PANT-GRUNTS IN WILD CHIMPANZEES (PAN TROGLODYTES SCHWEINFURTHII): THE VOCAL DEVELOPMENT OF A SOCIAL SIGNAL

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(*Pan troglodytes schweinfurthii*):
the vocal development of a social signal

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

August 2010

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I, Marion Laporte, hereby certify that this thesis, which is approximately 45,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree. I was admitted as a research student in September, 2006 and as a candidate for the degree of Doctor of Philosophy in June 2007; the higher study for which this is a record was carried out in the University of St Andrews between 2006 and 2010.

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General Abstract

While the gestural communication of apes is widely recognised as intentional and flexible, their vocal communication still remains considered as mostly genetically determined and emotionally bound. Trying to limit the direct projections of linguistic concepts, that are far from holding a unified view on what constitute human language, this thesis presents a detailed description of the pant-grunt vocalisation usage and development in the chimpanzees (*Pan troglodytes schweinfurthii*) of the Budongo forest, Uganda.

Pant-grunts are one of the most social vocalisations of the chimpanzee vocal repertoire and are always given from a subordinate individual to a dominant. The question of how such a signal is used and develops is critical for our understanding of chimpanzee social and vocal complexity in an ontogenetical and phylogenetical perpective. Results suggest that pant-grunt vocalisations can be used in a flexible way, both in their form and usage within a social group.

More specifically, chimpanzees seemed to take into account the number and identity of surrounding individuals before producing these vocalisations. At the acoustic level, pant-grunts seem to be very variable vocalisations that corresponded to different social situations commonly encountered. Grunts are one of the first vocalisations produced by babies but they are not first produced in social contexts. Although some modifications of the social grunts form and usage could not entirely be attributed to maturation only, the role of the mother seemed to be restricted. Her direct influence was perhaps more visible in the rhythmic patterns of chorusing events. Taken together, this thesis suggests that chimpanzee vocalisations are more flexible in their usage, production and acquisition than previously thought and might therefore be more similar to gestural communication.

Chapter one: General introduction

"And if I did not expect that our young men, learned and studious as they are, would very shortly present us here, one with a large collection of examples drawn from the land, the other with his from the sea, I should not have denied myself the pleasure of giving you countless examples of the docility and native capacity of beasts. Let us leave this subject, therefore, fresh and untouched for them to exercise their art upon in discourse."

Plutarch, 959 B.C.

Summary

The overall aim of this thesis is to describe the morphology and use of a social vocalisation in chimpanzees both in a developmental perspective and common use between adults. This chapter first reviews some of the more complex features of animal vocal communication and shows how they relate to aspects of human language from a comparative perspective. The focus is particularly put on notions such as referentiality, intentionality and vocal flexibility to investigate in what ways these terms are useful in animal communication studies and how they relate to the social lives of animals.

Introduction

Why are we so eager to understand non-human primate's vocal communication systems? Their vocalisations have now been studied for decades, with increasingly sophisticated equipment that can measure with precision numerous subtle acoustic parameters of vocal emissions. One of the underlying aims is to "crack the vocal code" that, under the biological foundations of language hypothesis, evolution and selection, would permit a direct comparison with the features of human language and would thus constitute an elegant way of re-evaluating the human-animal boundary characteristics. In this study, I am looking at one of the most social vocalisations of one of our closest living relatives: the pant-grunt of the chimpanzees. My initial aim was to describe the development of this vocalisation only, but I rapidly expanded it to include adult vocalisations, which have been largely ignored.

Animal communication systems in the light of human language

Human language and evolution

The nature of human language is still a popular, hotly debated and controversial topic in the sciences and humanities. Plato's writings about language are some of the earliest documents on the particularities of language, and notably the capacity to arrange different elements together to form a meaningful entity (at least the onoma and rhema, the noun and the verb) (The Sophist, 360 B.C. in Auroux 2008). For most scholars, this feature, i.e. "grammar" or "syntax", is considered the most important to distinguish animal communication from human language (Chomsky 1980). Concerning the origins of language, there have been two main schools of thought, embodied in the discontinuity and the continuity hypotheses. Supporters of the former refute the idea that animal models can help us understand the origins of our language, particularly because the language faculty is considered as undecomposable and no part of it could have been used by hominoids independently from other parts (Jackendoff 2002). Supporters of the later typically argue that language is such a complex system that it could only have emerged gradually, by progressive additions of crucial features, that is, the product natural selection (Christiansen & Kirby 2003; Masataka 2003). Support comes from biologically oriented studies, for instance those that have stressed the necessity of a specific vocal apparatus together with special neural circuitry and genes for the normal production of language as we know it. For example, one study managed to date the fixation of the mutations of a gene involved in orofacial movement control, the FOXP2 gene, to some 200 000 years ago, long after the separation from chimpanzees and bonobos (Enard et al. 2002, but see Coop et al. 2008 and Fitch 2010). This roughly coincides with the emergence of modern humans that possess the adequate vocal apparatus to produce speech (Lieberman 2001).

Anatomical features, such as specific vocal tracts and the neural hardware to control them, have changed slowly over the course of evolution. They also constitute a relatively small part of the conditions required for language. Numerous authors have stressed the importance of a number of key cognitive capacities, and some of these may be found in other animals, and especially primates, although sometimes serving different functions (Byrne 2000; Hauser et al. 2002). “Exaptation” could be one of the most important process in evolution (Gould 1991), providing a useful framework for understanding the emergence of different phenomena, such as language, as caused by the recruitment and interplay of basic capacities originally used for other functions.

Whether or not earlier forms of human communication were largely gesturally or vocally based is another much disputed topic. As such, some authors stress a gestural origin of language, highlighting the flexibility and intentionality shown by our closest cousins the great apes when using gestural signals, compared to their vocal signals, which have traditionally been considered as innate and bound to emotions as most of other non-human species (Arbib et al. 2008; Corballis 2003).

The opposing view is based on studies of primate vocal communication, which has been stressing parallels or relationships with some key features of human language, such as syntax (Arnold & Zuberbühler 2006; Zuberbühler 2002), referentiality (Zuberbühler 2000b), intentionality (Hostetter et al. 2001) and ontogenetic modification (Seyfarth & Cheney 2005). Additionally, primate vocal communication and human language are social behaviours that occupy an important place in the regulation of social interactions within a social group and might have thus been under similar social selection pressures (Hausberger et al. 2008; Masataka 2003). Studying primate vocalisations in tight connection with their social life is thus a means to explore the possible features shared with human language, but also, and perhaps most importantly, to get insights into their "Umwelt" (see von Uexküll 1934).

In this thesis, I am particularly interested in the interconnectivity between vocal communication and sociality or, in other words, how social cognition affects the production of vocalisations and their acoustic features both in adults and during earlier stages of development.

Studying natural vocalisations in animals and the problem of meaning

Many species possess a specific vocal repertoire, constituted of an array of vocalisations, which can be distinguished acoustically and contextually across individuals. Because of the sometimes tight link between acoustic morphology and call context, a first relevant question concerns the notion of meaning, that is, if such signals are comprehended by listeners as indicators of external events. As it is generally impossible to know the internal state of an animal and as it is often difficult to know the exact reasons for the production of a specific signal, one way around is to describe the specific context during call production and the reactions of the surrounding individuals. If there is a consistent relation, something can be inferred about the meaning of the call. This method is generally used in animal communication studies, but has also been used intensively to understand foreign human languages, with more or less success. For example, the Greenlandic word "panygmah" was translated in 1586 as "needle" (Hakluyt 1586) while we know today it relates to the possessive of "girl" or "daughter". The confusion appears to have come from a misunderstanding between the researcher and his informant when pointing to a needle (Dorais & Dorais 1996). Quine (1960) goes even further with the famous example of "gavagai", postulating that we cannot have access to the meaning of this utterance if we do not live in the social group using it. These examples highlight the fact that, although we can derive broad contextual understanding of a vocal emission, its meaning cannot always be fully understood, even between human languages.

This concept of meaning is often put in parallel with human semantics and referentiality. In the field of animal communication, it is largely assumed that signals encode information that is passed on from a sender to a receiver. This view is directly derived from the information theory, first used to describe the transfer of information in technical systems such as telecommunications. However, there is still some disagreement on this point both in animal communication (Rendall et al. 2009) and in human language (Auroux 2008; Rastier 2006). For Rendall and colleagues (2009), the concept of information is misleading in animal studies, because it creates an unnatural metaphor between animal communication and human language that involves intentionality and representations. But some linguists also consider 'information' as misleading in human language studies, largely because it implicitly requires an internalistic stance that humans possess a mentalese that can be encoded into vocal utterances and decoded by receiver(s) having the same representations. Some of these authors go further by postulating that a more fruitful way of thinking about language is to conceptualise it as constituting a milieu with society as the only language organ (Rastier 2006) and others even consider that the signifier and signified are not indissociable because their correspondence is dynamic (Calvet, 2010). Following these views, an acoustic signal does not contain any information per se, but the comprehension of these features is the result of experience and interpretative capacities of listeners, together with a historic conventionalisation (Auroux 2008).

While these views provide interesting frameworks, they are relatively far from the theories underlying current research in animal communication. Because of the problem of meaning and the need for testable hypotheses, the link between a vocal signal and external events is transformed into the problem termed "functionally referential" communication (Seyfarth et al. 2010).

"Functionally referential" communication

Most research in animal communication has focused on the behaviour of the individual receiving the signal, and the principle effort is to determine whether the signal produced functions as if it was referential. For a signal to be functionally referential, it must meet a production and a perception criterion (Macedonia & Evans 1993). First, it must be closely associated with a specific context of emission or stimulus and it should not be used in different contexts (production criterion). Second, the signal alone should be sufficient to elicit an appropriate response in the receiver (perception criterion) and this response must be consistent across different contexts of perception (presence or absence of the eliciting context). Under such conditions, receivers can infer the situation of emission of the signal and can select an appropriate response, even if not directly involved with the object or event.

The first and best-known example of functionally referential communication is Struhsaker's (1967) study on vervet monkey (*Chlorocebus aethiops*) alarm calls. He observed that these primates produce at least three different discrete classes of call types that can be distinguished by ear and on a spectrogram. Each call type was directly related to a specific escape tactic, depending on the type of predator. For a terrestrial predator alarm call, vervets usually run into a tree; for an aerial predator call, they climb down and move into cover and for a snake call, they usually stand bipedally and scan the ground. However, in order to meet the perception criteria and to reject the possibility that contextual cues influenced these responses, the eliciting stimulus must be separated from the surrounding context. Playback experiments during which recordings of different call types are played back to naïve receivers in the absence of both the predator and the caller are the method of choice (Seyfarth et al. 1980). Many authors have recognised the power of this approach and the playback method is now the standard way of providing evidence for the perception criterion of functionally referential communication.

Studies of functionally referential alarm calling have been conducted in various animal species, including chickens: *Gallus gallus* (Evans & Marler 1995), ground squirrels: *Spermophilus beecheyi* (Macedonia & Evans 1993; Owings & Virginia 1978), suricates (Manser 2001; Manser et al. 2001), and primates (Lemurs: *Lemur catta* and *varecia* (Macedonia 1990), Diana monkeys: *Cercopithecus diana* (Zuberbühler 2000b; Zuberbühler et al. 1997) and chacma baboons: *Papio ursinus* (Fischer et al. 2001)). However, even though all of these species produce different types of alarm calls, the different calls do not always refer to a particular type of predator. In California ground squirrels, for example, the different alarm calls appear to reflect different levels of urgency, regardless of the biological class of the predator (Macedonia & Evans 1993). If an individual is chased by a ground predator, it sometimes produces ‘whistles’, a call normally given in response to attacking aerial predators. This highlights the fact that alarm calls may be the direct product of the urgency perceived by the caller or, in other words, the caller’s motivation. It is important to point out that ’referential’ and ‘motivational’ are not considered as mutually exclusive interpretations, but simply address different properties of such communicative events (Evans 1997; Macedonia & Evans 1993). A central point is that receivers may be perfectly capable of extracting some information about the nature of an event, even if the signal is a direct readout of different types of motivations (Seyfarth & Cheney 2003; Seyfarth et al. 2010). For example, suricates (*Suricata suricatta*) respond with acoustically distinct alarm calls to different predators, but their call structure also varies with the level of urgency (Manser 2001). Similarly, Diana monkey ground and aerial predator calls are correlated with the type of predators perceived, together with additional information about the distance and elevation of the threat (Zuberbühler 2000b).

Research on functionally referential communication has not been conducted in the context of predation only, but also in social contexts, such as food discovery (Evans & Evans 1999; Slocombe & Zuberbühler 2005b), agonistic interactions (Slocombe & Zuberbühler 2005a) or sexual interactions (Semple 1998). However, as these contexts are more difficult to categorise, evidence for functionally referential communication is often scarce or disputed. For example, Evans and Evans (1999, 2007) presented some evidence for referential use of food calls by chicken. More generally, food calls can be affected by food quantity (Dittus 1984; Hauser et al. 1993), food preference (Elowson et al. 1991) or quality. For example, Hauser (1998) showed that the different calls produced by rhesus macaques (*Macaca mulatta*) when discovering food were referring to two categories of food: two calls were linked with a low quality food and three calls with a high quality food. Crockford and Boesch (2003) showed that chimpanzees produced acoustically distinct bark variants in different contexts, suggesting that this call type could function referentially for listeners. Similarly, there is evidence that chimpanzee rough grunts given in response to discovering food could function referentially (Slocombe & Zuberbühler 2005b), and it has been suggested that in some cases this may even lead to the labelling of different types of food (Slocombe & Zuberbühler 2006).

Intentionality and flexibility in vocal communication

As we saw earlier, in order to elicit the right type of reaction from listeners, there is no need for the vocalisation to be voluntarily emitted but it can also be the result of emotions and motivation. In humans, the question of intentionality is generally solved by the theory of mind, i.e., attributing mental states to others. This however cannot be postulated for non-humans where the evidence is for theory of mind is scarce although there are a certain number of isolated anecdotes of tactical deception in the primate literature (Byrne & Whiten 1988). Non-humans and especially primates have been shown to manipulate the behaviour of others but not their mental states or beliefs (Seyfarth & Cheney 2003; Tomasello & Call 1997). One way to test the degree of intentionality is to observe whether the emission of vocalisations is affected by the presence of others (i.e. audience effect). For Tomasello and Call (1997), intentional communication can only be achieved with flexible signals that vary in production and use depending on the situation encountered. They also stress the role of learning in a social group through the process of ritualisation (Tomasello & Call 1997). Following their arguments, the following sections will review evidence for flexibility in the usage of vocalisations revealed by audience effects as well as the flexibility in production of calls produced by adults and during development.

Audience effects

Audience effects refer to cases where the signalling behaviour in a specific context is influenced by the presence, the behaviour or identity of others. It includes both the cases where the audience is the recipient of the communicative event (as for example in gestures (Tomasello and Call 1997) or where the audience is represented by the bystanders that could influence the outcome of a signalling interaction between a signaller and a receiver or in cases of a broadcasted signal. For example, male chickens produce food calls that can be modulated by the presence of a hen (Evans & Marler 1994). Similarly, resident male thomas' langurs only stop alarm calling when all the female of his group have counter-called, showing that he takes their behaviour into account to modulate his own vocal production (Wich & de Vries 2006) and female chimpanzees modify their copulation calls and their screams as a result of the social position of bystanders (Slocombe & Zuberbühler 2007). Audience effects are thus not restricted to our closest cousins, but might be present in a large number of species. One should remain cautious when interpreting these modulations as the result of intentional and tactical production, done to modify the behaviour of others. Calling motivations are still out of reach and potentially encompass a larger range of behavioural and contextual correlates that might not fit our categorical preconceptions (Smith 1991). Still, looking at the effects of bystanders on the production of vocalisations permits some insights into the social fabric of the group, to assess flexibility and control over vocal production and, together with the observation of other behavioural flexibilities or directionalities, allows for intentional conclusions. Can vocalisations be emitted in an apparently intentional fashion to affect the behaviour of others, as reported for gestures? For Tomasello and Call (1997), intentional communication requires some flexibility and control over signal production to adapt to the social situation encountered.

Vocal flexibility in adult animals

Observations have shown that vocal flexibility can exist over different time frames. Over long time periods, vocalisations can progressively resemble each other within a social group, while diverging from other groups, creating local dialects. This was first described in sparrows: *Zonotrichia leucophrys* (Marler & Tamura 1964) and later also observed in a variety of other species, such as seals: *Mirounga angustirostris* (Le Boeuf & Petrinovich 1974), whales:

Megaptera novaeangliae (Noad et al. 2000; Riesch et al. 2006), and primates (Japanese macaques coo calls: *Macaca fuscata* (Green 1975), pigtail macaque recruitment screams: *Macaca nemestrina* (Gouzoules & Gouzoules 1990), barbary macaques “shrill barks”: *Macaca sylvanus* (Fischer et al. 1998), mouse lemurs: *Microcebus ssp*. (Zimmermann & Hafen 2001) or chimpanzees “pant-hoots”: (Crockford et al. 2004; Mitani & Brandt 1994; Mitani et al. 1992, 1999). It is often difficult to attribute these acoustic differences to behavioural control of vocal production because other factors can also interplay. They can be attributed to genetic differences, for instance in the case of subspecies or ecological variations, and some variations of the signal acoustic features can be explained with habitat differences (Janik & Slater 1997). The most cognitively demanding possibility is that the differences found are the result of socially motivated active call modification from individuals to match others, a mechanism is usually known as acoustic convergence. Another possibility is that the calls change as the result of a slow drift from one generation to the next, a process that would then require vocal learning.

At a small timescale, individuals can alter their vocalisations to match those of individuals they are chorusing or interacting with. For example, bottlenose dolphins (*Tursiops truncatus*) are likely to match another individual’s signature whistle during vocal interactions, in captivity as well as in the wild (Janik 2000; Janik & Slater 1997). Similarly, playback experiments showed that Japanese macaques tend to modify some of the acoustic features of their ‘coo calls’ depending on the individual they just heard (Sugiura 1998) and in their natural habitat, chimpanzees produce pant hoots varying along with those of their chorusing partners (Mitani & Gros-Louis 1998). These local variations due to the changing social situations can progressively stabilise, creating the dialects previously described. Humpback whales of the Australian west coast, for example, have picked up a new song, introduced by few immigrants from a distant ocean, and this new song progressively replaced the old one in the population (Noad et al. 2000). As found in whales, a pant-hoot variant introduced by only one individual can progressively spread to other group members in captivity (Marshall et al. 1999), and Poole and colleagues (2005) reported a case of an African elephant (*Loxodonta Africana)* vocalising like an Asian elephant after having shared the same enclosure for 18 years. Snowdon and Elowson (1999) found that pygmy marmosets *(Cebuella pygmaea)* modify their call structure rapidly after pairing and the new structure of the vocalisation subsequently stabilises, as found in campbell's monkeys: *Cercopithecus campbelli* (Lemasson & Hausberger 2004).

Social contact with individuals thus play an important role in driving acoustic convergence in primates and other animals (Elowson & Snowdon 1994), supporting the hypothesis that an active modification of calls permits to differentiate from others, but also to converge with community members, thus reinforcing group affiliation (Crockford et al. 2004) and are sometimes useful for recognising members of different clans (Riesch et al. 2006).

At small timescales, genetic factors are not likely to play a role, but as individuals can locally alter their vocalisations if in an open or closed habitat, ecological factors can still have an effect on vocal plasticity. For example, baboons *Papio hamadryas anubis* increase their grunt rate and duration when they are in forest habitat as opposed to the savannah, permitting a better sound propagation (Ey et al. 2009).

Social learning of vocalisations

Vocal plasticity occurs in adults of different primate species as the result of social forces acting between members of social groups over long (e.g.: elephants) or short (e.g.:

chimpanzees pant hoots) timescales. In cases where vocal dialects are found, these could further be the consequence of ontogenetic learning. More parsimonious explanations of adult vocal convergence are generally considered to be environmental conditions and genetic differences; for vocal learning they are constituted by the maturation processes (Janik & Slater 1997). For example, as the body grows, the lungs expand and the vocal folds lengthen and thicken, allowing the individual to produce longer vocalisations with lower frequencies (Fitch & Hauser 1995). These modifications are thus not the result of social experience with others. In studies of vocal development, it is difficult to separate the different mechanisms at work that are likely to be all mingled.

In an attempt to clarify the different types of learning that could be involved during ontogeny, a framework was proposed by Janik and Slater (1997; 2000). Vocal production learning is defined as a modification of a vocal signal's spectrotemporal features through auditory experience, mainly by imitating other individuals' vocalisations (Janik & Slater 1997; Seyfarth & Cheney 2005). It is contrasted with vocal usage learning and vocal comprehension (or response) learning, summed up by Janik and Slater (2000) as "contextual learning". In contextual learning, a signaller learns to use a signal in different contexts, while a receiver learns to link a particular signal to a context. This distinction has been useful in highlighting interesting parallels and differences between bird song and human language. Learning is thought to be one important features of human vocal development, in contrast to other animal species (Tomasello 2003). Speech and language are acquired through learning within a social group, at the individual level, whereas animal communication appears to be more hardwired, with vocal signals emerging in a species-specific way (Arbib, 2003). In humans, learning facilitates the generation of novel sound, which are prerequisites for the generation of potential infinite means (Janik & Slater 2000; Nottebohm 1972).

Darwin (1871/2009) already noted the presence of "provincial dialects" and practice in canary birds *Serinus canaria*. Only recently, the dialects and developmental plasticity of songs in different bird species were systematically investigated (Marler & Tamura 1962, 1964). It was found that learning was essential for the correct acquisition of songs in finches, an interesting parallel with human speech development (Kuhl 2003, 2004; Nottebohm 1972). However, only three out of twenty orders of birds actually show vocal learning. They are all the members of the songbirds (*Passeriformes*), hummingbirds (*Apodiformes*) and parrots (*Psittaciformes*) (Janik & Slater 1997). As they are not directly phylogenetically related and their neural circuitries for vocal control differ in a numerous ways, vocal learning could have evolved at least three times independently (Brenowitz 1997; Nottebohm 1972).

If songbirds are deafened at birth, they will not produce normal songs as for example zebra finches: *Taeniopygia guttata* (Nottebohm 1972). The result is the same if they are reared in isolation. Hand-reared bullfinches (*Pyrrhula pyrrhula*) can learn the canary songs they hear during their development that they further transmit to the next generation (Nicolai 1959, reviewed in Nottebohm 1972) and cross-fostered zebra finches can learn bengalses finch (*Lonchura striata*) songs (Kuhl 2003). These parallels between bird songs and human language are interesting because they highlight the neural and genetic mechanisms that are required for vocal learning. However, the bird model mostly concerns songs, an acoustic signal that principally functions in reproduction and territory defence. Indeed, the learning capacity seems to be a determining factor in mate attraction as females assess the quality of their potential mates through the complexity of their songs (Nowicki et al. 1998). Birdsong relevance is thus very limited for studies on the relationship between intentionality and context-relatedness of calls. One should thus be cautious when applying these models to other phylogenetic groups. For example, following these lines of research, early studies have raised primates in isolation to test for the role of social input and to examine the species-specific vocal repertoire. However, the individuals that underwent such treatment suffered from such deep behavioural problems if they survived, that is was difficult to draw any meaningful conclusions from their behaviour (Harlow 1958; Newman & Symmes 1973). In chimpanzees, socio-emotional contacts with caregivers are essential and isolation-rearing also causes persistent cognitive deficits (van Ijzendoorn et al. 2009). Overall these primates were more similar to humans than birds, when exposed to the same conditions. Kaspar-Hauser experiments of this kind were also performed on humans, allegedly by monarchs such as Psammeticus (663-609 BC), Frederick II of Hohenstaufen (1194-1250), King James IV of Scotland (1473-1513), or Akbar (1542-1605) (Rastier 2006). All tried language deprivation experiments with children who were raised in semi-isolation with muted surrogate mothers. Unsurprisingly they developed severe language deficiencies and the surviving ones were generally described as barely human. These examples emphasise the importance of social relationships for normal development in the primate lineage.

Primate vocalisations are often described as largely “innate” in terms of their acoustic features. Interestingly, it was recently noted by Seyfarth and Cheney (2005) that before 1987, 79% of published studies were in favour of a totally determined vocal repertoire, while 71% published after this date supported some acoustic changes during development.

A typical example for the genetic determinism of production comes from the studies on squirrel monkeys (*Saimiri sciureus*). From 1973 to 1982, researchers argued that the squirrel monkeys’ vocal repertoire was fully present from one week of age (Lieblich et al. 1980), was not affected by deafening or social isolation (Winter et al. 1973) and that hybrids from subspecies develop structurally intermediate isolation peeps in line with changes in the facial features (Newman & Symmes 1982). More recently, Winter and colleagues' study was repeated, using a more fine grained acoustic analysis and acoustic changes were found in all types of vocalisations but could all be explained by maturational factors (Hammerschmidt et al. 2001). In contrast, Roupe and colleagues (2003) found that auditory deprived marmosets failed to develop adult-like calls and usually continued to use immature vocalisations.

Interestingly, cross-fostering and hybrid studies have not shed more light on the question of innate versus learned vocal repertoire. Call analysis of hybrid gibbons (*Hylobates pileatus* x *Hylobates lar*) by Geissmann (1984) indicated that 7 of the 10 song characteristics examined had an inheritable component. Additionally, a male hybrid gibbon (*Hylobates muelleri* x *Hylobates lar*) presented some male-specific song elements of both parental species while the hybrid female's song elements differed from both parental species (Tenaza 1985). Japanese monkeys reared by rhesus mothers were shown to produce rhesus-like type of food calls and vice versa (Masataka & Fujita 1989), although it has been argued that there were no significant acoustic differences between the food calls of the two species (Owren et al. 1992). For both primate groups, these results suggest a close relatedness between species but imply that definite conclusions on genetic inheritance are impossible to draw on these grounds (Geissmann 1984; Owren et al. 1992).

All these experimental studies show little evidence in favour or against vocal production learning. Indeed, the small sample sizes, the kinds of vocalisations tested, the few spectrographic features studied and the equipment used to analyse the vocalisations often prevented a deeper understanding of the relevant mechanisms involved during vocal development. Snowdon and colleagues (2005) further argued that all call types might not be equivalent and proposed a distinction between calls of urgency and distress, such as alarm calls, that may not need to be learned and social or affiliative calls that could allow for more flexibility.

Modifications of the vocal structure of calls during normal development have been found in different primate species, indicating some flexibility and presenting a prerequisite for vocal production learning (Egnor & Hauser 2004). In free-ranging vervet monkeys, at least three different vocalisations undergo gradual changes during ontogeny, differing significantly from adults' vocalisations (Hauser 1989; Seyfarth & Cheney 1986, 2005). Similarly, Gouzoules and Gouzoules (1989 a, b; 1995) found age and sex differences in call production that cannot be explained by body growth only. Several authors thus advocate that the changes observed are certainly a combination of all the factors at work during development, such as the development of organs and growth, the increase in coordination as much as social experience that might lead to learning (Seyfarth & Cheney 2005).

In contrast to vocal production learning, there is good evidence for plasticity and ontogenetic flexibility in the usage and comprehension of primate vocalisations. The best known example is how vervet monkeys gradually learn how to use their 'grunts' (Seyfarth & Cheney 1986), 'intergroup wrrs' (Hauser 1989) and different alarms calls for their different predators: leopards, eagles and pythons (Seyfarth & Cheney 1980). As individuals grow older, they gradually sharpen the association between the context and the appropriate response. The response to some external events can also be learned. For example, vervet monkeys gradually learn the appropriate response to different starling alarm calls (Hauser 1988). In pigtail macaques, infants use four distinct scream variants with little consistency across acoustic contexts and only with experience learn to use them more specifically (Gouzoules and

Gouzoules 1989a; 1995). Similarly, young pygmy marmosets give ‘trills’, ‘J calls’ and ‘chirps’ indiscriminately of context. Their organisation long sequences that promote social interaction with adults resemble in many aspects to human babbling (Snowdon et al. 2005).

Overall, non-human primates present relatively little control over their vocal production and although the acoustic features of their calls undergo some modifications during development, they can most of the time be imputed to maturational factors. The only changes that appear to be influenced by the social environment are the usage and the comprehension of these relatively “fixed” vocal productions. Quite surprisingly, very little is known on the vocal development of apes in general and chimpanzees in particular. A first general overview of chimpanzee social structure is necessary to understand the problematic of chimpanzee vocalisations and development.

Chapter two: Chimpanzee social structure and vocalisations

"At the office all morning and did business; by and by we are called to Sir W. Batten's to see the strange creature that Captain Holmes hath brought with him from Guiny; it is a great baboon, but so much like a man in most things, that though they say there is a species of them, yet I cannot believe but that it is a monster got of a man and she-baboon. I do believe that it already understands much English, and I am of the mind it might be taught to speak or make signs".

Samuel Pepys, 24th of August, 1661

Social structure

In the wild, chimpanzee societies are organised in communities of twenty to more than a hundred individuals of all age–sex class that fluidly associate in small groups, which continuously change over time (van Lawick-Goodall 1968). This fission-fusion organisation is relatively atypical amongst animals. Other exceptions are dolphins, bats, elephant, spotted hyenas, spider monkeys, muriquis and bonobos (reviewed in Aureli et al. 2008). Chimpanzee females tend to leave their natal community at adolescence (10-14 years) and generally have their first offspring after they have fully transferred to a new community, although it is not always the case (Pusey et al. 1997, personal observation).

In chimpanzees, males are the philopatric sex and consequently there is a relatively high degree of relatedness between them (Goodall 1986). They also constitute the core of the group, displaying higher levels of social behaviour than females, including affiliative behaviours and competition for status (Goodall 1986; Mitani 2009b). Female chimpanzees have generally been perceived as passive and peripheral individuals, not really taking part in the social life of the community (Mitani 2009a). However, this view is beginning to change with recent studies showing that females can also behave competitively and even tactically at food sources (Kahlenberg et al. 2008; Murray et al. 2007; Pusey et al. 2008). Infanticide by females has been observed, possibly a response to increased resource competition imposed by a sudden influx of immigrant females (Townsend et al. 2007). Still, females rarely associate with other community members apart from their own dependent offspring or when foraging with others at large food sources or in nursing parties (Murray et al. 2007; Pusey 1983). At Gombe National park, females spend nearly two thirds of their time foraging alone with their dependent offspring (Pusey 1983).

While male rank is often linear and achieved through direct competition, grooming or alliances, female status is generally attained as a function of age and temperament (Bygott 1979; de Waal 1982). Due to their low interaction rates, even in captive settings, their social relations are harder to decipher (Mitani 2009a).

Communication

The chimpanzee vocal system is highly graded (van Hooff 1973; Marler & Tenaza 1977). There is no true delimitation from one call type to the next and there is considerable acoustic variation within the different call types. Graded vocal repertoires are more difficult to apprehend than discrete ones because the categorical boundaries perceived by human listeners may be different from those perceived by the species producing them. Whether or not the greater acoustic flexibility is reflected in their flexibility of usage is yet not so clear (Slocombe & Zuberbühler 2006).

The chimpanzee vocal repertoire is composed of variations of four main call types, the grunts, the barks, the screams and the hoots. Nevertheless, researchers relying on their own perceptions discriminated between 12 (Reynolds 2005) to 34 (Goodall 1986) vocalisations types, with added sub-categorisations of calls usually according to their usage in different contexts. Currently, the number of vocalisations discriminated through spectro-temporal features and contextual use is around a dozen call types (Arcadi 2000; Slocombe 2005, see Table 2.1). These calls can be given as part of longer sequences and are sometimes combined in context-specific ways (Crockford & Boesch 2005). For example, panting is a short and breathy call type that occurs in different contexts, such as long distance communication (pant-hoot), greeting (pant-grunt), grooming (pant) or copulation (copulation pant) (Goodall 1986).

Table 2.1: Categories of vocalisations used in this study, adapted from Arcadi (2000), Marler & Tenaza (1977), and Goodall (1986).

In this study	Marler and Tenaza 1977	Goodall 1986	Context Goodall 1986
Soft grunt	Grunt	Soft grunt Nest grunt	Foraging or travelling Nesting
Waa-bark	Waa-barks	Waa-bark	Agonistic contexts, mainly given by bystanders
Bark	Bark	Bark	Social excitement
Extended grunt	Grunt	Extended grunt	Resting
Hoo	Whimper	Huu Hoo	Surprise, mild anxiety Contact call (mother/infant contact)
Pant-grunt	Pant-grunt	Pant-grunt Pant-bark Pant-scream	Greeting up hierarchy Greeting up hierarchy, mild threat Greeting up hierarchy, fear
Pant hoot	Pant hoot	Roar Pant hoot Arrival Pant hoot Inquiring pant hoot Spontaneous pant hoot	Charges, stranger contact, social excitement Arrival at food source Travelling Resting, Feeding
Pant	Pant	Pant	Greeting, grooming
Food grunt	Grunt Rough grunt	Food grunt Food aaa	Feeding calmly Excited feeding
Squeak-Scream	Squeak Scream	Squeak Victim scream Tantrum scream SOS scream Copulation scream Crying	Response to threat by dominant When attacked Weaning conflict, frustration Appeal for help after attack Copulation (females) Whimpers and tantrum (Infants/Juveniles)
Cough	Cough	Cough	Mild threat given to lower ranking individuals
Whimper	Whimper	Whimper	Distress
Copulation pant	Copulation pant	Copulation pant	Copulation (males)
Laughter	Laughter	Laughter	Play
Whraah	Whraah	Whraah	Alarm

The chimpanzee pant-grunt

Acoustics

Pant-grunt utterances constitute an acoustically heterogeneous signal, which usually consists of a sequence of grunts joined together by voiced inhaled elements (Crockford & Boesch 2005, Fig. 2.1). However, this organisation can be modulated and the grunts can also be panted or can grade into barks or screams (Goodall 1986). Acoustically, the grunt elements are relatively variable in length (between 30 and 200 ms), with a low fundamental frequency (between 70-200Hz) and are generally very noisy (Crockford & Boesch 2005). This noisiness can be produced by chaotic tissue vibrations or turbulent airflow in the vocal tract that blurs the harmonic structure of the call (Buder et al. 2008). When the call grades into exhaled panting, it looses its fundamental frequency and becomes breathy. On the other end of the continuum, grunts can grade into barks with an increase in fundamental frequency and the apparition of clear frequency bands. The inter-grunt inhalations, with the air inhaled back to the lungs, can be voiced or not.

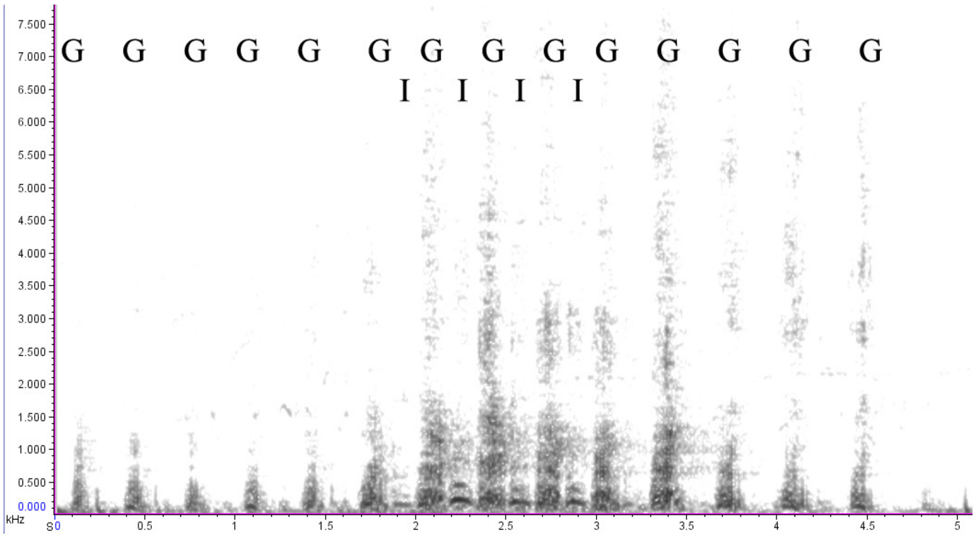


Figure 2.1: Spectrographic illustration of a pant-grunt vocalization given by the alpha female Nambi to the alpha male Nick, containing voiced inhalations (I) and grunts (G).

The social function of pant-grunts

Pant-grunts are social signals. In the current literature, their function is unanimously regarded as unidirectional greeting, given as a token of respect from a subordinate individual to a dominant in a variety of contexts, such as during travelling, feeding, or resting (Bygott 1979; Goodall 1986; de Waal 1982). The direction of pant-grunts is considered as a reliable way to assess dominance relationships between individuals. Pant-grunts are thus commonly used by researchers to construct social dominance hierarchies. In captive chimpanzees, pant-grunts are also often accompanied by ritualised behaviours of subordination, such as bobbing, crouching, or presenting (de Waal 1982). In the wild, where individuals are freer in their choosing or avoiding of social interactions, pant-grunts are often given without additional signals (Goodall 1986, personal observation). Newton-Fischer (1997; 2004) observed that they seem to be given spontaneously to others and not as a direct response to threat or agonistic behaviour. Pant-grunts are also used in reconciliations and Arnold and Whiten (2001) noted that about half of the reconciliations observed were preceded by a pant-grunt.

Overall, there does not seem to be a typical situation in which individuals produce pant-grunts. Both individuals can approach each other in calm or in an agonistic situation and the greeting can result in either agonistic or affiliative reactions, although neutral situations where the receiver does not produce any noticeable behaviour seem to be more the rule than the exception. This contrasts with greeting in some other animal species where both individuals typically participate in the greeting and follow a sequence of ritualised behaviours (baboons: (Colmenares 1990) howler monkeys: *Alouatta palliata* (Dias et al. 2008) or hyenas: *Crocuta crocuta* (East et al. 1993)). For example, in howler monkeys the initial approach is accompanied by vocalisations by both individuals. They then grab each other’s shoulder with one hand while sniffing the other individual’s armpit and proceed to a mutual rump-to-face position sniffing each other’s genitals before terminating the greeting (Dias et al. 2008).

In chimpanzees, it has been observed that pant-grunts are neither given to all higher-ranking individuals, nor are they compulsory at the time of encounter (Boesch & Boesch-Achermann 2000; Newton-Fischer 1997; Nishida & Hosaka 1996; Takahata 1990a). For example, Newton-Fischer (1997) noted that pant-grunts were observed in only 28% of possible dyads in a wild community of chimpanzees. These observations, done mostly on males-male interactions, could reflect uncertainties in the callers' perceived social position or the fact that some dominance relationships were unstable or ambiguous, a possible reflection of tactical behaviour (Newton-Fischer 1997; Nishida & Hosaka 1996). It has further been suggested that pant-grunts are not submissive behaviours but are a means to indicate subordinate status (Goodall 1986; Newton-Fischer 1997). Although pant-grunts are normally strictly unidirectional, some researchers have noted that they can sometimes be given in bi-directional ways, especially in females (Emery Thompson et al. 2008; Newton-Fischer 2006). While it has been shown that pant-grunts have an appeasing function, especially after conflicts (Arnold and Whiten 2001; de Waal 1982), they can also elicit aggressive response from receivers (Hayaki 1990).

Overall, these observations show that relatively little is known about the motivations to call and the flexibility in usage of this vocalisation, especially in females, although the vocalisation is commonly used by researchers in studies of chimpanzee social behaviour. Chapters 4 and 5 will address some of these questions. In Chapter four, I will address the question of intentionality and flexibility of this vocalisation by looking at the factors that influence the production of pant-grunts and the role of audience effects. In Chapter five I will focus on the acoustic structure of this vocal signal, while trying to address the questions of signal specificity and production flexibility in different contexts.

Development

In chimpanzees the development period from birth to adulthood is relatively long for a mammal and even compared to other primates. For example, chimpanzee females spend twice as much time nursing their infants as capuchins (Fragaszy & Bard 1997) and this long neonatal dependence is thought to have a strong influence on a species' cognitive capacities (Gómez, 2004). The development of chimpanzees before adulthood has often been divided into four major periods, the baby stage, the infant stage, the juvenile stage, and the subadult/adolescent stage, all of which are separated by major behavioural changes (van Lawick-Goodall 1967, 1968; van de Rijt-Plooij and Plooij 1987; Matsuzawa, 2003; Reynolds, 2005 Table 2.2). The mother-infant bond is crucial for normal development of young individuals and infants below the age of four generally do not survive to their mother's death (Pusey 1983) although cases of successful adoption have been reported (Boesch et al. 2010). The tie between the mother and her infant persists even after the acquisition of independence by subadults and they usually maintain a special relationship.

Table 2.2: Age classes and noticeable behaviours occurring within these age classes.

Age class (this study)	Reynolds (2005)	Matsuzawa (2003)	van de Rijt-Plooij and Plooij (1987)	Goodall (1968)	Goodall (1967)	Age	Noticeable behaviours
Baby: 0 to 6 months	Infant: 0 to 4years	Infant: 0 to 4years	Baby: 0 to 6 months	Infant 1: 0 to 6 months	Infant 1: 0 to 6 months	0 to 2 months	Ventral position
						3 to 6 months	Able to support its own weight, break of mother-infant contact, beginning to ride dorsally and eating solid food
Infant: 6 months to 4 years			Infant: 6 months to 5 years	Infant 2: 6 months to 2 years	Infant 2: 6 months to 2 years	7 to 11 months	Rides dorsally
						1 to 3 years	More independent, goes away from the mother
				Infant 3: 2-3½ to 4 years	Infant 3: 2 to 3-3 ½ years	3 to 4 years	End of infancy, beginning of weaning, resumption of the mother's menstrual cycle
Juveniles: 5 to 10 years	Juveniles: 5 to 10 years	Juvenile: 4 to 8 years	Juvenile: 5 to 9 years	Juvenile: 3½ - 4 to 7 years	Juvenile: 3-3½ to 6-7 years	5 to 6 years 7 to 10 years	Weaned, still travelling with the mother but not riding dorsally
Subadult: 11 to 15 years	Subadult: 10 to 15 years	Adolescent:s 8 to 12 years	Adolescent: 9 to 14 years	Adolescent: 7 to 10-13 years	Adolescent: 6-7 to 11-13 years	11 to15 years	Mostly independent, beginning of sexual maturity

Babies

As neonates, chimpanzees are extremely helpless. They cannot hold their head up for more than ten seconds; neurobiologically they rank closer to human neonates than capuchins (Fragaszy & Bard 1997). In the first few days, newborns do not move much. They seem unable to hold onto the mother without assistance and show distress with “infant screams” whenever the mother is moving or the ventro-ventral contact is lost (van de Rijt-Plooij & Plooij 1987). The mother usually supports her newborn with one hand and adopts the “hunched gait” to support her infant with her thighs while walking (van Lawick-Goodall 1967). The baby’s grabbing capacities stabilise around the second week of age but the mother continues to secure it until the second to third month (van de Rijt-Plooij & Plooij 1987). Babies are generally first seen to ride dorsally around the third month but this does not constitute their principal way of being carried until month six to nine (van Lawick-Goodall 1967). The first breaking of mother-infant contact does not occur before the fourth month and babies begin to regularly initiate excursions around month seven. At around the same age, babies who were principally relying on their mother’s milk for food begin to eat and chew solid food with the emergence of their teeth (Hiraiwa-Hasegawa 1990).

Infants

According to Plooij (1984), infancy starts in the sixth month, on the basis of major behavioural changes, such as dorsal riding, eating solid foods or able to go away from the mother without whimpering (Table 2.2). It ends when the mother resumes cycling, shortly followed by weaning and the birth of a new sibling, when the infant is between three and six years old. During infancy, chimpanzees also begin to socially interact with others (Plooij 1984). They are very attractive to older infants that initiate interactions with them more often than the other way around (Tomasello et al. 1990). From six months onwards, chimpanzees begin to manipulate objects in captivity and their interactions depend on the encouragement given by a caregiver (Russel et al. 1997). Around two years, they develop new skills, such as grooming their mothers for more than a minute (Nishida 1988) together with adult-like postures and gestures (van Lawick-Goodall 1967). Infants also progressively acquire the same diet as their mother through food sharing and the mother’s control over her infant’s food intake (Hiraiwa-Hasegawa 1989, 1990). Infants are first seen to make nests from about one year of age (Plooij 1984) although they still sleep in their mother’s nest at night until weaning (van Lawick-Goodall 1967). From two to three years of age, mothers do not always carry their infants during travelling anymore and from four years, infants travel more often independently than being carried dorsally (Hiraiwa-Hasegawa 1990). Weaning begins when the mothers resume oestrus, a long process punctuated by infants tamper tantrums, and first signs of some degree of social awareness (Nishida 1990).

Juveniles

After weaning, juveniles still spend most of their time with their mother and almost exclusively travel with her until they are about 8 to 10 years old, which is when puberty begins (Pusey 1990). Because of their small size of about 50% of adult body weight, (Pusey 1990) and the fact that they are not being carried dorsally anymore, juveniles become a constraint for their mother’s ranging patterns (Pontzer & Wrangham 2006). Juveniles of both sexes direct their grooming principally to their mothers with females generally grooming more than males (Pusey 1990). This is also the period of time when most playing occurs. Juvenile males play more with larger individuals than juvenile females (Pusey 1990) and it has been hypothesised that play is one of the mechanisms by which young chimpanzees test the degree of cooperation and competition among the playmates and their relatives (Palagi 2007). Juvenile males already show all the pattern of courtship and copulation behaviour. They have been observed to copulate mostly with females who do not have fully developed sexual swellings (Pusey 1990). In females, the first swellings are associated by active solicitations by males, especially infants and juveniles, while adult males are not interested in young females until her first oestrus (Pusey 1990) and more generally are more attracted by older females (Muller et al. 2006). Juvenile males generally do not receive much aggression from adult males and while some of them may begin to threaten adult females, they do not receive pant-grunt from them nor do they give pant-grunts to them (Pusey 1990).

Subadults

The patterns described in juveniles change in subadults. As males gain in social dominance over some adult females, they also receive higher rates of aggression from adult males (Pusey 1990). The amount of charging display also increases with age in males. Juvenile and subadult males joined in pant-hooting choruses more often than females and only subadults of both sexes were observed initiating pant-hoots (Pusey 1990). Individuals also acquire all the foraging skills such as terming fishing around five years of age (Lonsdorf 2006), but they do not master the nut-cracking behaviour before they are ten (Boesch 1991). A decrease in association between the mother and her offspring is observed in this period and seem to derive from diverging social priorities and not direct conflict (Pusey 1983). As subadults, individuals still have privileged interactions with their mothers and they spend about the same amount of time grooming them as they are groomed by them (Nishida 1988).

Maternal influence on offspring sociability

In the chimpanzee fission-fusion social system, the only long-term party consists of the mother with her dependent offspring. Given the close association of the mother and her offspring during travelling, the mother is very likely to have an influence on both the identity of individuals her offspring can socialise with and the amount of time of socialisation (Goodall 1986, Greengrass 2005), a finding also reported for other primates. For example in baboons, offspring of high-ranking females display higher rates of social interactions and play more than other offspring (Altmann, 2001). Also, because chimpanzee females associate mostly with females of similar rank in nursery parties, the social network of their offspring tends to mirror that of their mother at least until they become independent, a pattern observed both in captivity and in the wild (Evans & Tomasello 1986; Greengrass 2005).

Mothers seem to invest in each sex in a different way, partially depending on their own rank. For example when using the inter-birth interval as a measure of maternal investment, Boesch (1997) found that high ranking mothers nurse their sons about two years more than their daughters while low-ranking mothers nurse their daughters about eleven months more than their sons. On the other hand, Greengrass (2005) reported that in the Gombe community of Tanzania, females support their daughters more often than their sons in agonistic interactions. Other studies did not find any differences in other maternal behaviours towards sons and daughters, such as the amount of carrying time during travel (Hiraiwa-Hasegawa 1990) or the amount of interaction with other group members (Brent et al. 1997). These different rearing conditions potentially influence the future behaviour of males and females when interacting with others in adulthood. Mothers are also initially very protective over their newborn, possibly because of the risk of infanticide from both males and females (Goodall 1986; Townsend et al. 2007). Siblings are the first to be allowed to approach the infant and the mother is progressively more tolerant with other individuals (van Lawick-Goodall 1967). Mother-infant mutual gazing has been reported in captivity and corresponded to a decrease in cradling behaviour by the mother (Bard 2005; Matsuzawa 2006; Tomonaga et al. 2004).

Thesis outline

As part of a general research effort to better understand chimpanzee vocal communication and social world complexity, this thesis focuses on pant-grunt vocalisations with two principal goals. The first goal was to systematically investigate pant-grunts usage in adult individuals in different contexts to tackle the questions of intentionality and flexibility and the second goal of this study was to explore the development of this social signal both in its form and function within a social group.

Chapter four examines pant-grunts that adult females give to adult males and how this production is influenced by the presence, number and identity of other individuals (i.e. audience effects). Building up on Chapter four, Chapter five systematically investigates the acoustic variability of pant-grunts in three different contexts of emission that adult chimpanzees regularly encounter: approaching the alpha male, approaching another male and approaching the alpha male and grooming him.

The question of how this vocalisation develops from primary forms of grunts is addressed in chapters six and seven. Chapter six concentrates on the usage of grunt-like vocalisations from the first grunts produced in babies and describes the development of grunts produced in different contexts and especially in the social context when directed to an individual, which is the context in which pant-grunts are produced. The question of the similarity with adults' pant-grunts and more specifically the mother's is then studied, particularly in terms of the frequency of production and individual targeted. Chapter seven is a follow-up of Chapter six, which focuses on the acoustic modifications taking place during development and the similarity with the mother model.

Chapter three: General Methods

"[…] vue de l'intérieur, cette masse confuse devient un univers monumental. La forêt cesse d'être un désordre terrestre; on la prendrait pour un nouveau monde planétaire, aussi riche que le nôtre et qui l'aurait remplacé."

Claude Lévi-Strauss, 1955 (See Appendix A for translation)

Study Site

Data were collected over a 16-month study period divided in three field periods: a pilot study between January and April 2007, and two main study periods between August 2007 and February 2008 and between July and December 2008 in the Sonso chimpanzee community of Budongo Forest, Uganda. Budongo forest covers 428 km² of moist, semi-deciduous tropical forest situated in the Masindi district in the North-East of Uganda, between 1°35' and 1°55' N and 31°08' and 31°42' E (Fig. 3.1). The study site is located at an altitude of 1,100m with temperatures varying between 19°C and 32°C and a mean annual rainfall of about 1,600mm (Reynolds 2005). This region of Uganda has two rainy seasons a first one between March-May and a second one between July-November interspaced by a long and a short dry season respectively.

The forest composition varies across the reserve and comprises four main types of vegetation as a result of a long history of logging between 1930 and 1990 (Eggeling 1947; Plumptre 1996, Fig. 3.2): (1) Swamp forest around the two rivers intersecting in Budongo, the Sonso river and the Waisoke river both flowing into Lake Albert. This forest type is least common and contains species such as *Raphia farnifera*. (2) Colonizing forest is found in large blocks at the edge of the forest with dominant species such as *Maesopsis emineii* or *Cordia millenii*. (3) Mixed forest is characterised by high species diversity, large trees including the logged mahogany species *Khaya anthotheca* and is the most common type of forest found in Budongo. (4) Ironwood forest is possibly the climax forest type, containing the fewest species, including *Cynometra alexandrii*.

Figure 3.1: Map of Uganda indicating the location of the Budongo Forest reserve. Courtesy of Oxford Cartographers, (c) Oxford Cartographers. www.oxfordcartographers.com.

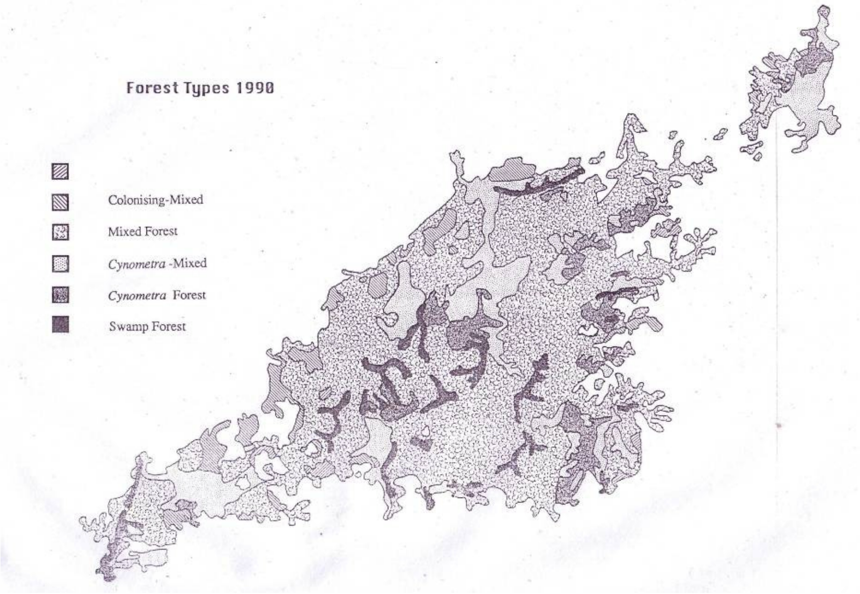


Figure 3.2: Map of the Budongo forest types covers in 1990 (Plumptre 1996). Printed with permission of A. Plumptre.

Fauna

A population of about 650 chimpanzees (*Pan troglodytes schweinfurthii*) inhabits the forest with four other species of diurnal primates: the red-tailed monkeys (*Cercopithecus ascanius*), the blue monkeys (*Cercopithecus mitis*), the black and white colobus monkeys (*Colobus guereza*) and the olive baboons (*Papio anubis*). Other large mammals include blue duikers (*Cephalophus monticola*), red duikers (*Cephalophus natalensis*), bushbucks (*Tragelaphus scriptus*) and bushpigs (*Potamochoerus porcus*) and there are several species of smaller mammals including genets (*Genetta genetta*), civets (*Civettictis civetta*), tree hyraxes (*Dendrohyrax arboreus*) and fruit-eating bats (Reynolds 2005).

The Sonso community

The chimpanzees of the Budongo forest are part of the Eastern or long-haired subspecies of chimpanzees (*Pan troglodytes schweinfurthii*) that are also found at other field sites, such as the Kibale Forest National Park of Uganda and the Gombe and the Mahale Mountains National Parks. The Budongo chimpanzees were first studied in the 1960s but habituation of Sonso community only began in 1990, without employing any provisioning methods and individuals have been continuously monitored ever since. The home range of the adult males was estimated to be around 7km² in 1994-1995, when the community consisted of 46 individuals (Newton-Fisher 2003, see Fig. 3.3).

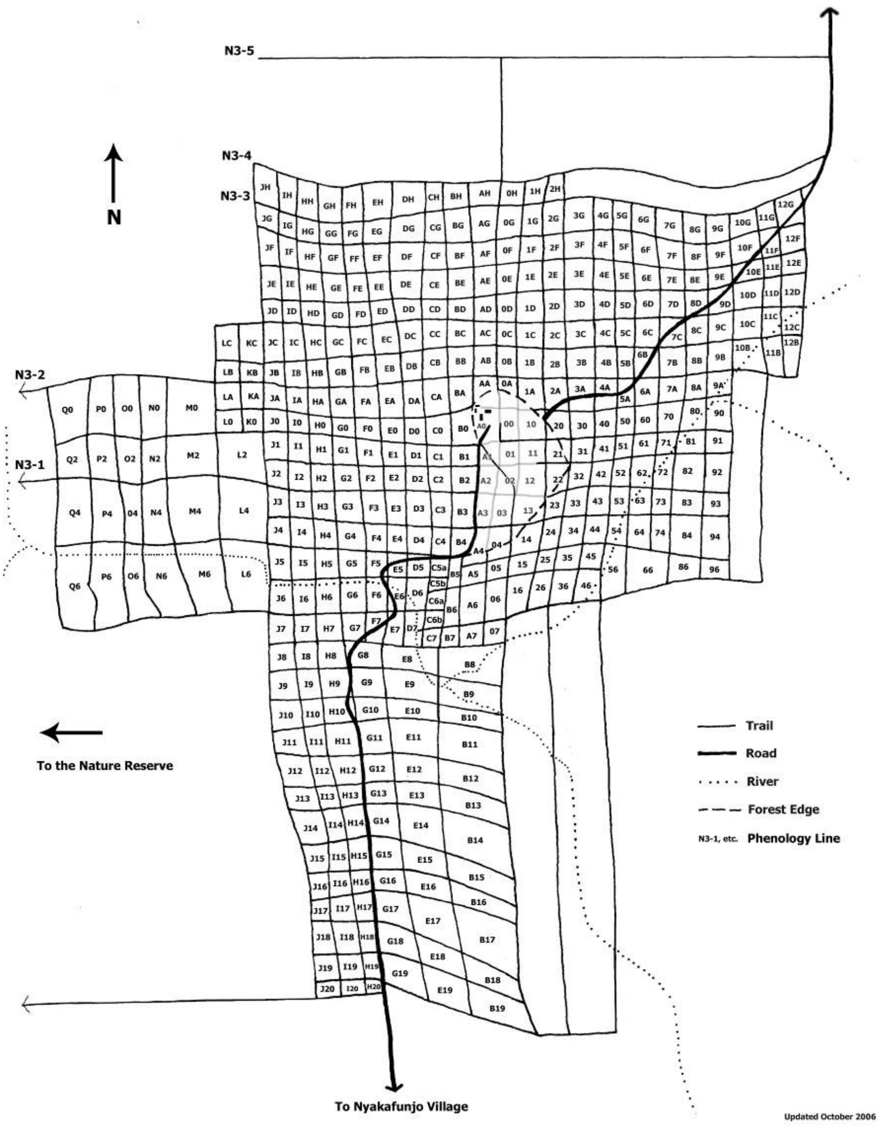


Figure 3.3: Map of the grid system of the Sonso area. To aid navigation through the forest, N-S and E-W lines have been given letters or numbers that determine the block number's name at each crossing point. The dark line represents the Royal Mile that provides access to the study site, at the centre of the map (courtesy of BCFS).

At the beginning of the study, the community consisted of 78 individuals (10 males, 25 females, 8 subadult males, 5 subadult female, 13 juveniles 12 infants and 5 babies (Table 3.1 and Appendix B for details per type of individuals). All individuals are named and given a two-letter code, usually according to their family relations (Table 3.2, 3.3). Males were generally more habituated than females but some core area females show habituation levels similar to males. Most of other females, and especially the peripheral ones, were shyer but the increased research effort on them substantially augmented their habituation over the course of this study.

Table 3.1: Community size for each month of study with births, disappearances and changes of age class: B: Baby, I: Infant, J: Juvenile, S: Subadult.

Year	Month	Total number of individuals	Disappearance	Births	Change of age class
2007	January	78		Karibu, Sharlot	
	February	79		Kox	
	March	79			
	April	79			Klauce (B-I)
	May-July		Bob, Mark, Banura	Rafia	Faida, Sokomoko (B-I)
	August	76	Zana		Karibu, Sharlot (B-I)
	September	76			Kox (B-I)
	October	76	Sean	Marion	
	November	77			Zak (I-J)
	December	76			
2008	January	75	Lola		Rafia (B-I)
	February	73	Duane, Gashom		Night (I-J)
	March-June				Marion (B-I), Monika (I-J), Rachel, Zig (J-S)
	July	74		Kathy	
	August	72	Maani, Polly		Kasigwa (I-J)
	September	73			Ramula (I-J)
	October	73		Kaspa	
	November	73			Rose (J-S)
	December	73			

Table 3.2: Adult females and their offspring present in the community during the study period. Asterisks denote individuals that died or disappeared during the study. Residence status are described as R: residential, P: peripheral. Age classes are described in Chapter two: B: baby; I: infant; J: juvenile; S: subadult; A: adult.

Females	**Code**	**Age**	**Status**	**Offspring**	**Code**	**Sex**	**Age class**
Anna	AN	17	R	-	-	-	-
Banura*	BN	39	P	Zefa	ZF	M	A
				Beti	BT	F	J
Beatrice	BC	31	P	Squibs	SQ	M	A
				Birungi	BG	F	I, J
Flora	FL	28	P	Fred	FD	M	S
				Frank	FK	M	J
				Faida	FA	F	B,I
Gladys	GL	32	P	Gina	GN	F	-
				Goria	GR	?	-
Harriet	HT	29	P	Hawa	HW	M	S
				Helen	HL	F	J
				Honey	HY	F	I
Janie	JN	23	P	Janet	JT	F	J
				James	JS	M	I
Juliet	JL	17	R	-	-	-	-
Kalema	KL	28	R	Bahati	BH	F	S
				Kumi	KM	F	J
				Klauce	KC	M	B,I
Kewaya	KY	24	R	Katia	KA	F	J
				Kox	KX	F	B,I
Kigere	KG	32	P	Keti	KE	F	J
				Kuki	KI	F	I
				Kaspa	KP	F	B
Kutu	KU	28	R	Kato	KT	M	S
				Kana	KN	F	J
				Kasigwa	KS	M	I,J
				Kathy	KH	F	B
Kwera	KW	26	R	Kwezi	KW	M	S
				Karo	KR	F	J
				Karibu	KB	F	B,I
Lola	LL	20	R	-	-	-	-
Melissa	ML	25	P	Mark*	MK	M	S
				Monika	MN	F	I,J
Mukwano	MK	27	P	Marion	MI	F	B,I
Nambi	NB	45	R	Musa	MS	M	A
				Nora	NR	F	S
				Night	NT	F	I
Polly*	PL	23	P	Pascal	PS	M	J
				Polina	PN	F	I
Ruhara	RH	39	R	Nick	NK	M	A
				Rose	RS	F	S
				Ramula	RM	F	J
				Rafia	RF	F	B,I
Sabrina	SB	26	P	Sally*	SA	F	S
				Sean*	SN	M	J
				Sharlot	SH	F	I

Table 3.2: (continued).

Females	**Code**	**Age**	**Status**	**Offspring**	**Code**	**Sex**	**Age class**
Sarine	SE	36	R	Simon Sokomoko	SM SK	M M	S I
Wilma	WL	26	R	-	-	-	-
Zana*	ZN	26	P	Zalu Zed	ZL ZD	M M	S I,J
Zimba	ZM	39	R	Zig Zak	ZG ZK	M M	J,S I,J

Table 3.3: Adult males present in the community during the study period. Asterisks denote individuals that died or disappeared during the study. Genotyping of adult males and individuals born between 1982 and 2002 permitted to conduct paternity analyses (Newton-Fisher et al. 2010).

Adult males	**Code**	**Age (2007)**	**Known offspring**
Bob	BO	18	-
Bwoba	BB	20	-
Duane*	DN	41	RS, KE, JT, KM
Gashom*	GS	20	-
Maani*	MA	49	KR
Musa	MS	16	-
Nick	NK	25	-
Squibs	SQ	16	-
Tinka	TK	47	-
Zefa	ZF	25	-

Data collection

Two-hundred and seventy days were spent in the forest following or looking for chimpanzees, usually from 7.00 am to 4.30 pm. Females and their infants are especially difficult to locate and follow because they are ordinarily silent when alone or in nursery groups. The usual methods to locate them were to de-nest them at their previous nesting site or to follow vocal cues by males and/or females, usually pant-hoots. Active fruiting trees were also checked and if the chimpanzees could still not be found, random searches were carried out along the trails. Often, the focal females were part of a larger mixed-sex party but they could also be found alone or in nursery groups.

Sampling method

As my primary goal was to study the development of the grunting behaviour, I focussed on females and their dependent offspring during the whole study period (i.e. babies and infants). From July to December 2008, I also added the juveniles and subadults, which could already be independent from their mothers or not. A mixture of sampling regimes was used, employing scan sampling, focal animal sampling and all occurrence sampling (Altmann 1974).

Focal animals were chosen opportunistically, as the first individual spotted during the day, unless the individual had already been sampled sufficiently. Special efforts were made to collect data on peripheral or shy females and their offspring. Another focus was to sample females with babies and young infants. Focal samples lasted one hour in general, but if a mother-offspring dyads was difficult to find it could be extended to two hours. A sample was stopped whenever the focal individual was out of view. This could be when animals were moving too fast or in dense areas and we lost track of them, or simply because the individual could not be seen properly and its behaviour could not be assessed reliably. This conservative method allowed us to record 501 hours of focal animal sampling during the whole study period.

Recordings of vocalisations were made continuously during the focal period with a Marantz PMD 660 with state recorder and a Sennheiser MKH 416T microphone. All vocalisations emitted by a mother and her offspring were recorded and a spoken description of the context of emission was given and transcribed later. An ‘encounter’ was defined as any individual entering a 10 m radius surrounding the focal animal. Ten metres were chosen because this roughly corresponded with an individual’s visual range in which most social interactions, such as grooming, competition over food, or sexual interactions, took place (Hayaki 1990). The radius was estimated together with my field assistant, Geresomu Muhumuza for every encounter, regardless of whether or not the focal animal produced pant-grunts. Subsequent encounters with the same individual had to be separated by at least five minutes to be considered as independent events. For each encounter, I noted whether or not the mother and her offspring produced a pant-grunt (within 2 min).

Scan sampling data were taken on the focal mother-infant dyads by my field assistant every five minutes as general behavioural data. Each scan sample consisted of an instantaneous description of the social situation at that moment including: (1) the time of the scan; (2) the location in the grid system (i.e.: block name), and (3) the name of the focal individual (offspring). (4) The activity of the mother was described in terms of fundamental activities: *resting* –individual in a stationary position, sitting or lying; *travelling* – individual walking on the ground or moving in branches over long distances; *moving* – individual moving over a short distance; *feeding* –individual foraging and handling food; *grooming* – individual engaged in a grooming session and *playing* – individual engaged in a play session alone or with another individual. (5) The activity of her offspring was described in the same terms and (6) the distance between the mother and her offspring was noted, using the following criteria: (a) mother-offspring body contact: *v* for ventral, *d* for dorsal or *bc* for any other body contact, (b) no direct contact: distance estimate in metres (c) *nv*: not visible but in party, (d) *np*: not in party. (7) The distance between the researchers and the focal individual in meters was also noted, as were (8) the names of the individuals in the 0-10 meters and (9) the names of the individuals within the party defined as a 35 m radius around the focal individual (Newton-Fisher 2004).

Finally, a derived measure for individuals that were within our visual range was used (i.e. 10 meters of our focal individual). For these individuals, the emission of pant-grunts together with the duration of time spent within our visual range could be determined with accuracy and permitted to calculate frequencies of productions. These data were called “focal 10m” and resulted in a total of 531 hours of observation. This method allowed us to determine the frequencies of production as well as having a very detailed account of what kinds of vocalisations each individual produced and was exposed to.

Because grunting in young chimpanzees can be a rare phenomenon, focal and focal 10m data were complemented with all occurrence data. Thus, all types of grunts by individuals that were neither our focal nor within the ten meters surrounding our focal were acoustically recorded as well and a spoken description of the context of emission was added whenever all the parameters could be determined without hindering the ongoing focal follow (Fig. 3.4).

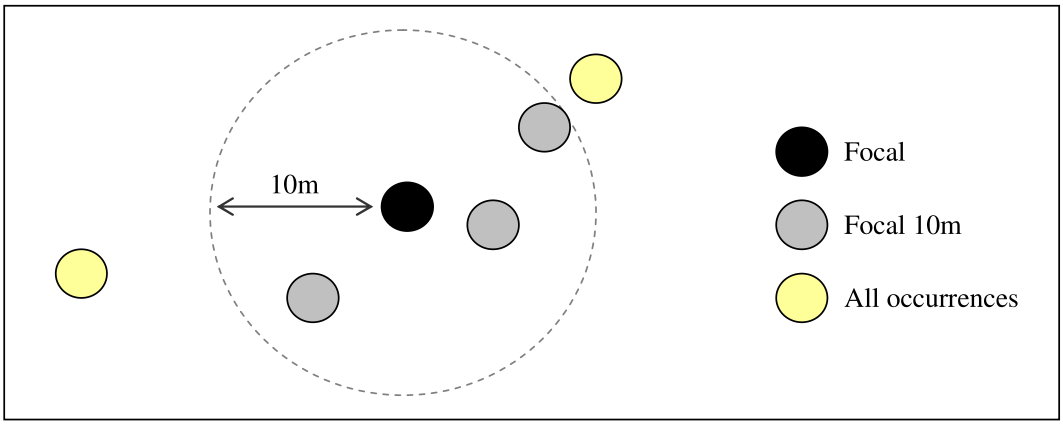


Figure 3.4: Sketch representing the three sampling methods used in the study.

Behavioural and contextual description of vocalisations

For each vocalisation recorded, a contextual description was given, including: (1) the emitter's identity and (2) the broad context of emission:*V*: after a vocalisation*, I*: to an individual, *IV*: to an individual and after a vocalisation or *O*: for no apparent reason. If these vocalisations were given to an individual in the presence or not of a vocalisation, then additional data were also taken: (3), the identity of the receiver's, (4), the approaching pattern: each individual could approach, retreat or stay stationary and (5) the intensity of the interaction: affiliative (grooming, touching, and kissing), neutral (no noticeable behaviours) or agonistic (display, chase, hit). If the vocalisation was given after a vocalisation, I also noted (6) the type of vocalisation emitted and (7) the identity of the emitter (if applicable).

Vocal data and Acoustic analysis

To compare the types of grunts and grunt sequences given by chimpanzees across situations, structural and spectral measurements were taken, using PRAAT 4.3.12. In PRAAT, the following spectral settings were applied: Gaussian windows shape was chosen because it does not give sidelobes in the spectrogram and it analyses twice as many samples per frame than the other possible windows (Square, Hamming, Hanning, Bartlett or Welch) see PRAAT manual online), windows length=0.025s, maximum frequency=2000Hz, dynamic range (lower limit of the signal's range)=50dB, Number of time steps (temporal resolution)=1000; Number of frequency steps (frequency resolution)=4096). Because pant-grunts are given in sequences involving different call types, different levels of sequence analysis were considered. Three levels of analysis appear the method of choice to encompass the communicative abilities of animal vocalisations (Bouchet et al. 2010; Hauser 2000). For each vocal emission of immatures and adults, were thus considered the total sequence, the grunt sequence and the grunt element levels of analysis. The aim was to make as comparable as possible the analyses made for different age classes and highlight the major modifications of grunts during development. Therefore, all the parameters that could only be taken for adult pant-grunts or immature social grunts were discarded. For example, because of the noisiness of adult pant-grunts and the tonality of most immature social grunts, formant analyses would have been possible for adult pant-grunts only while harmonic structure analyses would have been possible for immature social grunts only. Spectral analyses were thus limited to simple frequency measures at the middle of each call: the minimum frequency of the call (minimum frequency) and the frequency at which there is most of the energy (peak frequency).

1- For each sequence, the following structural measurements were determined:
(a) The total number of elements within a sequence (grunts, inhalations, pants or other elements like barks), (b) The total length of the sequence (in seconds), (c) The rate of the calling sequence: number of elements per second, (d) The number of calling bouts within a sequence: number of grunts bouts separated by at least one second, (e) The proportion of grunts within a sequence.

Grunts are generally noisy elements that can also be quite tonal, with low fundamental frequencies and generally little energy above 1500Hz (Crockford & Boesch 2005; Marler & Tenaza 1977) (Fig. 3.5.a), (f) the proportion of inhaled elements within a sequence. Inhalations (i.e. ingressive calls (Davila Ross et al. 2009)) are usually produced in between grunts or pants, when the airflow is inhaled by the caller. On a spectrogram, they are more tonal than the grunts with higher frequencies but can also be breathy (Marler & Tenaza 1977) (Fig. 3.5.b), (g) the proportion of panted elements within a sequence. Panted elements are unvoiced, breathy calls that are often difficult to spot on a spectrogram but can usually be detected by ear (Crockford & Boesch 2005) (Fig. 3.5.c).

The proportion of other vocalisations like barks (Fig. 3.5.d) or whimpers within a pant-grunt sequence was not analysed because of its low frequency and thus its low significance in the dataset.

2- For each sequence of grunts, structural measurements were determined:

(a) The total number of grunted elements in a sequence, (b), (c), (d) Proportion of n-shaped, u-shaped and w-shaped grunts. Melodic contours: these were determined by eye, derived from Papousek and Papousek (1989)'s classification system: the minimum frequency could be u-shaped, n-shaped (inverted u) or w-shaped (sinusoidal) (see Fig.3.6 a, b, c), (e) Proportion of tonal grunts in the grunt sequence: single calls were determined as tonal when the fundamental and its harmonics could be seen clearly or noisy when the call was harsh.

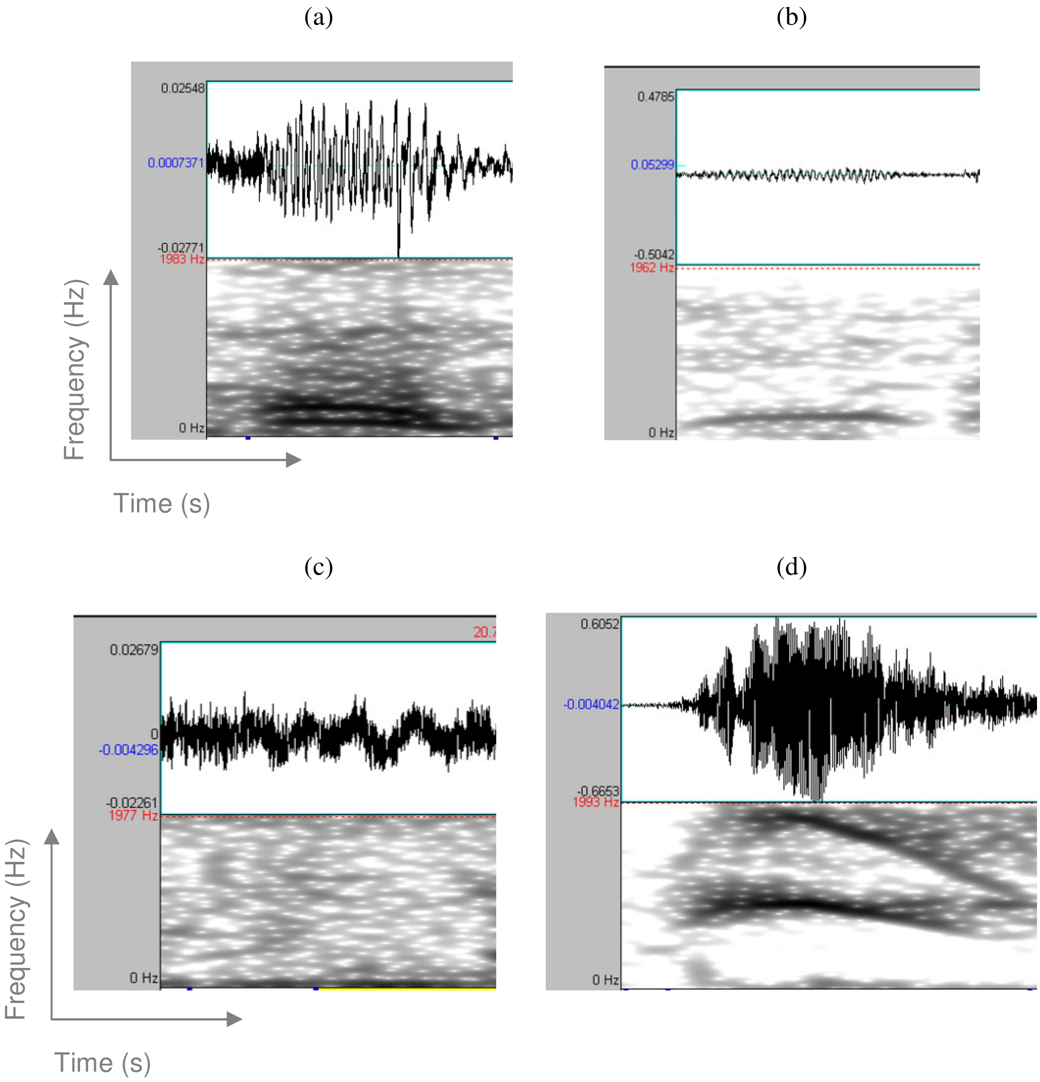

(a) (b) (c) (d)

Figure 3.5: Types of call elements encountered in pant-grunts sequences (a) Grunts, (b) Inhalations, (c) Pants, (d) Other elements, for example barks.

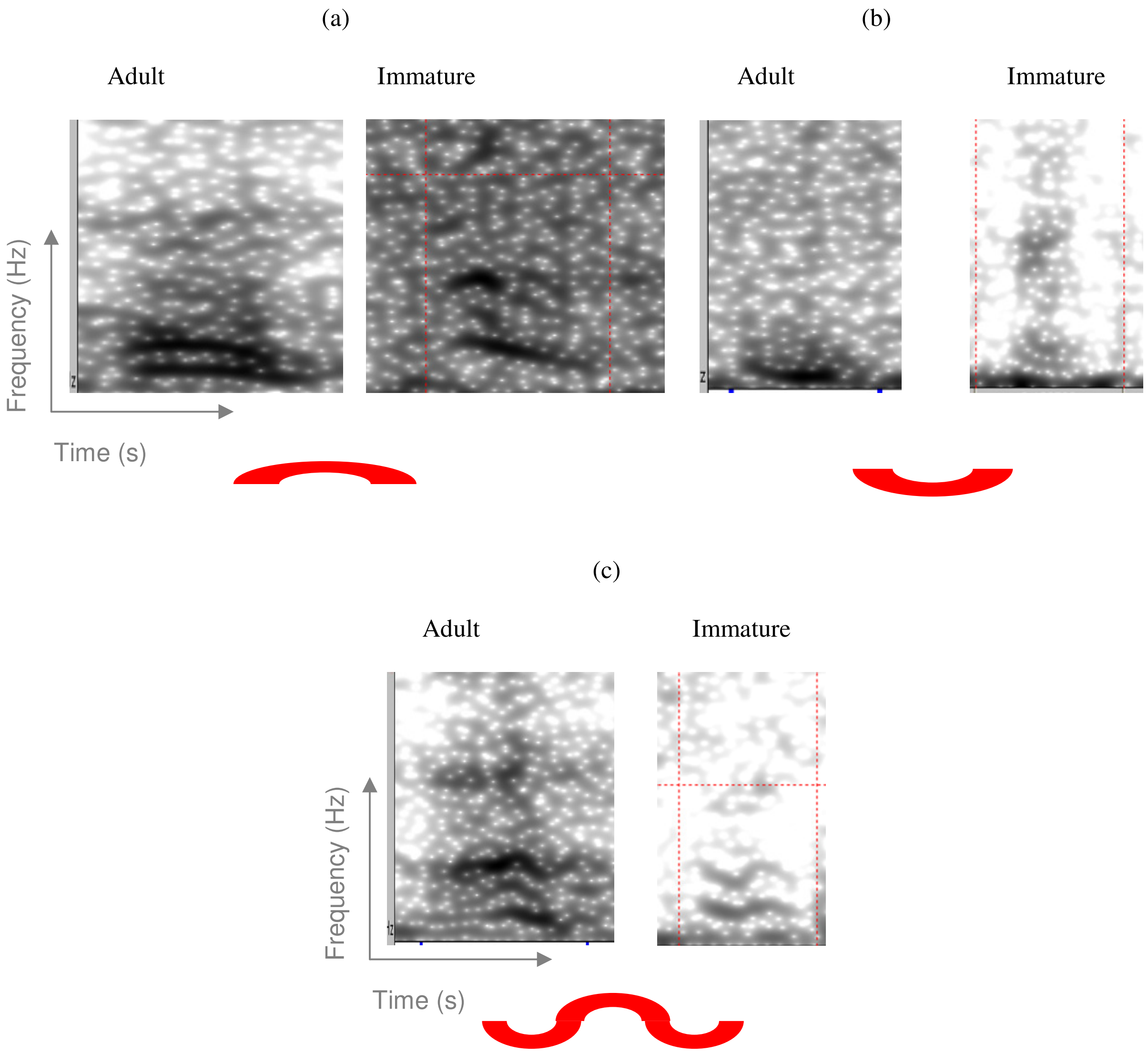


Figure 3.6: Melodic contours of grunts observed in adult females and immatures (0-15years) adapted from Papousek and Papousek (1989). a: n-shape, b: u-shape, c: w-shaped (sinusoidal).

3- At the individual grunt level, the following temporal and spectral measurements were taken:

(a) Grunt length (s) (Fig. 3.7), (b) Intercall length (s): duration of the interval between two grunts (Fig. 3.7), (c) Peak frequency (Hz) of the middle of the call: frequency where is the maximum of the acoustic energy at this point of the grunt represented as the highest peak of frequency seen on the spectrum (Fig. 3.8.a), (d) Minimum frequency (Hz) of the middle of the call: lowest frequency of the call determined by the vibration of the vocal folds only represented as the first peak of frequency seen on the spectrum (Fig. 3.8.b).

Grunts are naturally noisy vocalisations with very low frequencies. Spectral measurements of such aperiodic signals are more difficult to measure than harmonically structured signals and lowest frequencies might merge with background noise that can vary with the time of the day or the localisation of the recording. As these factors could not be controlled for in the present study, the spectral analyses were restricted to the parameters that could be taken with most accuracy across recordings (i.e.: minimum frequency and peak frequency). Overall, the differences between the parameters chosen in different age classes or situations could thus be roughly determined.

For each analysis involving acoustic data, the mean value of each parameter per sequence and per individual and the mean standard deviation of each parameter in a sequence were used. The standard deviation was used as an indicator of the variability of an acoustic parameter within a sequence.

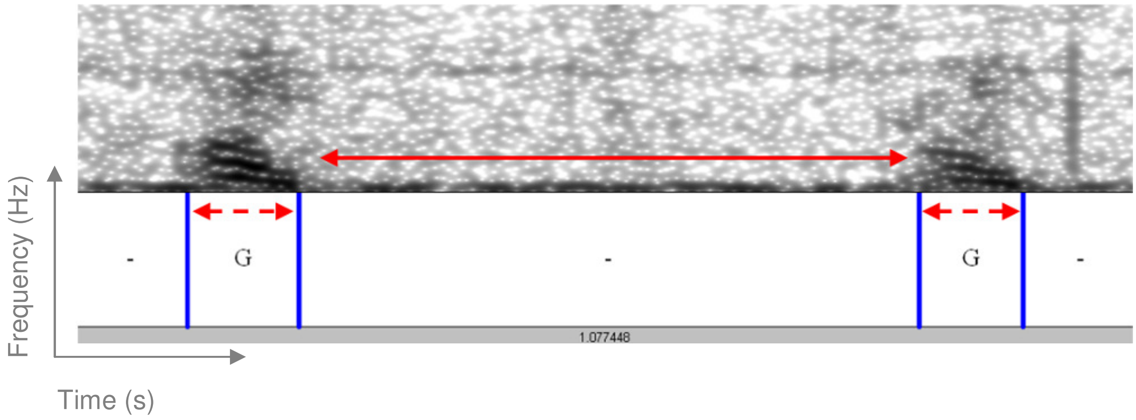


Figure 3.7: Temporal parameters of grunts: Dotted arrow, grunt length, Full arrow: intercall length.

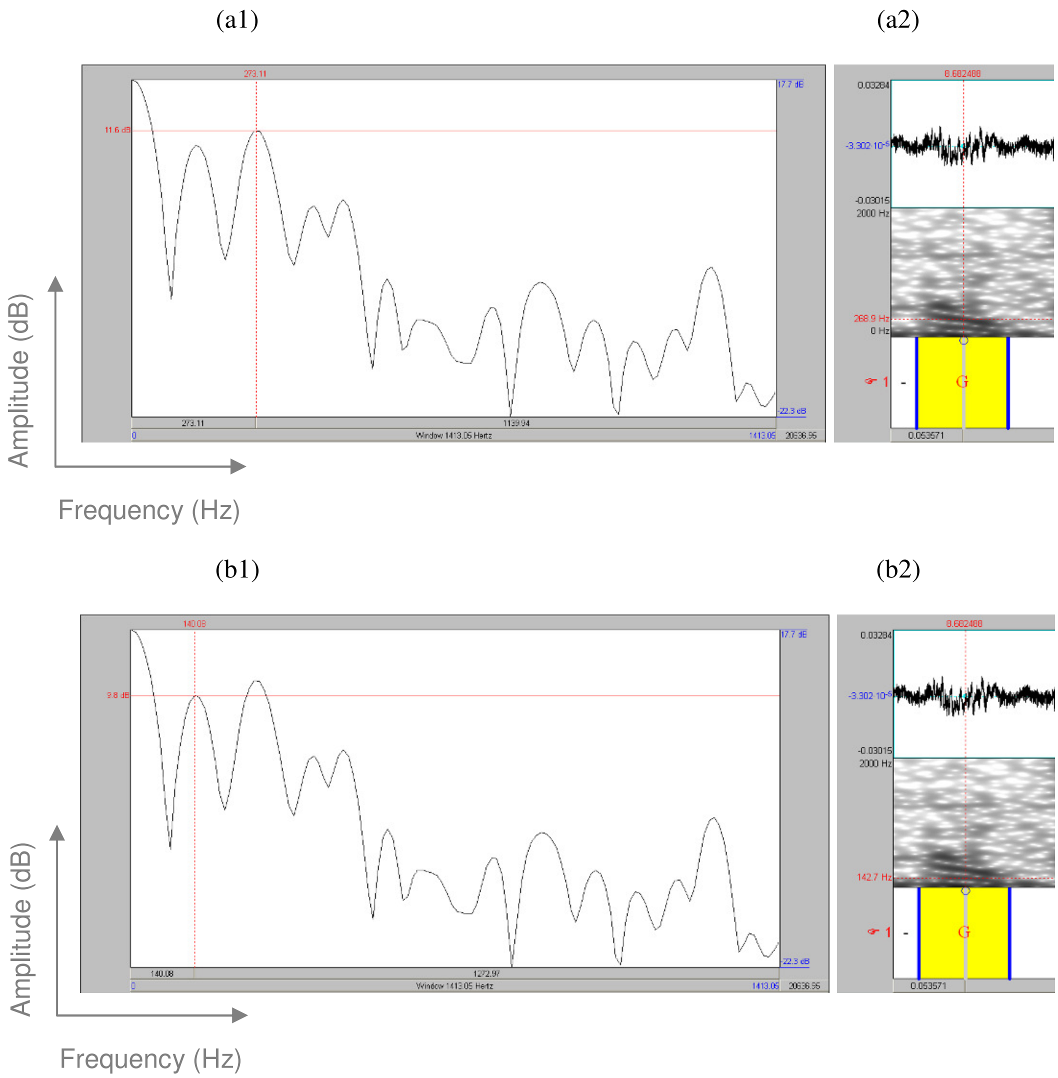


Figure 3.8: Illustration showing how spectral parameters were taken at the middle of each grunt element. The higher spike of the spectrum (a1) represents the peak frequency that can be seen as the darker energy band on the spectrogram (a2). The first spike in the spectrum (b1) denotes the minimum frequency at the middle of the call, also the lowest energy band seen on the spectrogram (b2).

Statistical analyses

Data were analysed at the individual level, depending on its age-class. Generally, frequency data were not transformed while proportional data were transformed with an arc sin of square root function and as recommended by Snedecor and Cochran's (1980) for $N<50$, a 1/4N transformation was applied for proportions equal to zero and for proportions equal to one, a 1-1/4N transformation was applied with N=total number of occurrences. Parametric tests were used whenever the data were normally distributed (Shapiro-Wilk test) and having homogeneous variances (Levene's test). If these conditions were not met, nonparametric tests were used. All tests were two-tailed with significance levels set at $\alpha=0.05$. For small sample sizes, exact p-values were calculated (Mundry & Fischer 1998). Post-hoc comparisons were done using a Sidak corrected alpha set at $\alpha=1-(1-\alpha)^{1/n}$. All analyses were conducted with SPSS 17.0. Details of the various statistical tests and specific methodologies used in this study are provided in the relevant chapters.

Chapter four: Vocal greeting behaviour in wild chimpanzee females

"Soiés resolus de ne servir plus, et vous voila libres; je ne veux pas que vous le poussies ou l'esbranlies, mais seulement ne le soustenés plus, et vous le verrés comme un grand colosse a qui on a desrobé la base, de son pois mesme fonder en bas et se rompre."

Étienne de la Boétie, 1574 (See Appendix A for translation)

Summary

Chimpanzees, *Pan troglodytes*, are unusual among primates in that they express their social position with a unique vocal signal, the pant-grunt. The call is only produced when encountering a higher-ranking group member and has thus been interpreted as a 'greeting' signal. The calling behaviour of nine adult females in a group of free-ranging chimpanzees, the Sonso community of Budongo Forest, Uganda was monitored, when encountering higher-ranking adult males. The results revealed that call production was by no means rigid, but that calls were given only if certain social conditions were met. Although all adult males received pant-grunts from females, the alpha male received a significantly larger proportion of calls. The number of pant-grunts given to males was not correlated with their hierarchical position or with the level of anticipated aggression. Instead, females were significantly more likely to vocalize to other males if the alpha male was absent, suggesting that their calling behaviour was moderated by social inhibition. The presence of the alpha female had a similar yet weaker inhibitory effect. Social inhibition was further increased with increasing numbers of bystanders, especially males. The results of this chapter thus demonstrate that chimpanzees use their 'greeting' signals flexibly by taking into account the social fabric of their community.

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

Laporte, M. N. C. & Zuberbühler, K. 2010. Vocal greeting behaviour in wild chimpanzee females. Animal Behaviour, 80, 467-473.

Introduction

‘Greeting’ behaviour has been observed in a range of social animals, although its biological function appears to vary between species. For example, greeting signals are often produced during intragroup conflicts, either to decrease or increase levels of aggression (e.g. mantled howler monkeys (Dias et al. 2008); baboons, *Papio hamadryas* and *P. cynocephalus*: (Colmenares 1990); spotted hyenas (East et al. 1993); spider monkeys, *Ateles geoffroyi*: (Aureli & Schaffner 2007; Schaffner & Aureli 2005). Other reported functions have to do with assessing another individual’s willingness to interact socially at that particular moment or with testing long-term bonds between familiar individuals (Guinea baboons, *Papio papio*: (Whitham & Maestripieri 2003); black-horned capuchins, *Cebus apella*: (Lynch Alfaro 2008)).

In most species, greeting signals are visual, usually part of an individual’s species-specific communication repertoire. In chimpanzees, however, greeting is conducted in the vocal domain, the so-called ‘pant-grunts’ (Bygott 1979; Goodall 1986; de Waal 1982). A remarkable feature of chimpanzee pant-grunts is that the signal is given only by lower-ranking individuals when encountering a more dominant group member, which contrasts with the greeting behaviour of other primates and nonprimates, such as baboons (Colmenares 1990), howler monkeys (Dias et al. 2008) or hyenas (East et al. 1993). In captive chimpanzees, pant-grunts are often accompanied by ritualized behaviours of subordination, such as bobbing, crouching or presenting (de Waal 1978). In the wild, where individuals are freer in their choosing or avoiding of social interactions, pant-grunts are often given without additional signals, although the acoustic structure can vary from soft grunts to loud pant screams (Goodall 1986).

Although pant-grunts are among the most common signals in the chimpanzee vocal repertoire, the social variables driving their production are not well understood. The notion of rank-related 'greeting' is largely uncontroversial, but there are a number of reports in the literature that indicate that the communicative function of pant-grunts is more complex than merely expressing subordination. First, pant-grunts are not compulsory when encountering someone higher ranking (Newton-Fischer 1997; Takahata 1990a), suggesting some kind of social assessment by the signaller. Second, although pant-grunts are mostly given to higher ranking group members, in some social dyads they can temporarily be given in bidirectional ways, perhaps reflecting uncertainties in the callers' perceived social position (Emery Thompson et al. 2008; Newton-Fischer 2006; Townsend et al. 2008). Third, pant-grunts sometimes trigger aggressive responses from previously calm higher-ranking receivers (Hayaki 1990) but they also appear to play some role in reconciliation and appeasement following conflicts (Arnold and Whiten 2001; de Waal 1982). Overall, these observations suggest that call production might be the product of relatively complex social assessments rather than a rigid response to encountering a high-ranking group member. These reports are relevant for an ongoing discussion about modality and flexibility in primate communication.

One dominant argument is that primate vocalizations, including those of apes but not humans, are not very flexible, especially if compared with gestures, and as such not very relevant for understanding human language evolution (Arbib et al. 2008; Corballis 1992; Pollick & de Waal 2007). A key empirical finding is that ape gestures are often socially directed and in this sense intentionally produced. In contrast, primate vocalizations appear to be broadcast in socially less specific and untargeted ways, often to a larger audience, an observation that tends to attract arousal-based interpretations (Arbib et al. 2008; Pollick & de Waal 2007). However, other studies have found that primate vocalizations have directional and intentional components, mainly because production can vary depending on the audience (Mitani and Nishida 1993; Slocombe & Zuberbühler 2007; Wilson et al. 2001, 2007) or the attentional state of a human receiver (Hopkins et al. 2007; Hostetter et al. 2001). Chimpanzee pant-grunts are particularly interesting for this discussion because they represent one of the few vocalization types that are always directed to a specific receiver.

To address the problem of flexibility more systematically, I investigated whether pant-grunt vocalizations were influenced by the presence of bystanders in a group of wild chimpanzees, the Sonso community of Budongo Forest, Uganda. Although audience effects are widespread in animal communication (e.g. yellow mongoose, *Cynictis penicillata*: (le Roux et al. 2008); chickens (Marler et al. 1986); brown capuchins, *Cebus apella*: (Pollick et al. 2005), in chimpanzees they seem to be the product of a considerable degree of social awareness and strategic impulse (Slocombe & Zuberbühler 2007; Townsend et al. 2008). I investigated the use of pant-grunts by female chimpanzees to understand the social patterns and motivations that drive call production in this species. The focus was on adult females because in chimpanzees they are formally subordinate to all adult males (Goodall 1986; Noë et al. 1980; Reynolds 2005). This chapter was interested in how flexible females were when using this vocal signal, and whether they took the wider audience into account. If pant-grunts merely functioned as a ritualized signal of subordination, call production should be determined by the relative rank of the receiver, regardless of other social factors, such as the composition of the nearby audience, or the nature of the ongoing social interaction.

Methods

Study Site

Data were collected on the individuals of the Sonso community of Budongo Forest, Uganda. At the beginning of the study, the community consisted of 78 individuals (10 males, 25 females, 8 subadult males, 5 subadult female, 13 juveniles 12 infants and 5 babies, see Chapter two).

Data collection

Pant-grunt utterances are an acoustically heterogeneous signal, which usually consists of repeated grunts that can be panted and that can grade into barks or screams (Fig. 4.1). Given in a variety of contexts, such as during travelling, feeding or resting, they are always directed to a specific receiver within a relatively short distance. As mentioned earlier, calling can be accompanied by other behaviours, such as presenting, crouching or bobbing. The calls typically do not result in noticeable responses in the receiver, although sometimes they are followed by agonistic (display, chase, hit) or affiliative (grooming, touching, kissing) interactions.

Focal animal sampling and 5min scan samples of focal individuals were used (Altmann 1974). For each scan sample, the behaviour of the focal animal and target individual was recorded, as was the identity of all individuals within a radius of both 10m (i.e. the average visual range) and 35m (i.e. the average spread of the travel party; (Newton-Fisher 2004)). An 'encounter' was defined as any individual entering a 10m radius surrounding the focal animal. Ten metres were chosen because this roughly corresponded with an individual's visual range in which most social interactions, such as grooming, competition over food or sexual interactions, took place (Hayaki 1990). The radius was estimated jointly with my field assistant for every encounter, regardless of whether or not the focal animal produced pant-grunts. Subsequent encounters with the same individual had to be separated by at least 5 min to be considered as independent events. For each encounter, whether or not the focal animal produced a pant-grunt was noted (within 2min). The level of threat experienced by the caller was assessed as (1) low (affiliative interactions: present, groom, touch), (2) neutral (no noticeable social behaviour) or (3) high (agonistic interactions: threat posture, display, chase). For the audience effect analyses, all individuals present within a radius of 10m (roughly corresponding to the average visual range) were considered, while male and female presence was assessed separately.

Dominance hierarchy

In chimpanzees, the social dominance hierarchy is heavily sex-biased (de Waal 1982). Males constitute the core of the group and all adult males are dominant over all adult females, as assessed in terms of agonistic interactions (Noë et al. 1980; Takahata 1990a). The aim was to evaluate how females were reacting to the male hierarchy. To increase precision, the dominance indexes were calculated separately for males and females. My own and the project’s long-term data were used (Zuberbühler and Reynolds 2005) to determine the social status of group members. In natural habitats, rank relations between males are somewhat dynamic and susceptible to sometimes rapid change (Newton-Fischer 1997), a possible result of their fission-fusion social organisation (Muller 2002). For example, three adult males (MA, DN, GS) died during the study period, which appeared to increase the social dynamics between group members. I therefore did not attempt to determine a linear dominance hierarchy for the entire study period. Instead of trying to assign an exact rank to each of the nine adult males, I calculated a relative cardinal rank value for each male while taking into account the total observation time for each dyad, a reflection of his average social position within the community throughout the study period. To this end, I used the "conferred respect equation" developed by Newton-Fisher (1997; 2004) and based on Fournier and Festa-Bianchet (1995):

Conferred Respect={[N (pant-grunts received) * DC] +1}/ {[N (pant-grunts performed) * DC] +1}

DC=Dyad Correction=(N scan samples of most seen dyad)/ (N scan samples of dyad studied).

For the males, the long-term project data were used over the 16 months study period, which consisted of 15 min scan samples, in which the simultaneous presence of two individuals in the same party was recorded. For females, my own data were used. They were more detailed in that they consisted of 5 min scan samples where the two females were seen within 10 m of each other.

Results were as follows: males: alpha: NK=3.45; ZF=0.16; DN=-0.05; BB=-0.15; MS=-0.68, TK=-0.97, SQ=-0.99; MA=-1.05, GS=-1.19; females: alpha: NB=2.13; ZM=1.92, RH=1.45; KY=0.45, KU=0.22; KL=-0.11, MK=-0.19, KW=-0.53, JN=-2.35. Because different dyad correction factors for males and females were used, these numbers are only meaningful in relation to other members of the same sex.

Statistical analyses

Many Sonso females lead relatively solitary lives. As a result the number of encounters remained low for some of them, and as a consequence not all females were able to contribute to all analyses. A minimum of 12 male encounters was required to be included in the analyses, which lead to a final sample of 9 females (JN, KL, KU, KW, KY, MK, NB, RH, ZM) encountering a total of 9 males (BB, DN, GS, MA, MS, NK, SQ, TK, ZF; N=301 encounters). The data of three additional females (FL, HT, and SE) contributed to calculations of encounter rates. Calling rates during encounters were determined for each female separately. Raw data were transformed with the arc sin of the square root; (Snedecor and Cochran 1980) and checked for normal distribution (Shapiro-Wilk test) and homogeneity of variances (Levene's test). If conditions were met, parametric tests, such as paired samples t-tests were used. The data generally did not meet the conditions of normal distribution and homogeneity of variances, in which case non-parametric Friedman's ANOVA for multiple matched comparisons, Wilcoxon-matched-pair tests and Spearman's correlations were used. All tests were two-tailed with significance levels set at $\alpha=0.05$. For small sample sizes, exact p-values were calculated (Mundry and Fischer 1998). All analyses were conducted with SPSS 17.0. Means are given±SE.

Results

General patterns

During 455 hours of focal observations were encounters could be reliably determined, 1,346 encounters of focal individuals were witnessed (adult females, subadult and juvenile males or females) with other group members, 211 of which led to pant-grunts (16.4%). During 301 hours of focal observations, 755 encounters of adult females with juveniles (N=156), subadults (N=157), adult females (N=129), adult males (N=227) and the alpha male (N=86) were recorded.

Effects of target individual identity

Across the twelve adult females, encounters rates with different types of individuals varied significantly (Friedman's ANOVA N=12, $\chi^2(3)=10.103$, $p_{exact}=0.014$). Encounters with adult males were generally rare (mean 1.02±0.5 encounters per hour), but more frequent than encounters with other females (mean 0.41±0.21 encounters per hour; Wilcoxon-test N=12, T(11)=-2.903, $p_{exact=}0.001$), subadults (mean 0.56±0.41 encounters per hour; N=12, T(11)=-2.401, $p_{exact=}0.014$) and juveniles (mean 0.55±0.35; N=12, T(11)=-2.275, $p_{exact=}0.021$; Sidak-adjusted alpha, α=0.017). For seven females, there were enough data to compare their behaviour across males. Although all seven females pant-grunted to all nine males, they did so significantly more to the alpha male than the other males (mean probability of calling: alpha=0.63±0.17 vs. non-alpha=0.35±0.06; $N_{females}=7$; T(6)=-2.366; $p_{exact=}0.016$; Wilcoxon-test; Fig. 4.1). Despite this bias towards the alpha male, it was not the case that male social status per se explained the females' pant-grunting behaviour. There was no significant correlation between the average rank value for the nine males and their likelihood of receiving pant-grunts when encountering a female ($N_{males}=9$, σ=0.293, p=0.444; Spearman-rank correlation). Similarly, the rank of the female caller also did not explain her likelihood of giving a pant-grunt when encountering a male ($N_{females}=9$, σ=-0.192, p=0.620; Spearman-rank correlation).

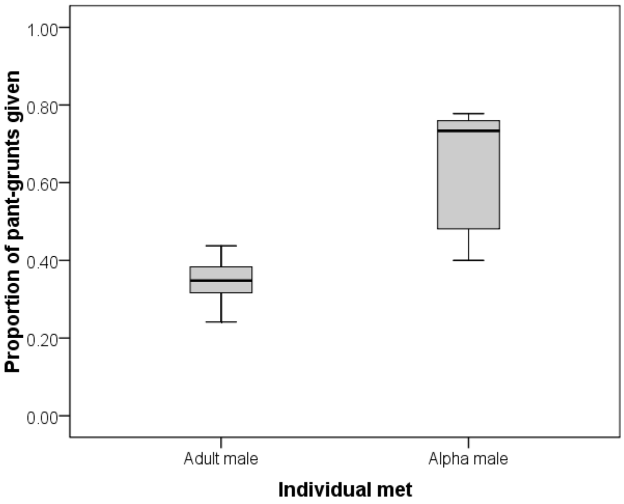


Figure 4.1: Proportion of pant-grunts given by adult females when meeting the alpha male versus another adult male. Boxplots show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range.

Effects of target individual behaviour

Compared to other adult males, the alpha male NK could be very violent towards other group members. Whether pant-grunting could be explained by the level of threat experienced by the caller during an encounter was therefore tested. During neutral encounters and the females' average probability of producing a pant-grunt was relatively low ($N_{females}$=9; mean probability of pant-grunting=0.36±0.08). The probability was higher in aggressive contexts ($N_{females}$=4; mean probability of pant-grunting=0.65±0.27) but highest in affiliative contexts ($N_{females}$=4; mean probability of pant-grunting=0.89±0.13), demonstrating that level of threat was not associated with elevated levels of pant-grunting (Fig.4.2.).

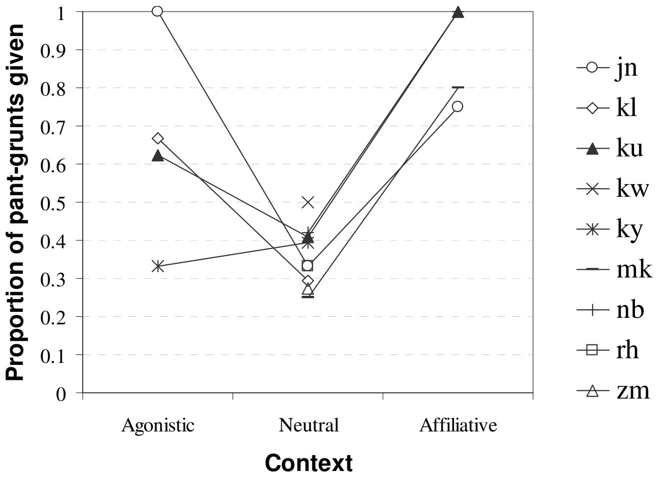


Figure 4.2: Proportion of pant-grunts given by adult females when meeting a male in the three levels of threat encountered.

Audience effects: alpha male and female

Whether the composition of the audience affected female pant-grunt production was investigated. Overall, the presence of the alpha male significantly reduced the likelihood of females' pant-grunting when encountering another male (T-test: $t(7)=-4.368$, $N_{females}=8$, $p=0.003$, Fig. 4.3.a). Encounters with males can be single encounters (if a single male joins the female's travelling party) or group encounters (if the female joins a group of males). In both conditions, the alpha male can be present or absent. To further investigate the audience effect exerted by the alpha male, the single male encounter sub-sample only was analysed. The effect remained the same, albeit only as a trend (Wilcoxon $T(4)=-2.023$, $N_{females}=5$; $p_{exact=}0.063$, two-tailed).

Whether the presence of the alpha female had an effect on the production of pant-grunts when encountering a male was also tested. I managed to compare matched data for four females, with or without the alpha female present within 10 m, whilst encountering a male. The probability of pant-grunting to adult males was about three times higher when the alpha female was absent than present (0.42±0.11 vs. 0.14±0.17), suggesting an inhibitory effect comparable to that of the alpha male (Fig. 4.3.b).

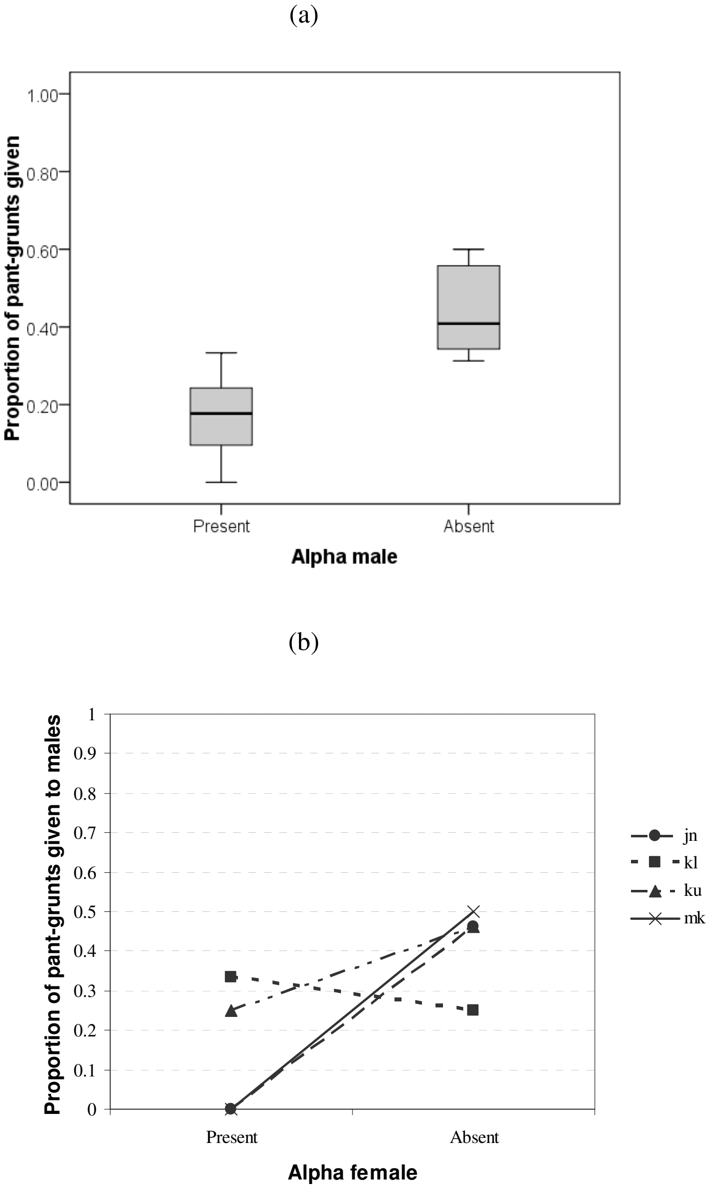


Figure 4.3: Proportion of pant-grunts given by adult females when meeting: (a) one or more adult males in the presence or absence of the alpha male (b) one or more adult males (excepting the alpha male) in the presence or absence of the alpha female. Boxplots show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range.

Audience effects: group size

When encountering the alpha male, the size of the audience had no effect on the likelihood of females' producing a pant-grunt. This was because the mean number of individuals in the vicinity of a female was not different in cases she did or did not give a pant-grunt (mean N individuals present with calls: 1.136±0.655; without calls: 1.143±0.627; t6=-0.019, $N_{females}$=7, p=0.984). However, when encountering another male, the size of the audience mattered greatly, and this was not due to the presence of the alpha male within 10m (mean N individuals present with calls: 0.484±0.452; without calls: 1.082±0.454; t(8)=-3.252, $N_{females}$=9, p=0.012, Fig. 4.4.a). The group size effect on calling behaviour was stronger for male than female audiences. As the number of males increased, the likelihood of females pant-grunting to another male decreased (mean N_{males} present with calls: 0.052±0.090; without calls: 0.38±0.335; Wilcoxon T(7)=-2.028, $N_{females}$=8, $p_{exact=}$0.047; Fig. 4.4.b) whilst only a trend in the same direction for the number of females present within ten meters was found (mean N females present with calls: 0.432±0.442; without calls: 0.702±0.370; t8=2.218, $N_{females}$=9, p=0.057; Fig. 4.4.c).

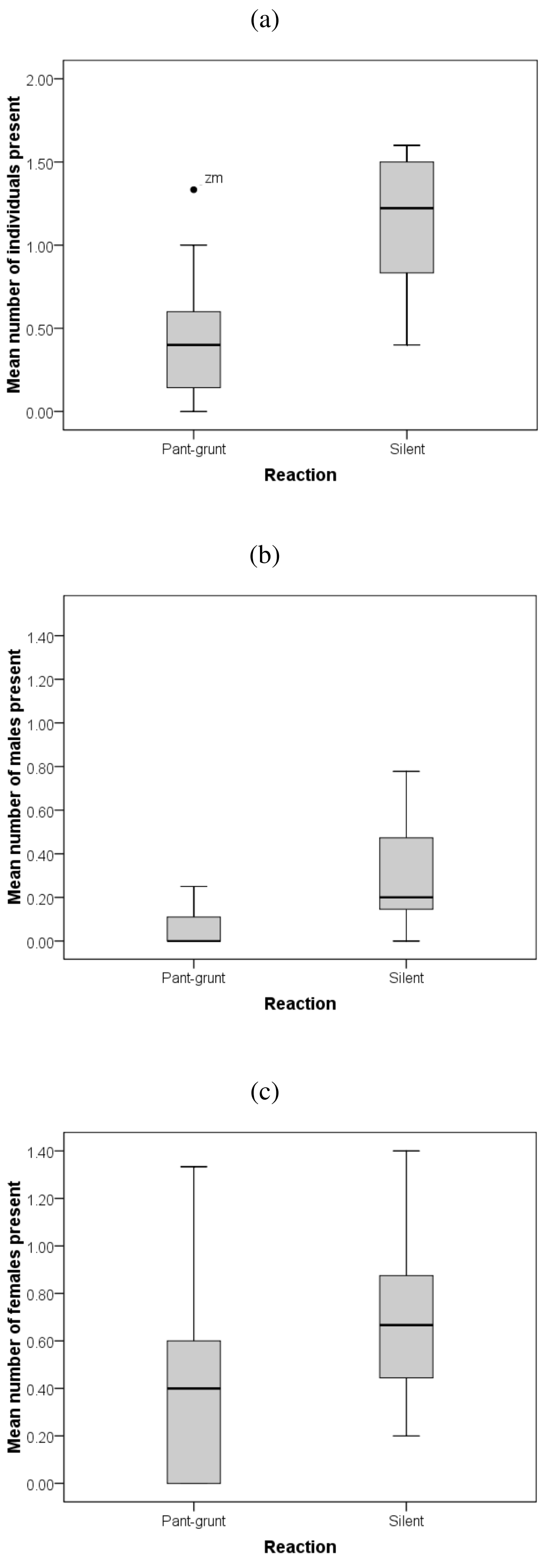


Figure 4.4: Number of individuals present with a focal female when encountering an adult male with or without pant-grunting: (a) all individuals; (b) adult males only; (c) adult females only. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outliers.

Discussion

A key element in the debate over human uniqueness is whether animals are intended addressees or mere accidental eavesdroppers of communication signals produced by conspecifics. This chapter has addressed this problem to some extent with this study on pant-grunting in wild chimpanzees. Data have revealed that wild chimpanzees adjust the production of pant-grunts in flexible ways. All individuals monitored in this study produced pant-grunts when encountering higher-ranking group members, but call production was not mandatory during such encounters and depended on a number of social variables. The probability of pant-grunting was highest during affiliative interactions, compared to agonistic or neutral situations. It is therefore not likely that pant-grunts function specifically to appease aggressively motivated group members or to express fear. Another finding was that the alpha male obtained a particularly large share of all pant-grunts. However, the relative social position of the call receiver failed to explain the production patterns of pant-grunts. Similarly, the social position of the caller also did not explain individual differences in the likelihood of calling. A further finding was that the presence of the alpha male had a powerful socially inhibitory effect, which might also be the case for the alpha female. In the presence of these individuals, the females typically refrained from greeting other group members, who under other circumstances were regular receivers of pant-grunts.

Although the sample size was too low to make statistical comparisons for the alpha female audience effect, some differences in the likelihood of calling in all individuals were observed. A number of anecdotal observations are in line with this interpretation. Once I observed a low-ranking female (KL) approaching and pant-grunting to the alpha male, followed by an attempt to groom him. The alpha female was also nearby but was probably not noticed by KL, as they were out of view from each other. While attempting to groom the alpha male the alpha female suddenly approached and aggressively chased KL away, something that probably would not have happened, had KL remained silent. Chimpanzee females are generally less gregarious than males but nevertheless are confronted with considerable intra-sexual social competition (Emery Thompson et al. 2008; Newton-Fischer 2006; Townsend et al. 2008), as indicated by this and other observations.

Previous research has shown that chimpanzee vocal behaviour can be flexible both in terms of acoustic morphology and call use (Slocombe & Zuberbühler 2006). Most chimpanzee vocalisations are acoustically graded and there is evidence for some acoustic variants to be meaningful to receivers (Slocombe et al. 2009; Slocombe & Zuberbühler 2005b). Another recurrent finding is that callers take into account the identity of all nearby individuals, as well as their potential relevance during an ongoing social event (Slocombe & Zuberbühler 2007; Townsend et al. 2008). In this study, I found further evidence that the presence and identity of bystanders had a significant impact on an individual's willingness to produce a vocal signal.

One consequence of these results is that the notion of pant-grunts as a behaviourally rigid and phylogenetically ritualised signal of subordination in chimpanzees becomes questionable, which is in line with other research (Emery Thompson et al. 2008; Newton-Fischer 1997, 2006; Takahata 1990a; Townsend et al. 2008). More likely, pant-grunting is a socially flexible behaviour that appears to be the product of a variety of motives (see also Hayaki 1990). Pant-grunting appears to be a reflection of a caller's wish to interact with a socially relevant group member, a way of probing a recipient's mood and motivations, and a vocal tool to make one's presence known and to convey respect. Pant-grunting, in other words, is part of a chimpanzee's tool kit to build social relations, rather than a straightforward consequence of a social hierarchy. There are some interesting parallels to human greeting, for which it has been argued that it also serves to attract attention, to signal intent, to enter a relationship, to reduce social anxiety and to mark social status, especially during tense situations (Firth 1972).

Social complexity is thought to be one of the major driving forces of cognitive evolution (Byrne & Whiten 1988; Humphrey 1976) and the findings of this chapter fit well with this more general idea. Chimpanzees live in a fluctuating social system where individuals' motives and alliances can vary rapidly. This fusion-fission social system, combined with the difficult visual conditions of the forest habitat, has the effect that individuals typically only witness a very small proportion of the ongoing social events, a possible selection factor towards enhanced cognition (Aureli et al. 2008; Barrett et al. 2003). Female chimpanzees are frequent targets of male aggression, suggesting that they benefit from initiating social interactions strategically in order to control the possible social consequences. Acoustically, pant-grunts are individually distinct, something that can be discriminated by other chimpanzees (Kojima et al. 2003). In the wild, the calls are audible over a considerable distance of up to 50 m (personal observation), indicating that they provide a rich source of social information to nearby listeners.

Why should a caller be sensitive to the presence of certain bystanders during encounters with higher-ranking group members? First, greeting others in the presence of the alpha male could be risky if it elicits aggressive behaviour by him. Out of eleven cases of females pant-grunting to another male in the presence of the alpha male, two cases of aggression towards the female within the next 5 min were observed. On the other hand, pant-grunts sometimes elicited aggressive behaviour from the receiver, especially towards subadult individuals (Hayaki 1990), suggesting that being addressed with pant-grunts is not always perceived as a positive event. Another provocative hypothesis is that females may contribute to the social climbing of their favourite males by allocating their pant-grunting behaviour strategically (de Waal 1982). Although it seems plausible that females are interested in social stability (to successfully raise their offspring), the data presented here data cannot really contribute to this debate in a meaningful way.

There is no doubt that apes have demonstrated high levels of flexibility in their gestural communication signals and that they sometimes use them to manipulate the behaviour of others to their own benefits (Liebal et al. 2004; Pika et al. 2003, 2005). Whether this kind of communicative flexibility is entirely restricted to the gestural domain, however, becomes increasingly more controversial. This study does not fit well with the notion of structurally rigid, contextually inflexible, and cognitively uninteresting vocal communication (Arbib et al. 2008; Tomasello 2008). More likely, both gestural and vocal communication are susceptible to the same cognitive processes and architecture that govern social behaviour in primates (Leavens et al. 2004; 2010; Slocombe & Zuberbühler 2007; Townsend et al. 2008).

Overall, pant-grunts are clearly interesting vocalisations because they enable group members to signal, interpret, maintain or potentially even change social relationships with or between other group members. The notion of chimpanzees as strategic individuals who are in constant assessment of each other's dominance relationships has largely emerged from captive research on adult males in their relations with each other (de Waal 1982). My study is in line with this general stance, but highlights that subordinates are possibly as strategic as dominants when interacting with other group members.

Chapter five: Acoustic structure of chimpanzee pant-grunts co-varies with the receiver's social class and intended type of interaction

" Il écrit une seconde lettre, et après les avoir cachetées toutes deux, il se trompe a l'adresse; un duc et pair reçoit l'une de ces deux lettres, et en l'ouvrant y lit ces mots: Maitre Olivier, ne manquez, sitôt la présente reçue, de m'envoyer ma provision de foin.... Son fermier reçoit l'autre; il l'ouvre, et se la fait lire: on y trouve: Monseigneur, j'ai reçu avec une soumission aveugle les ordres qu'il a plu a votre grandeur...."

Jean de La Bruyère, 1688 (See Appendix A for translation)

Summary

Pant-grunts are used in a flexible way depending on the individuals present in the vicinity (Chapter four). This chapter tries to evaluate whether this behavioural flexibility can also be reflected acoustically, depending on the situation encountered or the social position of the targeted individual. Following the hypothesis that pant-grunts are actively produced in their usage and given that they are highly variable signals, Chapter four was interested in testing whether this variability could be used flexibly in different contexts encountered. Acoustic analyses showed an inter-individual variability that concerned different acoustic parameters than those modified depending on the social situation encountered. More specifically, the grunts were consistently modified when approaching the alpha male as opposed to other males (increase in sequence length and increase in the proportion of n-shaped grunts) and individuals actively signalled their intention to interact in an affiliative way (grooming) by increasing the proportion of panting elements within a sequence with grunts that were lowered in their mean frequency and produced with shorter and more regular intervals. Taken together, these results support the hypothesis of an active production of pant-grunts, but also highlight the fact that chimpanzees are able to actively alter their vocal production depending on the situation encountered and that some of the variability was achieved by recruiting other types of elements within a sequence.

Introduction

Pant-grunts are highly social vocalisations that seem to be voluntarily produced by emitters when encountering and approaching higher ranking individuals. While they function as subordinate signals, this seem to be the overall result of different underlying functions such as making one's presence recognised or testing the relationship with the dominant individual (Hayaki 1990). As shown in the previous chapter, adult chimpanzees give the impression that they weigh the social situation before they greet an individual with a pant-grunt. In this sense, this vocalisation that was perceived as directly deriving from the hierarchical organisation of the community does not seem as rigid as previously described (de Waal 1982). The form of greeting interactions appears to be very variable depending on the primate species studied. Greetings can involve vocal signals or be only constituted by a succession of characteristic behavioural patterns (Colmenares 1990; Dias et al. 2008). Social vocalisations such as contact calls or greetings that regulate social interactions are believed to allow for more acoustic variability than alarm calls as a result of relatively lower evolutionary constraints (Snowdon et al. 2005). In addition, a flexible communication system permits a rapid adaptation to environmental change and it might be more adaptive to not have a totally fixed correspondence between signals and contexts (Snowdon 2008). The selection pressure in these cases might thus act on the flexibility processes rather than on the signal morphology and correspondence to the external world.

Concerning social signals, vervets use acoustically distinct types of grunts, when approaching a dominant or subordinate individual, when moving into a new area, or when observing another group and these that are meaningful for receivers (Cheney & Seyfarth 1990). Similarly, baboons use two different acoustic variants of grunts when moving into an open area and when attempting to handle infants (Rendall et al. 1999). However it is often not known what influence a small contextual variation has on the social call produced, such as the identity of the target of the call or the type of interaction.

In the vocalisations usually studied, the targets of the calls (or eliciting stimuli) are often different food types (Clay & Zuberbühler 2009; Elowson et al. 1991; Slocombe & Zuberbühler 2006), different predators (Schel 2009; Seyfarth et al. 1980; Zuberbühler 2000b, 2001) or different contexts (Notman & Rendall 2005) but the identity of individuals generally act as regulating forces called "audience effect". For example, chimpanzees not only produce different scream types depending on their role in the aggressive encounter, but their screams also vary with the intensity of the threat, taking into account the potential role of bystander (Slocombe & Zuberbühler 2005a, 2007).

Female chimpanzees seem to also modify their copulation calls depending on the rank of her mating partner (Townsend et al. 2008). Of course, considering that mating partners are the intended recipients of the copulation calls can be debated and it is also likely that copulation calls signal the occurrence of a copulation to males, promoting competition around the calling females while being regulated by social competition with other females (Semple 1998; Semple et al. 2002; Townsend et al. 2008). Although animal signals have been considered for a long time as genetically determined and emotionally bound (Fichtel et al. 2001; Smith 1965), these examples among others provide continuing evidence that monkey and ape vocalisations can present some flexibility beyond motivational state only.

Pant-grunts are very variable signals as described in Chapter two and they are believed to present more intra-individual variability and less inter-individual variability than pant-hoots possibly as a result of selective forces on acoustic signal dispersion (Mitani et al. 1996).

However, pant-grunts are highly variable sequences that are produced in a range of situations suggesting a potential for acoustic flexibility.

Within a community, chimpanzees have different social values and individuals react differently depending on the type of individual encountered. The alpha male usually receives most of the pant-grunts produced by community members while other males received pant-grunts in a less reliable way (Newton-Fischer 1997; Takahata 1990b). In this study, the first aim was to check whether this difference in the contextual usage of pant-grunts could be reflected in the acoustic features of these calls. To this end, the pant-grunt sequences of seven adult females to the alpha male were compared to the pant-grunts produced to the other males.

Pant-grunts are commonly used when meeting another individual. A reunion can lead to aggressive, neutral or affiliative behaviours as seen in the previous chapter and the second aim of this chapter was to determine whether there were acoustic differences between neutral and affiliative behaviours and particularly grooming that reinforces bonding between individuals. The pant-grunts emitted during aggressive encounters often grade into barks and screaming bouts that seem to be highly dependent on the fear experienced by the emitter (Goodall 1986), limiting the possibilities of detecting voluntary modulations within this calling family. I thus restricted the contextual analysis to calling sequences that were emitted to the alpha male in neutral situation (i.e.: diminution of the distance between these two individuals) and when the emitter approached the alpha male and groomed him.

Methods

Study Site

Data were collected during three field periods between January - April 2007, August 2007 - February 2008 and July - December 2008 in the Sonso chimpanzee community of Budongo Forest, Uganda (Reynolds 2005).. At the beginning of the study, the community consisted of 78 individuals (10 males, 25 females, 8 subadult males, 5 subadult female, 13 juveniles 12 infants and 5 babies, see Chapter two).

Data collection

Pant-grunts were collected during both focal animal sampling (females) and all occurrence sampling (Altmann 1974) for which I had enough information about the context of emission.

Selection of pant-grunts

In total, I recorded 888 grunts sequences produced by ten adults (3 males, 7 females, more than 15 years old). To conduct acoustic analyses, I selected the first three sequences of calls for each individual per context in my dataset that were free from extensive background noise and were produced in a non-agonistic context to limit the effects of strong emotional reaction displayed. As described above, I concentrated on three different contexts of pant-grunt emission in calm situations to compare the morphology of the pant-grunts used. First, the pant-grunts emitted by six females when encountering the alpha male or encountering another male were compared. In a second analysis, the production of pant-grunts of three females and three males when approaching the alpha male only or when approaching the alpha male and grooming him were compared. For an example of the grunt sequences examined, see Appendix C. This resulted in 767 grunts constituting 69 calling sequences (Table 5.1).

Table 5.1: Number of grunts analysed per individual per context of emission. The three categories are mutually exclusive. To limit the possible rank effects between males, only the vocalisations produced by females for the analysis on the receiver's identity were considered.

Individual	Sex	Approaches other males	Approaches alpha male	Approaches alpha male and grooms	Total
BB	M	-	25	21	46
JN	F	15	49	33	97
KL	F	19	83	51	153
KU	F	23	41	-	64
KW	F	14	26	9	49
KY	F	78	91	-	169
MS	M	-	15	12	27
NB	F	7	61	-	68
ZF	M	-	23	15	38
ZM	F	20	36	-	56
Total		176	450	141	767

Acoustic analysis

To compare the types of grunts and grunt sequences given by chimpanzees across the situations described above, structural and spectral measurements were taken, using PRAAT 4.3.12. As explained in Chapter three, pant-grunts are given in sequences involving different call types and different levels of sequence analysis were considered. Three levels of analysis appear the method of choice to encompass the communicative abilities of animal vocalisations (Bouchet et al. 2010; Hauser 2000).

1- For each sequence, the following structural measurements were determined:

(a) The total number of elements within a sequence (grunts, inhalations, pants or other elements like barks), (b) The total length of the sequence (in seconds), (c) The rate of the calling sequence: number of elements per second, (d) The number of calling bouts within a sequence: number of grunts bouts separated by at least one second, (e) The proportion of grunts within a sequence. Grunts are generally noisy elements that can also be quite tonal, with low fundamental frequencies and generally little energy above 1500Hz (Crockford & Boesch 2005; Marler & Tenaza 1977), (f) the proportion of inhaled elements within a sequence. Inhalations (ingressive calls (Davila Ross et al. 2009) are generally produced in between grunts or pants, when the airflow is inhaled by the caller. On a spectrogram, they are generally more tonal than the grunts with higher frequencies but can also be breathy (Marler & Tenaza 1977), (g) the proportion of panted elements within a sequence. Panted elements are unvoiced, breathy calls that are often difficult to spot on a spectrogram but can usually be detected by ear (Crockford & Boesch 2005). The proportion of other vocalisations like barks or whimpers within a pant-grunt sequence was not analysed because of its low frequency and thus its low significance in the dataset.

2- For each sequence of grunts, structural measurements were determined:

(a) The total number of grunted elements in a sequence, (b), (c), (d) Proportion of n-shaped, u-shaped and w-shaped grunts. Melodic contours: these were determined by eye, derived from Papousek and Papousek classification system (Papousek & Papousek 1989): the minimum frequency could be u-shaped, n-shaped (inverted u) or w-shaped (sinusoidal), (e) Proportion of tonal grunts in the grunt sequence: single calls were determined as tonal when the fundamental and its harmonics could be seen clearly or noisy when the call was harsh.

3- At the individual grunt level, the following temporal and spectral measurements were taken:

(a) Grunt length (s), (b) Intercall length (s): duration of the interval between two grunts, (c) Peak frequency (Hz) of the middle of the call: frequency where is the maximum of the acoustic energy at this point of the grunt, (d) Minimum frequency (Hz) of the middle of the call: lowest frequency of the call determined by the vibration of the vocal folds only (source).

Statistical analysis

As not all individuals contributed to the different situations, sample sizes varied between analyses. All tests were two-tailed with significance levels set at $\alpha=0.05$. All data were checked for normality (Shapiro-Wilk) and homogeneity of variances (Levene's test) and paired-sample t-test or Wilcoxon T-tests were used accordingly. Exact p-values as recommended for small sample sizes were calculated (Mundry & Fischer 1998). All analyses were conducted with SPSS 17.0.

Results

Individual identity

To investigate if individuals gave individually distinctive pant-grunts, I analysed 767 calls and 69 calling bouts recorded from ten individuals (three males and seven females). For normally distributed data with equal variances, ANOVAs revealed that three parameters out of seven varied significantly amongst individuals: the mean grunt length ($F(9)=2.353$, $p=0.025$), the mean minimum frequency ($F(9)=2.604$, $p=0.014$) and the proportion of inhalations within a sequence ($F(9)=2.514$, $p=0.016$). For the other parameters that did not fill the parametric requirements, Kruskal-Wallis analysis showed that two of the thirteen parameters presented individual differences as a trend: the number of grunts within a sequence ($\chi^2(9)=16.301$; $p=0.061$) and the mean peak frequency across the calling sequence ($\chi^2(3)=15.401$; $p=0.080$).

Receiver's status

To determine whether individuals produced different types of pant-grunts depending on the receiver's rank, the acoustic and structural features of calling sequences given to the alpha male and to other males were compared (BB, HW, KT, MA, MS, SM, SQ,TK and ZF).

The acoustic parameters that presented significant differences depending on the individual encountered were all situated at the grunt sequence level of analysis. Adult females produced significantly more grunts (Wilcoxon $T(7)=-2.366$, $p_{exact}=0.016$) that were more n-shaped (Wilcoxon $T(7)=-2.366$, $p_{exact}=0.016$) and less w-shaped (Wilcoxon $T(7)=-3.059$, $p_{exact}=0.022$) when encountering the alpha male. At the sequence level, these vocal productions tend to be longer (Wilcoxon $T(7)=-1.859$, $p_{exact}=0.078$) and contain more bouts (Wilcoxon $T(7)=-2.032$, $p_{exact}=0.063$).The type of individual encountered did not affect any of the spectral or temporal parameters in a significant way at the grunt element level (Table 5.2, Fig. 5.5, 5.6and 5.7).

Table 5.2: Statistical output of the comparisons between the acoustic measurements of the grunt sequences produced when encountering the alpha male and other males. Depending on the result for normality tests (Shapiro-Wilk) and equality of variances (Levene's test), matched sample t-tests and Wilcoxon T tests (with exact p-value) were used. Bold: Significant at α<0.05, Italics: Trend at 0.1<α<0.05.

Level of analysis	Parameter	Test	Value	Sig.(2tailed)	Figure
Total sequence	Number of elements	Wilcoxon	-.608	.565	1a
	Total length	*Wilcoxon*	*-1.859*	*.078*	*1b*
	Rate	T test	-.608	.565	1c
	Number of bouts	*Wilcoxon*	*-2.032*	*.063*	*1d*
	Proportion of grunts	T test	-1.280	.248	1e
	Proportion of pants	Wilcoxon	-1.014	.375	1f
	Proportion of inhalations	T test	.482	.647	1g
Grunt sequence	**Number of grunts**	**Wilcoxon**	**-2.366**	**.016**	**2a**
	Proportion of tonal grunts	T test	-.530	.615	2b
	Proportion of n-shaped grunts	**Wilcoxon**	**-2.366**	**.016**	**2c**
	Proportion of u-shaped grunts	**Wilcoxon**	**-2.197**	**.031**	**2d**
	Proportion of w-shaped grunts	**T test**	**-3.059**	**.022**	**2e**
Grunt element	Mean grunt length	T test	-.869	.418	3a
	Standard deviation of the grunt length	T test	1.092	.317	3b
	Mean intercall length	T test	.281	.788	3c
	Standard deviation of the intercall length	T test	1.188	.280	3d
	Mean peak frequency	T test	.567	.591	3e
	Standard deviation of the peak frequency	T test	.333	.750	3f
	Mean minimum frequency	T test	.509	.629	3g
	Standard deviation of the minimum frequency	T test	1.146	.295	3h

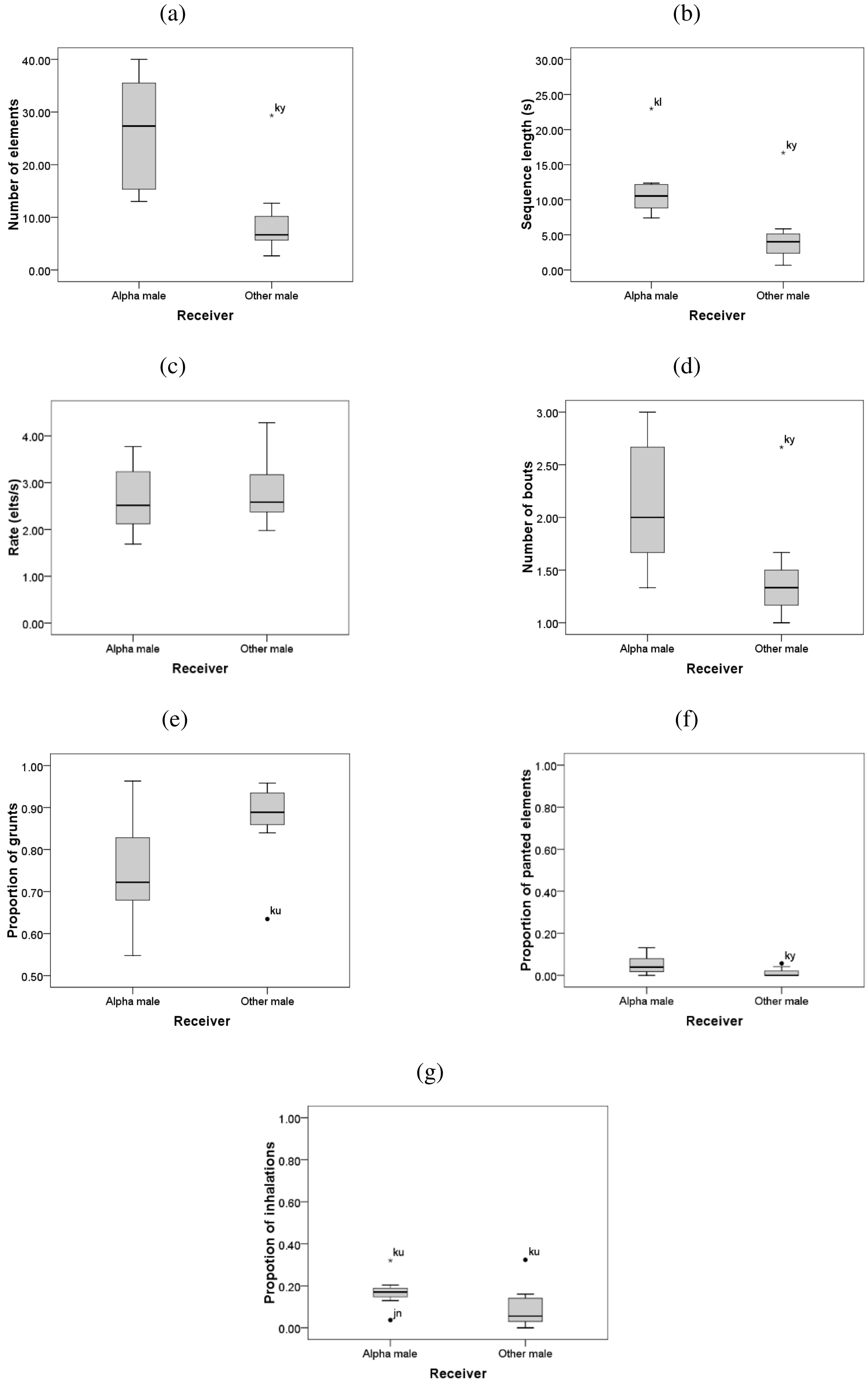
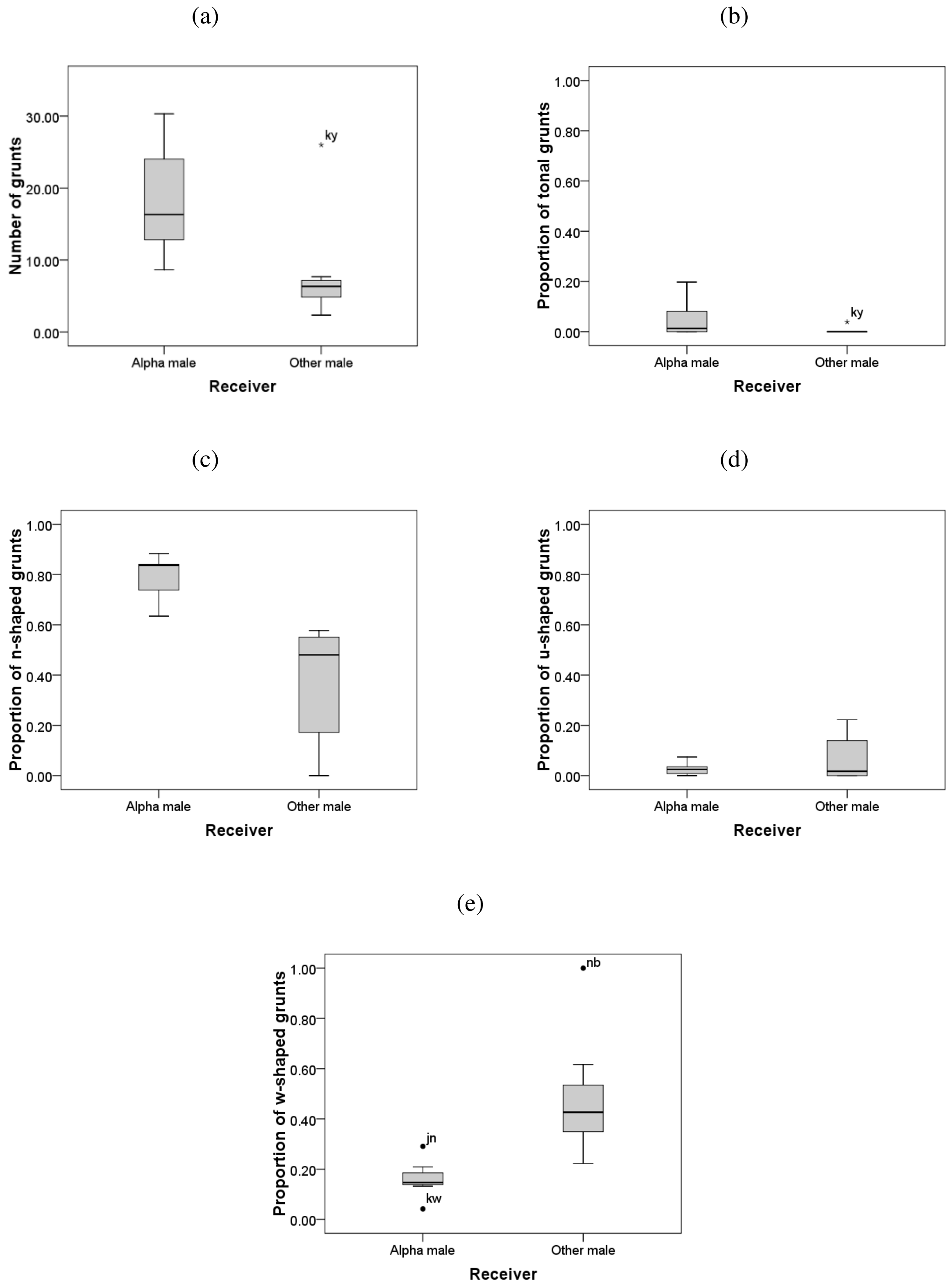


Figure 5.1: Phrase level acoustic analysis for encounters with the Alpha male or Other males: (a) total number of elements within a sequence (grunts and inhalations), (b) total length of a sequence, (c) sequence rate, (d) number of bouts in a sequence, (e) proportion of grunts within a sequence, (f) proportion of panted elements within a sequence, (g) proportion of inhaled elements within a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.


(a)

(b)

(c)

(d)

(e)

Figure 5.2: Grunt sequence level acoustic analysis for encounters with the Alpha male or Other males: (a) total number of grunts within a sequence, (b) proportion of tonal grunts within a sequence, (c) proportion of n-shaped grunts within a sequence, (d) proportion of u-shaped grunts within a sequence, (e) proportion of w-shaped grunts within a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

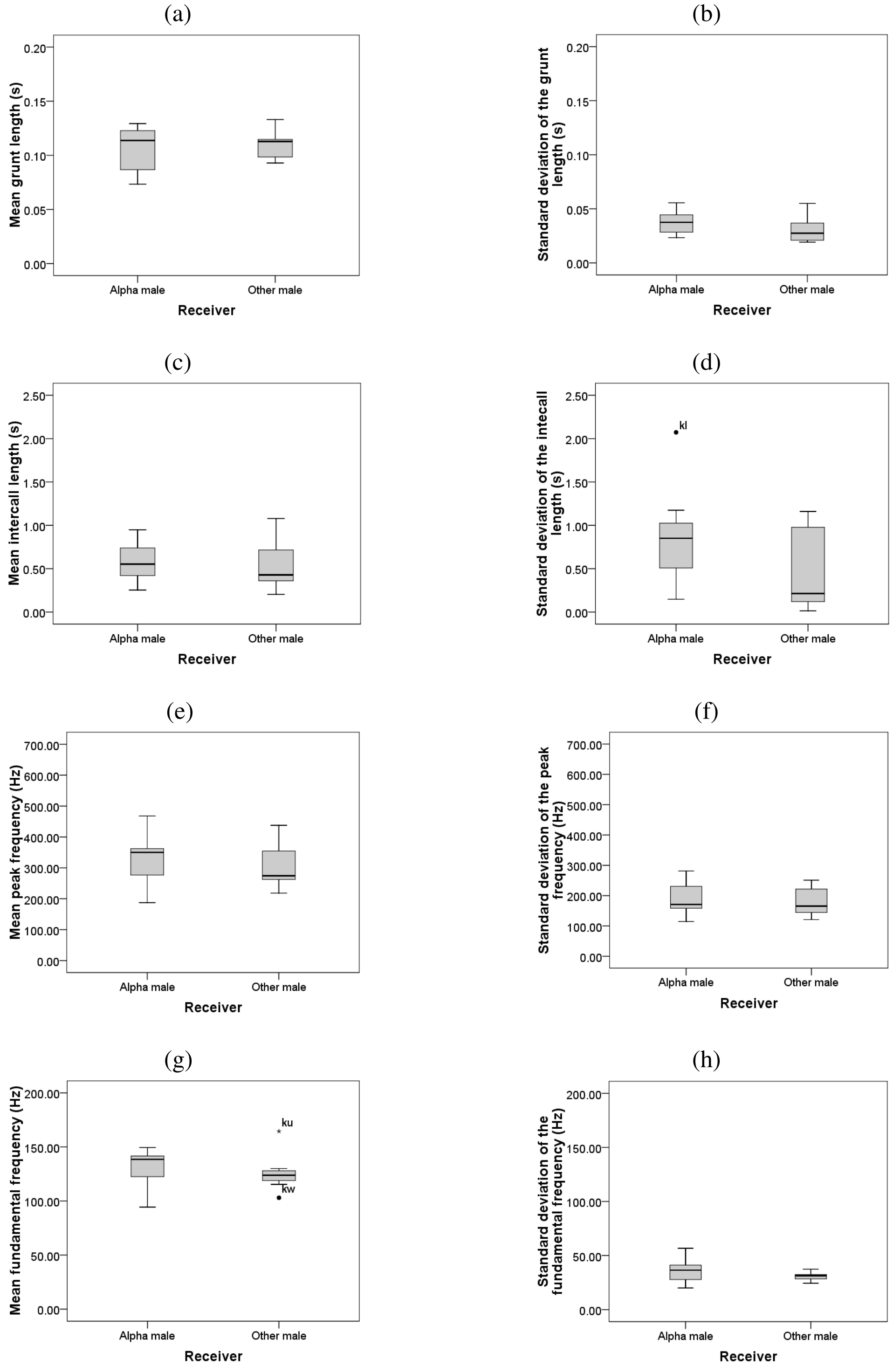


Figure 5.3: Grunt element level acoustic analysis for encounters with the Alpha male or Other males: (a) mean grunt length, (b) standard deviation of the grunt length, (c) mean interval length, (d) standard deviation of the mean interval length, (e) mean peak frequency, (f) standard deviation of the peak frequency, (g) mean minimum frequency, (h) standard deviation of the minimum frequency. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

Context of emission

To determine if individuals' pant-grunts vary acoustically with the context of emission, the pant-grunts from six individuals (three males and three females) constituting 36 calling sequences containing 362 grunts were analysed. Matched-pairs comparisons revealed that, when encountering and grooming the alpha male, the absolute number (t(5)=3.003, p=0.03) and the proportion (T(5)=-2.201, p=0.031) of grunts decreased together with the mean (T(5)=-2.201, p=0.031) and the standard deviation (T(5)=-2.201, p=0.031) of the intercall length and the peak frequency (t(5)=2.862, p=0.035), while the overall rate (t(5)=-2.968, p=0.031) and the proportion of pants increased (T(5)=-2.201, p=0.031) compared to when they approached the alpha male without grooming him. The number of bouts also slightly decreased (t(5)=2.390, p=0.062) (Table 5.3, Fig. 5.4, 5.5,5.6).

Table 5.3: Statistical output of the comparisons between the acoustic measurements of the grunt sequences produced when encountering the alpha male and approaching him or approaching and grooming him. Depending on the result for normality tests (Shapiro-Wilk) and equality of variances (Levene's test), matched sample t-tests and Wilcoxon T tests (with exact p-value) were used. Bold: Significant at α<0.05, Italics: Trend at 0.1<α<0.05.

Level of analysis	Parameter	Test	Value	Sig.(2tailed)	Figure
Total sequence	Number of elements	T test	-1.590	.173	4a
	Total length	Wilcoxon	-.105	1.000	4b
	Rate	**T test**	**-2.968**	**.031**	**4c**
	Number of bouts	*T test*	*2.390*	*.062*	*4d*
	Proportion of grunts	**Wilcoxon**	**-2.201**	**.031**	**4e**
	Proportion of pants	**Wilcoxon**	**-2.201**	**.031**	**4f**
	Proportion of inhalations	T test	1.089	.326	4g
Grunt sequence	**Number of grunts**	**T test**	**3.003**	**.030**	**5a**
	Proportion of tonal grunts	T test	1.789	.134	5b
	Proportion of n-shaped grunts	Wilcoxon	-1.153	.313	5c
	Proportion of u-shaped grunts	T test	-1.003	.362	5d
	Proportion of w-shaped grunts	T test	-1.108	.318	5e
Grunt element	Mean grunt length	T test	-1.256	.265	6a
	Standard deviation of the grunt length	T test	.257	.807	6b
	Mean intercall length	**Wilcoxon**	**-2.201**	**.031**	**6c**
	Standard deviation of the intercall length	**Wilcoxon**	**-2.201**	**.031**	**6d**
	Mean peak frequency	**T test**	**2.862**	**.035**	**6e**
	Standard deviation of the peak frequency	Wilcoxon	-.943	.438	6f
	Mean minimum frequency	Wilcoxon	-.105	1.000	6g
	Standard deviation of the minimum frequency	T test	1.200	.284	6h

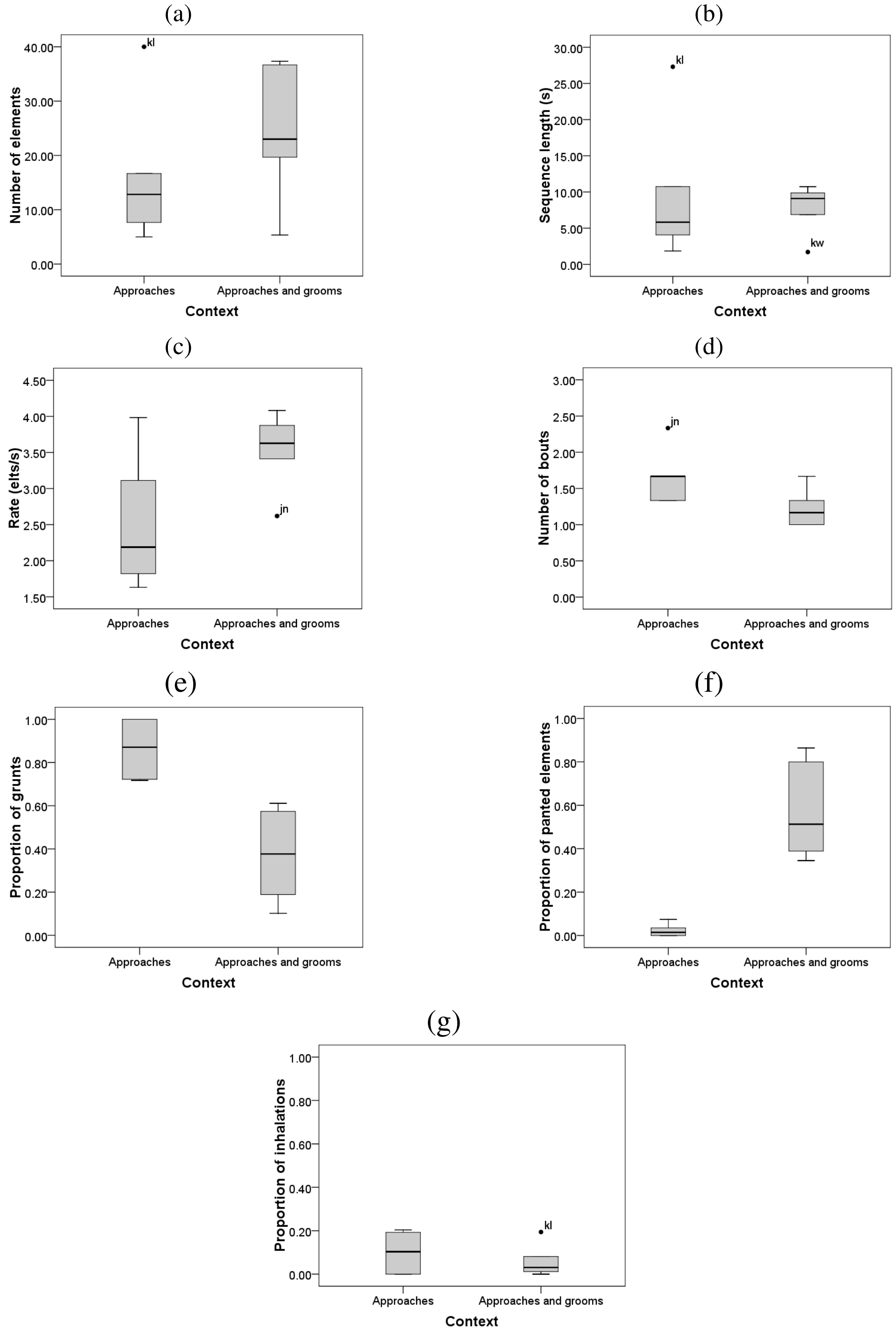
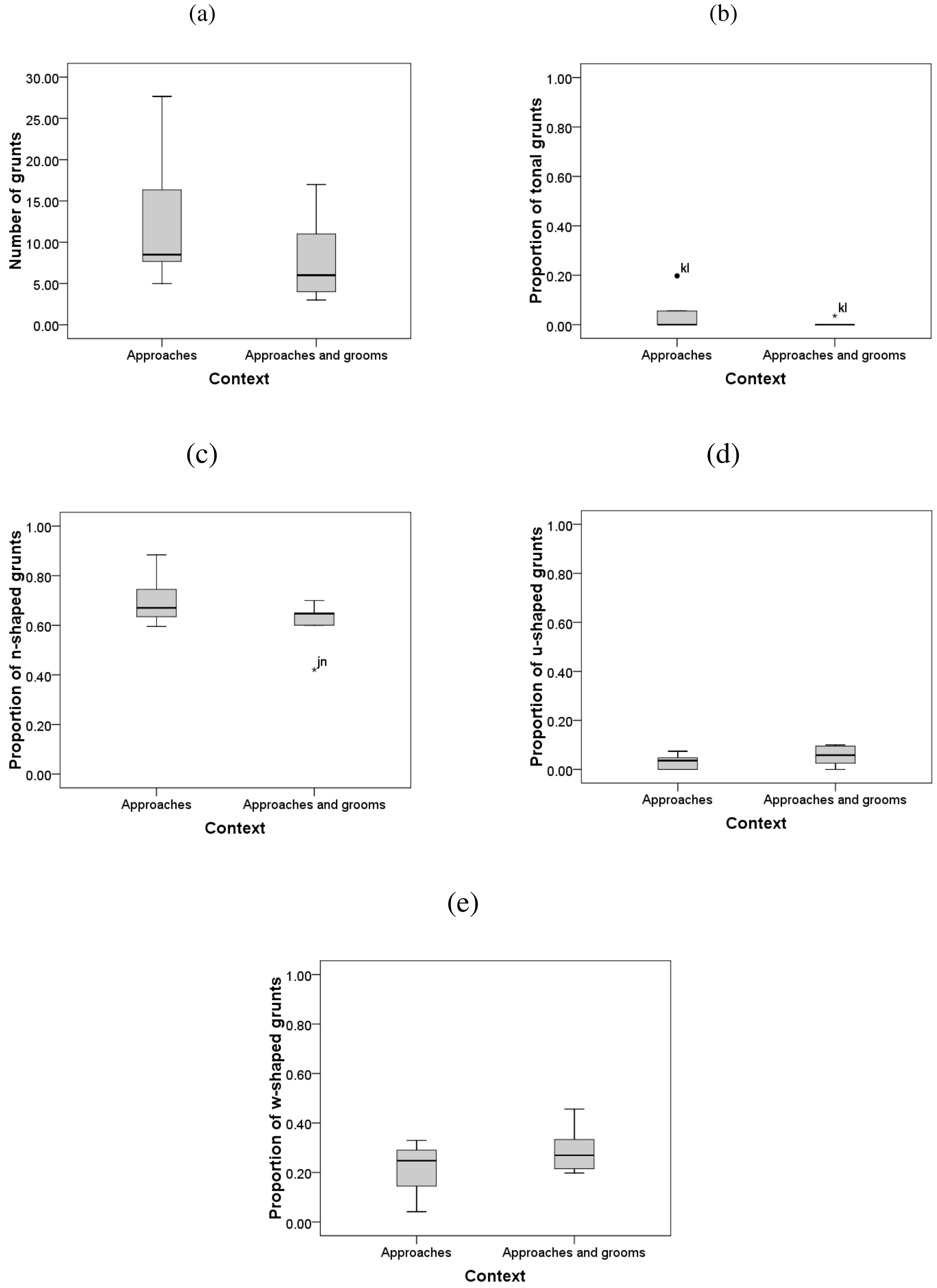


Figure 5.4: Phrase sequence level acoustic analysis for encounters with the Alpha male with Approach only or with Approach and groom: (a) total number of elements within a sequence (grunts and inhalations), (b) total length of a sequence, (c) sequence rate, (d) number of bouts in a sequence, (e) proportion of grunts within a sequence, (f) proportion of panted elements within a sequence, (g) proportion of inhaled elements within a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.



(a)

(b)

(c)

(d)

(e)

Figure 5.5: Grunt sequence level acoustic analysis for encounters with the Alpha male with Approach only or with Approach and groom: (a) total number of grunts within a sequence, (b) proportion of tonal grunts within a sequence, (c) proportion of n-shaped grunts within a sequence, (d) proportion of u-shaped grunts within a sequence, (e) proportion of w-shaped grunts within a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

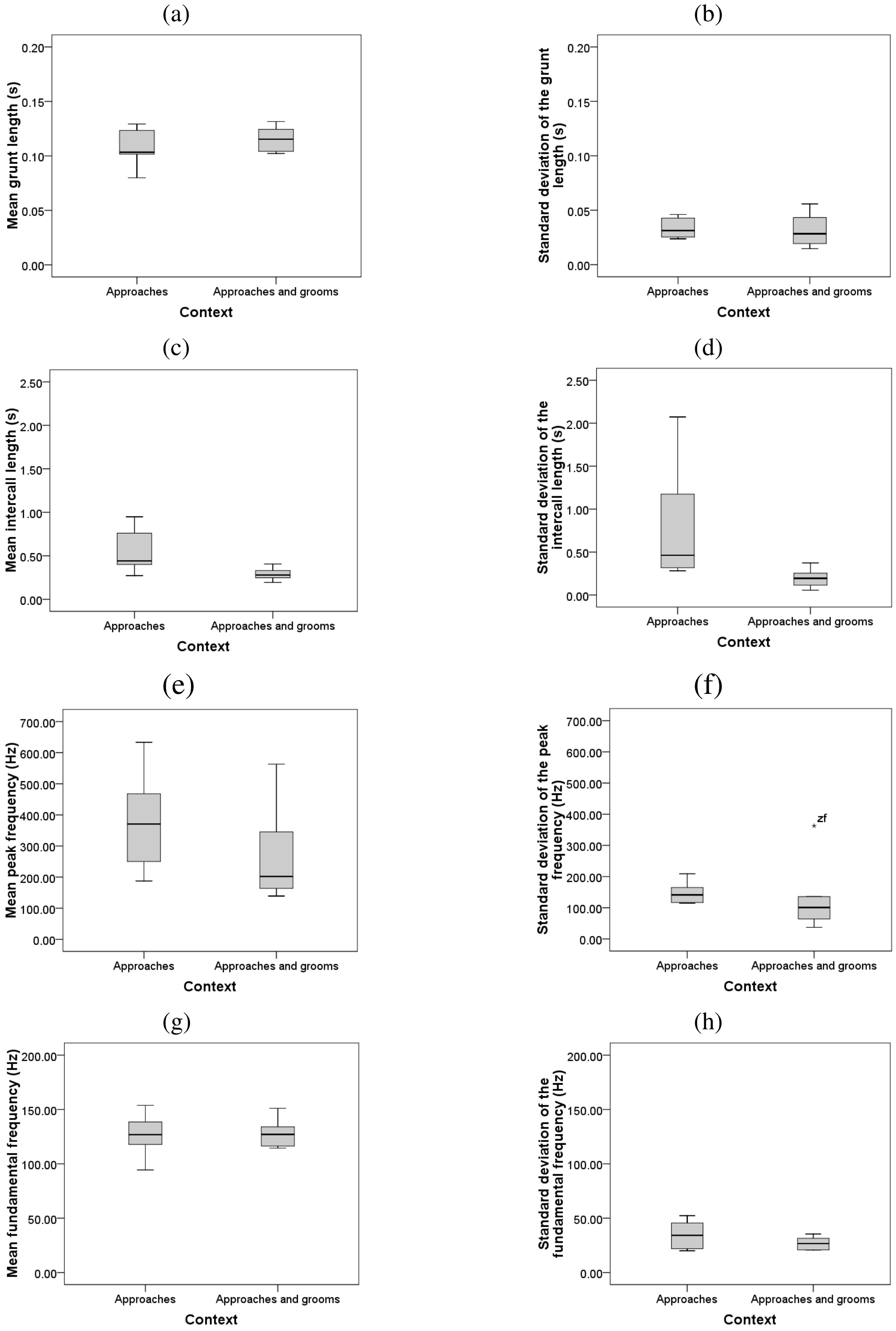


Figure 5.6: Grunt element level acoustic analysis for encounters with the Alpha male with Approach only or with Approach and groom: (a) mean grunt length, (b) standard deviation of the grunt length, (c) mean interval length, (d) standard deviation of the mean interval length, (e) mean peak frequency, (f) standard deviation of the peak frequency, (g) mean minimum frequency, (h) standard deviation of the minimum frequency. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

Discussion

Most of the studies investigating chimpanzees' vocalisations with fine-grained techniques of structural and spectral analyses found that they were used in flexible and potentially strategic ways (Slocombe & Zuberbühler 2005a; Townsend et al. 2008). The previous chapter demonstrated that pant-grunts were not automatic responses to the presence of a higher-ranking individual, but that their emission also depended on the surrounding social factors. The results of this chapter further support these findings and indicate that pant-grunts, although presenting some individual differences, also varied in their structural and spectral parameters depending on the rank of the individual met and the situation encountered.

Some individual variation in the pant-grunts produced was found mostly in the mean grunt length, the mean minimum frequency and the proportion of inhalations within a sequence and some other parameters varied depending on the target of the call or the action performed. For example, individuals produced longer calling sequences with proportionally more n-shaped grunts when encountering the alpha versus other males and when signalling an affiliative interaction (grooming), they increased the proportion of pants in their sequence and lowered the peak frequency of their grunts that were produced with shorter and more regular intercalls (see Table 5.4 for a summary of these results). Taken together, these results suggest that chimpanzees have some control over their pant-grunts.

There are two interesting findings in this study concerning the motivation to call and the tangible anticipation of future events. First, we have seen in the previous chapter that most of the pant-grunts produced are directed to the alpha male. One of the hypotheses was that as the alpha male could be relatively violent toward other group members, showing respect to him could be a way to avoid attacks. In this study, the vocalisations analysed were all emitted in affiliative or neutral situations in order limit the importance of confounding variables. Still, the parameters that were modified when encountering the alpha male do not specially reflect apprehension or fear but could be the result of an increase in motivation. For example the sequences were longer, which could reflect that individuals take more time to greet the alpha male while no increase in frequency (peak and fundamental) or in rate was found that could have reflected an increase in apprehension (Morton 1977; Schehka et al. 2007; Theis et al. 2007). Individuals thus seem to put more efforts in the production of pant-grunts given to the alpha than to the other males, which supports Hayaki (1990)'s hypothesis that one important function of pant-grunts is to make sure that one's presence is recognised and accepted by the dominant individual present.

The second interesting finding of this study is that pant-grunts that are given to the alpha male when approaching and grooming him seem to be often constituted by two different types of elements: the grunts and the pants. Panting has been described as occurring during grooming sessions or as a prelude to open-mouth kissing when one or both individuals do the panting (Goodall 1986; Marler & Tenaza 1977) but in the cases studied here, only the subordinate produced a vocalisation and always succeeded in his grooming attempt. While the panting alone is often given during grooming sessions, it seems to have been included at the end of the greeting sequence of pant-grunts, before any physical attempt of grooming and can also continue during grooming. This vocalisation thus suggests that the caller somehow anticipates a future action and advertises the receiver of his intentions by combining a greeting with the sound usually produced during grooming sessions. Chimpanzees' calls, as other primates' vocalisations, are often organised into sequences combining two or more vocal signals (Arnold & Zuberbühler 2006; Clay & Zuberbühler 2009; Ouattara et al. 2009; Schel 2009; Zuberbühler 2002). However, it is often not very clear what the meanings of the individual calls are and how this meaning is affected by combination. In other words, when combining units into sequences, animals display what has been termed "phonological syntax", while human have the possibility to combine meanings into hierarchical structures that confers its infinite expressive power to language, termed "lexical syntax" (Hauser et al. 2002; Marler 1977). In this study, pant-grunts in different contexts seem to be more an addition of meanings (Cleveland & Snowdon 1982) in anticipation of a future action. This simple process of concatenation of signals linked to two different social situations, the greeting and the grooming and in anticipation of the latter, could be one of the possible mechanisms by which lexical syntax could have emerged in animal communication systems. Overall, it seems that the pant-grunting in chimpanzees is closer to physical or physiological influences and motivation (Notman & Rendall 2005) than truly labelling the identity of the receiver or their own actions.

Of course, specific close range playbacks experiments would now be required to evaluate what chimpanzees understand from these greeting vocalisations and whether they can infer specific social situations from the acoustic and structural features of these calls. However, it seems reasonable to hypothesise that surrounding individuals take into account these variations. One observation suggests that at least the panting at the end of the calling sequence is meaningful for eavesdroppers: In the example given in the previous chapter, the alpha female Nambi chased the subordinate female Kalema away from the alpha male just after she heard her producing a pant-grunt terminated by a panting sequence. As Nambi was unable to see Kalema from her localisation (in a thick undergrowth and turning her back), it is not impossible that she could infer the actual affiliative interaction between this subordinate female and the alpha male by the composition of the call only.

In the same vein, recent experiments with other types of calls further suggest that chimpanzees can understand the nature of social events (Slocombe et al. 2009). If chimpanzees can infer from the calls the identity of the emitter and the receiver as well as the nature of the interaction, then the lack of visibility typical of forests with dense undergrowth would not be a such a problem anymore when making behavioural decisions of joining a party or not and updating relative ranks between group members.

Table 5.4: Summary of the significant modifications of pant-grunt sequences. Bold parameters represent individual variability and arrows denote the direction of change. The final level of variation corresponds to changes that appear to be specific to the situation encountered: R=Receiver (alpha male or other males) and C=Context (grooms or not).

Parameter		Approaches other male	Approaches alpha male	Approaches alpha male and grooms	Level of variation
Total sequence	Number of elements		=	=	
	Total length		↗	=	R
	Rate		=	↗	C
	Number of bouts		↗	↘	
	proportion of grunts		=	↘	C
	Proportion of pants		=	↗	C
	Proportion of inhalations		=	=	
Grunt sequence	Number of grunts		↗	↘	
	Proportion of tonal grunts		=	=	
	Proportion of n-shaped grunts		↗	=	R
	Proportion of u-shaped grunts		=	=	
	Proportion of w-shaped grunts		↘	=	R
Grunt element	**Mean grunt length**		=	=	
	Standard deviation of the grunt length		=	=	
	Mean intercall length		=	↘	C
	Standard deviation of the intercall length		=	↘	C
	Mean peak frequency		=	↘	C
	Standard deviation of the peak frequency		=	=	
	Mean fundamenal frequency		=	=	
	Standard deviationof the fundamental frequency		=	=	

Chapter six: The development of a greeting signal in wild chimpanzees

"Gargantua, depuis les trois jusques à cinq ans, fut nourry et institué en toute discipline convenente, par le commandement de son père, et celuy temps passa comme les petits enfants du pays: c'est à savoir à boire, manger et dormir; à manger, dormir et boire; à dormir, boire et manger."

Rabelais, 1542

Summary

Adult chimpanzees produce a unique vocal signal, the pant-grunt, when encountering higher-ranking group members. The vocalisation is typically directed to a specific receiver and has thus been interpreted as a ‘greeting’ signal. The alpha male obtains a large share of calls followed by the other adult males of the group. In this study, the development of pant-grunting behaviour from the first grunt-like calls of newborn babies to the fully developed pant-grunts in adults is described. As babies, chimpanzees produce simple grunts in a reflex-type way, but from infancy calls gradually change into acoustically distinct social grunts given to other group members. While the specificity in use increases, a sharp decline in calling activity in older infants and juveniles was found. During adolescence, call production increases again with grunts given most frequently to socially relevant individuals. As chimpanzees are closely affiliated to their mothers for the first decade of their lives, the calling patterns of mothers and their offspring were also compared and revealed some influences in the patterns of pant-grunt acquisition. In conclusion, the acquisition of pant-grunting behaviour in chimpanzees is a long-lasting process with distinct developmental phases that results from a combination of maturational and learning processes.

The results from this chapter have been submitted for future publication:

Laporte, M. N. C. & Zuberbühler, K. (under revision). The development of a greeting signal in wild chimpanzees. Developmental Science.

Introduction

The vocal behaviour of great apes has remained a relatively neglected area of research until recently. Early attempts to communicate with apes in enculturated settings produced ambiguous results. Paradigms based on vocal signals were much less successful compared to those using in sign language and lexigrams (Gardner & Gardner 1969; Hayes 1951; Savage-Rumbaugh et al. 1986). One result of this work was a widespread perceived dichotomy between gesturally-flexible and vocally-rigid apes. At the same time, the natural vocal behaviour of chimpanzees and other great apes has hardly been studied, with vocal development being especially poorly investigated. Two early development studies of captive apes included some observations on vocal productions (Jacobsen et al. 1932; Ladygina-Kohts et al. 1935/2002). However, they were conducted with single chimpanzees who were human-raised and had no contact with conspecifics. Plooij's (1984) study then described the general developmental patterns in five wild chimpanzees during their first two years of life. More recently, Bard (1994b) studied development of emotions and cognition in different rearing conditions and Kojima (2001) described some of vocalisations produced by a captive chimpanzee during the first 18 weeks, but apart from these I am not aware of any systematic studies of ape vocal development in the wild or in captivity.

A dominant theme in studies of vocal development in primates relates to the question of vocal learning. The established view is that non-human primates possess little control over call production, particularly call morphology, which typically results in limited vocal repertoires (Janik & Slater 1997, 2000). Flexibility is generally greater in other domains of vocal behaviour, such as context-specific call use and call comprehension (Cheney & Seyfarth 2009; Seyfarth & Cheney 1986, 1999). Some observations of adult individuals suggest that social and individual learning mechanisms are likely to be involved, but the details are not well understood. For instance, Diana monkeys of Tai Forest, Ivory Coast, can discriminate between chimpanzee screams given during social conflict and to a leopard, provided they have had sufficient experience with chimpanzees (Zuberbühler 2000a). Similarly, Diana monkeys living on Tiwai Island, Sierra Leone, a habitat with no leopards, give alarm calls to leopard models, but their calls do not differ from the alarm calls given to general disturbances, suggesting that some aspects of call production are controlled by ontogenetic experience (Stephan & Zuberbühler 2008). In chimpanzee, there is documented acoustic variability in the pant hoot vocalisations between communities, which has also been taken as evidence for learning (Crockford et al. 2004; Mitani et al. 1992).

As described in Chapter two, another line of research comes from vervet monkeys. Young monkeys initially produce eagle and leopard alarm calls to a broad range of events and only with experience learn to give these calls to the dangerous predator classes (Cheney & Seyfarth 1990). Similarly, the amount of experience with intergroup encounters was closely linked to the onset of “wrr” production in young vervet monkeys, a call type produced when detecting a neighbouring group (Hauser 1989). In the laboratory, adult cotton top tamarins (*Saguinus oedipus*) produce specific calls when feeding with their infants, as opposed to when feeding alone (Joyce & Snowdon, 2007), suggesting that the adult vocal behaviour functions to promote infant learning. Infants initially produce a large number of call types but over time converge towards a narrower range also used by adults (Roush & Snowdon, 2001). Overall, socialisation and experience with group members seem to be important in the development of vocal behaviour, suggesting that vocal development should be studied in natural group settings.

In this study, I focus on one potentially interesting vocal signal in chimpanzees, the pant-grunts. Pant-grunts are an acoustically heterogeneous and graded group of calls, which serve important social functions. The call is exclusively given by individuals when encountering a more dominant group member. Hence, this type of calling behaviour is interpreted as a greeting signal and commonly used as an indicator of dominance relationships (van Hooff 1973; Goodall 1986; Noë et al. 1980), although pant-grunts can also be produced in appeasement and reconciliation contexts (de Waal 1982). In the laboratory, pant-grunting decreases if groups are kept under crowded conditions where social tension is high (Aureli & de Waal 1997), suggesting that additional variables govern call production. In the wild, callers appear to be aware of the potential consequences of producing pant-grunts to certain group members (Chapter four). For example, in the presence of the alpha male, females typically refrain from producing pant-grunts to other high-ranking males, who would normally obtain such calls. Pant-grunts are frequently produced by all individuals apart from the alpha male and some high-ranking males (Clark 1993) and there is evidence that they are individually recognisable (Kojima 2003).

Grunts are some of the first vocalisations produced by chimpanzees in the wild (Plooij 1984) and captivity (Kojima 2001; Bard 2003). Plooij (1984) reported that first grunts were given as part of physical efforts (the “effort grunts”), the result of air release during muscular contraction (Plooij 1984). Other early vocalisations were staccato grunts and whimpers given in reaction to loss of contact with the mother or to a sudden loud noise (Plooij 1984; Kojima 2001). In captivity, Bard (2003) reported greeting vocalisations in their first week of life while earlier studies did not report them before the second month (Jacobsen 1932), possibly due to differences in rearing conditions or methodology (Bard 1998). Other work has shown that chimpanzees are tuned to conspecifics vocalisations from very early on, possibly as a result of prenatal experience (Berntson & Boysen 1989). From about three to four months, chimpanzees begin to produce grunts at the sight of other group members (Plooij 1984; Hiraiwa-Hasegawa 1989) or human caretakers in captivity (Jacobsen 1932; Ladygina-Kohts 1935/2002; Bard, 2003). In the wild, infants stay in constant ventro-ventral contact with their mothers until about seven months of age (van de Rijt-Plooij & Plooij 1987). Even after starting to move independently, mothers and their offspring usually stay close to each other and travel together for another ten years or so, until adolescence (Pusey 1990). The mother-offspring dyad, in other words, provides a particularly important context for exploring vocal development in chimpanzees.

Here, the development of context-specific grunt production from birth to adulthood in a large number of individuals in a free-ranging group of chimpanzees, the Sonso community of Budongo Forest, Uganda was systematically studied. The basic developmental patterns across the different age groups was described and the relationship between the vocal behaviour of the mother and of her offspring was examined to assess the role of the mother in the acquisition of vocal greeting behaviour.

Methods

Study site

Data were collected during three field periods between January - April 2007, August 2007 - February 2008 and July - December 2008 in the Sonso community of Budongo Forest, Uganda (Reynolds 2005). At the beginning of the study, the community consisted of 78 individuals (10 males, 25 females, 8 subadult males, 5 subadult female, 13 juveniles 12 infants and 5 babies, see Chapter two).

Data collection

In total, I followed 34 babies, infants, juveniles and subadults belonging to 15 different families (Table 2, Chapter three). Due to the slow development of chimpanzees, both cross-sectional and longitudinal data collection were used, by comparing four major periods of development, adapted from Goodall (1986) and Plooij (1984) (see Chapter two). Focal animal sampling ("focal": N=501 hours) and 5 min scan samples of focal individuals were used (Altmann 1974). For each scan sample, the behaviour of the focal animal and his or her mother was recorded, as was the identity of all individuals present within a radius of both 10m (average visual range) and 35m (average spread of a travel party (Newton-Fisher 2004)). During focal animal samples, all vocalisations produced by the infant and the mother were noted down, together with the context of production on an all-occurrence basis. An additional dataset consisted of all individuals remaining within a 10m radius surrounding the focal animal during at least two consecutive scans ("focal 10m": N=531 hours). To calculate call rates and to carry out context analyses, the two datasets were combined ("focal + focal 10m": N=1,032 hours, Table 6.1). All occurrence data were taken for all visible individuals situated further than ten meters from the focal. For some specific contexts involving sometimes low numbers of vocalisations produced by individuals, I calculated the proportion of each grunt type produced relative to all grunts produced, for which the data collected during all occurrence sampling was included.

Table 6.1: Time focal (hours) for each individual in each basic age classes discriminated in this study based on definitions by Plooij (1984; 1987), Goodall (1986), and Hiraiwa-Hasegawa (1990). See Appendix D for the participation of each individual in each analysis..

Focal Individuals	Baby 0-6 months included	Infant 7 months-4 years included	Juvenile 5 years to 10 years included	Subadult 11-15 years included	Total
Kathy	42.25				42.25
Faida	1.08	6.33			7.42
Klauce	15.50	66.75			82.25
Kox	6.92	48.08			55.00
Karibu	16.33	65.17			81.50
Marion	10.00	11.33			21.33
Rafia	7.00	25.00			32.00
Honey		15.42			15.42
James		46.33			46.33
Sokomoko		17.50			17.50
Sharlot		3.00			3.00
Night		18.50	31.92		50.42
Kasigwa		30.25	31.00		61.25
Zak		10.58	21.92		32.50
Ramula			15.67		15.67
Monika			4.33		4.33
Zed			30.91		30.91
Helen			10.00		10.00
Karo			24.50		24.50
Kumi			26.42		26.42
Janet			14.50		14.50
Pascal			21.65		21.65
Frank			15.75		15.75
Katia			33.58		33.58
Kana			23.25		23.25
Zig			7.75	17.75	25.50
Rose			7.00	6.17	13.17
Nora				31.67	31.67
Zalu				40.08	40.08
Bahati				28.67	28.67
Kwezi				37.25	37.25
Fred				20.50	20.50
Kato				27.50	27.50
Hawa				28.33	28.33
Simon				10.83	10.83
Total	99.08	364.25	320.14	248.75	1032.23

Vocalisations

Chimpanzee babies produce grunt-like calls and whimpers from their first day of life (Kojima, 2001; Plooij 1984). These grunts probably serve as the substrate for a wider range of call types, including various grunts, but maybe also hoots and barks. Early grunts produced by babies and infants are produced in a range of situations. Some contextual distinctions have been made by Plooij between the “effort grunts” and the “social grunts” (labelled “staccato grunts” and “uh-grunts”). Adult grunts fall into at least three distinct categories, based on acoustic structure and contextual use: rough grunts given to food, travel grunts given in relation to movement, and pant-grunts given when encountering a higher ranking group member (Goodall 1986). Although rough grunts have been shown to acoustically vary with the type of food (Slocombe & Zuberbühler 2006), no systematic acoustic analyses have been done to specifically distinguish between the different types of adult grunts. The relationship between the acoustic variation in adult and infant grunts will be investigated in the next chapter. The grunt-like calls of immatures were labelled according to their contextual use.

Context analysis

For offspring grunts, the call rates (grunts per hour) of any grunt-like vocalisation produced by all offspring were determined. As contexts, the following events were discriminated: (1) no apparent external events, (2) hearing vocalisations only, (3) encountering food with individuals around and possibly other vocalisations, and (4) encountering group members while possibly hearing vocalisations. These contexts were mutually exclusive. Grunts rates were calculated in a preliminary analysis per month of development for the first two years and then per year of development until 15 years of age, i.e. the onset of adulthood. This detailed representation of the total number of grunt-like vocalisations emitted by any individual over the total number of hours of observation for this specific period of development generated an overview of the contextual usage of calls during development. The low number of individuals per observational month, the relatively low call rate, and the imprecise age estimates of some older individuals prevented us from conducting meaningful statistical analyses at this level. I thus chose to proceed at the individual level, by comparing grunt rates and proportional data on call usage. To this end, the immatures were divided in four age classes following previous studies and based on the physical and social development of individuals: Baby: from birth to the onset of dorsal riding (0-6 months); Infant: from dorsal riding to weaning (7 months - 4 years); Juvenile: from weaning to puberty (5-10 years) and Subadults: from puberty to adulthood (11-15 years) as described in Chapter two (van Lawick-Goodall 1967; van de Rijt-Plooij 1987; Plooij 1984; Hiraiwa-Hasegawa 1989). A minimum of five hours of observation for an individual was required to be included in the frequency analyses and a minimum of three calling events to be included in proportional analyses. According to this division, the number of individuals per age class varied between 5 and 15 depending on the analysis conducted (See Appendix D for the participation of each individual in each analysis). The first contextual analysis divided the grunts into four contextual categories and subsequent analyses were conducted at the individual level as well.

Response to the type of vocalisations and the identity of the emitter

The aim of this analysis was to reveal the importance of other group members' pant-grunts vocalisations as triggers for the production of grunts. To this end, I investigated what proportion of pant-grunts (relative to other vocalisations) were triggering grunt-like vocalisations in immatures, using those that were produced after any other vocalisation only or together with the presence of food or another individual (Analysis 2a). Secondly, I examined the provenance of these vocalisations to observe the relative importance of the vocal behaviour of different types of individuals in triggering the grunt-like calls (Analysis 2b). Emitters of these vocalisations were thus divided emitters in six different possibly meaningful categories: *Adult males*, *Adult females*, *Mother*, *Subadult*, *Group of individuals* (at least two) or *Other* (Juveniles individuals or younger, not determined) (Analysis 4).

Response to the presence of individuals

Socially directed grunts are relatively easy to identify, even in very small babies who are difficult to observe within the mother's fur. At this early age, call production required considerable efforts both in terms of attention and physical strength. It was not rare to see a baby seemingly preparing for a grunt, with body and lip posture directed towards a specific individual over several seconds before producing a grunt, with sometimes no sound produced. Using all the grunts clearly directed to individuals, in the presence or not of a vocalisation, I examined the relative importance of the identity of the target over development using call rates (Analysis 4a). One of the most important figure receiving pant-grunts in adults is the alpha male (Chapter four) and I thus divided the receivers in Alpha male, Adult male, Adult female and Subadults. For this analysis, I also considered the adult frequency of pant-grunting represented by the mothers of the immatures studied ($N_{mothers}$=11).

Influence of the mother

To investigate whether certain aspects of social grunting behaviour are possibly influenced by the production of the mother, I conducted a number of comparisons between the vocal behaviour of the mothers and their offspring. A first one concerned the question of whether more vocal mothers have more vocal offspring (Analysis 4b). To investigate this, I compared the females' overall vocal activity of pant-grunting with the vocal activity of their offspring of social grunting. As the production of social grunts was likely to be age-dependent, I conducted a follow-up analysis to test whether offspring were more likely to rank closer to their own mother than other females. To this end, I considered the relative distance between the mother and her offspring and compared it to the relative distance to the mean call rate of other females.

Number and identity of targets

To assess the influence of the mother in terms of the number and identity of targets, I first checked whether mothers and their offspring correlated in the number of group members that received grunts over development (Analysis 4c). In terms of the portfolio of targets, I tested whether the target of immatures' social grunts were part of their mother's portfolio by calculating the proportion of all social grunts produced by immatures that were directed individuals that were part of their mothers portfolio (Analysis 4d).

Overall, the study consisted in ten analyses that are summarised in Fig. 6.1.

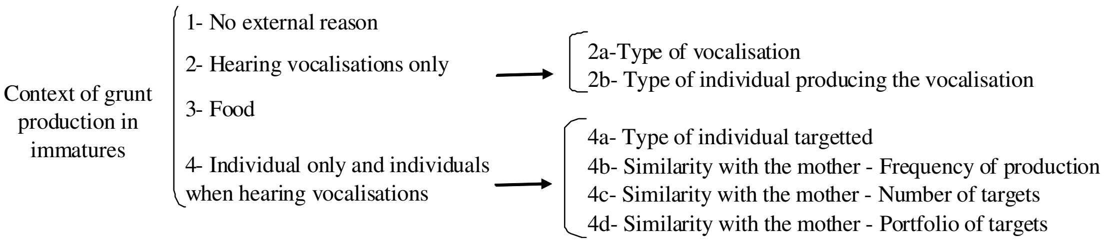


Figure 6.1: Schematic representation of the analyses performed in this chapter.

Statistical analysis

All proportional data were transformed using an arcsine of square root function and following recommendations for $N<50$, a $1/4N$ transformation was applied for proportions equal to zero and for proportions equal to one, a $1-1/4N$ transformation was applied with N=total number of occurrences (Snedecor & Cochran 1980). As not all individuals contributed to the different situations, sample sizes varied between analyses. Raw data per individuals were subsequently checked for normal distribution (Shapiro-Wilk test) and homogeneity of variances (Levene's test). If conditions were met, parametric tests were used, such as ANOVAs, Student t-tests, or Pearson correlation. The data, however, did not always meet the conditions of normal distribution and homogeneity of variances, in which case we used non-parametric Kruskal-Wallis tests for multiple unmatched comparisons with Jonckheere–Terpstra tests, Mann-Whitney tests and Spearman's correlations. The Jonckheere–Terpstra procedure tests for ordered patterns across the medians of groups compared with a Kruskal-Wallis test. If the z-score is greater than 1.65 independently of the sign, there is a significant difference between groups. The direction of the difference between groups is given by the sign of the z-value (positive for ascending medians, negative for descending medians). All tests were two-tailed with significance levels set at $\alpha=0.05$ otherwise stated. For small sample sizes, exact p-values were calculated (Mundry & Fischer 1998). Post-hoc comparisons were done using a Sidak corrected alpha set at $\alpha=1-(1-\alpha)^{1/n}$. All analyses were conducted with SPSS 17.0.

Results

Contexts of grunt-like call production

1-Grunts produced with no external reason

As noted by Plooij (1984), we observed that in the first three months of life, most grunts of chimpanzee babies are given mostly with no apparent external reason and appear to be by-products of physical effort, produced when moving on their mothers' body. As infants start to move independently such "effort grunts" become rarer, but they remain in the vocal repertoire, even in adulthood. In older individuals, grunts produced with no apparent reason do not seem to be the result of physical effort any more, as they are often produced when sitting or lying down. Overall, a significant change in the production of grunts produced with no apparent reason was observed, due to a significant decrease between babies and infants (U=6, z=-2.816, p_{exact}=0.003, Mann-Whitney test, Sidak-corrected α=0.017) and not to an overall decrease with increasing age (H(3)=12.586, p=0.006, Kruskal Wallis test, two-tailed; J=297, z=-0.848, r=-0.129, Jonckheere's test; Fig. 6.2a).

2-Grunts produced to other vocalisations

A first indicator of grunts as communication signals is when babies respond with grunts to the vocalisations of other group members. I found a significant negative relationship with age for grunts given in response to vocalisations by other group members (H(3)=9.141, p=0.027; J=250, z=-1.916, r=-0.29; Fig. 6.2b).

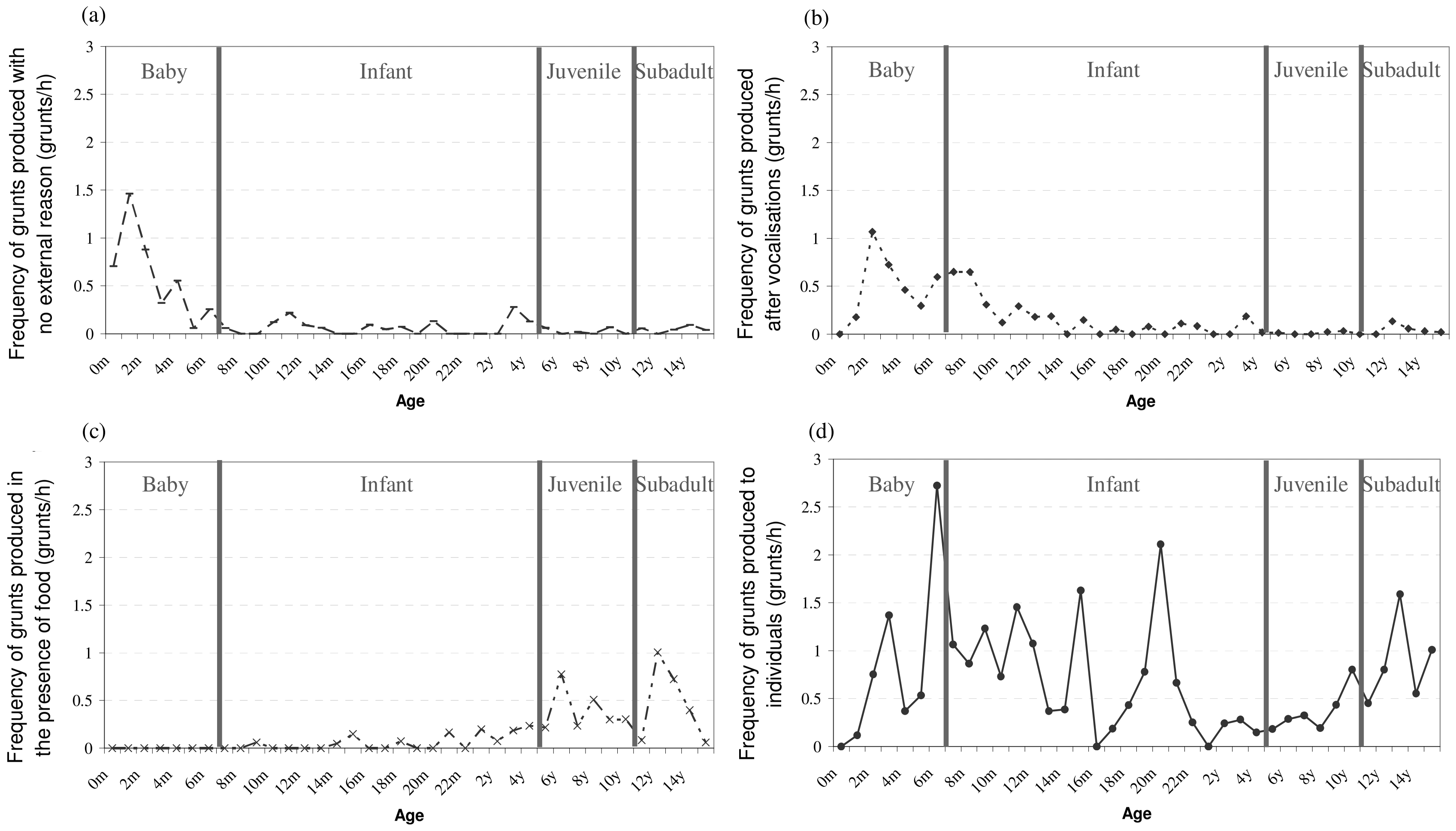


Figure 6.2: Frequency of grunts-like vocalisations produced in different contexts for (a) Grunts given when there is no apparent reason, (b) Grunts given in response to vocalisations, (c) Grunts given to food, (d) Grunts given to individuals Frequencies per hour are presented for each month of development until two year and per year of development from two to 15 years (Total number of vocalisations produced by all individuals divided by the total number of hours focal for this period).

2a- Type of vocalisation triggering grunt-like vocalisations in offspring

Not all call types were equally effective in eliciting grunts. Even in older babies and infants, when vocally-elicited grunting is first observed, individuals did not respond to any vocalisations, but mostly after the pant-grunts produced by other group members (pant-grunts preceding vocal responses: 47%±34%, N_{babies}=5; 69%±20%, $N_{infants}$=11; 82%±14%, $N_{juveniles}$=8; 87%±9%, $N_{subadults}$=9; ANOVA, F(3, 29)=5.097, p=0.006, and there was a significant linear trend F(1,29)=15.10, p=0.001 indicating that proportion of pant–grunts preceding any type of grunt like vocalisations by immatures increased with age Fig. 6.3). Sidak corrected post-hoc tests revealed significant differences between babies and juveniles (p=0.032) and between babies and subadults (p=0.006).

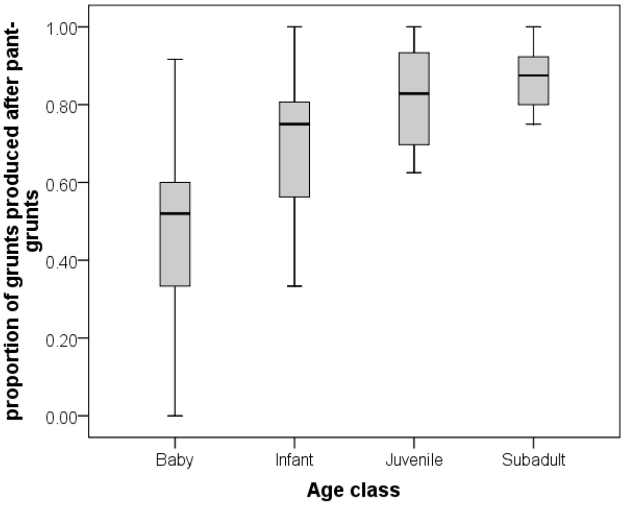
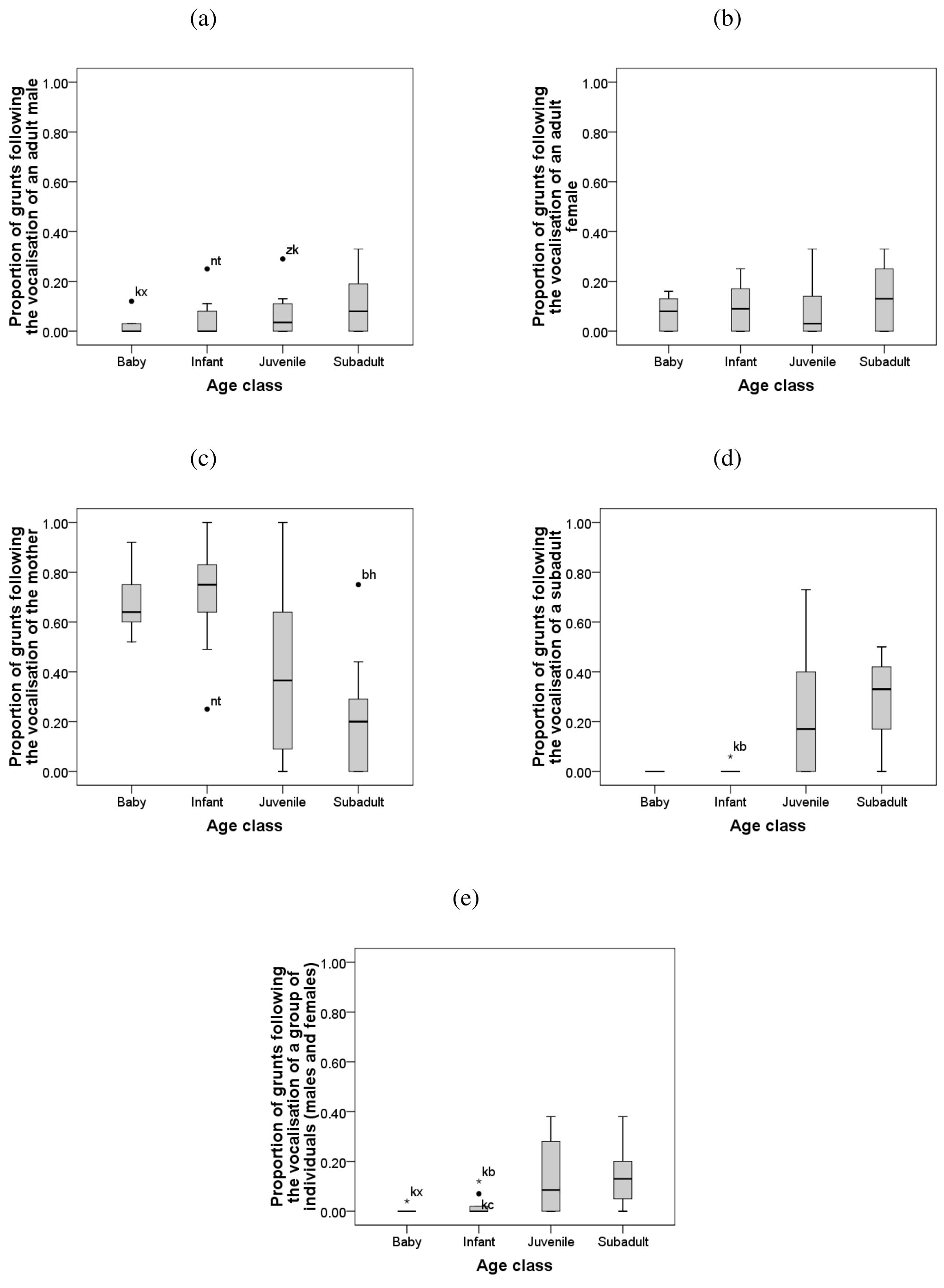


Figure 6.3: Proportion of grunts produced by developing individuals after pant-grunts produced by other individuals. N_{babies}=5, $N_{infants}$=11, $N_{juveniles}$=8, $N_{subadults}$=9. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

2b- Type of individuals producing the vocalisations that trigger grunt-like calls in offspring

The largest percentage of grunts produced by chimpanzee immatures was in response to any vocalisation by their mother until the subadult age where they begin to equally respond to other subadults (Fig. 6.4). The relative importance of mother vocalisations as triggers of offspring vocalisations significantly decreased with age ($H(3)=13.316$, $p=0.004$, Kruskal Wallis test, two-tailed; $J=91.00$, $z=-3.302$, $r=-0.584$, Jonckheere’s test) while subadults’ vocalisations as grunt triggers acquired more importance during development ($H(3)=18.047$, $p=0.0004$, Kruskal Wallis test, two-tailed; $J=312.00$, $z=4.183$, $r=0.740$, Jonckheere’s test). In contrast, adult male and female vocalisations were very ineffective as triggers of vocal behaviour with no significant changes through the age classes ($H(3)=4.574$, $p=0.206$, and $H(3)=0.707$, $p=0.872$, Kruskal Wallis test, two-tailed).


(a)

(b)

(c)

(d)

(e)

Figure 6.4: Proportion of grunts following the vocalisations produced by (a) an adult male, (b) an adult female, (c) the mother, (d) a subadult, and (e) a group of males and females. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

3-Grunts produced when encountering food

I found positive relations between age and the propensity to produce grunts to food, which constitutes one of the main contexts of grunt production in adult chimpanzees, especially males (Clark 1993; Marler 1976) However, grunts to food (the likely precursors to chimpanzee 'rough grunts') did not appear regularly until the second year of life (Fig. 6.2c) but from then on these calls occupied a significant amount of all grunts produced and significantly increased with age (H(3)=18.778, p=0.0003; J=517, z=3.986, r=0.607).

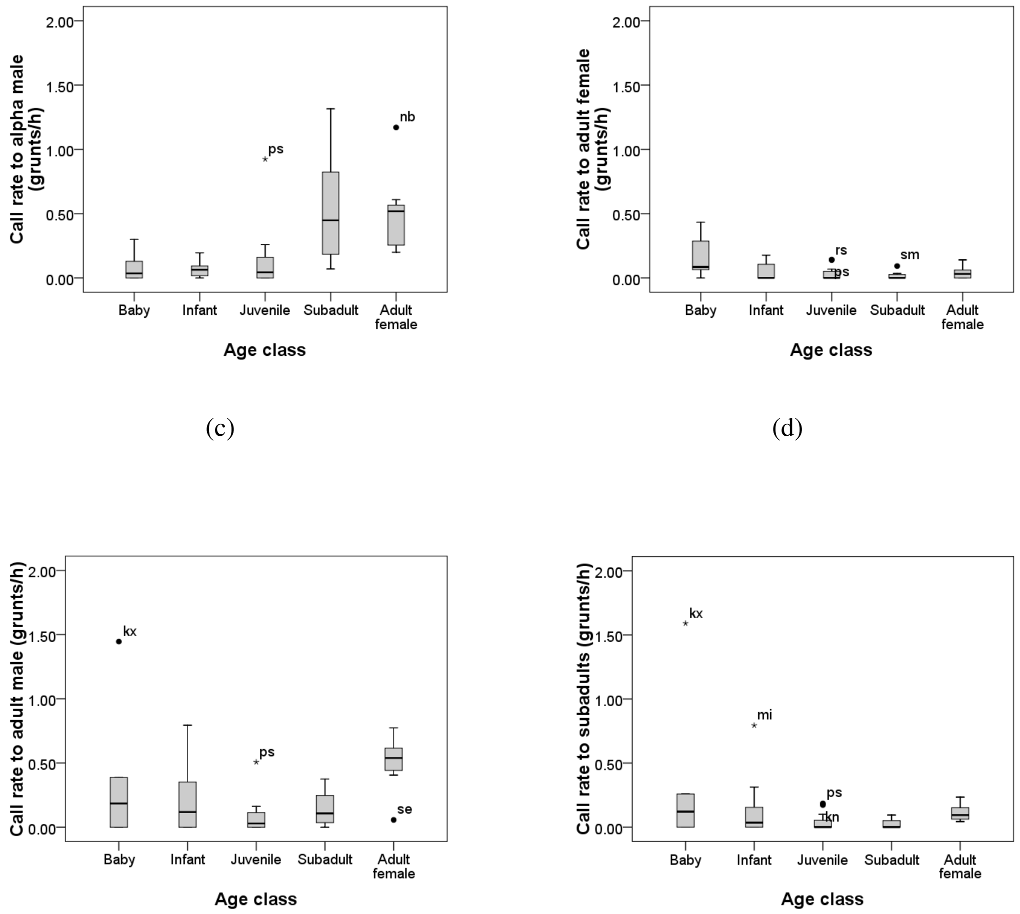
4-Grunts produced when encountering group members

Grunts to other group members ('social grunts', the likely precursors of adult 'pant-grunts') was the most common context of call production but it developed in a peculiar non-linear way (Fig.6.3d). Initially, call rates started out very high but then decreased to reach a negative peak at around five years of age. Afterwards, call rates increased again steadily until reaching adult levels. Analysis at the age class level revealed an overall significant increase (H(3)=8.664, p=0.034; J=374, z=0.842, r=0.128; Fig. 6.2d).

4a- Type of individuals targeted by offspring' social grunts

The first social grunts given by very young babies were all directed to siblings (KB to KZ and KX to KA, personal observation). The age-related changes of different group members were compared and a significant increase with age of the frequency of social grunts directed to the alpha male was observed (H(4)=28.604, p=0.00001; J=870.5, z=4.594, r=0.625, Fig. 6.5a). Although he was the individual receiving most of the pant-grunts from adult females (Chapter four), the alpha male did not appear as a relevant recipient until adolescence. In contrast, call rates to adult males remained low in all ages, despite relatively high call rates by the mothers

(H(4)=18.785, p=0.001; J=733.00, z=2.488, r=0.339, Fig. 6.5b). Call rates to adult females were uniformly low with no significant changes over time (H(4)=7.886., p=0.096; J=506.00, z=-1.100, r=-0.150, Fig. 6.5c). Call rates to subadults, finally, were also low but showed a significant variation across age (H(4)=12.919, p=0.012; J=610.5, z=0.604, r=0.0821, Fig. 6.5d).


(a)

(b)

(c)

(d)

Figure 6.5: Frequency of grunts produced by developing individuals to different classes of group members (a) Grunts produced to the alpha male, (b) Grunts produced to adult males, (c) Grunts produced to adult females and (d) Grunts produced to subadults. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

4b- Frequency of production

Females differ in their overall sociability and willingness to produce pant-grunts during social interactions with other group members (mean 1.15 calls/h; range 0.34-2.08). The pant-grunts rates of each mothers were thus compared with the social grunts rates of their offspring. Non-parametric correlations between the rates of the mothers and their offspring did not reveal any significant relationships in any age group ($N_{babies}=6$, $\sigma=-0.486$, $p=0.329$; $N_{infants}=11$, $\sigma=-0.009$, $p=0.979$; $N_{juveniles}=12$, $\sigma=0.225$, $p=0.481$; $N_{subadults}=8$, $\sigma=0.476$, $p=0.233$, Table 6.2).

4c- Number of targets

In a second analysis, I tested whether there was a relation between the number of individuals that the mothers' and their offspring's interacted with vocally by producing grunts. Significant correlations in the younger, but not older age classes were found ($N_{babies}=6$, $R=0.839$, $p=0.037$; $N_{infants}=11$, $R=0.707$, $p=0.015$; $N_{juveniles}=12$, $\sigma=0.356$, $p=0.256$; $N_{subadults}=8$, $R=0.229$, $p=0.585$, Table 6.3), indicating that mothers and offspring became increasingly different in the number of group members targeted with grunts.

Table 6.2: Social grunt rates and absolute difference between immatures and their mothers and other females per individual and per age class.

Age Class	Immature name	Mother name	Immature social grunt rate	Mother pant-grunt rate
Infant	Sk	Se	0.00	0.34
Subadult	Sm	Se	0.28	0.34
Infant	Zk	Zm	0.09	0.77
Juvenile	Zk	Zm	0.23	0.77
Juvenile	Zg	Zm	0.00	0.77
Subadult	Zg	Zm	0.45	0.77
Baby	Kx	Ky	3.47	0.85
Infant	Kx	Ky	0.96	0.85
Juvenile	Ka	Ky	0.09	0.85
Baby	Rf	Rh	0.29	0.91
Infant	Rf	Rh	0.20	0.91
Juvenile	Rm	Rh	0.00	0.91
Juvenile	Rs	Rh	0.29	0.91
Subadult	Rs	Rh	0.16	0.91
Infant	Js	Jn	0.82	1.17
Juvenile	Jt	Jn	0.21	1.17
Infant	Fa	Fl	0.47	1.21
Juvenile	Fk	Fl	0.32	1.21
Subadult	Fd	Fl	0.73	1.21
Baby	Mi	Mk	0.70	1.22
Infant	Mi	Mk	1.85	1.22
Baby	Kc	Kl	0.84	1.30
Infant	Kc	Kl	0.21	1.30
Juvenile	Km	Kl	0.04	1.30
Subadult	Bh	Kl	0.21	1.30
Baby	Kb	Kw	0.12	1.35
Infant	Kb	Kw	0.46	1.35
Juvenile	Kr	Kw	0.08	1.35
Subadult	Kz	Kw	1.83	1.35
Baby	Kh	Ku	0.38	1.42
Infant	Ks	Ku	0.17	1.42
Juvenile	Kn	Ku	0.34	1.42
Juvenile	Ks	Ku	0.19	1.42
Subadult	Kt	Ku	0.36	1.42
Infant	Nt	Nb	0.00	2.08
Juvenile	Nt	Nb	0.09	2.08
Subadult	Nr	Nb	0.82	2.08

Table 6.3: Overall number of different individuals that have been observed to receive social grunts or pant-grunts from each mother and her offspring for each age class.

Period of development	Mother-Offspring dyad	Number of targets mother	Number of targets offspring
Babies	Kl Kc	11	9
	Ku Kh	14	13
	Kw Kb	7	3
	Ky Kx	7	10
	Mk Mi	5	4
	Rh Rf	5	2
Infants	Fl Fa	4	3
	Jn Js	15	15
	Kl Kc	11	8
	Ku Ks	13	3
	Kw Kb	12	14
	Ky Kx	12	20
	Mk Mi	8	9
	Nb Nt	9	0
	Rh Rf	5	1
	Se Sk	4	0
	Zm Zk	1	0
Juveniles	Fl Fk	5	2
	Jn Jt	15	2
	Kl Km	15	0
	Ku Kn	15	6
	Ku Ks	9	2
	Kw Kr	13	2
	Ky Ka	15	2
	Nb Nt	9	1
	Rh Rm	10	0
	Rh Rs	10	1
	Zm Zg	8	0
	Zm Zk	8	1
Subadults	Fl Fd	5	3
	Kl Bh	15	3
	Ku Kt	15	1
	Kw Kz	13	9
	Nb Nr	13	5
	Rh Rs	10	0
	Se Sm	4	2
	Zm Zg	8	3

4d-Portfolio of targets

Finally, the proportion of grunts produced by every individual in each age class that corresponded to a usual target of the mother was assessed. This proportion of similarity between mothers' and offspring's portfolio of targets, significantly increased with age (proportion of similar vocalisations to mother: N_{babies}=5: 62%±26%; $N_{infants}$=11: 87%±14%; $N_{juveniles}$=7: 90%±14%; $N_{subadults}$=9: 96%±4%, ANOVA, F(3,27)=6.066, p=0.003, with a significant linear trend F(1,27)=16.652, p=0.0003 Fig. 6.7).

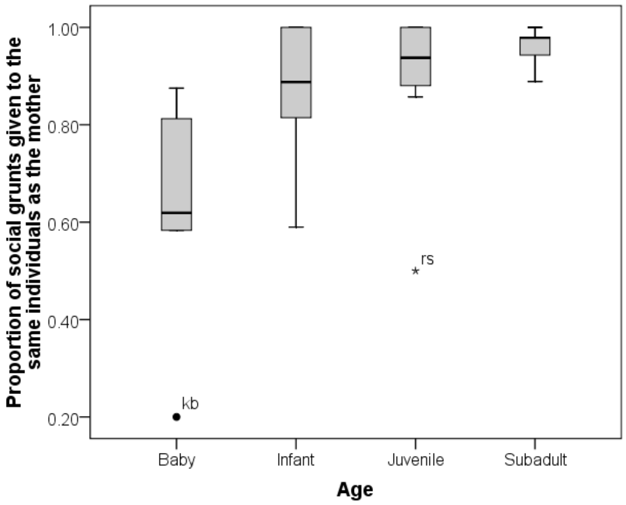


Figure 6.6: Proportion of social grunts given to the same individuals as the mother. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

Discussion

Pant-grunts are an interesting example of chimpanzee vocal behaviour because it is based on a considerable amount of social awareness (Chapter four). The calls are only given to higher-ranking group members, but call rates are determined by various social factors suggesting that personal experience underlies the production of this vocal signal. Whether this is based on observing other animals interacting with each other or whether it is based on personal experience is largely unknown.

My primary goal in this study was to document the emergence of this important social signal in free-ranging chimpanzees from the first days of life to adulthood. The second goal was to assess the potential role of the mother on the calling behaviour development of young chimpanzees.

Overall, the results report a general path of the grunt-like calls usage towards the adult pant-grunting patterns regarding the response of calls heard and individuals seen. In the following, the observed development of grunt-like vocalisations is regarded under the light of socialisation within the general behavioural development pattern of chimpanzees.

Early stages: birth to weaning

The first grunts produced by chimpanzee babies seem to be linked to moving on the mother's body, a mere by-product of physical activity (Plooij 1984). These calls are not produced in a socially targeted or voluntarily way, but when the infant is trying to reach a specific locomotor goal (changing position, reaching the mother's nipple, grasping to prevent fall, and so forth). How the transition to communicatively active signals takes place is unclear. It is interesting that older infants, who are producing socially directed grunts, often try to touch their targets or extend their bodies towards them. Following arguments that have been made for the development of grunts, this suggests that social grunts could be action-based signals that become ritualised and in a phylogenetical perspective, it is interesting to note that similar arguments have been made for the development of human grunts from early infancy (McCune et al. 1996).

Socially-directed grunting appears around two months of age in the wild (Plooij 1984) (Fig. 6.2.d), and it is about the time when other social cognitive activities such as social smiling also emerge in captivity (Tomonaga et al. 2004). These grunts are typically produced when encountering other group members and often in response to the vocal behaviour of the mother. It is often difficult to extract the exact motivation of the young baby when producing a grunt, as hearing a vocalisations and seeing an individual can act in synergy to trigger these grunt-like calls. The calling frequency in this context increases significantly over the following months until the age of about seven months. Recognition of an interest in other group members thus emerges early and develops rapidly in chimpanzees. In captivity, human-reared chimpanzees have no trouble to adapt their social grunt production to human carers (Jacobsen et al. 1932; Ladygina-Kohts et al. 1935/2002; Hayes 1951). Human infants are also sensitive to faces from birth and remain attracted to them during later development (Johnson, et al. 1991; Lewis et al. 1998) but start using grunts communicatively somewhat later than chimpanzees, at around 12 months of age. Interestingly, their peak of grunt production occurs during the second year of life at the onset of referential word production. Some authors thus argue that grunts constitute an important step toward language acquisition (McCune et al. 1996; Roug-Hellichius 1998).

A characteristic feature at this early age in chimpanzees is that although grunt production can be considerable, there are no visible patterns in selecting targets. Nearly half of all grunts are directed to adult males, but they are also given to a wide range of other individuals (Figs 6.5). As a result, there are considerable differences between mothers and their offspring in terms of which group members are addressed vocally (Fig. 6.6). My general impression was that chimpanzee babies were keen to acknowledge the presence of any group member with a grunt, with little specificity, as reported in captivity (Jacobsen et al. 1932; Ladygina-Kohts et al. 1935/2002), perhaps similar to how young vervet monkeys produce alarm calls to a wide range of events and only with experience learn to narrow call production to biologically relevant events (Seyfarth & Cheney 1986; Hauser 1989).

Why are young chimpanzees interested in interacting with other group members vocally at such an early age? In the wild, mothers can receive significant aggression from other group members after returning to the group from parturition, especially from the alpha male (observed for Ky/Kx, Ku/Kh and Kg/Kp, Table 6.1). There is also evidence that infants under the age of three years can be exposed to considerable risks of infanticide by male and female group members (Clark & Wrangham 1999; Townsend et al. 2007). One possibility is that an infant's efforts to interact with other group members could lower infanticide risk, especially if vocal infants receive less aggression compared to silent ones and would thus constitute a selective force. The fact that some recently reported cases of infanticide in chimpanzees have occurred with the offspring of newly immigrated and poorly integrated females (Townsend et al., 2007) together with the observation that less vocal mothers also have less vocal offspring (Table 6.2) supports this hypothesis.

Intermediate stages: after weaning

In chimpanzees, weaning usually coincides with the arrival of a new sibling, generally when the previous offspring is between four to six years old. Infants continue to spend much time with their mothers, but increasingly also with peers. During this long period, a key observation was that the youngsters were very reluctant to give grunts to others (Fig. 6.2d), and would only do so in special circumstances, such as when separated from the mother by a more dominant individual or when encountering an adult male in the absence of the mother (personal observation), presumably because they perceived the situation as dangerous (van Lawick-Goodall 1967). Apart from such instances, they uniformly preferred to remain silent, while their mother produced pant-grunts during encounters at normal rates. If calls were given, then they were already produced in an adult-like way, with juveniles often showing the same individual preferences as their mothers (Fig. 6.7). Hence, although these young chimpanzees possess a tool to interact and explore their social world, they made little use of it. The observations reported here suggest that the lack of use was not the result of incompetence but could be explained with simple changes in motivation that plays an important role in human infant vocal development (Locke 1993).

Later stages: Adolescence

As subadults, chimpanzees of both sexes produce social grunts that, to the human ear (Hayaki 1990; Hiraiwa-Hasegawa 1989), are acoustically indistinguishable from adult pant-grunts. The calls are now used frequently and in socially competent ways. At this stage of development, individuals are very interested in the social fabric of the group, their encounters with other group members multiply, and they become socially active members with their own independent positions within the community. The change in social behaviour coincides with physiological changes, such as visible testes growth in males and sexual swellings in females (Pusey 1980; 1983). Subadult males no longer behave in a relaxed manner around adult males but produce frenzied submissive responses, a pattern also observed at other field sites (Hayaki 1990; Pusey 1990). Perhaps this is in response to higher rates of aggression, perhaps they are simply more interested in interacting with adult males, which also increases the likelihood of obtaining an aggressive response (Hayaki 1990). Because of growing independence, although most subadult individuals overlap largely with their mothers in terms of preferred individual call targets (Fig. 6.7), they seem to differ in the frequency of production and the number of targets.

Influence of the mother

Vocal development in non-human primates, and especially apes, is a particularly poorly researched area of science. Chimpanzees are famously unable to acquire spoken language (Hayes & Hayes 1951), although they can acquire artificial communicative system based on gestures or other visual symbols (Gardner & Gardner 1969). In terms of their own vocal signals, most complexities so far have been found in how subtle acoustic modifications of basic call types are used in relatively distinct contexts, which often appear to be meaningful to receivers (barks: Crockford & Boesch 2003; screams: Slocombe et al. 2009; food grunts: Slocombe & Zuberbühler, 2005b; copulation calls: Townsend et al., 2008). How these patterns are acquired and whether social learning from the mother and other group members plays a key role is largely unknown.

Although the mother is very important before weaning we did not observe any vocal interactions involving mutual gaze between mothers and their offspring which is thought to facilitate social and communicative learning in humans (Papousek et al. 1991, Trevarthen &

Aitken 2001, Bard & Leavens, 2009). This confirms earlier observations in the wild reporting that mothers pay little attention to their babies' faces before the second month of life and more when the baby begins to discover his mother's face by touching it and during play (Plooij 1979, 1984). In captivity, face-to-face interactions are observed more often and can involve mutual gaze (Bard 1994a, 1998; Bard et al. 2005). This discrepancy might be due to the paucity of the behaviour in the wild around human observers together with the fact that constant physical contact between the mother and her young infant seems to be correlated with little mutual gaze (Bard et al. 2005). The fact that affiliative mutual gaze has been reported in rhesus macaques (Ferrari et al. 2009) and that face-to-face interaction can be extremely rare or absent in some human societies due to cultural belief (Ochs & Schieffelin, 2009) further emphasize the diversity of mother-infant interactions within and between species.

In chimpanzees, a striking behavioural change was in the juveniles' overall decrease in grunt production (Fig. 6.2d). This change took place despite the fact that the close bonds to the mothers and opportunities to interact with others remained unchanged. The prolonged period of juvenile low production of grunts lasted several years, and was succeeded by the emergence of appropriate use of signal production during adolescence (Fig. 6.2d & 6.7). This pattern of vocal development is similar to the acquisition of a social signal in vervet monkeys. Vervet monkeys produce "wrr" calls from birth in the immature context of distress but only produce them in the adult context of intergroup signalling after a temporary gap in production from three to ten months (Hauser 1989). Hauser (1989) suggested that this phenomenon could be the result of the integration of other vocalisation in the repertoire producing some interference. Another non-exclusive hypothesis could be that during this period of low production, young chimpanzees begin to understand the social organisation of their community together with the contexts in which the call is normally uttered in adults and only produce this vocalisation when they are ready to integrate the social group as an independent individual.

In conclusion, during chimpanzee childhood, socially directed grunting changes from high production frequency and with low social specificity (babies, infants) to low production frequency with high social specificity (juveniles) to high production frequency with high social specificity (subadults), relative to adult female behaviour (Figs. 6.2d & 6.6). Babies and infants resemble the vocal behaviour of their mothers in the number of individuals targeted but not in the identity of individuals targeted, suggesting that despite similar experiences, mothers and offspring assess the same social situations differently or that the calls serve different functions. We suggest that, in babies and infants, social grunting does not function as a submissive signal, but as an expression of interest in other individuals combined with intention to interact with them socially (Jacobsen et al., 1932). Judging from these findings we suggest that chimpanzee pant grunting should not be conceptualised as a simple ritualised expression of submission but also as a desire to interact with another group member who is higher ranking (Hayaki, 1990; Laporte & Zuberbühler, 2010). Producing these ritualised vocal signals help the caller to indicate her social intentions which is likely to lower the probability of misunderstanding and escalated conflict..

Chapter seven: Modification of grunt morphology over development

"En somme, l'exemple et l'éducation n'ont guère servi qu'à appeler son attention sur des sons que déjà elle ébauchait ou trouvait d'elle-même, à provoquer leur répétition ou leur achèvement, à diriger de leur côté sa préférence, à les faire émerger ou surnager dans la foule des autres sons semblables. Mais toute l'initiative lui appartient."

Hyppolite Taine, 1876 (See Appendix A for translation)

Summary

Vocal development in great apes is poorly understood both in terms of call morphology and call use. It is not clear if it is the result of social or individual learning or simple maturation. Here, I documented the vocal development of young chimpanzees belonging to 15 different families of a free-ranging group, the Sonso community of Budongo Forest, Uganda. I focused on the development of social grunts and found no direct evidence that the general calling behaviour of the offspring was socially learned from the mother. However, when producing sequences of grunts jointly with the mother, infant call sequences were more similar to their mothers' pattern of emission compared to when the sequences were extracted from different instances in which they were also calling together. The morphology (grunt duration) of the infant calls produced in these two social conditions did not differ, suggesting that infants have some control over the structure of the call sequence, but not the morphology of individual calls. I discuss these results with regards to their relevance for evolutionary theories of primate communication.

Introduction

The standard view in the development of primate vocal communication is that call production is largely innate, while call usage and comprehension is subject to ontogenetic experience (Egnor & Hauser 2004; Janik & Slater 1997, 2000; Seyfarth & Cheney 2005). In contrast, various non-primate species show various forms of vocal production learning, most notably songbirds, hummingbirds, parrots, some marine mammals, elephants and humans (Janik & Slater 1997). This apparent discontinuity in the evolutionary roots of vocal development has been taken to suggest that the mechanisms responsible for vocal learning have evolved separately in different groups (Jarvis et al. 2000).

A well-documented case for the lack of vocal learning in non-human primates has been demonstrated in squirrel monkeys (Hammerschmidt et al. 2001; Lieblich et al. 1980; Winter et al. 1973). Auditory deprived individuals produced all their species-specific call types (Winter et al. 1973). Call comparisons between two squirrel monkey subspecies (as judged by differences in their facial features) also revealed acoustic differences in their isolation call from the first week after birth (Lieblich et al. 1980), while their hybrids developing structurally intermediate isolation calls (Newman & Symmes 1982). When replicating Winter and colleagues' study (1973), Hammerschmidt and colleagues (2001) found developmental modifications in most of the vocalisations that could all be attributed to maturation. Because of these findings, the conclusion has been that genetic factors are the main mechanism guiding vocal development in this primate (Winter 1973; Hammerschmidt et al. 2001).

It is generally very difficult to decide whether acoustic changes during development are due to learning or to basic changes in growth and maturation (Hammerschmidt & Fischer 2008). During development, organ growth and hormonal changes impact on the morphology of acoustic signals, for example call amplitude and duration will depend on the size of the lungs and the amount of air pressure produced (Fitch & Hauser 1995). Providing evidence for vocal learning (in the sense that call morphology changes due to experiencing the call morphology of other individuals (Janik & Slater 1997) is very difficult, especially in natural field conditions.

In this study, my aim was to describe the natural development of chimpanzees' social grunts, beginning with the very first grunt-like utterance produced by very young chimpanzees to individuals. During adolescence and adulthood, chimpanzee social grunts are used in highly context-specific ways, i.e. in response to encountering a higher ranking group member, the so-called pant-grunts (Chapter four). Calls of urgency and distress serve a very important evolutionary function from birth, suggesting that they should not depend on learning or experience before becoming functional. In contrast, social and affiliative calls, are usually part of more complex social interactions, suggesting that callers are more likely to benefit from enhanced flexibility (Newman & Symmes 1982; Snowdon et al. 1986, 2005). Pant-grunts are interesting signals in the chimpanzees' vocal repertoire, mainly because they are directed to specific individuals and are given in a range of social contexts, suggesting that the caller's arousal cannot directly explain call production as it has been done in other studies (e.g. isolation calls in *Saimiri sciureus* (Lieblich et al. 1980) and *Callithrix jacchus* (Pistorio et al. 2006); lost calls in *Papio usrsinus* (Ey et al. 2007), or agonistic screams in *Macaca nemestrina* (Gouzoules & Gouzoules 1989a)).

Chimpanzees and bonobos are the closest living relatives of humans and yet the acquisition of their vocal repertoire remains largely unexplored. In the 1950's Hayes and Hayes (1951) home-raised the chimpanzee Viki and tried to teach her spoken English, but with very little success. Observations in the wild focussed on vocalisations used for mother-infant coordination, such as the "hoo whimper" or the "infantile scream" (van Lawick-Goodall 1967, 1968) and on grunt vocalisations as a measure of infant activity (Plooij 1984). Hiraiwa-Hasegawa (1989) reported that gestures accompanying vocal signals were given from four months of age during mothers' pant-grunts. In captivity, the production of grunts and response to them are documented for the first 18 weeks but the relationship to the mother's calling behaviour was not explored (Kojima 2001; Matsuzawa 2006).

As reviewed in the previous chapters, infant chimpanzees produce grunt-like calls and whimpers from their first week of life (Kojima 2001; Plooij 1984). Plooij (1984) discriminated between three variants of infant grunts, termed “effort grunts”, “staccato grunts” and “uh-grunts”. Staccatos and Uh-grunts are given from the first day onwards in a series of contexts, such as to a sudden sound, an object moving in the visual field, a sudden movement of the mother or to other individuals (Plooij 1984). Efforts grunts are given by a baby moving or struggling over the body of its mother. As a result of muscular contractions, air is expelled from the lungs, producing a sound. This vocalisation is not given in response to an external event, but a direct product of body movement, which has also been observed in humans (Fig. 7.1).

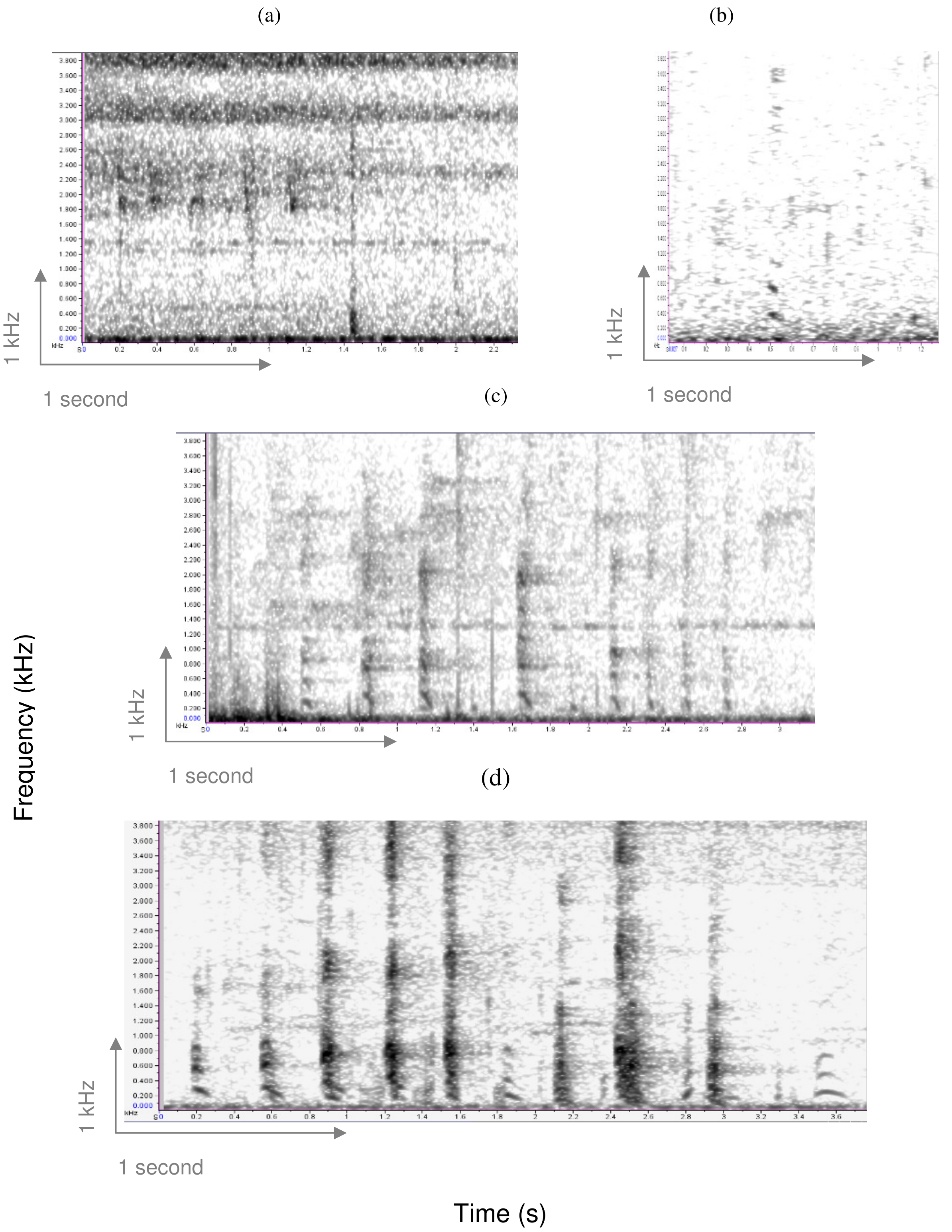


Figure 7.1.a.: Effort grunt produced by Kathy while moving on her mother when she was a month and a week old. b.: Uh-grunt/ social grunt produced by Karibu in response to the sight of her sister Karo when she was two months old .c. Staccato grunt produced by Kox in response to the sight of a juvenile female (Karo) when she was six months old. d.: Social grunt produced by James to a subadult male when he was 2 ½ years old.

Staccato sounds are short and breathy calls, produced in series, sometimes accompanied by phonations with frequency modulations. Uh-grunts (“grunts” in Kojima (2001)) are generally slightly more tonal, vowel-like sounds perceived as {u}, {o} or {a} by humans). During my study, I did not discriminate directly between the “staccato grunts” and “uh-grunts” acoustically as they were falling along a continuum and decided to describe their structure depending on their contextual use.

This chapter first goal was to describe the different types of grunts produced by infant chimpanzees in terms of their acoustic structure, especially the transition from baby socially directed grunts to subadult pant-grunts. The second goal was to understand the development of call use, which is how infant chimpanzees learn to use these grunts in a socially appropriate way and whether their mothers’ vocal behaviour played any role in this process. To this end, I considered three different levels of investigation. First, I recorded calls by babies in four different contexts: seeing another group member (visual presence), hearing another group member (auditory presence), hearing and seeing another group member (multi-modal presence) and no apparent stimulation (internal processes).

Second, I traced the changes in acoustic morphology of grunts during development in order to document their transition into adult-like pant-grunts. To explore whether the morphology of the mothers’ calls had any influence on the infant’s vocal development, I calculated the absolute difference in a number of acoustic parameters between the calls produced by mother-offspring dyads. If any kind of social learning took place at the level of call morphology, then the distance in call morphology should decrease with age in a dyad-specific way.

Third, adult-pant-grunting behaviour is based on sequences of calls and there seem to be individual differences in the sequential structure (Chapter five). A mother's pant-grunting is often contagious for her offspring especially in baby and infant age classes, suggesting these are the instances where some form of learning could take place. To this end, I considered two conditions of calling: when the mother and the offspring were calling together or when the offspring was calling alone. Values of morphological parameters were reported separately for the mother and her offspring and absolute difference between these mother and offspring values were calculated in three different conditions: (a) mother and offspring calling together considering sequences coming from the same event, (b) mother and offspring calling together considering sequences coming from different events, and (c) mother silent, but infant calling. I compared the acoustic structure of calls given by both and predicted that, if mothers had some influence over her offspring's calling, then the distance in the acoustic parameters should be smaller when calling together compared to when calling alone or when calls are extracted from different calling events.

Methods

Study Site

Data were collected during three field periods between January - April 2007, August 2007 - February 2008 and July - December 2008 in the Sonso chimpanzee community of Budongo Forest, Uganda (Reynolds 2005). At the beginning of the study, the community consisted of 78 individuals (10 males, 25 females, 8 subadult males, 5 subadult female, 13 juveniles 12 infants and 5 babies, see Chapter two).

Data collection

In total, I followed 34 infants, juveniles and subadults belonging to 15 different families (see Chapter two). Due to the slow development of chimpanzees, I used both cross-sectional and longitudinal data collection, by comparing four major periods of development and the adult age. I used calls collected during both focal animal sampling and all occurrence sampling (Altmann 1974) for which I had enough information about the context of emission and that were of sufficient quality.

As explained earlier, the study was organised around four main questions: 1- the contextual analysis in babies, 2- the development of call morphology, 3- the relation to the mother production and 4- the relation to the mother’s production during chorusing.

Context

For the analysis 1, I considered grunts that could be given in the four different contexts observed in the previous chapter: *I*: to an individual, *V*: to a vocalisation, *IV*: to an individual and a vocalisation, or *O*: to no apparent reason, which included calls given during movement (i.e. effort grunts) (Table 7.1).

Vocalisations

In total, I recorded 1798 grunt sequences produced by 34 developing individuals (0-15 years). For the acoustic analyses, I selected two call sequences for 20 individuals in the four contexts described before. I selected call sequences based on the order of recording, provided they were free from extensive background noise. Four individuals (KB, KC, KX, and MI) contributed to more than one age group. This resulted in 93 sequences for the 20 individuals, a total of 513 grunts. I was able to compare the infant vocal behaviour with the vocal behaviour of eight mothers, from whom I analysed 44 sequences containing 577 grunts. To address the question of whether infants and mothers converged on a common structure during joint calling, I was able to analyse 38 baby and infant sequences (consisting of 178 grunts) and 12 mother sequences (consisting of 87 grunts). Overall, I analysed 180 sequences, consisting of 1304 grunts (Table 7.1).

Table 7.1: Number of sequence and grunts (in brackets) produced when encountering an individual and analysed per individual per age class for each of the analyses. In italics, sequences and grunts taken from the contextual analysis and thus appearing twice ($N_{sequences}$=19, N_{grunts}=68). In this chapter, I analysed a total of 180 social grunts sequences totalising 1304 grunts.

Age class	ID Name	Context analysis 1		Development analyses 2 and 3		Chorusing analysis 4	
Baby	Kb	8	(13)	*4*	*(7)*	1	(2)
	Kc	6	(10)	*4*	*(8)*	1	(4)
	Kh	8	(22)	*4*	*(11)*	5	(13)
	Kx	8	(30)	*4*	*(20)*		
	Mi	6	(37)	*3*	*(22)*	2	(21)
	Rf			2	(7)		
Baby Total		36	(112)	21	(75)	9	(40)
Infant	Js			4	(7)	4	(16)
	Kb			4	(14)	6	(20)
	Kc			4	(13)	5	(15)
	Kx			5	(28)	10	(67)
	Mi			4	(20)	4	(20)
Infant Total				21	(82)	29	(138)
Juvenile	Fk			2	(31)		
	Jt			2	(11)		
	Ka			2	(8)		
	Km			2	(18)		
	Ps			3	(47)		
	Zd			2	(16)		
Juvenile Total				13	(131)		
Subadult	Bh			2	(11)		
	Fd			2	(15)		
	Hw			2	(26)		
	Kt			2	(23)		
	Kz			2	(29)		
	Nr			2	(28)		
	Zl			2	(18)		
Subadult Total				14	(150)		
Mother	Jn			6	(64)	2	(10)
	Kl			6	(102)	2	(14)
	Ku			6	(64)	2	(10)
	Kw			6	(40)	2	(6)
	Ky			6	(169)	2	(29)
	Mk			2	(14)	2	(18)
	Nb			6	(68)		
	Zm			6	(56)		
Mother Total				44	(577)	12	(87)
Grand Total		36	(112)	113	(1015)	50	(265)

To determine the relationship between the acoustic structure of grunt sequences and developmental stage and context, I measured a number of temporal and spectral parameters, using PRAAT 4.3.12.

For analyses 1, 2 and 3, each sequence was analysed at three different levels as detailed in Chapter three: the total sequence level, the grunt sequence level and the grunt call level.

For each sequence, I described its structure as follows: (a) the total number of grunts, (b) the total length of the call sequence (s), (c) the call rate of the sequence (number of elements per sequence), (d) the presence of other vocal signals within a sequence, mainly inhalations because other elements did not appear.

Grunt sequences contained between 1 and 25 grunts, which were analysed as follows. For each grunt, I measured: (e) grunt length (s); (f) interval length (s): duration of the inter-call interval (s); (g) minimum frequency (Hz) at call midpoint (i.e. oscillation of vocal folds); (h) peak frequency (Hz) at call midpoint (i.e. location of maximum acoustic energy); (j) melodic contour (u-, n- or w-shaped F0, following (Field 2009) (see Chapter three); (k) tonality: whether the F0 and harmonics could be seen clearly or whether call was noisy and harsh.

For each acoustic parameter I calculated the mean and standard deviation to assess variability per sequence. I then calculated the mean value for each sequence average and standard deviation per individual, so that each caller contributed with one value per parameter.

To assess the similarity between the mother and her baby or infant during chorusing (analysis 4), I used two high quality call sequences of six mothers and their babies or young infants (age range: 2-24 months) calling together or separately, a total of 38 sequences (Table 7.2). Within my dataset involving the mother and her offspring calling together, I selected the first two calling events that were free from extensive background noise and for which respective calls from the mother and her offspring could be determined with accuracy for all the calling elements within a sequence (See Appendix E for examples of sequences analysed). I restricted the analysis to baby and infant social grunts, firstly because I hypothesised that it was at this period that they would be more sensitive to their mother's production as a result of the close contact maintained.

Moreover, social grunts from older immatures are acoustically more similar to adult pant-grunts and are thus often impossible to distinguish from the mother's calls for the entire calling sequence. I compared the temporal features of the sequence, the mean grunt length, the mean interval length and the call rate per sequence. Some sequences produced by mothers contained non-grunt vocalisations (barks and inhalations), which were removed from analysis. In one case I only took data on the tonal extended grunts at the end of the mother's sequence and not the preceding panting sequence. Final sample sizes are summarised in Table 7.2. For each mother-infant pair, I calculated the difference between the mother's and her infant's measurements ($dM\text{-}I=|M-I|$ resulting in $N=76$ dM-I; Table 7.2). For each infant, I calculated the mean dM-I value and used paired comparisons.

Table 7.2: Number of calling sequences and distances between mother's and infant's values used for each individual in each situation. Generally, NdM-I=2xNcalling sequence because each infant value is tested against each mother's value.

Infant name	Infant calling alone		Infant calling after his mother during the same event		Infant calling after his mother during a different event		Grand Total	
	N calling sequence	NdM-I.	N calling sequence	NdM-I.	N calling sequence	NdM-I.	N calling sequence	NdM-I.
Js	2	4	2	2		2	4	8
Kb	3	6	2	2	2	6	7	14
Kc	3	6	2	2	1	4	6	12
Kh	2	4	2	2	1	4	5	10
Kx	3	6	2	2	5	12	10	20
Mi	2	4	2	2	2	6	6	12
Grand Total	15	30	12	12	11	34	38	76

Statistical analysis

All proportional data were transformed using an arcsine of square root function. For proportions equal to one, a 1/4N transformation was applied; for proportions equal to zero a 1-1/4N transformation was applied with N=total number of occurrences (Snedecor & Cochran 1980). Each individual contributed with its mean value per parameter for all the analyses, derived from the mean and standard deviation obtained per sequence. Data were checked for normal distribution (Shapiro-Wilk test) and homogeneity of variances (Levene's test).

1- Context-specific call morphology in babies

For the contextual analyses in babies, I used one-way related-sample ANOVAs or Friedman's ANOVAs, depending on the distribution of data for each variable. I then conducted Sidak-corrected post-hoc tests to determine which acoustic variable differed with the context and which contexts were statistically different from one another for each acoustic variable.

2- Developmental changes in call and sequence structure

For the development analyses, I first conducted a MANOVA with all variables that met the criteria for parametric tests. Multicolinearity checks were performed on these variables to see if they had a satisfactory variance inflation factor (VIF) of less than 8.00 (Slocombe & Zuberbühler 2007). A value superior to this limit reflects that the predictors have strong linear relationships that might affect the model (Field 2009). I then used a Discriminant Function Analysis (DFA) to assess how the variables could discriminate between the five age classes. I also conducted one way ANOVAs and Kruskal-Wallis tests for non-related samples and the Sidak-corrected post-hoc tests associated to determine which variables varied with age and more specifically whether they were going towards the adult model and at what age they stop being significantly different from the adult females.

3- Similarity within a mother-infant dyad

I first determined individual differences between females with Kruskal-Wallis tests. I then conducted Wilcoxon matched-pair tests to evaluate whether the absolute difference in each of the parameters was closer to the vocal production of their own mother or to other females.

4- Temporal matching between mothers and offspring during chorusing

Using the same method of the absolute difference, I assessed the influence of the mother on her baby or infant when calling together or not.

Not all individuals contributed equally to the different situations, so that sample sizes varied between analyses. All tests were two-tailed with significance levels set at $\alpha=0.05$. For small sample sizes, I calculated exact p-values (Mundry & Fischer 1998). All analyses were conducted with SPSS 17.0.

Results

1- Context-specific call morphology in babies

Because the grunt sequences produced by babies often contain very few grunts, and no other elements than grunts, some parameters could not be analysed or were redundant. Using Friedman's ANOVAs to explore the role of context (no apparent reasons, encountering a group member, encountering a group member with vocalisations, hearing vocalisations), I found significant effects in the grunt rate per sequence ($N_{infants}$=5; $\chi^2(3)$=8.265; $p_{exact=}$0.030), the duration of individual grunts ($N_{infants}$=5; $\chi^2(3)$=8.265; $p_{exact=}$0.030) and the proportion of n-shaped elements ($N_{infants}$=5; $\chi^2(3)$=7.596; $p_{exact=}$0.043); (Table 7.3 and Fig. 7.2, 7.3, 7.4), but posthoc Wilcoxon tests (with Sidak corrected alpha, α =0.0085) did not reveal any significant differences between contexts.

Table 7.3: Statistical output of the comparisons between the acoustic measurements of the grunt produced in the four different contexts of production in the baby age class. Because the data were neither normally distributed nor had equal variances, the non-parametric Friedman's ANOVAs were used. Bold: Significant at α<0.05, Italics: Trend at 0.1<α<0.05.

Level of analysis	Parameter	Test	Value	Sig. (2tailed) exact	Figure
Total sequence	Number of elements		n/a	n/a	
	Total length	Friedman's ANOVA	6.188	.104	2a
	Rate	**Friedman's ANOVA**	**8.265**	**.030**	**2b**
	Number of bouts	Friedman's ANOVA	2.833	.667	2c
	Proportion of grunts		n/a	n/a	
	Proportion of pants		n/a	n/a	
	Proportion of inhalations		n/a	n/a	
Grunt sequence	Number of grunts	Friedman's ANOVA	6.070	.105	3a
	Proportion of tonal grunts	Friedman's ANOVA	2.467	.522	3b
	Proportion of n-shaped grunts	**Friedman's ANOVA**	**7.596**	**.043**	**3c**
	Proportion of u-shaped grunts	Friedman's ANOVA	4.909	.184	3d
	Proportion of w-shaped grunts	Friedman's ANOVA	3.677	.333	3e
Grunt element	**Mean grunt length**	**Friedman's ANOVA**	**8.265**	**.030**	**4a**
	Standard deviation of the grunt length		n/a	n/a	
	Mean intercall length		n/a	n/a	
	Standard deviation of the intercall length		n/a	n/a	
	Mean peak frequency	Friedman's ANOVA	2.520	.521	4b
	Standard deviation of the peak frequency		n/a	n/a	
	Mean minimum frequency	Friedman's ANOVA	4.920	.210	4c
	Standard deviation of the minimum frequency		n/a	n/a	

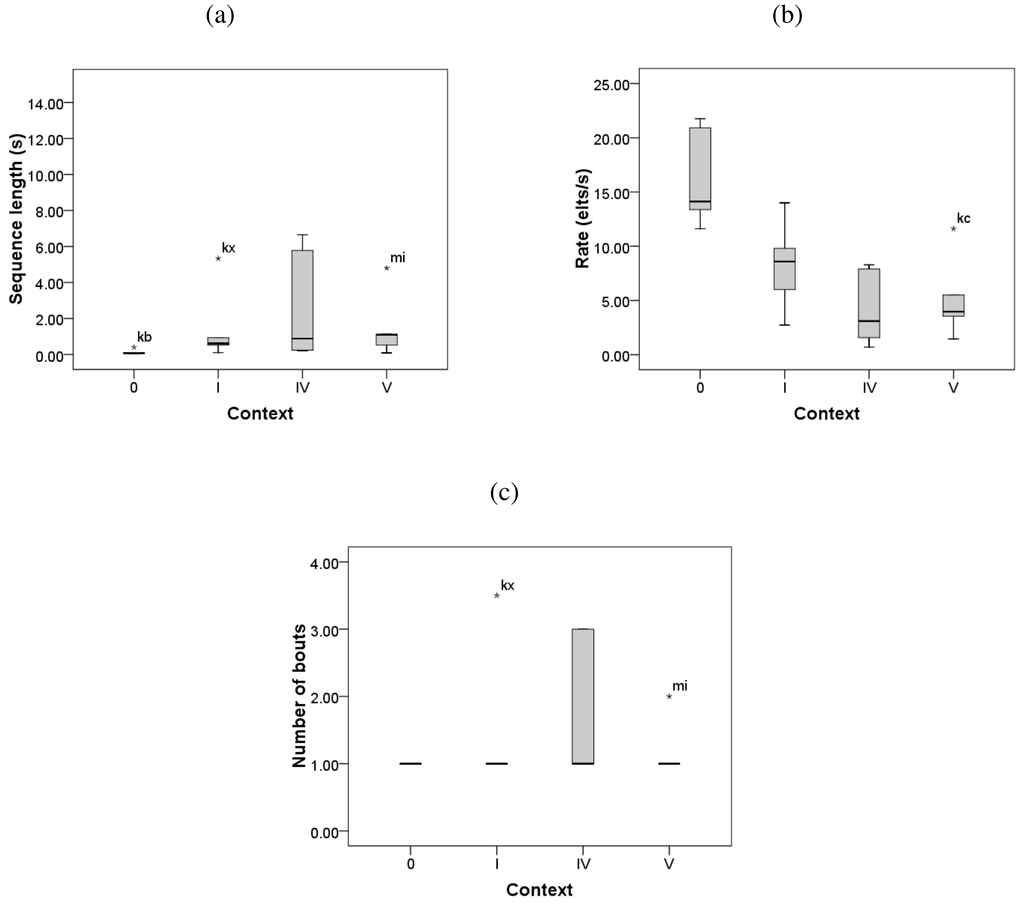


Figure 7.2: Boxplots representing the values for different acoustic parameters for each context at the phrase level (N=5 individuals) 0: no apparent reason; I: individuals; IV Individuals & Vocalisations; V: Vocalisations: (a) total length of a sequence, (b) sequence rate, (c) number of bouts in a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

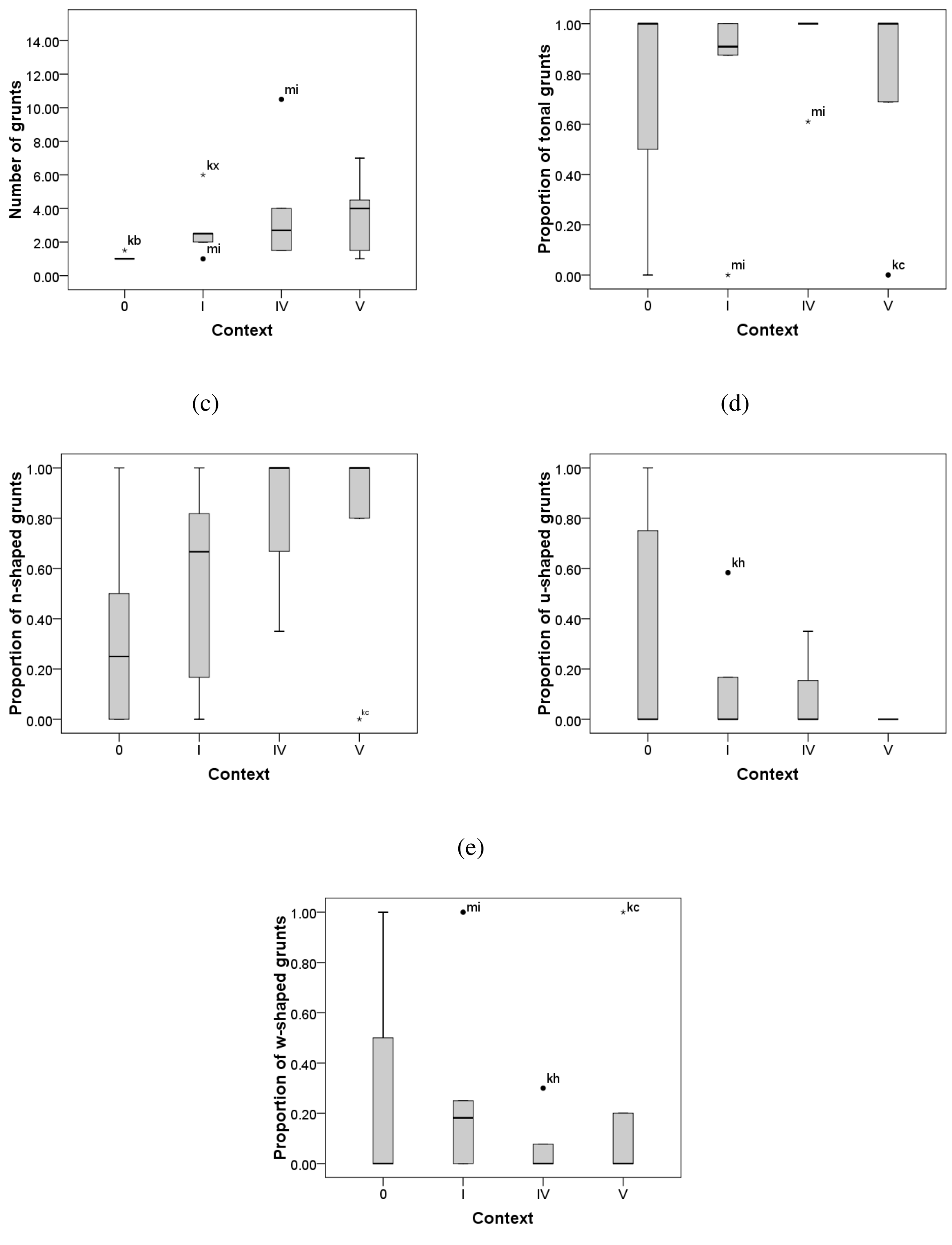
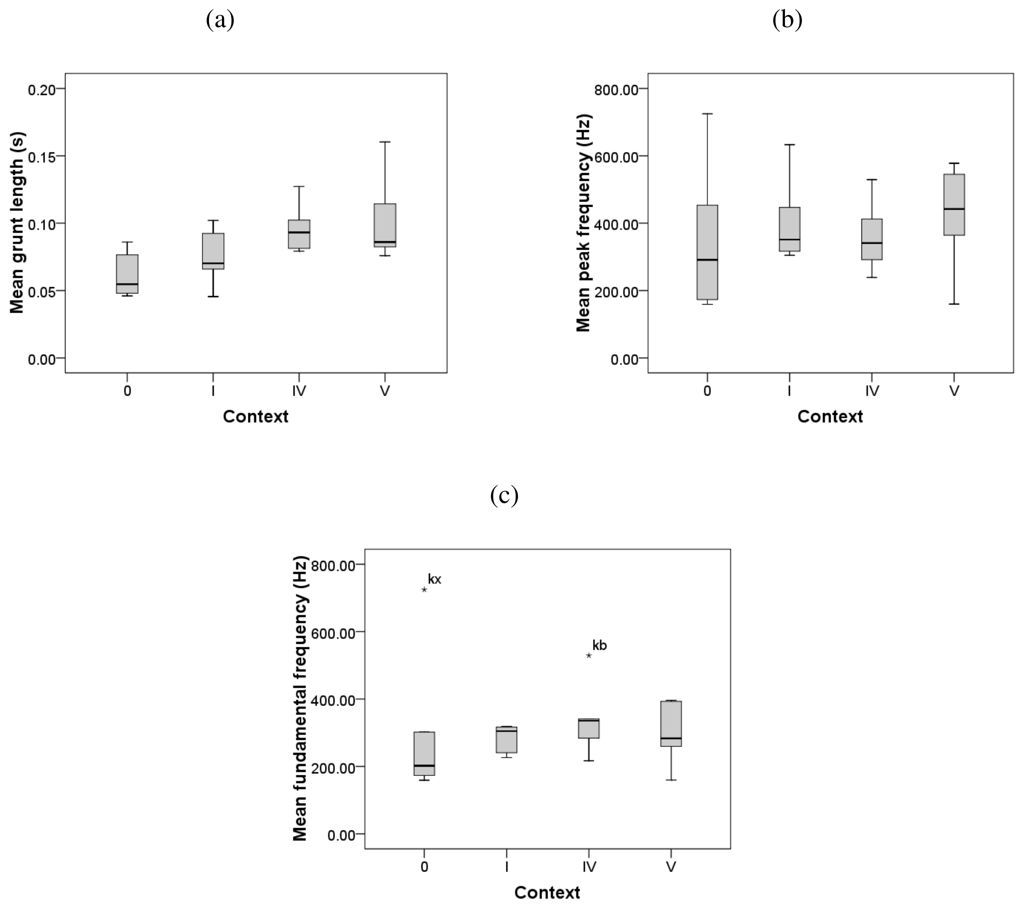

(a) (b) (c) (d) (e)

Figure 7.3: Boxplots representing the values for different acoustic parameters for each context at the grunt sequence level (N=5 individuals) 0: no apparent reason; I: individuals; IV Individuals & Vocalisations; V: Vocalisations: (a) total number of grunts within a sequence, (b) proportion of tonal grunts within a sequence, (c) proportion of n-shaped grunts within a sequence, (d) proportion of u-shaped grunts within a sequence, (e) proportion of w-shaped grunts within a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.


(a)

(b)

(c)

Figure 7.4: Boxplots representing the values for different acoustic parameters for each context at the grunt element level (N=5 individuals) 0: no apparent reason; I: individuals; IV Individuals & Vocalisations; V: Vocalisations: (a) mean grunt length, (b) mean peak frequency, (c) mean minimum frequency. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

2- Developmental changes in call and sequence structure

Next I described the developmental changes in the different acoustic parameters of social grunts in the two contexts of seeing someone (with or without hearing a vocalisation). For this analysis I considered all normally distributed acoustic variables with equal variances across the different age classes and multicolinearity checks were performed on these variables to see if they had a satisfactory variance inflation factor (VIF) of less than 8.00 (Slocombe & Zuberbühler 2007). The following N=8 variables fulfilled the criteria: (1) total length of the sequence, (2) proportion of grunts within a sequence, (3) proportion of tonal grunts, (4) proportion of u-shaped grunts, (5) mean grunt length, (6) mean peak frequency, (7) standard deviation of the peak frequency, and (8) standard deviation of the minimum frequency. A MANOVA showed that age significantly affected the acoustic structure of social grunts (F(32,92)=3.088, p=0.00001), while a discriminant function analysis based on these eight variables revealed that they explained a significant amount of variation across ages (Wilk's lambda Λ=0.012, $\chi^2(32)=108.490$, p=0.001; Fig. 7.5). Classification was possible with a high 87.5% accuracy (and cross-validated with the leave-one-out method at 68.8% of accuracy (22/32), Binomial test, p=0.05). Errors mostly occurred between the subadult and the adult age (Table 7.4).

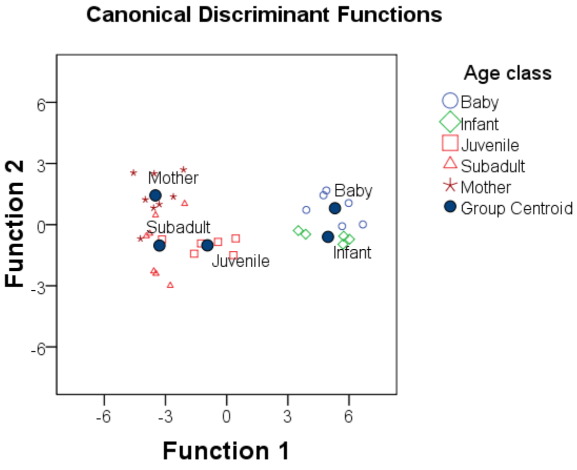


Figure 7.5: Distribution of discriminant scores along the two canonical discriminant functions established to discriminate age-related social grunts (Eigen values; Function 1=17.462, Function 2=1.322). Black squares represent group centroids.

Table 7.4: Confusion matrix for discriminant function classification of calls based on age.

Actual Age class	Predicted Age class					Total	
	Baby	Infant	Juvenile	Subadult	Mother		
Baby	6	0	0	0	0	6	100%
Infant	0	5	0	0	0	5	100%
Juvenile	0	0	5	1	0	6	83%
Subadult	0	0	0	5	2	7	71%
Mother	0	0	0	1	7	8	88%

In a subsequent analysis I investigated each acoustic variable separately, using one-ways ANOVAs and Kruskal-Wallis tests. Significant effects were found at all three levels of analyses (total sequence (Fig. 7.6), grunt sequence (Fig. 7.7) and grunt element (Fig. 7.8). I found significant age related differences for the mean number of elements in the total sequence (Kruskal-Wallis ($\chi^2(4)=21.073$, $p<0.0001$), the total duration of the sequence (ANOVA, $F(4)=6.974$, $p=0.001$) and the proportion of grunted elements within a sequence (ANOVA, $F(4)=2.903$, $p=0.04$). Significant age-related effects were also found at the grunt sequence level (Table 7.5) and at with individual grunt elements (mean grunt duration: ANOVA, $F(4)=6.208$, $p=0.001$), and standard deviation of the grunt duration (ANOVA, $F(4)=10.197$, $p=0.037$), the standard deviation of the peak frequency within a sequence (ANOVA, $F(4)=4.767$, $p=0.005$) and the mean minimum frequency (Kruskal-Wallis, $\chi^2(4)=24.353$, $p=0.00007$).

Table 7.5: Statistical output of the comparisons of social grunts acoustic parameters during development from babies to adults. Bold: Significant at α<0.05, Italics: Trend at 0.1<α<0.05.

Level of analysis	Parameter	Test	Value	Sig.(2tailed) exact	Figure
Total sequence	**Number of elements**	**Kruskal Wallis**	**21.073**	**.000**	**6a**
	Total length	**ANOVA**	**6.974**	**.001**	**6b**
	Rate	Kruskal Wallis	4.892	.299	6c
	Number of bouts	Kruskal Wallis	6.229	.183	6d
	Proportion of grunts	**ANOVA**	**2.903**	**.040**	**6e**
	Proportion of pants		n/a	n/a	
	Proportion of inhalations		n/a	n/a	
Grunt sequence	**Number of grunts**	**Kruskal Wallis**	**18.472**	**.001**	**7a**
	Proportion of tonal grunts	**ANOVA**	**54.833**	**.000**	**7b**
	Proportion of n-shaped grunts	**Kruskal Wallis**	**11.671**	**.020**	**7c**
	Proportion of u-shaped grunts	**ANOVA**	**4.947**	**.004**	**7d**
	Proportion of w-shaped grunts	**Kruskal Wallis**	**16.518**	**.002**	**7e**
Grunt element	**Mean grunt length**	**ANOVA**	**6.208**	**.001**	**8a**
	Standard deviation of the grunt length	**Kruskal Wallis**	**10.197**	**.037**	**8b**
	Mean intercall length	Kruskal Wallis	6.139	.189	8c
	Standard deviation of the intercall length	Kruskal Wallis	2.243	.691	8d
	Mean peak frequency	ANOVA	.915	.470	8e
	Standard deviation of the peak frequency	**ANOVA**	**4.767**	**.005**	**8f**
	Mean minimum frequency	**Kruskal Wallis**	**24.353**	**.000**	**8g**
	Standard deviation of the minimum frequency	ANOVA	.809	.531	8h

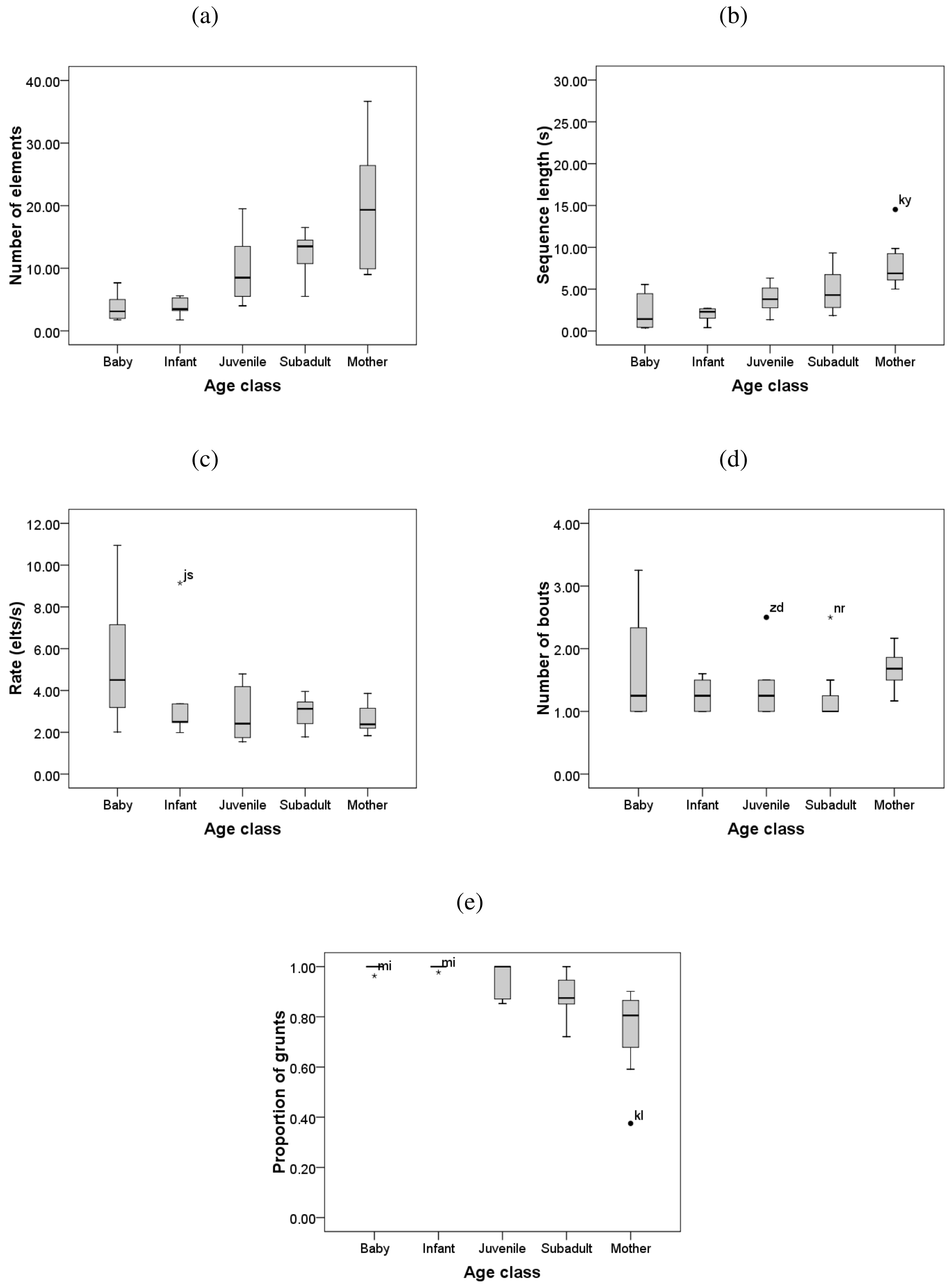


Figure 7.6: Mean values for each age class at the phrase level: Baby, Infant, Juvenile Subadult and Mother: (a) total number of elements within a sequence (grunts and inhalations), (b) total length of a sequence, (c) sequence rate, (d) number of bouts in a sequence, (e) proportion of grunts within a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

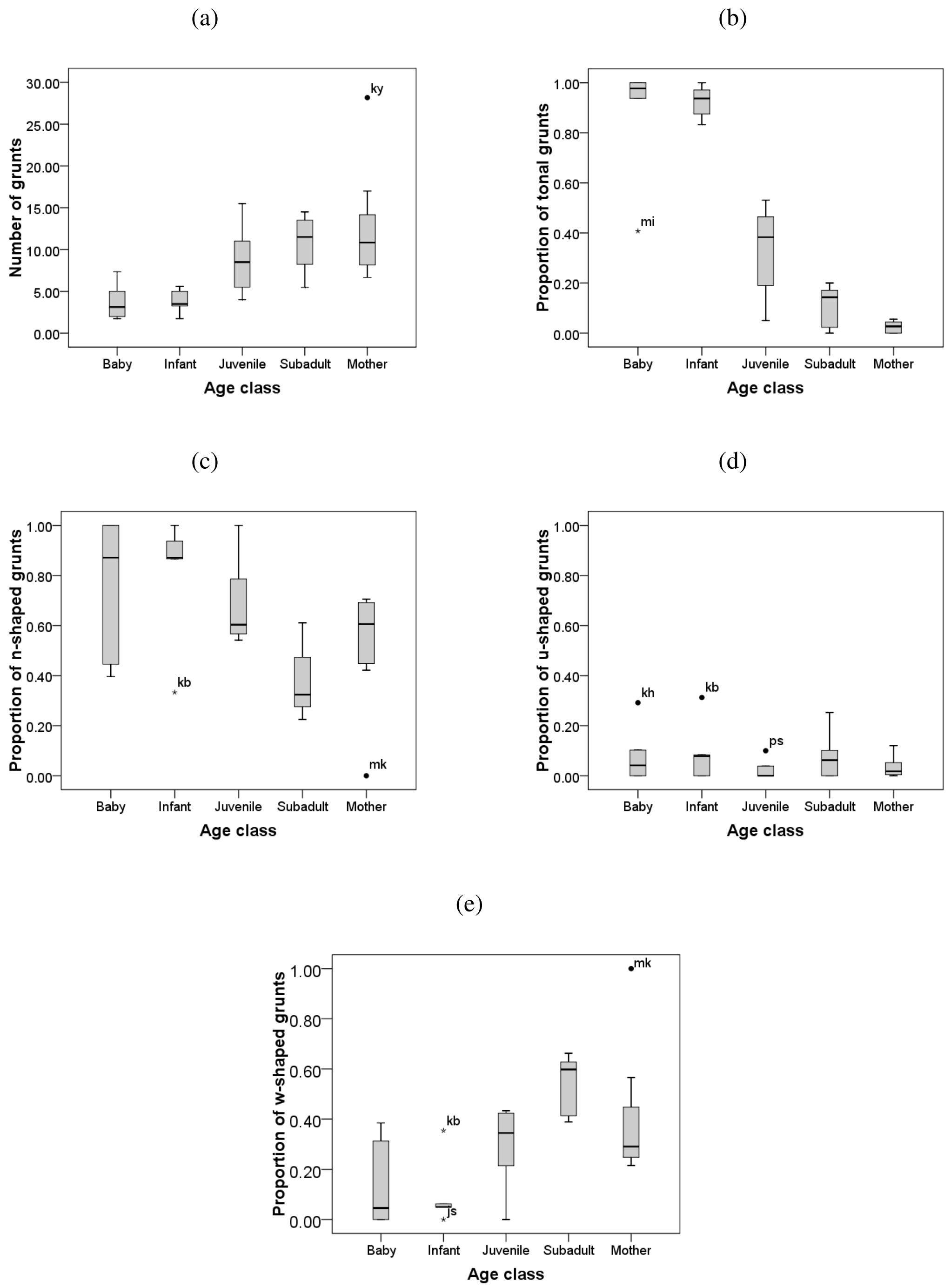


Figure 7.7: Mean and standard deviations for each age class at the grunt sequence level: (a) total number of grunts within a sequence, (b) proportion of tonal grunts within a sequence, (c) proportion of n-shaped grunts within a sequence, (d) proportion of u-shaped grunts within a sequence, (e) proportion of w-shaped grunts within a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

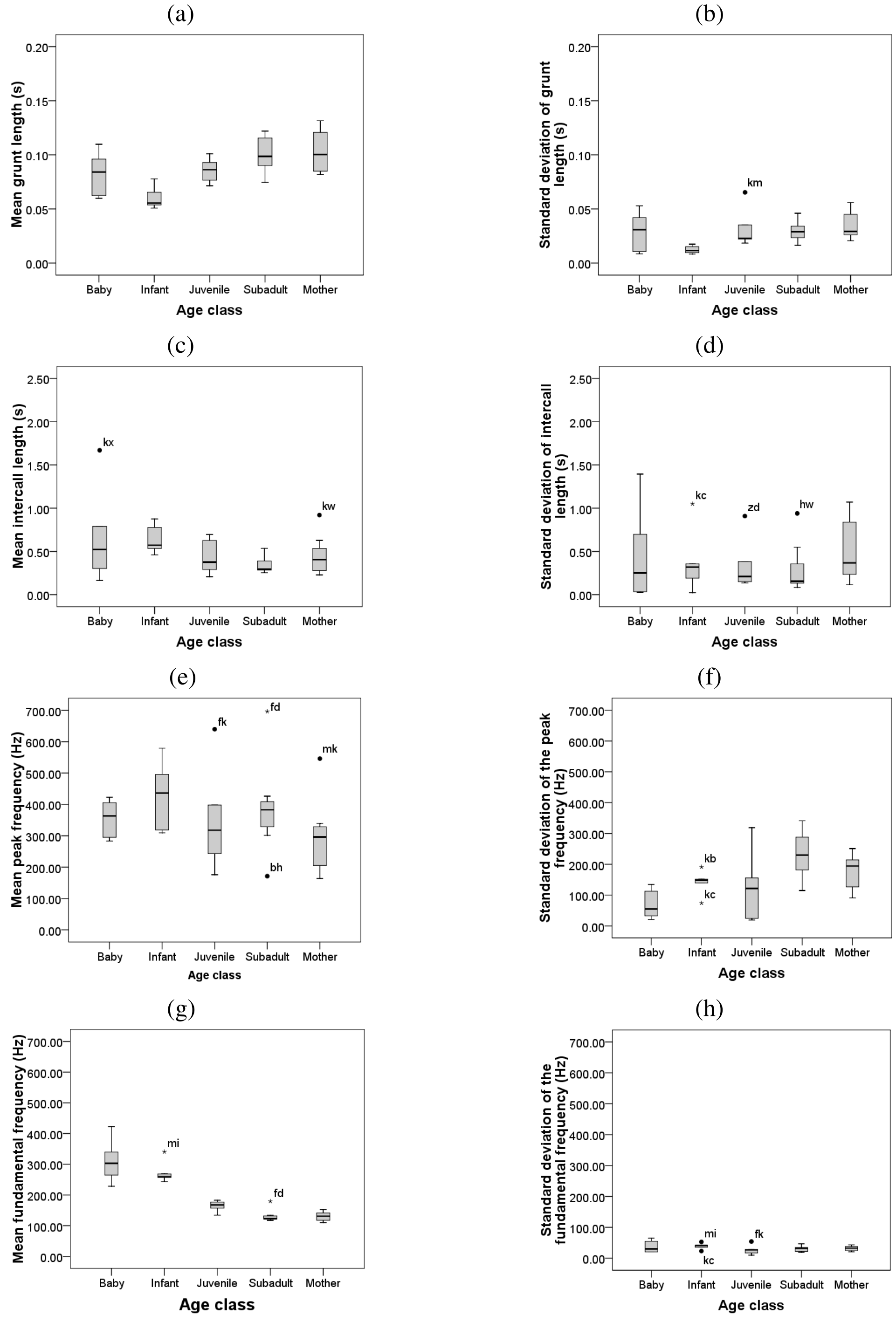


Figure 7.8: Mean and standard deviations for each age class at the grunt element level: (a) mean grunt length, (b) standard deviation of the grunt length, (c) mean interval length, (d) mean peak frequency, (e) standard deviation of the peak frequency, (f) mean minimum frequency, (g) standard deviation of the minimum frequency. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

To assess the developmental progression towards the adult model, I compared the acoustic structure of the offspring's social grunts with acoustic structure of the mothers' pant-grunts for each age class, using a Sidak corrected alpha set at α=0.013 (unmatched comparisons). There was a trend towards increased similarity with increasing age, but for some parameters, similarities already occurred at a very early age, while others were more reluctant to convergence (Table 7.6).

Table 7.6: Post-hoc tests realised after the parametric ANOVA and after the non-parametric Kruskal-Wallis test (t-tests and Mann-Whitney U tests significant when p<Sidak corrected alpha, α =0.013, white cells). Grey cells represent non-significant differences with the mother.

	Mother-Baby		Mother-Infant		Mother-Juvenile		Mother-Subadult	
	Test	p	Test	p	Test	p	Test	P
Total length	t(12)=-3.861	0.002	t(11)=-4.247	0.001	t(12)=-2.945	0.012	t(13)=-1.988	0.068
Proportion of grunts in sequence	t(12)=1.832	0.92	t(11)=2.266	0.045	t(12)=3.146	0.008	t(13)=1.624	0.128
Mean number of grunts	U(12)=2	0.003	U(11)=0.00	0.002	U(12)=14.5	0.241	U(13)=28	1
Mean grunt length	t(12)=-1.951	0.075	t(11)=-4.411	0.001	t(12)=-1.954	0.74	t(13)=-0.233	0.819
Standard deviation of the grunt length	U(12)=20	0.662	U(11)=0.00	0.002	U(12)=18	0.491	U(13)=23	0.613
Standard deviation of the peak frequency	t(12)=-3.886	0.002	t(11)=-1.218	0.249	t(12)=-1.118	0.285	t(13)=1.600	0.134
Mean minimum frequency	U=0.00	0.001	U(11)=0.00	0.002	U(12)=4	0.008	U(13)=27	0.955
Proportion of tonal elements	t(12)=12.966	2,00E-08	t(11)=18.846	1,00E-09	t(12)=4.454	0.001	t(13)=1.411	0.182
Proportion of n-shaped grunts	U(12)=13	0.181	U(11)=7	0.065	U(12)=14	0.228	U(13)=14	0.121
Proportion of u-shaped grunts	t(12)=3.625	0.003	t(11)=3.179	0.009	t(12)=-0.144	0.888	t(13)=0.872	0.399
Proportion of w-shaped grunts	U(12)=9	0.059	U(11)=6	0.045	U(12)=14	1	U(13)=10	0.04

3- Similarity within mother-offspring dyads

Adult pant-grunts differ individually (Chapter four). I was able to replicate this effect in this sample of mothers, who differed significantly in the number of call elements (Kruskal-Wallis $\chi^2(6)=12.849$, $p=0.045$), mean grunt length ($\chi^2(6)=16.165$, $p=0.013$) and minimum frequency ($\chi^2(6)=16.659$, $p=0.011$).

To test whether offspring ranked closer to their own mothers than to other females in for all the parameters considered above, I first calculated the absolute difference between the mother and her offspring for each variable and compared this with the mean difference of the offspring and all other females. Because of small sample size in mother-juvenile and mother-subadult dyads (N=3 and N=4 respectively) due to deaths or disappearances, I could not evaluate each age class separately. Over all age classes (N=17 immatures), most parameters did not present a difference between mother-offspring dyads absolute difference and other-female-offspring dyads absolute difference. Mother-offspring distance was significantly smaller than the distance of immatures with other females in the proportion of grunts, the proportion of tonal grunts, and the proportion of n-shaped grunts and w-shaped grunts while it was significantly higher for u-shaped grunts (Wilcoxon matched-pairs analyses, Table 7.7 and Fig. 7.9, 7.10, 7.11).

Table 7.7: Paired sample statistics for the absolute difference between Mother-Offspring values and Other female-Offspring values. Bold: Significant at α<0.05, Italics: Trend at 0.1<α<0.05.

Level of analysis	Parameter	Test	Value	Sig.(2tailed) exact	Figure
Total sequence	Number of elements	Wilcoxon	-1.306	.192	9a
	Total length	Wilcoxon	-.356	.722	9b
	Rate	Wilcoxon	-.047	.962	9c
	Number of bouts	Wilcoxon	-1.637	.102	9d
	Proportion of grunts	**T-test**	**-6.014**	**.000**	**9e**
	Proportion of pants	n/a	n/a		
	Proportion of inhalations	n/a	n/a		
Grunt sequence	Number of grunts	Wilcoxon	-.355	.722	10a
	Proportion of tonal grunts	**Wilcoxon**	**-3.153**	**.002**	**10b**
	Proportion of n-shaped grunts	**T-test**	**-5.323**	**.000**	**10c**
	Proportion of u-shaped grunts	**Wilcoxon**	**-2.018**	**.044**	**10d**
	Proportion of w-shaped grunts	**T-test**	**-6.682**	**.000**	**10e**
Grunt element	Mean grunt length	Wilcoxon	-1.586	.113	11a
	Standard deviation of the grunt length	Wilcoxon	-.521	.602	11b
	Mean intercall length	Wilcoxon	-.260	.795	11c
	Standard deviation of the intercall length	Wilcoxon	-.402	.687	11d
	Mean peak frequency	Wilcoxon	-.071	.943	11e
	Standard deviation of the peak frequency	Wilcoxon	-.686	.492	11f
	Mean minimum frequency	T-test	.431	.672	11g
	Standard deviation of the minimum frequency	Wilcoxon	-1.633	.102	11h

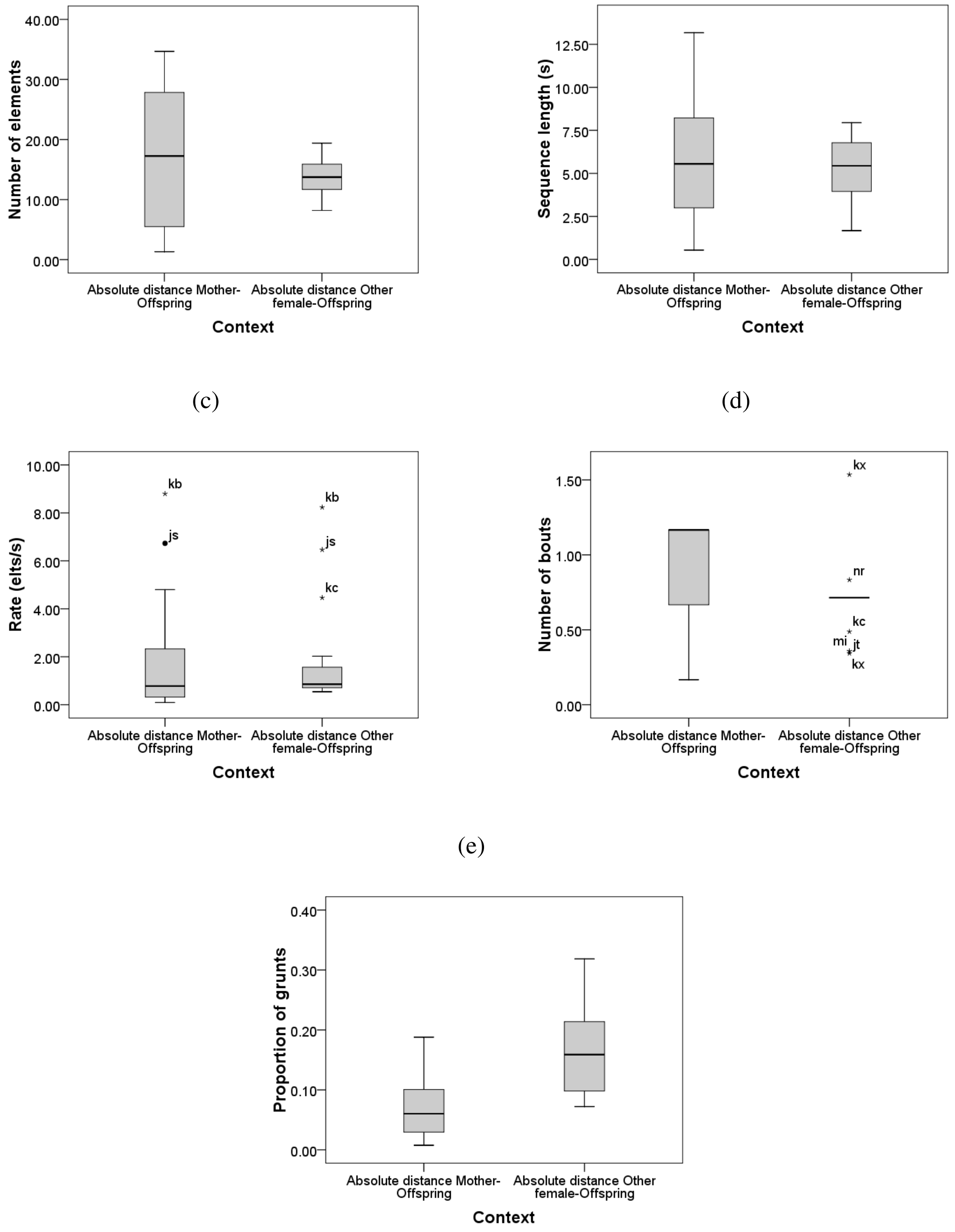

(a) (b) (c) (d) (e)

Figure 7.9: Absolute difference between the Mother –Offspring values and the Other female-Offspring values at the phrase level: Baby, Infant, Juvenile Subadult and Mother: (a) total number of elements within a sequence (grunts and inhalations), (b) total length of a sequence, (c) sequence rate, (d) number of bouts in a sequence, (e) proportion of grunts within a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

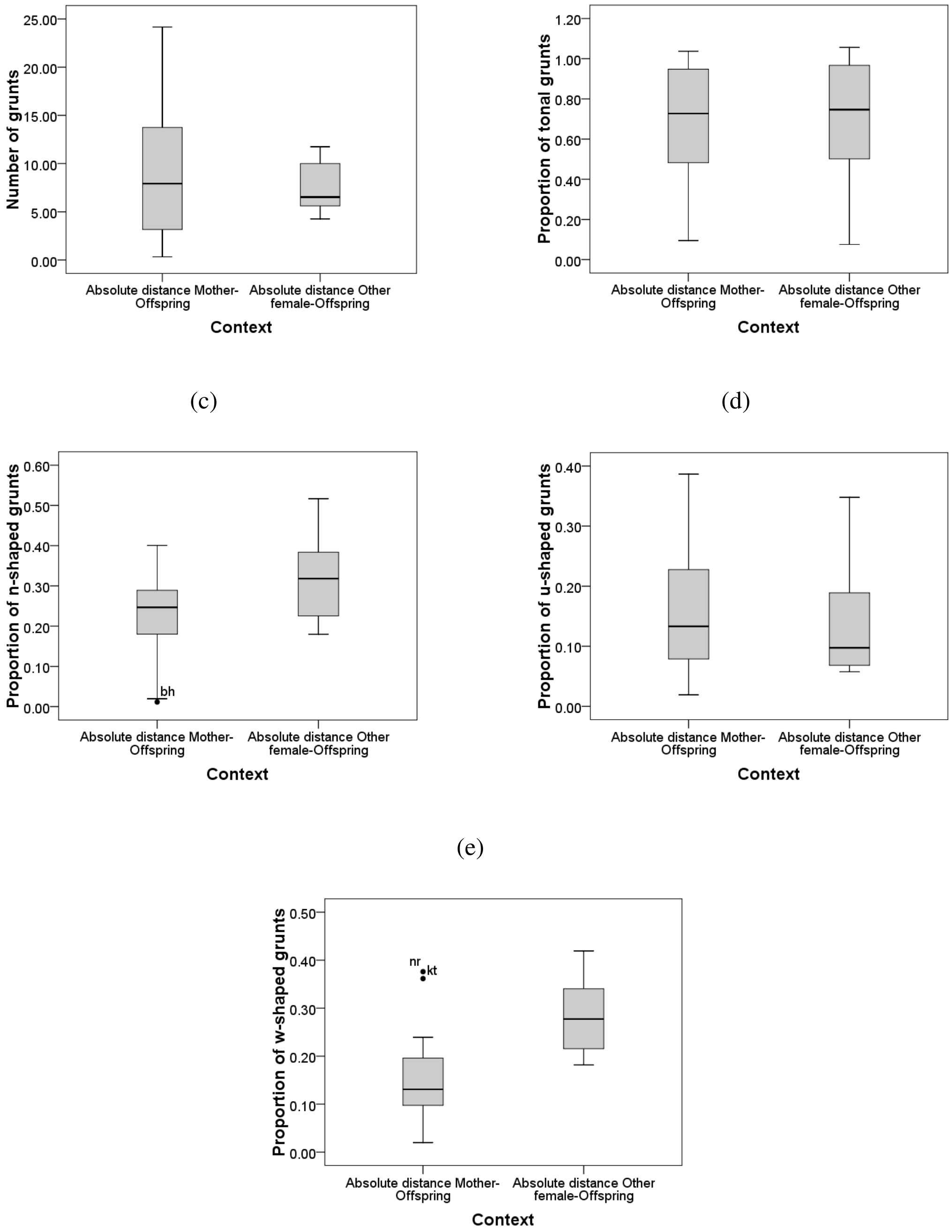

(a) (b) (c) (d) (e)

Figure 7.10: Absolute difference between the Mother –Offspring values and the Other female-Offspring values at the grunt sequence level: (a) total number of grunts within a sequence, (b) proportion of tonal grunts within a sequence, (c) proportion of n-shaped grunts within a sequence, (d) proportion of u-shaped grunts within a sequence, (e) proportion of w-shaped grunts within a sequence. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

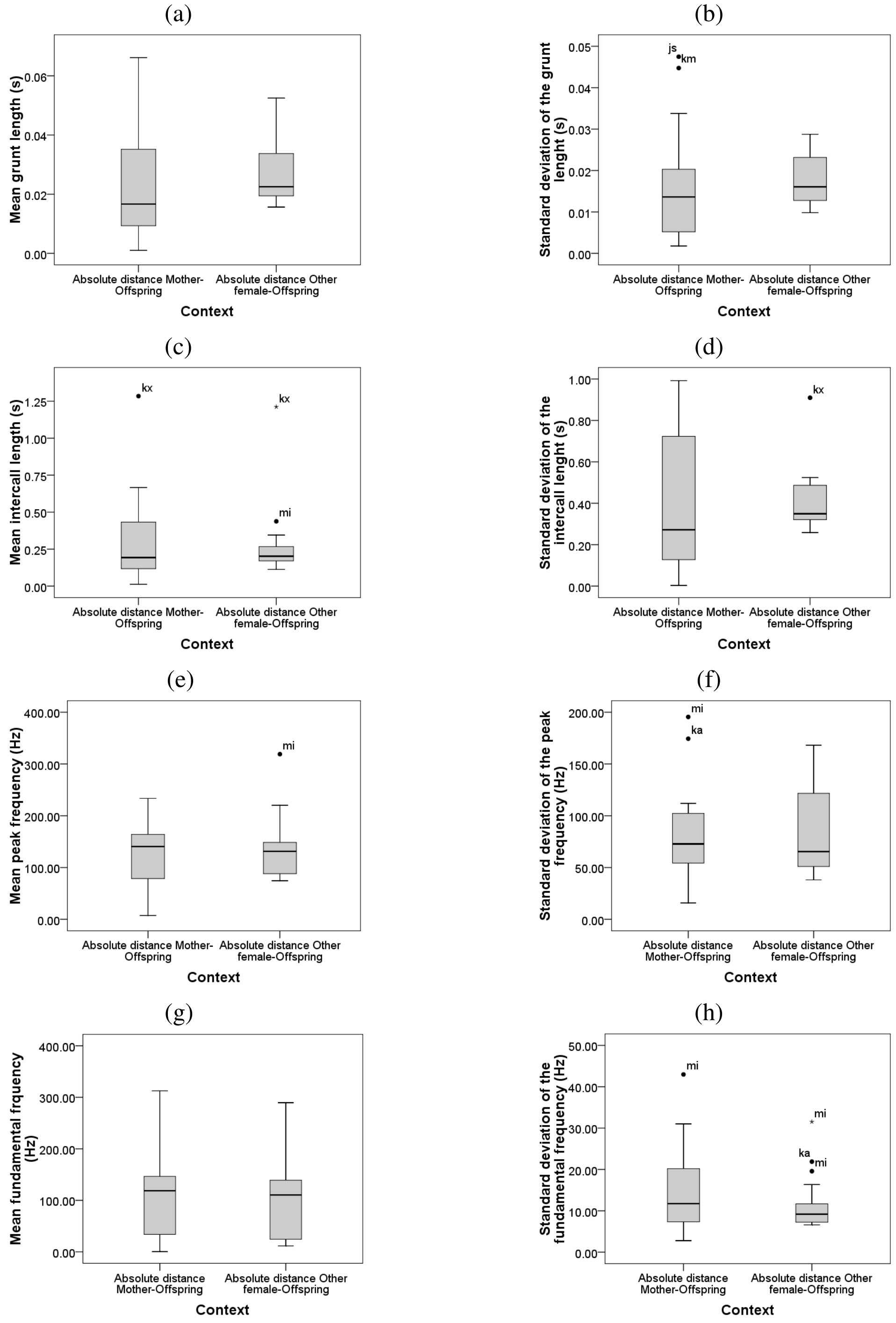
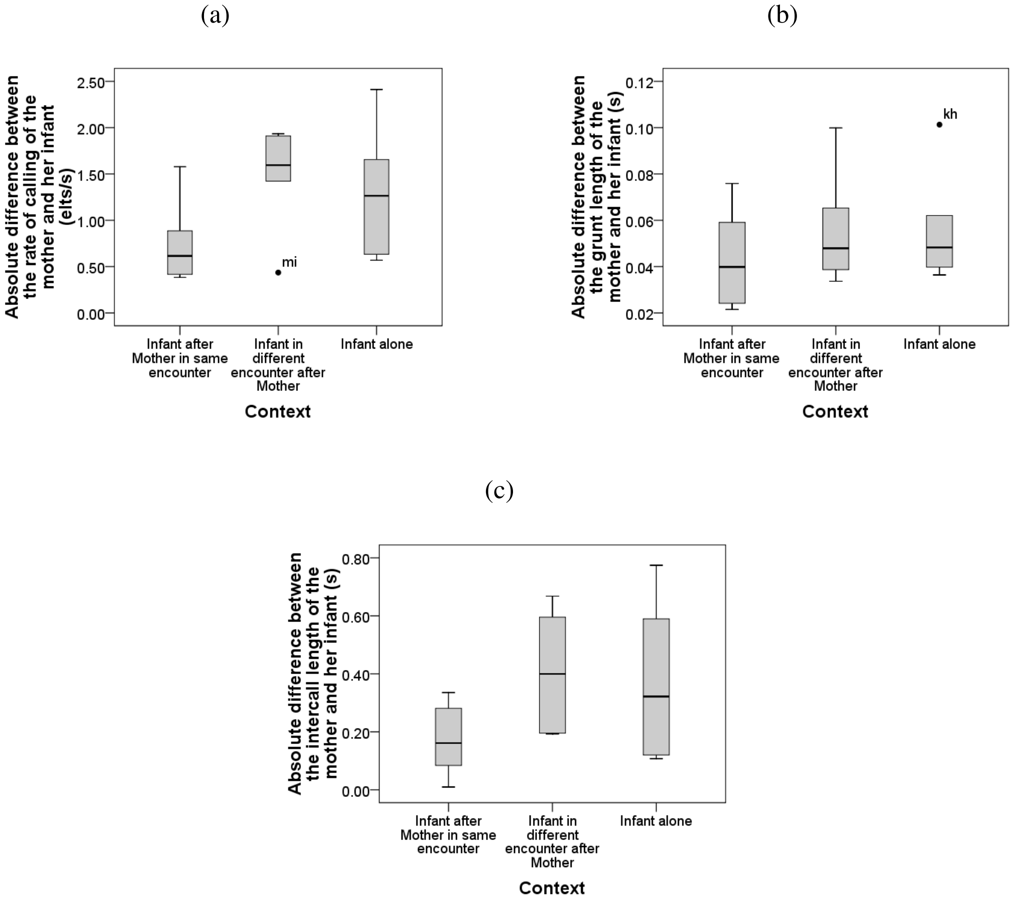


Figure 7.11: Absolute difference between the Mother –Offspring values and the Other female-Offspring values at the grunt element level: (a) mean grunt length, (b) standard deviation of the grunt length, (c) mean intercall length, (d) standard deviation of the intercall length (e) mean peak frequency, (f) standard deviation of the peak frequency, (g) mean minimum frequency, (h) standard deviation of the minimum frequency. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

4- Temporal matching between mothers and offspring during chorusing

To examine the influence of the mother at the level of the call sequence, I tested whether the calling sequences of the infant were more similar to their mothers' when calling together compared to when calling alone or calling in a different encounter.

Shapiro-Wilk test revealed that the data were normally distributed for call rate, grunt duration, and interval length. Using paired t-tests, I found that the infants' call rates and mean interval lengths (but not mean grunt durations) were affected by the mother's calling behaviour (Fig. 7.12). Calls produced after the mother during the same event and the calls produced after the mother during different calling events (respectively: rate: $t(5)=-2.908$, $p=0.033$, and interval length: $t(5)=-2.829$, $p=0.037$ that only represent trends using the Sidak correction for multiple comparisons set at $\alpha=0.025$) but not significantly different than when calling alone (respectively rate: $t(5)=2.302$, $p=0.07$ and interval length: $t(5)=1.353$, $p=0.234$). I found no difference between contexts in the mean grunt length (respectively: $t(5)=1.052$, $p=0.341$, $t(5)=-1.121$, $p=0.313$).


(a)

(b)

(c)

Figure 7.12: Boxplots representing the mean distance values for each context of production, for each parameter. (a) rate, (b) mean grunt length, (c) mean interval length. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; black circle indicates outlier.

Discussion

When comparing the call morphology of grunts given by baby chimpanzees some differences were found in the call rate, mean grunt duration and proportion of n-shaped grunts, but these differences could not be explained with context, mostly likely due to large variability. Comparing call morphology across the different age classes, however, yielded significant effects in spectral, temporal and structural features. Comparisons with adult call morphology revealed a gradual change from infant social grunts to adult pant-grunts. The acoustic structure of calls given by offspring were not more similar to the calls of their mothers compared to the calls of other adult females, suggesting that, in chimpanzees, the role of the mother in the specific acquisition of social grunts' spectral features is extremely limited. However, I found some instantaneous social learning effects in the youngest age classes. When calling jointly with their mothers, babies and infants produced social grunts that were acoustically more similar to each other than when calling separately.

The normal development of social grunts

Chimpanzees acquire the proper use of social grunts slowly during development, possibly as a result of learning within their social group (Chapter six). This chapter documented the numerous ontogenetic changes taking place in the acoustic morphology of social grunts during their transition into adult pant-grunts. Changes in body size are likely to drive some of these changes (Fitch & Hauser 1995), correlating with an enlargement of the vocal folds and larynx and lowering of the fundamental frequency (minimum frequency), although there are exceptions (Ey et al. 2007; Fitch 1997; Hauser 1993). Increased body size also correlates with an increase in lung capacity, which leads the capacity to produce longer and louder sounds (Hammerschmidt et al. 2000). Some of these effects were observed in the sample, such as a decrease in the minimum frequency an increase in grunt duration, and an increase in sequence length, with the associated increase in the number of grunts and elements. Increase in call duration has also been shown in the development of squirrel monkey, marmosets, and rhesus macaques (Elowson et al. 1991, 1992; Lieblich et al. 1980; Pistorio et al. 2006; Hammerschmidt et al. 2000). Decrease in frequency parameters during development has been reported for vervet monkeys (Seyfarth & Cheney 1986; Hauser 1989), pigtail macaques

(Gouzoules & Gouzoules 1989), marmosets (Elowson et al. 1992; Pistorio et al. 2006) and rhesus macaques (Hammerschmidt et al. 2000).

However, the overall structure of the social grunts changed. Young individuals produced more n-shaped calls than older ones, who produced more w-shaped grunts. This appears to be linked with an increase in the biphonations and noisiness of the social grunts. In adults, nearly all pant-grunts are noisy and contain aperiodic sounds (sounding like the quasivowel liquid “r”), as a result of turbulent airflows blurring the energy differences in the harmonic structure of the call. In contrast, the social grunts of infants are rarely noisy possibly due to their inability to contract the vocal tract either due to a lack of neuromuscular maturation or lack of muscular coordination (Boliek et al. 1996; Scheiner et al. 2002). However, when compared to other vocalisations, noisy calls usually require relatively little control over the vocal apparatus (Hammerschmidt et al. 2001; Scheiner et al. 2002) and should thus be easier to produce for immatures (Hollen et al. 2008).

Another difference is that adult pant-grunt sequences are composed of additional call types, such as panting, inhalations and barks, while the sequences of youngsters are essentially composed of grunts. In this sense, chimpanzees differ from some other non-human primates for which it has been observed that vocalisations become more stereotyped with age (Gouzoules & Gouzoules 1995; Roush & Snowdon 2001). In chimpanzees, I observed an increase in the structural diversity of the signals produced as part of a sequence, together with an increase in the variability of the peak frequency of grunts within a sequence (as assessed by the standard deviation). As a result, adult chimpanzee pant-grunts show a very low degree of stereotypy as already reported by Mitani and colleagues (1996). A second major difference compared to other species is that the development of this call type extends over an unusually long period. In some other primates, call development usually only takes a few years (three years for pigtail monkeys screams, (Gouzoules & Gouzoules 1995) and four years for vervet monkeys alarm calls (Seyfarth & Cheney 1986)). In chimpanzees, it is not before subadulthood (equivalent to about 10 years of development), when call structure is finally adult-like. This may be due to the fact that the infancy is comparatively longer in chimpanzees than in monkeys (Fragaszy & Bard 1997), which may also delay other types of behaviours, such as tool use which is not fully acquired before the age of six (Matsuzawa 2007). The fact that the mothers' pant-grunts and their offspring's social grunts are given in the same circumstances provides good evidence against the hypothesis that the observed acoustic differences are due to the calls serving fundamentally different functions (Gouzoules & Gouzoules 1995).

The role of the mother

Over the course of development, young chimpanzees converge towards the acoustic structure of adult calls, but not preferentially toward their own mother's style of pant-grunting. The variability of the peak frequency emerged in infants, then the number of grunts reached an adult level in juveniles and the length, the minimum frequency and the switch to noisy grunts totally occurred in subadults. However, none of these parameters were closer to the mother's model than to the other females sampled. The only parameters that ranked significantly closer to the mother's model than to other females concerned proportional variables. It is thus possible that the mother has a subtle influence over her offspring's production. It seems unlikely that the selection of elements or their shape would be genetically inherited because they are not the direct result of physical constraints such as lung size or vocal tract length. However, this is not likely to constitute an evidence for vocal learning either. First, the absolute difference was evaluated using all age-classes and thus could not take into account the development of individuals. Second, the observation of graphs revealed that the statistical significance concerning the proportion of u-shaped grunts was the result of more similarity with other females. Furthermore, the significantly smaller distance from the mother than from other females in the proportion of tonal grunts produced was extremely limited. One should thus be cautious when interpreting such results that are subtle and restricted to a few parameters. A conservative hypothesis would be that individuals accommodate their production in features requiring little articulatory control to the individuals with whom they interact most or spend more time with (Hammerschmidt et al. 2000). In humans, this process is commonly observed in the vocal behaviour of developing infants and has been termed “vocal accommodation” (Locke 1993).

This possible limited vocal accommodation to the mother’s production over the whole developmental period was also found, in a very immediate fashion although on different structural parameters. Babies and infant did echo their mother’s pant-grunt productions when calling together in their temporal features and rhythm. This could be the result of simple mechanisms of neonatal imitation such as the tongue click sounds or tongue protrusion (Bard 2007).

Vocal echoing also exists in humans from very early on (Malloch 1999). In humans, prematurely born babies are able to synchronise their vocal expressions with those of adults (Lester et al. 1985), and the appeasing effect of a beat of 72bpm on newborn babies is supposed to directly derive from the maternal heart rate heard prenatally (Lecanuet 1995; Trevarthen 2008). Mother’s voice propagates well through body tissue and bones (Lecanuet & Schaal 2002), suggesting that neonates’ ability to recognize the face of the mother is aided by prenatal learning of her voice (Sai 2005). Similar processes of prenatal associative learning in terms of the sounds heard have also been shown in chimpanzees and persist after birth (Nobuyuki et al. 2004).

In mother-infant communication, exchanges of signals are negotiated by both parties in a dynamic way and involve vocalisations as much as gestural, visual and affective aspects (O'Neil et al. 2005). This process of coordination between the infant and his mother is a kind of psychological basis on which affects and meanings can be built and permitting the anticipation of future events (Devouche & Gratier 2001). This thus constitutes an important feature of the young human vocal and social development. It is also considered as being at the roots of music (Bispham 2006; Dissanayake 2000) which shares a large number of its characteristics with human language and might have been constrained by the same evolutionary processes (Darwin 1871/2009; Fitch 2006).

In chimpanzees however, when the 'echoing' observed in this study does not concern vocal exchanges between the mother and her infant nor joint attention where the mother and her infant communicate about a third entity (Tomasello et al. 2005). Invariably, the mother directs her vocalisation to another individual and generally does not react to her infant's production by looking at it or responding vocally. Sometimes, she will produce another row of pant-grunts after her infant, but the phenomenon seem to be more likely linked to her appreciation of the external situation and thus not to her infant behaviour. This lack of behavioural responsiveness from the mother suggests that her behaviour is one of the important differences with human mother-infant dyads, which is further supported by studies on different rearing conditions of newborn chimpanzees. When reared by responsive humans, young chimpanzees present a better neonatal adaptation than when they are reared by their own unresponsive mothers (Bard 1994b). Nevertheless, it is very likely that this echoing capacity, that was possibly a feature of our common ancestor, plays a role in the acquisition of the social grunts by associative learning. Moreover, an additional row of pant-grunts produced by the mother after her infant could act as reinforcement without intentional components from the mother.

Another possibility, of course, would be that the mother and her offspring would react similarly when involved in the same event. Although this is an hypothesis that cannot be refuted at present, the young age of these babies and infants and the very subtle difference found between conditions suggest that offspring are likely to be influenced by the general rhythm of their mothers more than stereotypically answering different social situations without taking into account the vocal behaviour of their mothers.

Other studies have reported vocal convergence in adult chimpanzees, a phenomenon that appears to play a role in the management of social bonds between individuals (Crockford et al. 2004; Marshall et al. 1999; Mitani & Gros-Louis 1998). Vocal convergence has also been reported from other species of primates (pygmy marmosets; Elowson & Snowdon 1994; Rukstalis et al. 2003; Snowdon & Elowson 1999), cotton-top tamarins (Egnor & Hauser 2004; Weiss et al. 2001), Campbell monkeys, (Lemasson et al. 2005), Japanese macaques, (Sugiura 1998) and non-primates, such as elephants (Poole et al. 2005), bottlenose dolphins (McCowan & Reiss 2005), or bats *Phyllostomus hastatus* (Boughman 1998). Convergence is either very rapid, as in instantaneous vocal matching of chimpanzee pant-hoots, or it takes several years as illustrated by the vocal convergence of an elephant (Poole et al. 2005). Interestingly, echoing has also been observed gesturally in nut-cracking behaviour, where the observed behaviour is directly transformed in motoric response and it has been hypothesised that it could reflect mirror neurons activity that prepare the body for future actions and could thus constitute a learning facilitator (Marshall-Pescini & Whiten 2008; Rizzolatti et al. 1996). A perhaps related phenomenon of entrainment to music beats has also been observed in several bird species which led the authors to suggest a direct link with vocal mimicry (Patel et al. 2009; Schachner et al. 2009). Although the vocal convergence observed in very young chimpanzees is far from perfect, they might still draw on the same underlying mechanisms and as such be part of the numerous building blocks required for developing human language.

Chapter eight: General discussion

"On oublia l'origine de ces signes, aussi-tôt que l'usage en fut familier, et on tomba dans l'erreur de croire qu'ils étoient les noms naturels des choses les plus spirituelles. On s'imagina meme qu'ils en expliquoient parfaitement l'essence et la nature, quoiqu'ils n'exprimassent que des analogies fort impafaites. Cet abus se montre sensiblement dans les philosophes anciens, et il s'est conservé chez les meilleurs des modernes, et il est la principale cause de la lenteur de nos progrès dans la manière de raisonner."

Étienne Bonnot de Condillac, 1746, (See Appendix A for translation)

Aims of the study

Although chimpanzees are one of the most studied primate species, there are still domains that remain surprisingly unexplored. For historical reasons, the chimpanzee vocal repertoire and in particular one of its most social vocalisations, the pant-grunts, had not been systematically investigated. Despite a considerable amount of research efforts aimed at understanding the acquisition of the natural vocal repertoire in non-human primates, there were no comparable studies in our closest living relatives in captivity or in the wild, despite their significance for the evolution of human language.

The first aim of this thesis was thus to provide insight into the production of pant-grunts in adults. Although this vocalisation is constantly used by researchers as an indicator of social relations, the detailed usage and function of this signal within a social group has remained anecdotal. The second aim of this thesis was to tackle the development of this social signal, beginning with the first grunts produced by very young babies.

Research on animal communication systems has considerably been inspired by linguistic theories of human language, a unique communication tool with evolutionary roots in primate communication. Linguistics is a theoretically heterogeneous field influenced by research areas such as philosophy, psychology, neurophysiology or computer science. Primate and more specifically ape communication is currently receiving a renewed interest with the aim to provide a model for the evolution of human language. In the following, a summary of the key empirical findings is presented before drawing general conclusions concerning the relevance of pant-grunts in the chimpanzee social world and its development in light of its relevance for understanding language evolution.

Summary of the key empirical findings

The behavioural variability of adult pant-grunts production

Pant-grunt vocalisations are special in the chimpanzee vocal repertoire because they seem to be the result of an active decision by the caller to vocalise and they are not broadcasted but directed at specific individuals. Previous observations made in different chimpanzee communities had already suggested that pant-grunts might have a range of social functions and were not just mere reactions to the presence of a more dominant individual (Hayaki 1990; Newton-Fischer 1997). Chapter four aimed to test this assumption by looking more precisely at the contexts of emission of pant-grunts and the flexibility of their production, especially regarding the number and type of bystanders.

Looking at the pant-grunting activity of several females to the alpha male and to other males, the results were consistent with the hypothesis that females made an active choice with regards to production. In chimpanzees, the female social dominance hierarchy is independent from the males' (Goodall 1986; Noë et al. 1980). Although the alpha male received most of the pant-grunts, the female production patterns did not follow the male hierarchy nor did the females' own social position affect the production patterns. I also found that pant-grunts were not given compulsorily when encountering a higher-ranking individual. Moreover, they were produced more often in affiliative contexts than any other. Finally, I found that social variables influenced the production of the signal. For example, the presence of the alpha male in the vicinity had a powerful inhibitory effect and females refrained from producing pant-grunts to other males in his presence. Even in his absence, females seemed to monitor their audience; they were less likely to pant-grunt to a male with increasing numbers of other males in the audience. Females, and notably the alpha female, also influenced the production of pant-grunts by females to males, but the pattern was not very strong and failed to reach statistical significance. Overall, the data were consistent with the hypothesis pant-grunts are not produced in a stimulus-response way and that females seem to assess the social situation before actively deciding to produce this greeting signal.

Acoustic variability of adult pant-grunts

Assuming that pant-grunts are actively produced and highly variable signals, Chapter four focused on testing whether this variability could be used flexibly in different contexts.

Recordings of pant-grunts were made from seven females and three males in three different contexts: (1) encounters with any male in a neutral situation (females only), (2) encounters with the alpha male, and finally (3) encounters with the alpha male followed by a grooming session (both males and females). Acoustic analyses were performed on entire pant-grunt sequences at three different levels of analysis: (1) the total sequence level, (2) the grunt sequence level and (3) the individual grunt element level. Although individual pant-grunts showed individual acoustic differences, for example in terms of variations in the mean grunt length, the mean minimum frequency or the proportion of inhalations within a sequence, I found that grunts were consistently different when encountering the alpha male as opposed to other males (in terms of increased sequence length and increased proportions of n-shaped grunts). I also found that individuals actively appeared to signal their intention to interact in an affiliative way (grooming), notably by increasing the proportion of panting elements within a sequence and by producing grunts that were lowered in their mean frequency and produced with shorter and more regular intervals. Taken together, these results are in line with the notion of an intentional production of pant-grunts, as well as an ability to alter vocal production depending on the situation encountered partly by recruiting other types of elements such as pants or voiced inhalations within a sequence.

Behavioural variability of social grunts usage during development

The second major aim of this thesis was to document the emergence and development of the pant-grunting behaviour, from the first grunts produced to the adult-like pant-grunting behaviour described in Chapters six and seven. A key finding was that grunting appears to pass through stages in which these vocal signals become clearly socially directed (the "social grunts") and used only in social situations.

Grunts are produced very early in the life of chimpanzees and some authors have even reported a production from the first day of life (Kojima 2001). They are initially produced in very unspecific ways and most of them are produced as a result of physical effort, a mere expulsion of air from the lungs during locomotor activities (Plooij 1984). Grunt production then successively becomes more focused as responses to different environmental variables, such as hearing other individuals' vocalisations, the sight of other group members, or both. It is not until the juvenile and subadult stage that grunts begin to be produced to socially relevant individuals. While there are some patterns that suggest a progression towards the adult model of production (i.e. the mothers'), there was a remarkable gap in the frequency of production in the juvenile age before subadult use, which largely conformed to the patterns shown by adults. One possibility is that the mother involuntarily influences the grunting activity of her infant simply by navigating through her social networks. As subadults, chimpanzees travel already largely independently from their mothers and, as a result, their pant-grunting activity diverges more and more from their mother's.

Acoustic modification during ontogeny

Chapter seven is a follow up of Chapter six aimed at describing acoustically the first grunts emitted by babies in the different contexts they experience in the wild. A second aim was to relate the major acoustic changes of social grunts during development with the emission patterns of the mother. The final part of the chapter focussed on the instantaneous chorusing of some mothers and her babies and infants when pant-grunting.

Using the same three levels of analysis as Chapter four (i.e. the total sequence, the grunt sequence and the grunt element levels) revealed that babies' grunts did not show any evidence of significant context-specific acoustic differences. Significant modifications in acoustic parameters of social grunts occurred progressively. When comparing to the adult model (i.e. the mother group), the stage at which the parameters become adult-like could be determined. Analyses revealed that the mother does not seem to have a strong influence on the development of the acoustic form of her offspring social grunt. However, infants and babies seemed to have a tendency to match their mothers' vocalisations in terms of the rhythmic features, but only when calling together.

General discussion of the results

The pant-grunt, an important signal for sociality

For decades, pant-grunts have constituted a useful tool for researchers because they reliably reflect the hierarchical structure of a chimpanzee community. The conception of pant-grunts as mere expressions of subordination from one individual to another as a result of their dominance relationships was widespread, perhaps due to the way the signal has been used by researchers for studies of social behaviour. However, a main finding of this thesis has been that this conception of pant-grunting might have been too restricted.

Pant-grunts could be more than just vocalisations that are a direct result of dominance relationships. This thesis suggests that it could also be a social signal used in different social functions, such as to assess the relationship with another group member, and to advertise one's presence to other group members (Hayaki 1990; Newton-Fischer 1997). As a general pattern, pant-grunts somehow confer a superior status to the addressee. They are produced flexibly, taking into account the social fabric of the party and its eavesdroppers (Chapter four). In concert with other types of interactions, pant-grunts could thus be viewed as part of a dynamic process of constant updates of relationships, as individuals interact with each other. In Chapter four, I have described the pant-grunting behaviour of females to males. As the male and females dominance relationships are distinct and not overlapping (Goodall 1986; Noë et al. 1980), it is possible that females have a subtle, yet non negligible effect on the male dominance status, as already suggested by de Waal (1982). A working hypothesis could thus be that this kind of subtle social shaping is a way of constantly confirming and renewing the preference toward some individuals above others. This process could in turn have an effect of maintaining stability within the community or of creating it during instability.

Pant-grunts seem to be a demonstration of social interest, reflected not only by whether or not the signal is given, but also by its form. Chapter five showed that females produced acoustically different types of pant-grunts when addressing the alpha male compared to other males. Although there was no evidence that the acoustic structure of pant-grunts functions in a referential way, with different acoustic variants referring to different individuals it was still the case that the pant-grunt directed to the alpha male seemed acoustically more elaborated with females putting more efforts into call production compared to pant-grunts given to other males.

As a highly graded and variable signal used flexibly in different situations, pant-grunts do not seem to be likely to qualify as referential or functionally referential in the sense of Macedonia and Evans (1993) that derive from formal theories of language information transfer. They do not seem to transmit direct information through their morphological form, but seem to draw most of their meaning from contextual variables and function in social regulation. In this aspect, pant-grunting shows more similarities with some gestural than vocal signals (Call & Tomasello 2007).

In terms of comparisons with human communication, pant-grunting thus contributes most usefully to questions about the role of pragmatics (the third major area of linguistics, in conjunction with semantics and syntax) which has recently received a renewed interest from linguists and philosophers of language (Recanati 1998; Scott-Phillips 2010). The focus on pragmatics is interesting because it might offer alternative hypotheses about the possible link between animal communication and human language in practical terms of situated action and situated meaning.

One notion of pragmatics developed by “ordinary language philosophers” (Recanati 1998) emphasises a descriptive approach of natural languages, opposing their views to the “ideal language philosophers”, or formal positivists (Recanati 1998). Formal positivists hold a reductionist view of language, in that they assume a compositional link between semantics and syntax, which supposes that a signal’s meaning is fully specified by reference to its form and a decoding algorithm (Scott-Philips 2010). In contrast, the formers adopt a more empirical reductionism, which assumes that the function of language is to act in the world rather than to refer to it or to describe it (Austin 1962/1975). Somewhat related arguments have been made recently by Rendall and colleagues (2009) and Scott-Phillips (2010), who believe that we will gain a better understanding of animal communication if we understand it more as a matter of influence than information.

Traditional approaches of sound analysis, which generally assume that signals “contain” information, are still the method of choice to tackle problems in animal communication. One source of the current confusion in the field is that the psychological states underlying animal, and particularly primate, communication are largely unknown. Some consider that the acoustic variability seen in primate vocalisations mainly reflects emotions and terms such as meaning should thus be avoided (Owren & Rendall 2001; Rendall et al. 2009). Quite interestingly, researchers working on computational models of automatic speech recognition note that acoustic analysis of language has seldom been done in natural context of vocal exchanges (Kohler 2000), despite the fact that most of human language processing is deeply affected by the behavioural context, including attention and intention (Tanenhaus & Brown-Schmidt 2008; van Berkum 2008).

There are still a number of unresolved issues in the field of speech perception that might prevent a deeper understanding of how meaning is recovered in humans. For example, the overlap between phonetic units as a result of continuous vocal tract activity and individual natural variability of pronunciation does not allow for a direct and invariant correspondence between spectrogram features and meaningful units (Greenberg 1998). Perceptually, there is a rapid recognition of words, even before their offsets (Hagoort 2008), and if segments of a sentence are locally time-reversed, comprehension is not prevented (Saberi & Perrott 1999).

As a result, some authors consider that the phonetic or spectral constituents of speech are secondary to the rhythmic properties associated with prosody (Greenberg 1997). They also support the view that meaning is an integrative process involving different mechanisms together with the motor system to generate a global representation of the world (Davis & Johnsrude 2007; Todd et al. 2006). Taking into account these different issues faced by researchers working on both humans and non-humans' signal analysis, the following alternative ways are conceivable to address the possible primate roots of human language other than focalising on subtle acoustic variation only (Greenberg 1996).

First, according to the sensorimotor approach, pant-grunts could thus be viewed as communicative acts, similar to "speech acts" (Austin 1962/1975), which would not function directly as referring to the hierarchic relationship to another individual. Instead, pant-grunts may participate in relationship building due to its phatic nature, i.e. functioning mainly to keep the communication contact alive and to perform social tasks or, in Malinowski's (1923) words, "….the important social function of apparently meaningless small talk". Also, it should be noted that in humans, grunts are part of what is called "paralinguistic speech", which constitutes about half of all natural vocal sounds including speech. While they have been considered as emotional-only, it has recently been suggested that they also have an important social function in the speaker-interlocutor relationship and consequently contributing to the understanding of speech sounds (Campbell 2007). Even if they do not seem to serve the same function in chimpanzees, the communicative function of pant-grunts could be viewed as inherently dynamic and modulated in its production and interpretation by external events or shared knowledge about situations or past events.

Vocal development of communicative acts

Following the same arguments, the acquisition of a vocal repertoire can also be approached under a more pragmatic light. As described in Chapter one, vocal learning theories emphasise the importance of vocal production while neglecting vocal usage in contextually appropriate situations. It is also the case that researchers working with animal species living in socially complex groups struggle to explore the development of communicative abilities, possibly as a result of the emphasis on production compared to usage and comprehension. Here again, a pragmatic approach of communication could be fruitful in understanding how signals are acquired. Of course the form of the signal produced, as well as its function, are partly determined by a maturational process that may have strong genetic components or philogenetic roots (Gómez, 2005) as well as being shaped by individual experience and history (Varki et al. 2008). Indeed, individual experience can have an impact at all levels of organisation, even those that are thought as the most genetically-driven. In rats, for example, enriched environments promoting the voluntary activities, such as running, have a positive effect on neuro-genesis (Kempermann et al. 1997; van Praag et al. 1999). Similarly, there is an active reorganisation of neural circuitries in the acquisition and consolidation of new skills in mice (Yin et al. 2009). Finally, although the form of the vocal tract determines the limits over the range of sounds an individual can produce, it does not determine it (Fitch & Hauser 1995). At a bigger scale, the role of vocal tract changes during development and evolution is still debated and some authors argue that the vocal tracts of human babies, chimpanzees and Neanderthals have the potential to produce all phonemes found in modern human adult speech (Boë et al. 2007).

Sociality begins early

As reviewed in Chapter six and seven, social influences by the group and the mother may begin before birth if the foetus already begins to associate sounds and possibly emotional states of his mother. In humans, as soon as the hearing apparatus is developed, a foetus can hear its mothers' voice and heartbeat, as well as digestion and impact sounds. In the third trimester of pregnancy, a foetus begins to respond to external sounds by turning the head and accelerating the heart rate (Joseph 2000). Some researchers even suggest that the emotional and physical state of the mother is reliably perceived by her foetus through her internal sounds before receiving hormonal signal (Parncutt 2009). With repetition of the same pattern, it is suggested that the foetus comes to anticipate the emotional correlate of the sounds heard by a process of classical conditioning (Parncutt 2009). Prenatal experience thus seems important in shaping the future individual response to its environment in humans. Because of this, it is possible that chimpanzee foetuses begin to experience social sounds and their related physiological correlates before birth, as suggested by their early capacity in sound association (Nobuyuki et al. 2004).

In the early life of chimpanzee babies, the results of this study suggest that the emergence of social grunts cannot be explained by a single factor, such as physical maturation or imitation, but is the result of a combination of different processes. One of the first vocalisations emitted by chimpanzee babies are grunts produced when struggling over the mother's body. This reflex-type of vocalisation is likely to constitute a substrate for other grunts as the infant begins to react to chimpanzee vocalisations in resonance with his mother. The association between the production of grunts and the sight of an individual could be reinforced on the one hand by this resonance with his mother when she produces a pant-grunt and on the other hand by his own body reacting in a stereotyped way to the effort of trying to reach the individual spotted. During all infancy, young chimpanzees are thus possibly reinforced by these different factors and especially by their mother. Also, it could be hypothesised that the production of a second row of pant-grunts from the mother or her production after her infant could further reinforce her offspring's production. Overall, these empirical observations suggest that the production of grunts is deeply rooted in the action and the repetition of action conjointly with the mother. For some authors, these processes are the first prerequisites for the emergence of meaning (de Condillac 1746/2002). This ontogenetic acquisition of a signal does not require active teaching, but only a repetition of situations together with a progressive understanding of the social rules of the community. By navigating within the social group attached to its mother, the offspring experiences the social life of his group and learns how to adequately respond to its semiotic milieu (von Uexküll 1934).

While I did not find any influence of the mother on the general call morphology of social grunts of her infants, I found some influence at the rhythmic level which possibly derives from the foetal sensitivity to rhythm (see Trevarthen (2008) for evidence in humans). This also suggests that the influence of the mother could be subtle and possibly more readily detected on a short-term basis. Quite interestingly, I observed that chimpanzee infants play a major role in creating vocal synchrony as it has been observed in infant orang-utans when matching their mothers' gestures (Cartmill 2009). With age, individuals accumulate experiences and it is possible that they actively shape each other's vocalisations, as it has been shown during modification of the identity of social companions or relationships (Lemasson & Hausberger 2004; Snowdon & Elowson 1999).

As juveniles, chimpanzees largely refrain from pant-grunting to others and although they do use grunt sequences resembling the adults in form and function, they produce them only when forced to by the social circumstances. From my observations, while babies and infants readily grunt to individuals when attempting to reduce the distance between themselves and their targets, juveniles seem to often avoid the close presence of dominant individuals by staying away from them or even making detours while their mothers approach them (personal observation). In Budongo, I observed that two individuals who both lost their mothers when still very young, one male Zed (6 years old) and one female (most likely Polina, 4½ years) appropriately responded to other individuals with adequate pant-grunt sequences as soon as they were seen in the community again (personal observation). This is also consistent with the view that pant-grunts are active vocalisations used in behaviourally flexible ways to integrate the chimpanzee society but more work would be needed to test these hypotheses. For example, it would be interesting to follow the transfer of a female to another community to assess the amount of pant-grunt produced and her vocal variations.

Vocal and gestural communication

A significant fraction of the research community thinks of ape gestural communication is particularly flexible compared to their vocal communication (Arbib et al. 2008). This view might have taken its origin in the early attempts made to communicate with apes in enculturated settings. These attempts were generally unfruitful if the main goal was to teach them to talk (Hayes & Hayes 1951) compared to some success in sign language and lexigrams teaching programs (Gardner & Gardner 1969; Savage-Rumbaugh et al. 1986). Nowadays, despite increasing support for flexibility in the vocal domain, the dichotomy persists, with gestures possessing the following characteristics that are considered as absent in vocalisations. First, apes seem to gesture in a mostly intentional way depending on the attentional state of the receiver (Liebal et al. 2004; Pika et al. 2003, 2005) and often have single intentional meanings (Cartmill & Byrne 2010). In contrast to vocal signals, gestures have important variations in their form and new forms can be invented (Call & Tomasello 2007; Goodall 1986). The evidence for idiosyncratic signals that have been invented or imitated is much weaker in the vocal domain. In one study, chimpanzees produced attention-getting sounds such as the “raspberry” and the so called “extended grunt” in their interactions with humans holding food (Hopkins et al. 2007) and one orang-utan spontaneously imitated the whistling of humans, hereby controlling the duration and number of whistle (Wich et al. 2009). Another specific feature of gestures is that they are also less context-bound than vocalisations and can be used in a wide range of behavioural situations (Pollick & de Waal 2007). For these reasons, most gestural signals are not considered as referential in the sense used for vocalisations although they actively participate in the regulation of the social life (Call & Tomasello 2007). Gestures are considered as referential when they are used to direct the attention of another individual to a target as, for example, the pointing gesture of humans and possibly other apes (Gómez 2007; Leavens et al. 1996, 2005). Most likely, gestures are acquired by apes via the process of ontogenetic ritualisation, a form of social learning. In ontogenetic ritualisation, two individuals shape each other’s signals through repeated interactions. The anticipation of the interactants over the succession of predetermined actions can give a communicative function to that signal which is then incorporated in the communicative repertoire (Tomasello 1996; Tomasello & Call 1997). Overall, gestures are produced with great flexibility, as much in their usage than their production, and it is hypothesised that it is related to the fact that they usually signal less evolutionary urgent functions than vocal signals (Call & Tomasello 2007). This is interesting in regard to Sowdon and colleagues’ (2005) hypothesis that social calls might reveal themselves more flexible and subject to learning for the same reasons.

The discovery of mirror neurons has been used by some to argue in support of the hypothesis of a gestural origin of language (Corballis 2010; Rizzolatti & Arbib 1998). The initial discovery was that some neurons in the F5 area of the monkey brain discharge both when the monkey is performing an action and when he sees another individual performing the same action (Rizzolatti et al. 1996). These neurons thus have been interpreted as the biological underpinnings for action anticipation and representation, with a possible direct role in language evolution. Indeed, the F5 part of the ventral premotor cortex of the monkey is homologous to the Broca's area of the human brain (Arbib & Rizzolatti 1998) and both are involved in motoric response although F5 is more concerned with hands movements while Broca's area is involved in speech production (Rizzolatti et al. 1996). In humans, watching speech movements also activates the regions likely to involve the mirror system including Broca's area (Calvert & Campbell 2003). However, while recent single cell recordings showed the presence of mirror neurons in humans, these were only done in other regions than Broca's area, in hippocampus, parahippocampal gyrus, and entorhinal cortex, preventing any firm conclusions yet (Mukamel et al. 2010). Mirror neuron theories of language evolution incorporate these findings into evolutionary scenarios including a switch of communicative modality from hand to mouth (Arbib 2005; Corballis 2003) sometimes even considering that speech can be considered as a half swallowed facial gesture (Corballis 2009) in opposition to a vocal-only origin of language (Burling 2005).

While these scenarios propose an interesting account of communication as actions together with an account of the substrates for the mediation between perception and action, the transition from hand to mouth remains somehow speculative in the incorporation of vocalisations to the mirror system and the actual role of mirror neurons in speech perception (Burling 2005; Lotto et al. 2009). There is increasing evidence that perception and action are related, even in speech perception. The Motor Theory of speech perception proposed by Lieberman and colleagues in 1985 postulated that speech itself could be considered as a gestural system (considering the discrete movements of articulators) as being the function of a hard-wired language module (Liberman & Mattingly 1985). This rather strong position has found some renewed interest with the discovery of mirror neurons and is currently a subject of debate and theoretical controversies (Lotto et al. 2009; Schwartz et al. 2010; Wilson 2009).

However, it remains that these positions offer renewed lines of research on the actual link between production and perception. Pulvermüller and colleagues (2006) found an overlap between the cortical areas active during speech production and those active during passive listening to speech and D'Ausilio and colleagues (2009) recently found that the motor cortex specifically contributes to speech perception.

In chimpanzee, some synchronisation or “echoing” behaviour between individuals has been reported in the nut-cracking behaviour and it has been hypothesised that it could involve the mirror neuron system (Marshall-Pescini & Whiten 2008). It is still not known which neural mechanisms are involved in the matching of gestural or vocal behaviours between individuals but it seems reasonable to hypothesise that neural mechanisms of perception and action overlap.

In the macaque brain, while F5 is somato-topically organised with a predominance of hand gestures, there is also some representation of mouth and larynx movement in its ventral part (Rizzolatti & Arbib 1998). This further suggests that some links can also exist between gestural and vocal communication. During development, both human and chimpanzee infants are combining their vocalisations with hand movements. For example, canonical babbling in infants from 6 to 8 months is accompanied by rhythmic hand movement (Masataka 2001). Similarly, the extension of hand to grasp an object is accompanied by vocalisations (Bernardis et al. 2008), which is very similar to what has been observed in chimpanzees of the same age, when extending their hands toward individuals while grunting to them although only the grunts are rhythmically produced (Chapter seven). Combination of gestural and vocal communication persists in adulthood, as for example in requests to humans in captivity (Hopkins & Leavens 1998) or in displays in natural social groups (Arcadi et al. 1998, 2004) and the production of communicative gesture and vocal signals both involve the Broca's homolog (left inferior frontal gyrus) (Taglialatela et al. 2008).

Several classes of neurons that encompass several sensitive modalities have recently been discovered, such as the "echo neurons" that fire both when watching a meaningful grasping action and hearing its sound, such as breaking peanuts (Kohler et al. 2002) and the so-called "audiovisual mirror neurons" that fire whenever the actions are performed, heard or seen (Keysers et al. 2003). This close association between manual and vocal gestures at the neural level suggests that it might be fruitful to consider intentional gestures and vocalisations as a deeply related communicative system (Balter 2010).

Taken together, these findings suggest that, beyond the mirror neuron debate, perception, cognition and motor control might be integrated into overlapping neural networks (Pulvermüller & Fadiga 2010). Some authors propose that these neural networks of signal distribution can be based on learned experience (Southgate et al. 2009) and permit the brain to reconstruct an action from only one sensory input (Damasio & Meyer 2008). More generally, this integrative cross-modality system debated in neurosciences and neurolinguistics could help animal communication discipline to also approach it subject as a cross-modality system.

In sum, the results reported here support the view that ape communication can be used in flexible ways as much in their usage as in their production. Although the nature of the acquisition mechanisms still remains largely unclear as it is in other primates' species including humans, this research suggests that it cannot be considered as a result of unfolding maturation only. More generally, testing whether a vocal signal is genetically determined or learned does not seem to be a productive question (Johnson 1988) as both are likely to be involved (see, for example Bard et al. 2010) and methodologies to assess the relative importance of genetic or cultural influence on a trait observed in adult individuals are still difficult to implement (Langergraber et al. 2010). As for the acquisition of other cognitive abilities, it seems important to observe the vocal development of chimpanzees as sensitive to flexibility (Gómez, 2004).

When trying to understand what animals actually do when they vocalise, the dichotomies between innate versus acquired, internal versus external, or body versus mind might be too often taken as real facts about development and cognition rather than models that we construct to help ourselves categorise and understand our observations. Such a position could thus be misleading and unproductive. Several research teams working in linguistics (Recanati 1998; Tanenhaus & Brown-Schmidt 2008), animal communication (Johnson 1988; Rendall et al. 2009), animal behaviour (Barrett et al. 2007), development (Spencer et al. 2009) or even genetics (Varki et al. 2008) suggest that it might be more fruitful to switch to integrative approaches based on empirical observations. Alternative frameworks coupling perception and action in the real world could also be useful for the understanding of the emergence of meaning and communication, both during the ontogeny and during the phylogeny.

Future directions

Age classes

Because I chose a conservative within-individual approach without pooling all vocalisations produced by a specific age–class and because I was working with a restricted number of individuals or number of vocalisations per individual within specific age-classes, I was prevented from conducting some analyses. For example, the age classes that have been used in this first study are very broad and most of them encompass several years during which it would be interesting to extract critical periods. While I did not find any distinct long term impact of the mother on her offspring's vocalisations in this thesis, the mothers seem to have an influence on the rhythm of production on the short term. It would thus be worth looking more deeply at some crucial developmental stages such as the infant stage around seven month when infants begin to regularly break the contact with their mothers and the juvenile stage between five and six years when they seem to already understand the function of pant-grunts but produce very few of them. Due to a restricted number of individuals in these periods of development, it was difficult to directly test the influence of the mother, but I hope to further conduct these evaluations of vocalisations in these critical periods for pant-grunt development.

Sex classes

For the same reasons as stated above, I could not distinguish between male and female acquisition of pant-grunts during development although a differential rate or manner of acquisition is likely. In chimpanzees, females acquire tool use faster than males, essentially because they spend more time looking at what their mother is doing while males spent more time playing (Lonsdorf et al. 2004). This finding could be directly linked to the socioecological theory predicting that reproductive success of males and females are limited by different factors (Wrangham 1980): access to resources in females and access to mates in males. Accordingly, while females should primarily be interested in finding food, adult males should be more interested in social relations and in establishing themselves socially in their group (Wrangham 1980). Therefore, pant-grunt acquisition might occur earlier in males and might be more conservative in its form while females' pant-grunts might be more subject to variation as females leave their mothers later than males and transfer to another community where they might have to adapt their vocal production. Although it would be difficult to achieve, following an emigrating female to another community would certainly bring more light on how chimpanzees' signals can be modified.

Comparison with other communities

Similarly, it would also be interesting to compare developing individuals at Budongo with those of other communities. For example, Crockford and colleagues (2004) observed that pant-hoot varied between communities, forming local dialects that could have emerged through learned mechanisms within the social group. It would be important to study the emergence of pant-grunts in neighbouring communities or other Ugandan communities sharing the same genetic background. For example, patterns of male aggression toward females vary between communities (Stumpf & Boesch 2010) and individuals of the Kanyawara community of the Kibale forest are often considered to be more aggressive than Budongo chimpanzees. Comparing the vocal productions of individuals at different stages would possibly reveal group specific emissions of pant-grunts and/or different rates of acquisition linked to the specific social style of the community.

Development of other vocalisations

Other vocalisations, such as pant-hoots, need further studies. Pant-hoots are also compositional vocalisations that have been extensively studied in adults, showing contextual variability (Notman & Rendall 2005), group specificity (Crockford et al. 2004; Mitani et al. 1992;1999) and instantaneous convergence with calling partners (Mitani and Brandt 1994; Mitani & Gros-Louis 1998), suggesting that their acquisition might require learning with a continuous flexibility even in adulthood (Marshall et al. 1999). Pant-hoots seem to develop later than pant-grunts and perhaps require more control over the vocal production. As babies and infants respond to vocalisations, including long distance ones, with sequences of grunts and staccatos, it would be interesting to study the possible link between these early grunts and the first pant-hoots produced.

Playback experiments

Finally, pant-grunts are used flexibly in adult chimpanzees, but due to the low visibility of the forest, it would be interesting to test whether these variations are meaningful for eavesdroppers and sufficient for inferring the ongoing situation. For example, can individuals anticipate the arrival or the presence within a group of the alpha male by the pant-grunt they hear from another individual? Playback experiments are now beginning to be used with wild apes with low disturbances and successful outcomes (Slocombe et al. 2009).

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Appendix A

Translation of the citations

Chapter one: General introduction

"And if I did not expect that our young men, learned and studious as they are, would very shortly present us here, one with a large collection of examples drawn from the land, the other with his from the sea, I should not have denied myself the pleasure of giving you countless examples of the docility and native capacity of beasts. Let us leave this subject, therefore, fresh and untouched for them to exercise their art upon in discourse."

Plutarch, 959 B.C.

Chapter two: Chimpanzee social structure and vocalisations

"At the office all morning and did business; by and by we are called to Sir W. Batten's to see the strange creature that Captain Holmes hath brought with him from Guiny; it is a great baboon, but so much like a man in most things, that though they say there is a species of them, yet I cannot believe that it is a monster got of a man and she-baboon. I do believe that it already understands much English, and I am of the mind it might be taught to speak or make signs".

Samuel Pepys, 24th of August, 1661

Chapter three: General Methods

"[...] From the inside, this confused mass becomes a monumental world. The forest ceases to be a terrestrial disorder, it might be taken for a new planetary world, as rich as ours and which would have replaced it."

Claude Lévi-Strauss, 1955

Chapter four: Vocal greeting behaviour in wild chimpanzee females

"Be resolved to serve no more, and here you are free; I do not want you to push or unhinge him, but just to support him no more, and you will see him as a great colossus from which the base has been disrobed, in his own weight collapse and break down."

Étienne de la Boétie, 1574

Chapter five: Acoustic structure of chimpanzee pant-grunts co-varies with the receiver’s social class and intended type of interaction

"He wrote a second letter, and having sealed both, he mistakes the addresses, a duke and peer receives one of these two letters, and opening it to read these words: Master Olivier, do not miss, as soon as you receive this, to send me my supply of hay.... His farmer receives the other: he opens it, and asks for it to be read: it can be found: Sir, I received with a blind obedience the orders it has pleased to your greatness…."

Jean de La Bruyère, 1688

Chapter six: The development of a greeting signal in wild chimpanzees

Gargantua, from three to five, was nurtured and established in all proper discipline by the commandment of his father, and he spent time as the little children of the country: that is to eat, drink and sleep, to eat, sleep and drink, to sleep, drink and eat."

François Rabelais, 1542

Chapter seven: Modification of grunt morphology over development

"In sum, the example and education have done little else than to call her attention to the sounds that she was already sketching or found by herself, to cause their repetition or their completion, to lead on their side her preference, or brought them to emerge or float in the multitude of other similar sounds. But all initiative belongs to her."

Hyppolite Taine, 1876

Chapter eight: General discussion

"They forgot the origin of these signs, as soon as their use was familiar, and it fell into the mistake of thinking they were the natural names of the most spiritual things. They even imagined they would perfectly explain their essence and nature, although they expressed only very imperfect analogies. Such abuse appears significantly in the ancient philosophers, and it was preserved in the best of the moderns, and it is the main cause of slow progress in our way of thinking."

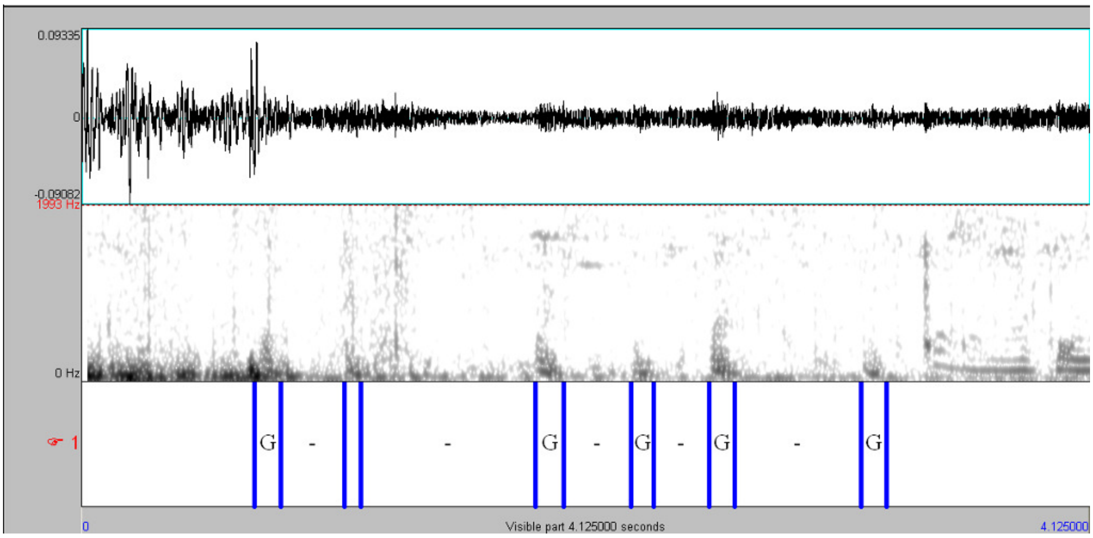
Étienne Bonnot de Condillac, 1746

Appendix B

Table B: Detail of the community composition during the 16 months of study.

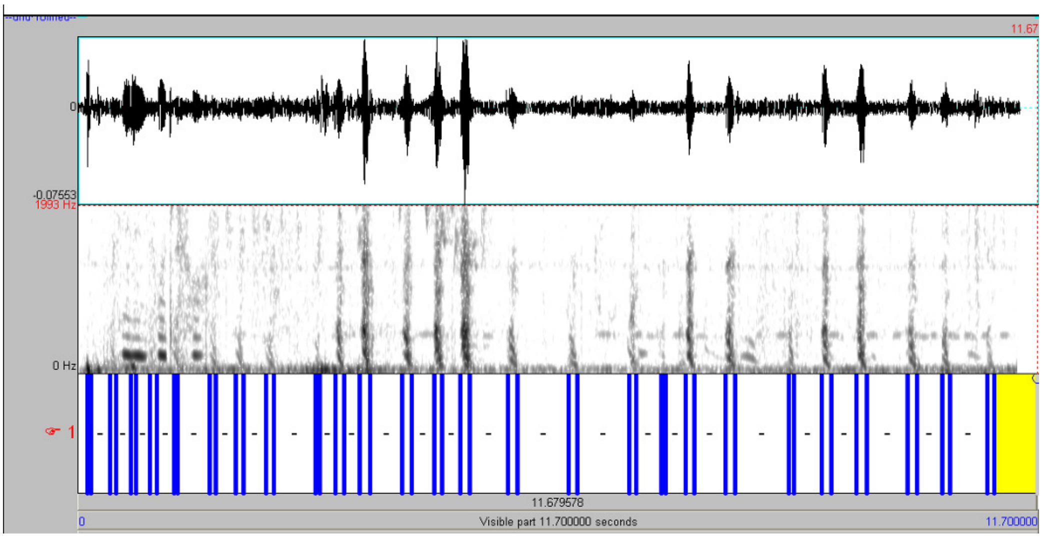
Year	Month	Adult males	Adult female	Subadult male	Subadult female	Juvenile male	Juvenile female	Infant males	Infant female	Baby male	Baby female	Total
2007	January	10	25	8	5	4	9	5	7	2	3	78
	February	10	25	8	5	4	9	5	7	2	4	79
	March	10	25	8	5	4	9	5	7	2	4	79
	April	10	25	8	5	4	9	6	7	1	4	79
	May-July											
	August	9	23	7	5	4	9	7	10	0	2	76
	September	9	23	7	5	4	9	7	11	0	1	76
	October	9	23	7	5	4	9	6	11	0	2	76
	November	9	23	7	5	5	9	6	11	0	2	77
	December	9	23	7	5	5	9	5	11	0	2	76
2008	January	9	22	7	5	5	9	5	12	0	1	75
	February	7	22	7	5	5	10	5	11	0	1	73
	March-June											
	July	7	22	8	6	4	10	5	11	0	1	74
	August	6	21	8	6	5	10	4	11	0	1	72
	September	6	21	8	6	5	11	4	11	0	1	73
	October	6	21	8	6	5	11	4	10	0	2	73
	November	6	21	8	7	5	10	4	10	0	2	73
	December	6	21	8	7	5	10	4	10	0	2	73

Appendix C



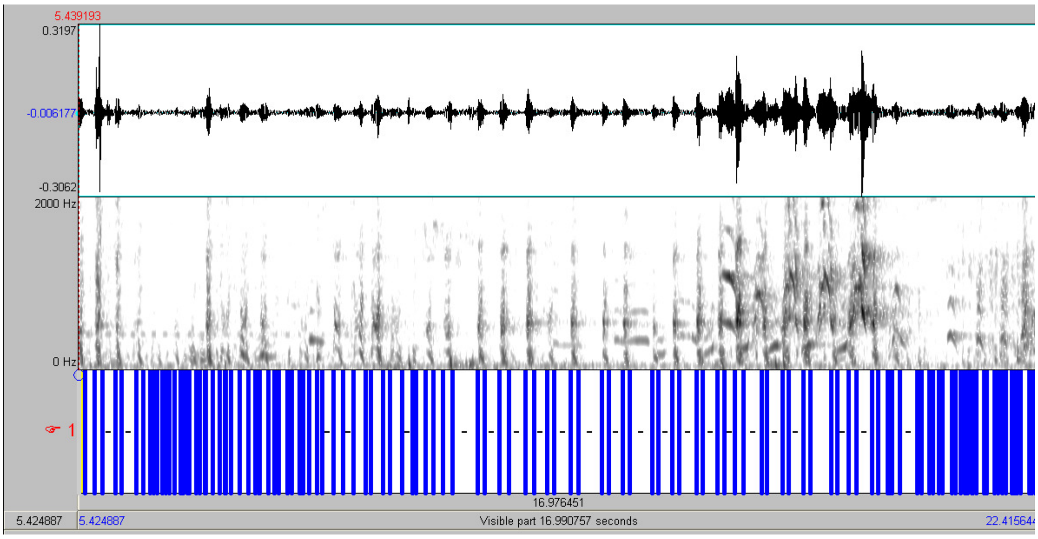
G1	G2	G3	G4	G5	G6

Figure C.1: Spectrogram and sequence description of pant-grunts given by the female Kalema (Kl) when encountering a male, Tinka. The colours and letters indicate G: Grunt, I: Inhalation and P: Pant.



G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	G11	G12	G13	G14	G15	G16	G17	P	G18	G19	G20	G21	G22	G23	G24	G25

Figure C2: Spectrogram and sequence description of pant-grunts given by the female Kalema (Kl) when encountering the alpha male, Nick. The colours and letters indicate G: Grunt, I: Inhalation and P: Pant.



G1	G2	G3	G4	I	G5	I	G6	I	G7	I	G8	I	G9	G10	I	G11	P	P	G12	I	I	G13	G14	G15	G16

P	G17	G18	G19	G20	G21	G22	G23	G24	G25	G26	G27	G28	G29	G30	G31	G32	G33	G34	G35	G36	I	G37	P	P	P

P	P	I	P	P	P	P	P	P	P	P

Figure C.3: Spectrogram and sequence description of pant-grunts given by the female Kalema (Kl) when encountering the alpha male and grooming him. The colours and letters indicate G: Grunt, I: Inhalation and P: Pant.

Appendix D

Table D: Participation of each immature individual to each type of analysis presented in Chapter six with reasons explaining why individuals did not participate to one or several analyses. Y: participates to the analysis, N: does not participate to the analysis. When immature individuals were observed in two periods of development, their participation in each age class were represented by one letter each with the lowest age class first.

Focal individual	Frequency analyses- general context - Analyses 1,2,3,4,4-a	Proportional analyses vocalisations- Analyses 2-a, 2-b	Similarity with mother- frequency analyses- Analyses 4-b, 4-c	Similarity with mother - Proportion analyses - Analysis 4-d	Reason
Kathy	Y	Y	Y	Y	
Faida	N-Y	N-Y	N-Y	N-Y	Time focal and number of grunts too low
Klauce	Y-Y	Y-Y	Y-Y	Y-Y	
Kox	Y-Y	Y-Y	Y-Y	Y-Y	
Karibu	Y-Y	Y-Y	Y-Y	Y-Y	
Marion	Y-Y	Y-Y	Y-Y	Y-Y	
Rafia	Y-Y	N-Y	Y-Y	N-Y	Grunt number too low
Honey	Y	Y	N	N	No mother
James	Y	Y	Y	Y	
Sokomoko	Y	N	Y	N	Grunt number too low
Sharlot	N	N	N	N	Time focal and number of grunts too low
Night	Y-Y	Y-N	Y-Y	N-Y	Grunt number too low
Kasigwa	Y-Y	Y-Y	Y-Y	Y-Y	
Zak	Y-Y	N-Y	Y-Y	N-Y	Grunt number too low
Ramula	Y	N	Y	N	Grunt number too low
Monika	N	N	N	N	Time focal and number of grunts too low
Zed	Y	Y	N	N	No mother
Helen	Y	N	N	N	Grunt number too low- No mother
Karo	Y	N	Y	Y	Grunt number too low
Kumi	Y	Y	Y	Y	
Janet	Y	Y	Y	Y	
Pascal	Y	Y	N	N	No mother
Frank	Y	Y	Y	Y	
Katia	Y	N	Y	Y	Grunt number too low
Kana	Y	Y	Y	Y	
Zig	Y-Y	N-Y	Y-Y	Y-Y	Grunt number too low
Rose	Y-Y	N-N	Y-Y	Y-N	Grunt number too low
Nora	Y	Y	Y	Y	
Zalu	Y	Y	N	N	No mother
Bahati	Y	Y	Y	Y	
Kwezi	Y	Y	Y	Y	
Fred	Y	Y	Y	Y	
Kato	Y	Y	Y	Y	
Hawa	Y	Y	N	N	No mother
Simon	Y	Y	Y	Y	

Appendix E

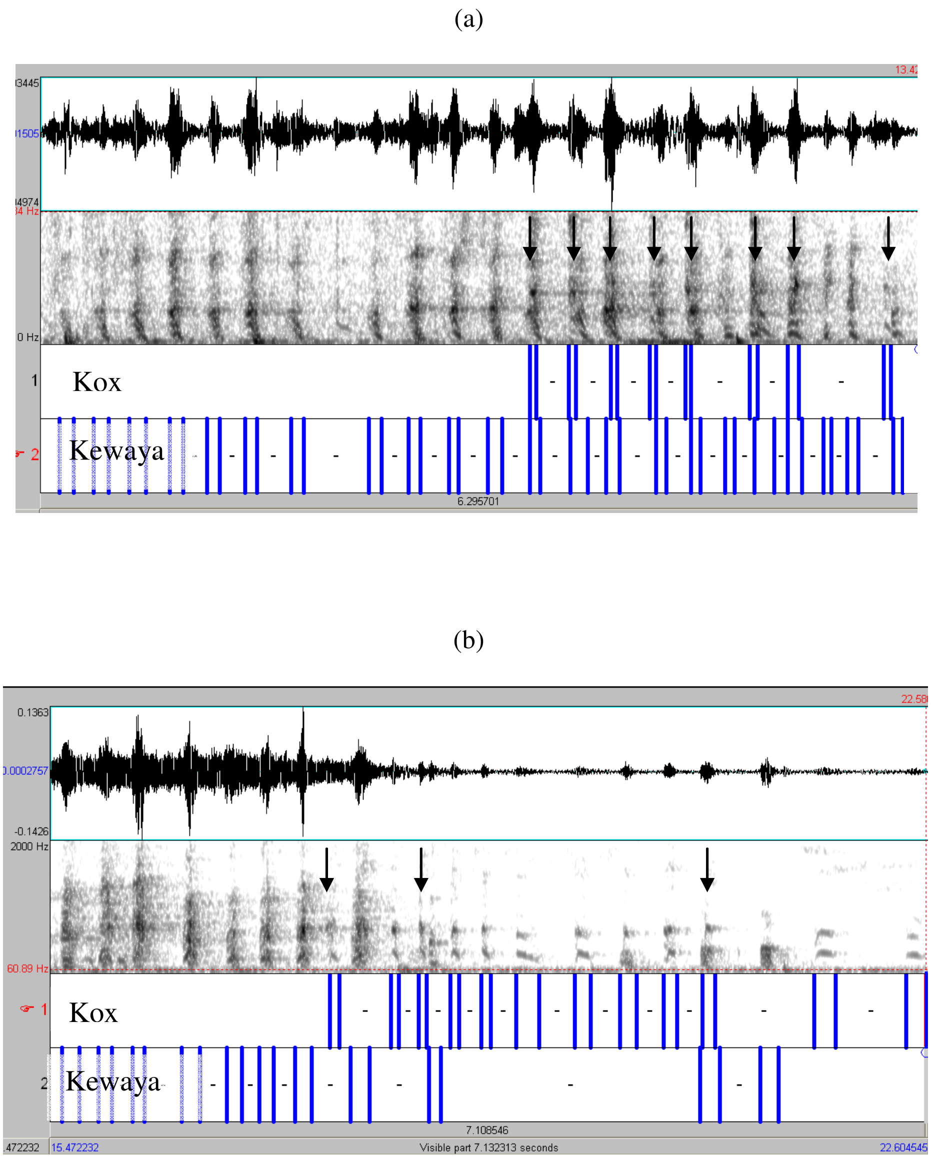


Figure E.1: Examples of grunt sequences produced by the mother and her infant when calling together. Temporal matching of grunts between Kewaya (line 2) and her daughter Kox (line 1) when pant-grunting to the male Bwoba, approaching him in two different encounters (a) and (b). Arrows represent calls that were produced at the same time.

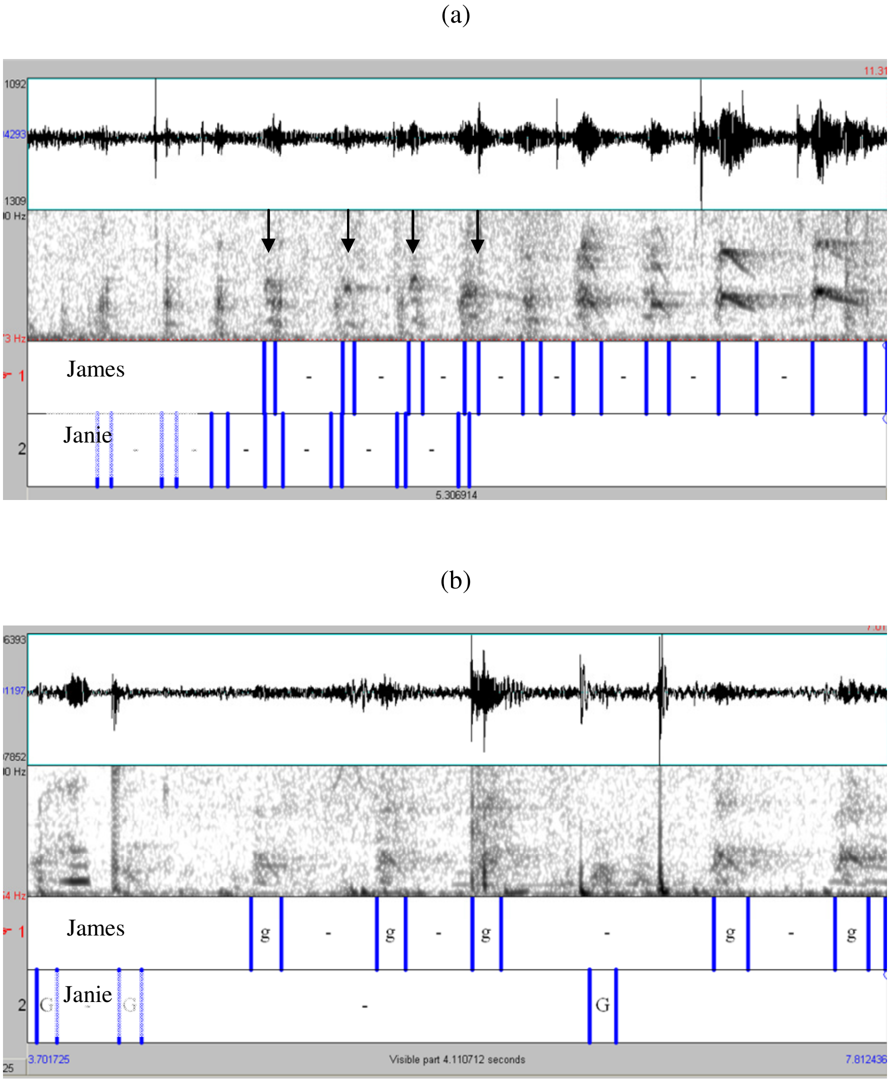


Figure E.2: Temporal matching of grunts between Janie (line 2) and her son James (line 1) when pant-grunting to (a) the male Bwoba not moving when he passed nearby and (b) the group of Kwezi, Kwera, and Kalema approaching them. Arrows represent calls that were produced at the same time.