.6
	Second Formant (Hz)	1236	1300	1092 - 1508	1268	1253	935 – 1570	1422	1441	1221.1 – 1659.9
	Peak Frequency (Hz)	531	533	473 – 592	547	557	478 – 636	572	658	443.1 – 873.1
	Number of pulses	22	21	12 – 29	13	12	9 – 16	13	13	11 – 16
	Fundamental Freq (Hz)	16	16	12 - 20	19	19	11 - 27	18	17	15 - 20
2 <sup>nd</sup> RS Last Phrase	Phrase Duration (ms)	397	380	192 – 568	471	370	-9 – 749	417	396	265.4 - 527
	HNR (dB)	2.43	2.93	-0.39 – 6.25	4.27	4.14	-1.19 – 9.48	3.7	4.05	0.55 -7.56
	First Formant (Hz)	618	600	496 – 704	610	633	458 – 807	727	705	587.6 – 823.4
	Second Formant (Hz)	1320	1280	1001 – 1559	1305	1307	906 – 1708	1445	1472	1241.8 -1701.5
	Peak Frequency (Hz)	446	466	373 – 559	547	527	334 – 719	496	575	370.3 – 779
	Number of pulses	7	7	3 – 11	6	7	-1 – 16	8	7	4 -10
	Fundamental Freq (Hz)	18	18	14 - 21	19	20	9.37 – 29.	17	18	15 - 20

**Table D.2.** Results of the statistical tests conducted on the first and last phrases produced within and between the three contexts. On the left hand side of the Table: exact p-values and effect size ( $r$ ) of the within-context comparisons of the first and last phrases of the first two Roaring Sequences produced (Wilcoxon Signed Ranks Test,  $\alpha=.05$ ). On the right hand side of the Table: asymptotic p values of between- context comparisons of first and last phrases of the first and second roaring sequences between the three contexts (Kruskall-Wallis Test,  $\alpha=.05$ ).

Acoustic variable		Within MC (First vs Last phrase)		Within NEE (First vs Last phrase)		Within PBE (First vs Last phrase)		Between MC, NEE and PBE	
		Exact p	r	Exact p	r	Exact p	r	First Phrase p	Last Phrase p
<b>1<sup>st</sup> RS</b>	Phrase Duration (ms)	<b>0.008</b>	0.63	0.156	0.45	<b>0.001</b>	0.63	<b>0.002</b>	0.953
	HNR (dB)	0.250	0.32	0.750	0.19	0.820	0.07	0.372	0.429
	First Formant (Hz)	0.461	0.21	0.844	0.09	0.465	0.17	0.345	0.097
	Second Formant (Hz)	0.844	0.07	0.563	0.21	0.413	0.19	0.299	0.435
	Peak Frequency (Hz)	<b>0.008</b>	0.63	0.063	0.58	0.969	0.01	0.883	0.168
	Number of pulses	<b>0.008</b>	0.63	0.125	0.49	<b>0.002</b>	0.60	<b>0.003</b>	0.510
	Fundamental Freq (Hz)	0.383	0.25	0.438	0.27	0.320	0.23	0.603	0.641
<b>2<sup>nd</sup> RS</b>	Phrase Duration (ms)	<b>0.008</b>	0.63	0.125	0.55	<b>0.002</b>	0.63	<b>0.036</b>	0.941
	HNR(dB)	0.148	0.39	0.875	0.13	0.383	0.23	0.491	0.542
	First Formant (Hz)	0.641	0.14	1.000	0.04	0.770	0.08	0.100	0.181
	Second Formant (Hz)	0.461	0.21	0.625	0.21	0.557	0.15	0.159	0.264
	Peak Frequency (Hz)	<b>0.023</b>	0.58	0.625	0.23	0.098	0.38	0.181	0.278
	Number of pulses	<b>0.008</b>	0.63	0.188	0.52	<b>0.004</b>	0.61	<b>0.036</b>	0.968
	Fundamental Freq (Hz)	0.250	0.32	1.000	0.04	0.301	0.26	0.422	0.622

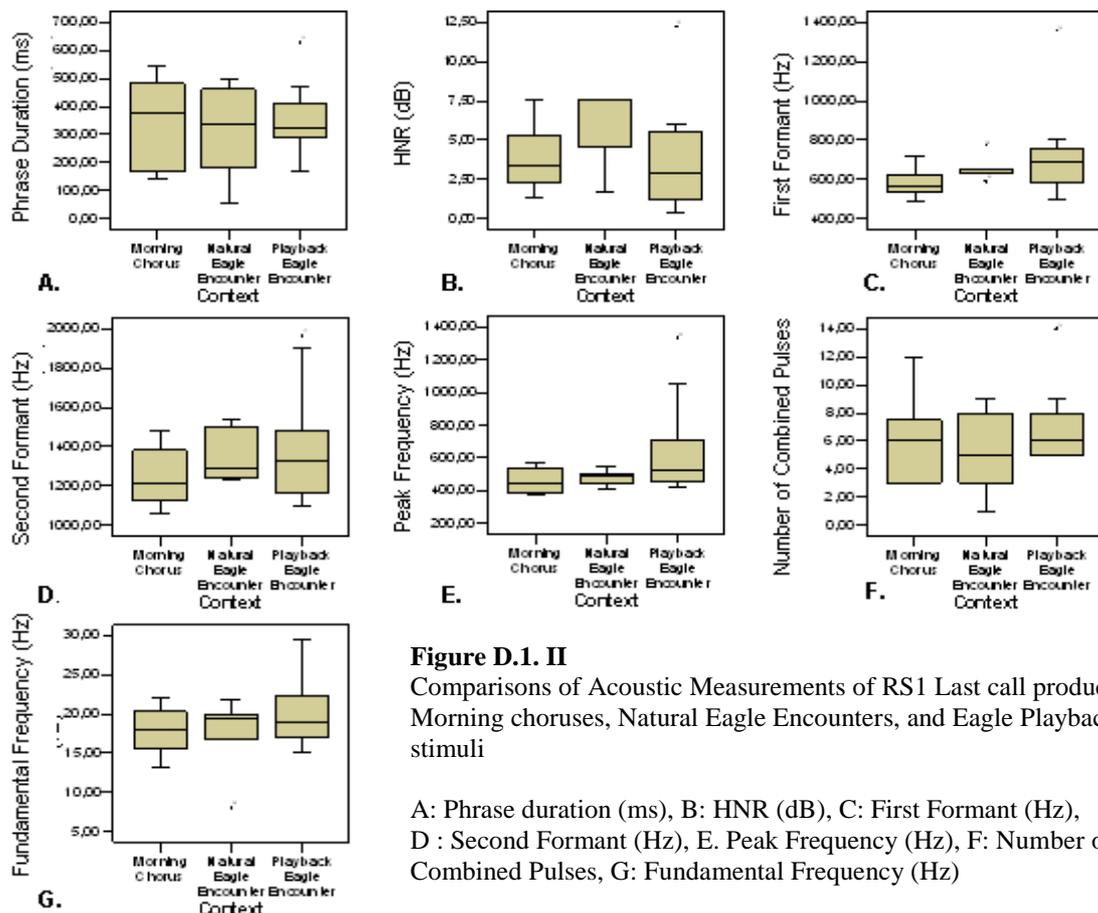
**Table D.3.** Exact p- values and corresponding effect sizes (r) of the Post-Hoc comparisons between acoustic characteristics of phrases produced in the first and second RS in Morning Chorus context, Natural Eagle Encounter context and Playback induced Eagle Encounter (Mann-Whitney U test,  $\alpha=0.05$ )

Acoustic variable		Between MC and NEE		Between MC and PBE		Between NEE and PBE	
		Exact p	r	Exact p	r	Exact p	r
1 <sup>st</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	<b>0.003</b>	0.76	<b>0.004</b>	0.64	0.098	0.41
	HNR (dB)	0.368	0.29	0.228	0.29	0.613	0.15
	First Formant (Hz)	0.228	0.35	0.238	0.28	1.000	0
	Second Formant (Hz)	0.491	0.21	0.129	0.36	0.660	0.12
	Peak Frequency (Hz)	0.637	0.14	0.791	0.07	0.863	0.05
	Number of pulses	<b>0.001</b>	0.79	<b>0.013</b>	0.57	0.091	0.42
	Fundamental Freq (Hz)	0.345	0.28	0.600	0.13	0.678	0.11
1 <sup>st</sup> RS Last Phrase	Phrase Duration (ms)	0.950	0.03	<b>0.058</b>	0.45	0.751	0.09
	HNR (dB)	0.261	0.37	0.408	0.21	0.353	0.28
	First Formant (Hz)	<b>0.029</b>	0.59	0.068	0.44	0.884	0.05
	Second Formant (Hz)	0.228	0.35	0.146	0.36	1.000	0
	Peak Frequency (Hz)	0.691	0.12	0.088	0.41	0.245	0.29
	Number of pulses	0.833	0.07	<b>0.024</b>	0.54	0.328	0.25
	Fundamental Freq (Hz)	0.685	0.12	0.606	0.14	0.884	0.0
2 <sup>nd</sup> RS 1 <sup>st</sup> Phrase	Phrase Duration (ms)	<b>0.030</b>	0.61	<b>0.058</b>	0.45	0.254	0.32
	HNR (dB)	0.683	0.15	0.408	0.21	0.374	0.26
	First Formant (Hz)	0.354	0.28	0.068	0.44	0.165	0.38
	Second Formant (Hz)	0.622	0.16	0.146	0.36	0.129	0.41
	Peak Frequency (Hz)	0.306	0.31	0.088	0.41	0.529	0.18
	Number of pulses	<b>0.044</b>	0.57	<b>0.024</b>	0.54	0.626	0.14
	Fundamental Freq (Hz)	0.284	0.32	0.606	0.14	0.364	0.27
2 <sup>nd</sup> RS Last Phrase	Phrase Duration (ms)	1.000	0	0.696	0.10	1.000	0
	HNR (dB)	0.368	0.29	0.442	0.21	0.933	0.04
	First Formant (Hz)	0.622	0.16	0.101	0.40	0.254	0.32
	Second Formant (Hz)	0.724	0.12	0.173	0.34	0.254	0.32
	Peak Frequency (Hz)	0.162	0.41	0.208	0.31	0.977	0.02
	Number of pulses	0.963	0.02	0.778	0.07	0.970	0.97
	Fundamental Freq (Hz)	0.550	0.18	0.829	0.06	0.371	0.37



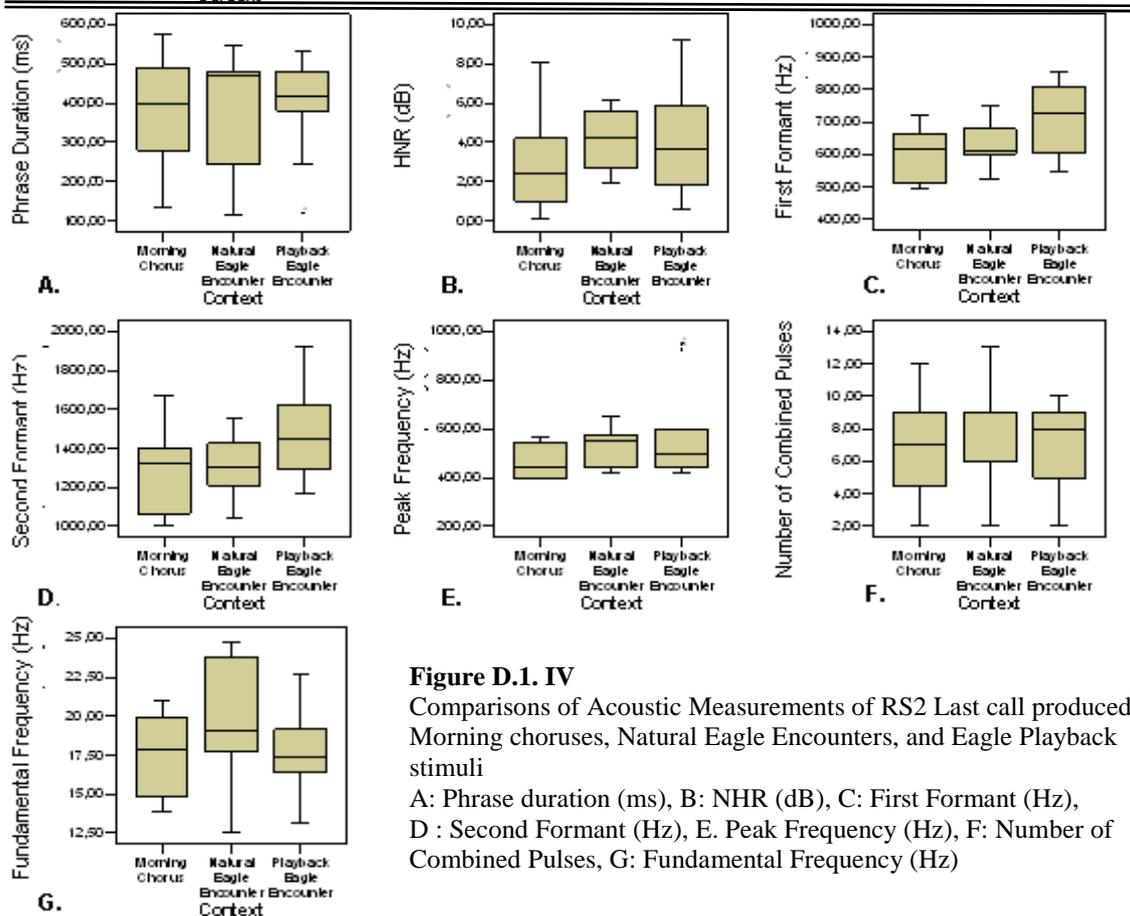
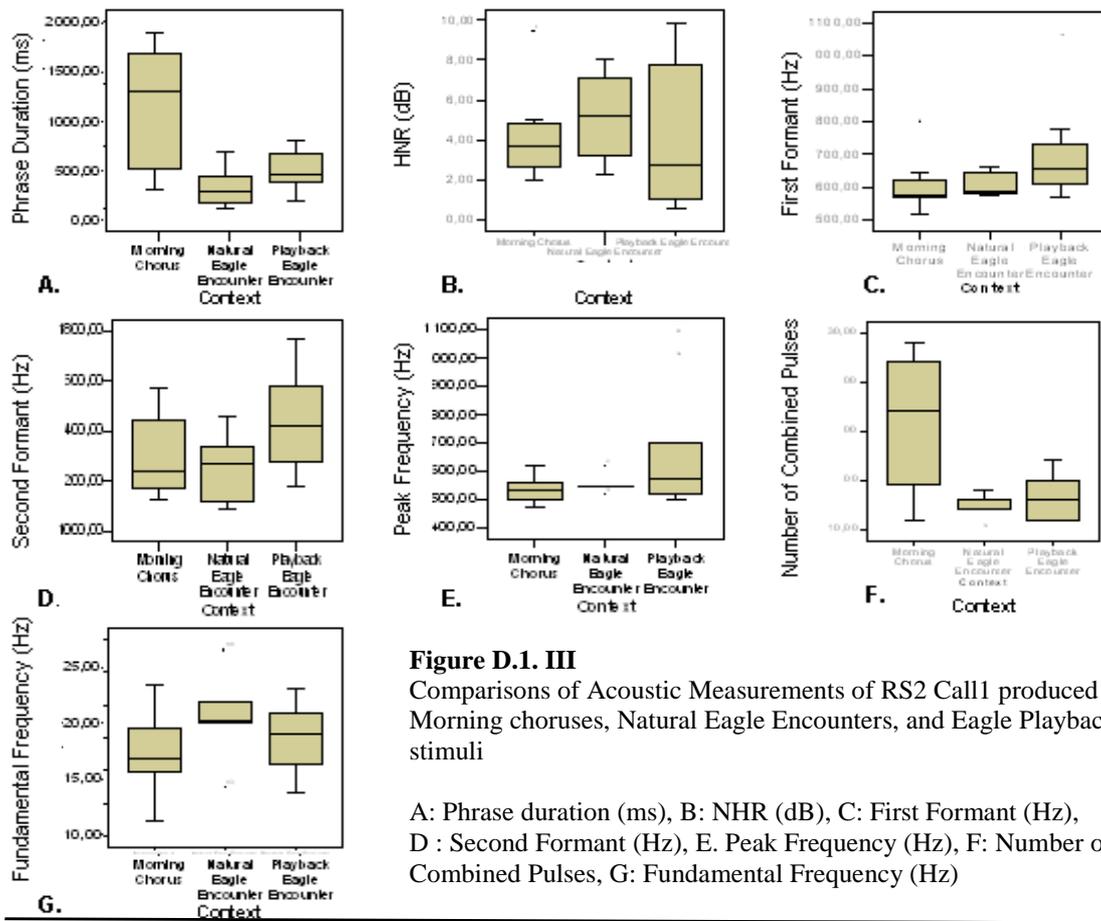
**Figure D.1. I**  
 Comparisons of Acoustic Measurements of RS1 Call1 produced in Morning choruses, Natural Eagle Encounters, and Eagle Playback stimuli

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz),  
 D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)



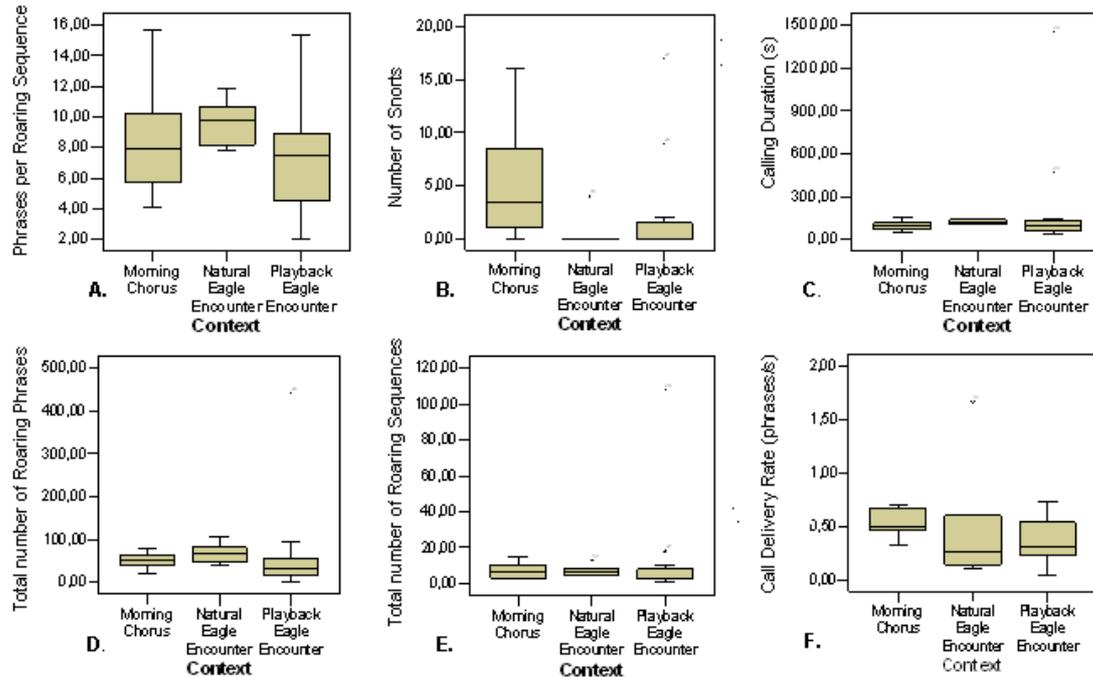
**Figure D.1. II**  
 Comparisons of Acoustic Measurements of RS1 Last call produced in Morning choruses, Natural Eagle Encounters, and Eagle Playback stimuli

A: Phrase duration (ms), B: HNR (dB), C: First Formant (Hz),  
 D : Second Formant (Hz), E. Peak Frequency (Hz), F: Number of Combined Pulses, G: Fundamental Frequency (Hz)

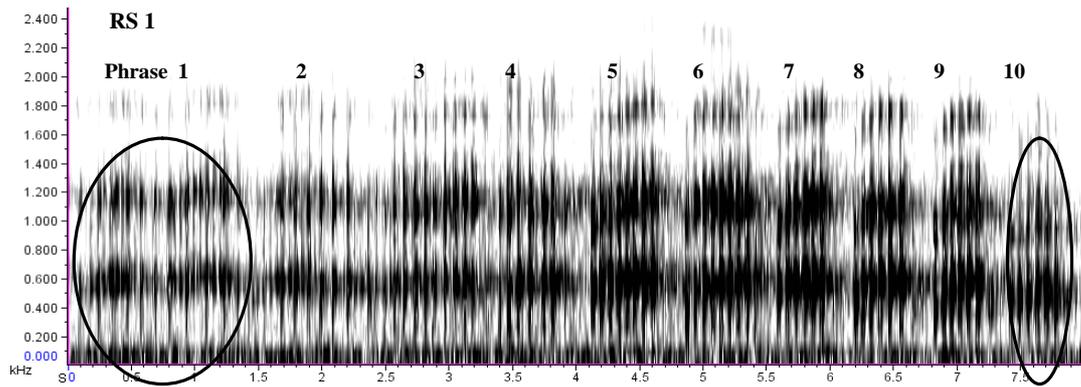


### Composition of Roaring Sequences

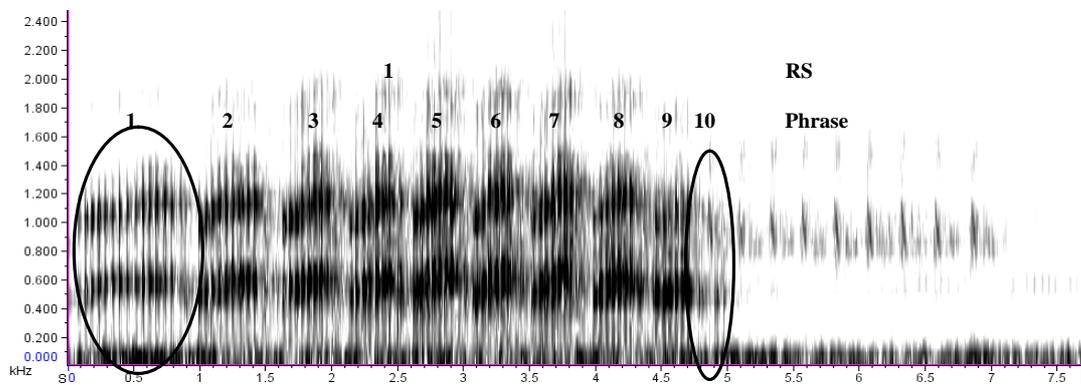
Finally, comparing the structural characteristics of the responses given in the three contexts, showed that there were no differences in structural composition (Figures D2, D3, D4, and D5; Table D4).



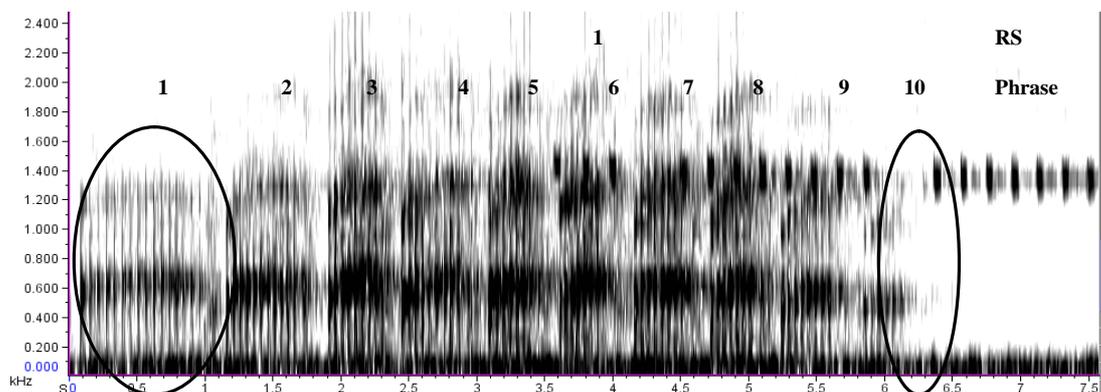
**Figure D.2.** Measurements of temporal response characteristics to acoustic leopard and eagle models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box). A: Number of phrases/ RS, B: Number of snorts, C: Calling duration (s), D : Total number of phrases, E. Total number of RS (Hz), F: Call delivery rate (phrases/s).



**Figure D.2.** 8 Seconds recording of a male producing one Roaring Sequence (RS) consisting of 10 phrases during a Morning Chorus. Encircled are the First and Last phrases produced in the RS.



**Figure D.3.** 8 Seconds recording of a male producing one Roaring Sequence (RS) consisting of 10 phrases during a Natural Eagle Encounter. Encircled are the First and Last phrases produced in the RS.



**Figure D.4.** 7.5 Seconds recording of a male producing one Roaring Sequence (RS) consisting of 10 phrases during a playback induced Eagle Encounter. Encircled are the First and Last phrases produced in the RS.

**Table D. 4.** Temporal measurements of vocal response characteristics to the eagle and morning stimuli stimuli. Mdn= median value, M= mean value and CI = 99% confidence interval. Statistical output (exact p-values ) of the Kruskal Wallis test to compare measurements across contexts are presented as well ( $\alpha=.05$ ).

	Calling Duration (s)			Total Number RS			Total Number Phrases			Phrases per RS			Number of Snorts			Call Delivery Rate (phrases/s)		
	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI	Mdn	M	CI
<b>Morning Chorus</b>	99.5	96.4	53 -139.8	7	7	2 - 13	51	51	27 - 74	8	8	4 - 13	4	5	-2 - 12	0.53	0.50	0.37 - 0.69
<b>Natural Eagle Encounter</b>	122.5	122.5	-864 -1109	6	6	2 - 12	68	68	28 - 108	10	10	7 - 12	0	1	2 - 3	0.53	0.51	-9.6 - 10.5
<b>Playback Eagle Encounter</b>	99	245	-154.7 -644.7	3	15	-15 - 45	32	73	-46 - 193	8	7	4 -11	0	3	-3 - 8	0.30	0.36	0.13 - 0.58
<b>Exact p value between MC, NEE, and PBE</b>	0.695			0.433			0.169			0.208			0.083			0.141		

In sum, the comparisons of roars produced in natural eagle encounters, playback induced eagle encounters and morning choruses have shown that these sequences are similar in their structural composition. Since it may be highly important for the Guerezas to clearly communicate the specified meaning of these different sequences -- because they are produced to serve very distinct functions; a male-male competition and/or spacing function for the morning choruses and a conspecific warning and/or predator communication for the eagle responses— the animals seem to have developed a system for this, based on differences in duration of phrases only: first phrases produced in morning choruses have a longer duration than first phrases produced in both eagle contexts.

The fact that the animals are using a calling system that both seems to make use of acoustically distinct calls produced within distinct roaring sequences in different contexts, is an interesting finding, that can also be related to the responses to the two ground predator contexts that were found to be very similar in structural composition, but may differ in subtle acoustic features.