N° Ordre de la thèse : 4531

Année/Year 2012

UNIVERSITE DE RENNES 1

-

UFR SVE

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UMR 6552 ETHOS

UNIVERSITY OF ST ANDREWS

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SCHOOL OF PSYCHOLOGY

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ORIGINS OF MIND

JOINT PHD

For the completion of the status of

DOCTEUR DE L'UNIVERSITÉ DE RENNES 1

sous le sceau de l'Université Européenne de Bretagne
Mention: biologie, Ecole Doctorale Vie Agro Santé

and

DOCTOR OF THE UNIVERSITY OF ST ANDREWS

Mention: philosophy

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SOCIAL LIFE AND FLEXIBILITY OF VOCAL BEHAVIOUR IN DIANA MONKEYS AND OTHER CERCOPITHECIDS

PhD viva held in Paimpont, on the 12th of july 2012, in front of the following committee:

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ACKNOWLEDGMENTS / REMERCIEMENTS

First of all, I am very grateful to all my PhD committee. Thank you to Pr Nicolas Mathevon and Dr Thomas Geissmann for accepting to read and comment my work. I would also like to thank Dr Roman Wittig and Pr Catherine Blois-Heulin for accepting to be examinators.

I am deeply grateful to Pr Klaus Zuberbühler , whom I first contacted 2008 and who accepted to give me a first experience in field primatology. He later accepted to co-supervise a joint PhD project and introduced me to Dr Alban Lemasson. Je suis profondément reconnaissante envers Dr Alban Lemasson que je connais depuis début 2009, pour avoir soutenu le projet d'une étudiante débutante en éthologie qui voulait partir trois mois en Côte d'Ivoire et boucler un rapport de master 2 en deux semaines ! Merci également de m'avoir poussée, d'avoir été compréhensif dans les moments difficiles et d'avoir cru en mes données parfois plus que je ne l'ai fait ! Mes remerciements vont à Martine Hausberger, directrice de l'UMR 6552 ainsi qu'à Daniel Cluzeau, directeur de la station biologique de Paimpont, pour m'avoir accueillie dans leur structure et m'avoir permis d'entreprendre une thèse dans de bonnes conditions.

Une thèse de doctorat, surtout lorqu'elle est co-encadrée et comprend de nombreuses missions à l'étranger, nécessite les compétences et l'efficacité de *nombreuses secrétaires* qui gèrent l'administratif (la paperasse !). Merci à Annick Guyomard, la secrétaire de l'Ecole Doctorale Vie, Agro, Santé, ainsi qu'aux secrétaires de la station biologique de Paimpont, Fabienne Perron et Catherine Racineux. Merci également à Béatrice Durand et Laetitia Ahimou du Centre Suisse de Recherches Scientifiques à Abidjan. I thank Mrs Helen Sunderland from the School of Psychology and Mrs Karen Rae from St Andrews foreign office at St Andrews University. Last but not least, 'hip hip hip, hourrah' à nos deux irremplaçables wonderwomen du secrétariat Rennais, j'ai nommé Sylvie Dufresne et Isabelle Simier!

A la station Biologique de Paimpont, petit havre de paix breton qui fournit des conditions de travail optimales, je remercie les animaliers Philippe et Arnaud pour leur conscience professionnelle et leur disponibilité. Un grand merci à nos « mamans » les cuisinières pour tous ces bon repas qui ont stimulé nos neurones (et engendré des siestes aussi) et ont fortement contribué au maintien de mon poids ! Merci enfin à Léon, notre gardien de la bonne humeur, même s'il n'a à ce jour pas réussi à me faire un « glaçon ». Merci aux châtelains pour leur hospitalité.

Au sein de *l'UMR6552*, je remercie dans l'ordre chronologique Hélène B qui m'a chaleureusement accueillie à mon arrivée et dépannée/éclairée/démystifiée en statistiques plus d'une fois. Merci à mes collègues et compagnons de galère Florent P, Agathe L, Carole S, Clémence L, Amandine C, le trio de choc Audrey M, Hélène T et Céline R, ainsi que Dorothée K, Jacques P, Séverine H, et Laure D. Une pensée pour Kévin R, ex-colloc parfait et Camille C, magnétiseuse et stagiaire hors pair! Merci à Caroline C. pour son soutien personnel dans un passage difficile ainsi que ses bons conseils pour la santé! Merci également à toute l'équipe des covoitureurs Rennes-Paimpont, d'avoir bien voulu balloter des boulets dans leurs bolides…

At the *School of Psychology*, I am thankful to Katy H and her cookies, Cat H, Marion L, Kate A, Thibaud G and all my other other PhD fellows. I am grateful to Brian the informatician for his patience with my French computer!

Au sein de l'*UMR6553*, je remercie Nelly Ménard pour avoir accepté la collaboration inter-labos dans le cadre des analyses génétiques. Un grand merci à Dominique V pour sa patience aves mes échantillons, ainsi qu'à Eric P pour sa contribution au stage de Camille et ses scripts magiques sous R. Merci aux « verdeterrologues » CharlèneB, Daniel C, Guénola P, Hoel H, Muriel G et Raphaël M pour leur dynamisme et pour avoir recruté un stagiaire Choletais. Merci également à Céline G, Mathieu L, Charlène B, Pascaline L et Radosoa A pour tous les bons moments passés ensemble.

Au *Centre Suisse de Recherches Sscientifiques*, je remercie profondément Pr Bonfoh et Dr Koné pour avoir accepté et soutenu mes missions de terrain. Merci à Karim Ouattara pour ses bons

conseils et son amitié et à Anderson Bitty pour son aide logistique. Une pensée pour la maman Béa, le tonton Rodrigue et la tata Geneviève, ainsi qu'aux cuisinières qui ont elles aussi fortement contribué à mon poids !

A *Abidjan*, je remercie chaleureusement ma cousine Johanna et sa famille pour la porte qui était toujours grande ouverte et les week-ends à Assini. Merci à Abdoulaye pour son hospitalité, ainsi qu'à Bernadin et Nina pour leur amitié.

Dans les *villages de l'ouest de la Côte d'Ivoire*, j'ai une pensée émue pour Germain, feu chef canton Oubi qui soutenait la cause des chercheurs. Merci au Lt Kramo pour son amabilité, à Natacha pour sa maison accueillante ainsi qu'aux habitants de Paulé Oula, Gouléako II et Taï pour leur chaleureux accueil, avec une pensée particulière à toutes les familles qui ont perdu des proches lors des évènements de 2011.

Au sein du *TMP*, Je remercie les Prs Zuberbühler et McGraw pour avoir accepté de m'envoyer sur le terrain et avoir rendu cette étude possible. Merci à Ferdinand pour m'avoir enseigné les bases du terrain en forêt de Taï (et toujours ramenée saine et sauve au campement), à Frédérique pour nos discussions, nos chansons (viens voir, viens voir…) et nos fous rires. Merci à vous deux pour le travail efficace toujours mené dans la bonne humeur. Merci également à Bertin, Gérard, Richard, feu Valentin et Cyrille pour les bons moments partagés au campement.

I thank all my '*fieldmates*' for sharing the great and sometimes pathetic situations we encounter in the field (car break, roof crash, army ant invasion…): Ryan, Mark and Henk.

From the *TCP& WCF*, I thank to the 'girls crew' for their warm welcoming: Nadin Livia, Lydia, Sonja, Geneviève and Emmanuelle. I am grateful to the *film crew* (Edward, James and Martyn) for the car trips and enjoyable company. Merci au Pr Christophe Boesh pour son soutien dans les moments de crise avec la population locale. Un énorme remerciement également à Sidiki, coursier et chauffeur tout terrain 24/7 même sans chaussettes dans ses bottes !

In the *zoos*, I thank Mark Kingston Jones and the primate keepers for permission to study the animals. I am also thankful to David & Maureen Jones as well as Warren for their welcoming home, our interesting discussions and for sharing the soul touching sounds of folk music.

Muchas gracias au groupe français Shaka Ponk pour avoir rythmé la rédaction de mon manuscrit !

Je remercie *tous mes proches* pour avoir suivi de plus ou moins près mon épopée simiesque. Merci à mes amies de toujours, Lucie et Elisa, pour continuer à m'accepter comme je suis malgré la vie qui parfois malmène nos amitiés et nous fait prendre des chemins très différents.

Merci à Mathias pour avoir fait un bout de chemin à mes côtés lors de ma thèse.

Merci à mes frères pour avoir grandi auprès d'une énergumène telle que moi, ainsi qu'à mes parents pour leur amour et leur support inconditionnel. Ce mémoire leur est dédié.

J'ai une tendre pensée pour le soutien et les attentions permanentes de Kevin.

Enfin, j'ai une dernière pensée pour les femelles Diane nommées Aya, Benja, Candy, Klg, Kemi, Nora, Paula, Bijou, Chérie, Eva, Fiona, Eva Java, Ikla, Melo et Nina qui ont toléré ma présence plus ou moins discrète et mon micro inquisiteur pendant plusieurs mois. Je souhaite du fond du cœur que leur forêt soit préservée afin que cette espèce fascinante se perpétue en Afrique et que nos générations futures puissent à leur tour s'émerveiller et apprendre d'elles.

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CHAPTER 1 – GENERAL INTRODUCTION

1.1 – Vocal communication and social life

1.1.1 – Communication is a social need

1. 1.2 – Communicating through a variety of signals

Communication, a process inherent to all living organism, is required for vital functions such as reproduction and is a prerequisite for social life (Goldberg 1998). As defined by (Smith 1969), communication requires an emitter, a receiver and a signal which can carry a variety of messages. Whether the concept of information carried through messages is relevant to animal communication is much debated (e.g. (Dawkins & Krebs 1978; Rendall et al. 2009; Carazo & Font 2010; Scott-Phillips 2010; Seyfarth et al. 2010b). Here, we will use Harper & Maynard Smith (2003)'s definition of a signal ("Any act or structure which alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved") and we will consider communication as an exchange of signals, that is to say the completion of signals and the corresponding responses (Carazo & Font 2010). The nature of signals can be very diverse (electric, chemical, tactile, visual or acoustic: vocal and non vocal). Signals are partly constrained by the emitter's morpho-anatomy, life mode and the environment of propagation. While communication is often multimodal, each sensory modality has its advantages and drawbacks. Vertebrate species living in visually reduced habitats rely strongly on vocal signals (birds: Catchpole & Slater 1995; cetaceans: (Tyack & Sayigh 1997); nonhuman primates: (Marler 1965; Gautier 1988). Communication through vocal signals becomes advantageous because their propagation is omni-directional (360 degrees) and can be addressed to a particular or a large audience at short and long distances depending on the communicative needs. Nonetheless, compared to other sensory modality, vocal communication suffers from the distortion of signals during propagation (Richards & Wiley 1980; Brown et al. 1995; Mathevon et al. 2008) and the time window for signal reception is extremely short. Nonhuman primates use olfactory communication, which is primarily used in nocturnal species (Schilling 1979), but also to a lesser extent in some diurnal species (De Brazza monkeys: Gautier-Hion & Gautier 1978; Gautier-Hion et al. 1999). They also use visual communication, mainly exploited for short range communication (such as threatening gestures) and particularly in species that live in open habitats (Hinde & Rowell 1962;

Kummer & Kurt 1965; Marler 1965). Tactile communication plays an important role in the short distance communication of all primate species (Deputte 1981). Eventually, vocal communication is widely used amongst primates, not to mention the fact that the majority of primate species live in African or South-American tropical forest. It is hence pertinent to focus on this mode of communication.

1.1.3 – Production, usage and comprehension of signals

Any mode of communication involves three components which are signal production (the acoustic structure of a vocal signal), signal usage (the mode of emission and the context of emission) and signal perception (the capacity to discriminate) and comprehension (the decoding of messages and subsequent behaviours), equally deserve attention because they may exhibit differences in the developmental processes or involve different neural mechanisms (Seyfarth & Cheney 2010). Production and usage enable us to study the social-signal link from the point of view of the emitter while perception and comprehension focuses on the point of view of the receiver. Social life puts strong selective pressures on all these aspects and social needs can hence be comprehended from all three aspects of communication.

1.1.4 – A co-evolution of communication with social needs

Given that social life and communicative needs are intimately entangled, it is intuitive to acknowledge a co-evolution between social systems and vocal capacities. Seyfarth et al. (2005) demonstrated with field experiments that baboon's knowledge of their companions' social relationships shows characteristics similar to properties of several mechanisms underlying language, because they are hierarchically structured, open-ended, rule-governed, and independent of sensory modality. These results suggest that the latter could have evolved from complex social knowledge in humans' pre-linguistic ancestors. In line with this idea, the social brain hypothesis suggests that brains of nonhuman primates have not evolved to deal with ecological problem-solving tasks but that large brains reflect the computational demands of the complex social systems that characterize the order (Dunbar 1988; Whiten & Byrne 1988). Dunbar proposed in 1998 the vocal grooming hypothesis which suggests that conversations in humans would function as a vocal grooming replacing the physical grooming, becoming too time consuming in bigger groups. Increased social needs would have lead to increased cognitive (Zuberbühler & Byrne 2006) and communicative (Lemasson 2011) abilities. Pinker (2003) has theorized that the human language faculty would be a complex biological adaptation for communication in a knowledge-using, socially interdependent lifestyle. Alongside with this theoretical 'social-complexity hypothesis for communication', McComb & Semple (2005) have demonstrated that increases in the size of vocal repertoires were associated with increases in group size but also time spent grooming in 42 species of primates. The hypothesis has also been tested on three species with different group structures, and the study revealed that the size but also the complexity (structural variability of the call types and patterns of units assembling) of their vocal repertoire, as well as females calling rates, paralleled the degree of complexity (groups composition and organisation) of species' social structure (Bouchet et al. submitted). This is not specific to primates, since correlations between the size of the vocal repertoire and the size (birds : (Freeberg 2006 or the group composition (marmots : Blumstein 2003) and the species mobility (orcas : May-Collado et al. 2007) have also been found.

1.1.2 – Vocal flexibility, a phylogenetic gap?

1.1.2.1 – Definitions

Here, we will define the vocal variability as the fact that a vocal signal can have a more or less variable structure amongst or between individuals, and the vocal flexibility as a qualitative (flexibility in production) or quantitative (flexibility in usage) modulation of a vocal signal over time. Social life is one of the motors of flexibility, but the link between sociality and flexibility in the production of calls is still debated in nonhuman primates (Hammerschmidt & Fischer 2008; Snowdon 2009; Lemasson 2011).

1.1.2.2 – Vocal flexibility in production in birds and non-primate mammals

Vocal flexibility is a well known and much studied phenomenon in songbirds (Hausberger et al. 1995; Brown & Farabaugh 1997), cetaceans (McCowan & Reiss 1995; Miller & Bain 2000) but also in bats (Boughman 1998). In songbirds, young individuals' vocal development contains a phase in which they learn their songs from a tutor and several species called open-ended learners can learn new songs throughout their life (Briefer 2008).

Bottlenose dolphins learn whistles from other group members and use them in vocal matching interactions (Janik 2000; Tyack 2000). Birds and cetaceans can also learn to produce other species' vocalisations (Pepperberg 1997; Foote et al. 2006; Kremers et al. 2011). Vocal learning has been extensively studied in animal kingdom, both concerning the production learning and the contextual learning (Heyes & Galef 1996; Janik & Slater 2000). In contrast, early studies on vocal flexibility in nonhuman primates through experiments of hybridization (Geissmann 1984; Brockelman & Schilling 1984), cross-fostering (Owren et al. 1992), deafening (Talmage-Riggs et al. 1972) or social deprivation (Winter et al. 1973; Newman & Symmes 1974) revealed that monkey' and apes' vocal repertoires are largely fixed and genetically determined (Seyfarth et al. 1997; Hammerschmidt & Fischer 2008). In addition, neurological studies revealed that the production of some vocalisations in squirrel monkeys is related to the limbic system and processed in sub-cortical areas associated with emotion, while humans possess a direct neuronal pathway between the motor cortex and the larynx which accounts for the subtle control of vocal production (Ploog 1981; Jürgens 2002). It has also been showed that electrical stimulations of the limbic and subcortical structures alone induce calling (Ploog 1981). Given the numerous analogies between birdsongs or cetacean calls and human speech, especially regarding their high level of acoustic flexibility and the importance played by the social experience of callers (Snowdon & Hausberger 1997), there seems to be a phylogenetic gap between humans, other nonhuman primates and birds or cetaceans (Lemasson 2011).

1.1.3 – Theories of origins of human language

There has been a long term controversy in the scientific community regarding the origins of language and human speech, sometimes considered as the hardest problem in science (Christiansen & Kirby 2003). Although there is no direct evidence of evolutionary paths, the origins and evolution of language becomes a tractable problem when tackled at an interdisciplinary level, which enhances the accuracy of ethological approaches on the spontaneous use of calls in primates (Hauser et al. 2002; Griebel & Oller 2008). Three main theories are currently debated to account for the emergence of language and human speech.

1.1.3.1 – Theory of vocal origins

This theory claims that human language finds its precursors in nonhuman primate calls, deep inside the primate lineage (Masataka 2003; Snowdon 2009; Zuberbühler et al. 2009; Lemasson et al. 2012). Several characteristics that are fundamental in language can indeed be described in a primitive form in nonhuman primates' vocal communication, such as semanticity (Diana monkeys: Zuberbühler et al. 1999, Vervet monkeys: Seyfarth & Cheney 2003) , syntax (gibbons: Clarke et al. 2006, Putty-nosed monkeys: Arnold & Zuberbühler 2006), social influences called audience effects (food calls of cotton-top tamarins: Roush & Snowdon 2000, screams of chimpanzees: Slocombe & Zuberbühler 2007) and conversations (pygmy marmosets: Snowdon & Cleveland 1984, squirrel monkeys: Symmes & Biben 1988). All these examples show that these properties can be found in some old world monkeys, some new world monkeys as well as in some apes. Increased control of vocal production would have been a major step in the emergence of language, but the limited flexibility in vocal production of nonhuman primates is the main weakness of the vocal origin theory, showing that human and nonhuman primates strongly differ in the mode of acquisition of their communicative abilities. Nevertheless, the defenders of this theory also claim that the flexibility of nonhuman primate calls have been strongly under-estimated (Snowdon 2009; Lemasson et al. 2012).

1.1.3.2 – Alternative theories

Several authors claim that human language presents properties that are unique, notably a recursive and generative grammar (Chomsky 1981; Corballis 2003) and symbolism (Deacon 1997), which require a theory of mind that does not seem to exist in other animal species (Cheney & Seyfarth 2010). Other scientists argue that such properties cannot have appeared de novo but that neurological and cognitive underlying structures must have emerged progressively, meaning that precursors are likely to be found in animals (Christiansen & Kirby 2003). Hence, some authors claim a gestural origin of language (Corballis 2003; Vauclair 2004). Defenders of this view argue that language is not uniquely oral, that gestures come ontogenetically before sounds in humans, and that gestural communication in apes are lateralized (the preferential use of the right hand revealing a control by the left hemisphere) and related to the activation of a part of the brain which is homologous to the area of Broca controlling language production in humans (Corballis 2003; Taglialatela et al. 2006). Apes' gestures and language share properties of flexibility in learning, usage, referentiality and intentionality (Meguerditchian & Vauclair 2008). Gestures of nonhuman primates hence seem more flexible and controlled than their vocalisations. In addition, the mirror system hypothesis (Rizzolatti & Arbib 1998; Arbib & Bota 2003) proposes that the mirror system, a region in the monkey brain in which neurons active when the monkey executes a specific hand action are also active when the monkey observes another primate carrying out that same action, is a key element in the emergence of imitation that was in turn a crucial step for the language property that utterances carry similar meaning for speaker and hearer (Arbib 2002). Recent developments claim that a vocal and a gestural origin are not necessarily exclusive and tend to a multimodal origin of language (Meguerditchian et al. 2011; Lemasson 2011; Taglialatela et al. 2011). We will now present new advances challenging the 'phylogenetic gap' associated with the supposed limited vocal flexibility of nonhuman primates, which is the basis of the disagreement between language-origin theories.

1.2 – Vocal flexibility under social influences in nonhuman primates

We will focus here on the flexibility of production and usage. There is no debate on the fact that social life has a motor role on call usage in nonhuman primates (Seyfarth et al. 2010a) but regarding production, while the vocal repertoire of the species is clearly genetically determined in nonhuman primates, a growing number of publications reveal that individuals remain able to change the detailed acoustic structure of their calls (see Snowdon 2009 for review and I am co-author of a more recent review that can be found in this manuscript as an annex). First, the recent technical progress in acoustic recordings and analyses (telemetry recording: Lemasson et al. 2004, acoustic analyses software: (Owren 2008) as well as the focus on social calls and a multi-level approach of repertoires (Hauser 2000) have favoured the discovery of unexpected subtle levels of flexibility. Second, the increased number of studied species, notably forest-dwelling species which rely on vocal signals to communicate due to poor visibility in their habitat, but also a shift in the scientists' interests from alarm calls to other more social call types, can also have favoured the discovery of unprecedented vocal flexibility (Lemasson 2011).

1.2.1 – Recent neurological findings

In chimpanzees, Taglialatela et al. (2011) have shown that some attention-getting vocalisations, when produced in addition to a gesture, reinforce the activation of the brain areas homologous to human language. In addition, it has recently been shown that the production of coo calls in Japanese macaques seems, to certain extends, to be under voluntary control via the involvement of cortical neurons when the emission has been experimentally conditioned but not when the emission is a mere reflex “coo call” in reaction to food (Coudé et al. 2011). Contrary to the conclusions drawn from the first neuro-atonomical studies, the control of vocal production and vocal usage is not limited to the limbic system and the sub-cortical areas. Behavioural studies confirmed the existence of such control in other species (playback of background noise interrupting tamarin’s calling: Miller et al. 2003, operant conditioning of call utterance in gibbons: (Koda et al. 2007).

1.2.2 – A multi-level approach of vocal repertoires

Most studies on vocal communication of nonhuman primates are confined to the analysis of repertoires at the call type level while a multi-level approach is commonly used to study human speech, bird and whale song (Payne & McVay 1971; Chomsky 1986; Catchpole & Slater 1995). Several studies adopting this approach have revealed interesting variability properties in nonhuman primates’ vocal repertoires. A vocal sequence will here be defined as a series of calls separated by a silent gap, a call as one or several sound units separated by a short silent gap, and sound units as basic sonor elements (Hauser 2000; Bouchet et al. 2010). There are two theoretical ways to generate acoustic variability, which are the variation of structural parameters (amplitude, frequency and duration) and the concatenation of discrete sound elements (i.e. sound units into calls and calls into vocal sequences).

1.2.2.1 – Variation of acoustic parameters within a signal

A focus on the characteristics of the acoustic structure (e.g. duration, frequency modulation pattern, energy distribution) at the call level of nonhuman primates’ vocalisations reveals a high variability in the fine structure of calls. This enables a distinction between subtypes of calls that can be classified in different functional categories such as alarm call subtypes coding for different types of predators (prosimians: Macedonia 1990– new world monkeys:

Wheeler 2010– old world monkeys: Cheney & Seyfarth 2010; Zuberbühler et al. 1997, apes: Slocombe et al. 2008), food call subtypes coding for features of the feeding event (new world monkeys: Benz 1993, old world monkeys: Hauser & Marler 1993, apes: Slocombe & Zuberbühler 2006; Clay & Zuberbühler 2009), distress calls coding for the role of the protagonists involved in a conflict (old world monkeys: Gouzoules et al. 1984; apes: Slocombe & Zuberbühler 2007; Slocombe et al. 2009), copulation calls coding for the presence/absence of ejaculation during copulation (old world monkeys: Pfefferle et al. 2008). There are also subtle subtypes of contact calls sand call variants within the subtypes coding for social affiliations in several old world monkeys (macaques: Green 1975, vervets: Cheney & Seyfarth 1982b), Campbell's monkeys: Lemasson et al. 2003; Lemasson & Hausberger 2011).

1.2.2.2 – Concatenation of sounds

Many calls are composed of discrete units concatenated in various ways (i.e. repetition, affixation, combination), and calls can also be concatenated into sequences (as defined above). Complex calls can be produced by the repetition of units, for example red-capped mangabeys produce single 'Ti' as well as multiple 'Titi' (Bouchet et al. 2010). Combinations of units into calls are also frequent, such as the 'TiUh' call of red-capped mangabeys emitted during call exchanges. Calls can result from an affixation process where a 'root' unit is followed by a 'suffix', for example male Campbell's monkeys can affix an 'oo' unit to the 'hok' and the 'krak' calls, which respectively code for an eagle alarm and a leopard alarm (Ouattara et al. 2009a). The 'hokoo' signal codes for a general canopy alarm while the 'krakoo' signal codes for a general ground disturbance. Campbell's monkeys affix to the SH1 unit (encoding matriline membership) an arched frequency modulation (encoding social affinities) to form the very common CH call (Lemasson & Hausberger 2011). Calls can in turn be combined into sequences of calls, such as 'Pyows' and 'Hacks' of male putty-nosed monkeys which are both emitted in predatory contexts but generate a new message of group departure when combined into a 'P-H' sequence (Arnold & Zuberbühler 2006) or the 'wa', 'hoo' and 'waoo' notes of Gibbons combined into sequences named songs that were either coding for a predatory context or not (Clarke et al. 2006). Red-capped mangabeys utter vocal sequences which length and complexity seem to vary with the size of the audience (Bouchet et al. 2010). Eventually, studies on the organisations of acoustic structures at higher levels show the existence of sequences of calls which potentially carry information in the type and order of components as well as the rhythm of delivery. Food calls of bonobos are emitted in sequences which composition varies (Clay & Zuberbühler 2009; Clay & Zuberbühler 2011) while in tamarins (Elowson et al. 1991; Caine et al. 1995), chimpanzees (Hauser et al. 1993) and macaques (Dittus 1984), the number of repetitions of the same call varies with the amount of food available. Male Campbell's monkeys produce 6 types of loud calls ('Boom', 'Krak', 'Krak-oo', 'Hok', 'Hok-oo' and 'Wak-oo') that are usually emitted in sequences of 2 to 40 units. Analyses revealed a complex combinatorial system relying on associations and order of succession of these calls to encode diverse information such as the nature and proximity of a danger, the type of predator and the emitter's activity (Ouattara et al. 2009a). They even combine call sequences together, for example a sequence coding for tree falls is composed of a sequence coding for group gathering and departure followed by the sequence coding for acoustic predator detection. The rhythm of emission also carries information about the level of danger emergency and the emitter's intention to counter attack the predator or not (Lemasson et al. 2010b).

1.2.2.3 – Acoustic variability and social value of a signal

We presented so far examples of intra-individual acoustic variability with the context of emission, but these signals can also present inter-individual acoustic variability carrying identity information (Seyfarth & Cheney 2003). Several authors hypothesized that there is a link between the degree of structural variability (at the intra- and the inter-individual levels), and the social value of a call and its context of emission (Snowdon & Hausberger 1997; Griebel & Oller 2008). Vocalisations regulating intra-group relationships and directed to one or several receivers are likely to be under social pressures that favour high variability, encoding the emitter's identity but also the emotional state and the intended behaviours. In contrast, calls emitted in a less social context and directed to the whole group could be under selection pressures favouring stereotypy that guarantees the absence of ambiguities in the signal. This hypothesis has been recently validated by studies assessing the degree of variability in the vocal repertoire of several monkey species. Affiliative calls presented the highest degrees of variability in the structure of the calls and encoded most reliably identity (macaques: Rendall et al. 1998– babouins : Rendall et al. 2009–Campbell's monkeys : Lemasson & Hausberger 2011– Red-capped mangabeys : (Bouchet et al. 2012). On the contrary, alarm calls and food calls were more stereotyped (Campbell's monkeys: Lemasson & Hausberger 2011– Red-capped mangabeys : (Bouchet et al. 2012).

1.2.3 –Social context of communicative interaction

When compared to the vocal development of birds or cetaceans, little is known about the vocal development of young nonhuman primates, probably due an apparent lack of interest by researchers due to the strong fixity and genetic determinism observed in the past. Still, in adults, there is a good overview of the flexibility in production and usage.

1.2.3.1 – Development of acoustic structures in juveniles

As mentioned before, several early experiments lead the scientists to the conclusion that monkey and apes' calls were highly genetically determined. Still, the debate about vocal production ontogeny remains open because results are contradictory (Egnor & Hauser 2004). For example, cross-fostering in macaques revealed in one case some vocal learning (Masataka & Fujita 1989) while the same experiments lead to the conclusion of very limited modifications (Owren et al. 1993). In addition, most vocalisations of young primates were first described as similar to those found in adults (Newman & Symmes 1982; Seyfarth & Cheney 1997; Hammerschmidt & Fischer 2008), while other authors described acoustic variability due to maturational changes (Hauser 1989; Hammerschmidt et al. 2000). (Snowdon & Elowson 2001) described a "babbling" phenomenon in young pygmy marmosets, which first produce poorly formed trills and infant calls and progressively switch to well-formed trills and adult variants. Importantly, a longitudinal study in macaques has shown that inter-population differences do not appear until the age of 6-7 months old, suggesting an influence of experience and social learning (Tanaka et al. 2006).

1.2.3.2 – Flexibility of acoustic structures and social status in adults

Flexibility can be observed at several levels of vocal production, which will be described here after. First, several species are said to produce sex-specific call types, due to morphologic and hormonal differences. Indeed, several acoustic parameters are correlated with the physical properties of phonation organs (Riede 2010), correlated in turns with individual's body size and weight, or to specific features (Fitch & Hauser 1995; Ey et al. 2007). For example, male loud calls of guenons and mangabeys cannot be emitted by females due to the absence of extra-laryngeal vocal bags (Gautier 1971; Gautier & Gautier 1977; Waser 1982). Still, a number of anecdotic reports claim that sex-specific calls are not necessarily reflecting the other sex's incapacity to emit them. For instance, male squirrel monkeys can produce so-called female specific calls when stimulated electrophysiologically (Jürgens 1979; Smith et al. 1982). Female guenons can emit male alarm calls in case of impending danger if the latter remain silent (Ouattara et al. 2009b; Bouchet et al. 2010). Besides, several females gibbons have been reported to sing the part of their male partner's song (Geissmann 1983; Chen et al. 2008) and a few male individuals were reported to imitate the song phrase of a female (Geissmann 2002). It is hence possible that sex differences in vocal repertoires might reflect individual preferences for some call types, in agreement with the social role of the corresponding gender (Smith et al. 1982; Hohmann 1991; Bouchet et al. 2010), rather than an impossibility to emit some calls of the other sex.

Second, intra-group social bonds (affiliative and agonistic) guide the structuring of individuals' repertoire. Within social groups, partner preferences can be reflected in vocalisations, such as the "vocal sharing" phenomenon described in Campbell's monkeys, where females with strong affiliative bonds emit the same variants of contact calls while isolated females diverge from others (Lemasson et al. 2003). This phenomenon is dynamic and reflects the evolution of social preferences within the group over time through vocal convergences and divergences over long periods of time (Lemasson & Hausberger 2004). In Campbell's monkeys, it has been shown that degrees of similarity in females' calls are positively correlated to the strength of their social bond (Lemasson et al. 2011b).Long term convergence in the structure of social vocalisations have also been observed in marmosets several weeks after pairing (Snowdon & Elowson 1999) and in captive chimpanzees from diverse origins (Marshall et al. 1999) Hierarchical ranks can also be reflected by the acoustic structure of individual's vocalisations ('wahoo' of baboons: Fischer et al. 2004). Again, there is an adjustment in parallel with the dynamic of social networks, with the modification of acoustic parameters when dominance is lost (baboons: Fischer et al. 2004).

Third, the analysis of vocal interactions revealed a short-term phenomenon of vocal convergence where the receivers vocally respond to the emitter using a call which structure converges for one or several acoustic parameters (chimpanzees: Mitani & Brandt 1994; Mitani & Gros-Louis 1998; Japanese macaques: Sugiura 1998; gibbons: Geissmann 1999). Conversely, macaques can "exaggerate" their calls with higher pitch and longer duration when they are not answered, which augments the probability to obtain an answer (Masataka 1992; Koda 2004).

Fourth, flexibility can be observed in reaction to changes in the habitat, such as noise or visibility. For example, Brumm et al. (2004) found that common marmosets increased the sound level of their spontaneous calls in response to increased levels of white noise broadcast to them. Visibility also influences some characteristics of the acoustic structure of social calls (Japanese macaques: Koda et al. 2008; baboons: Ey et al. 2009). This phenomenon could be explained by an increased need of social cohesion due to the poor visibility.

Fifth, group membership also influences the flexibility of calls. Inter-group comparisons have revealed in several species that some calls reflect the belonging to a social group, a phenomenon described as dialects within groups (lemurs : Hafen et al. 1998) or between groups (e.g. chimpanzees : Mitani et al. 1999; Mitani et al. 1999; Crockford et al. 2004; Crockford et al. 2004; Braune et al. 2005 ; macaques : Tanaka et al. 2006 ; marmosets : de la Torre & Snowdon 2009). This could be explained by a genetic drift or differences in the habitat acoustic properties, but the explanation of a social learning phenomenon is highly plausible. For example, these dialects cannot be explained by genetic differences in lemurs (Hafen et al. 1998) or macaques (Tanaka et al. 2006), and cannot be explained by environmental factors in lemurs, chimpanzees and marmosets (Hafen et al. 1998; Crockford et al. 2004; de la Torre & Snowdon 2009).

Differences in the production and use of calls are also described between wild and captive animals (Lemasson & Hausberger 2004; Ouattara et al. 2009b). Eventually, captivity can be considered as a new ecological niche that has favoured the apparition of “vocal innovations” in Campbell’s monkeys (human alarm calls, Lemasson et al. 2004), chimpanzees (‘extended grunts’ and ‘raspberry’, Hopkins et al. 2007) and acoustic innovations in Orang-utans (whistling, Wich et al. 2009).

1.2.3.3 – Social learning of appropriate contexts of emission in juveniles

There are several evidences that young nonhuman primates learn to use vocalisations in the appropriate context from congeners (Seyfarth et al. 1997; Snowdon & Hausberger 1997; Naguib et al. 2009). There is a progressive refining of the contexts of emission during development, notably through observations of adults. For example, young vervet monkeys first emit eagle alarm calls in reaction to any flying object, then restrict this alarm call to any bird, then preferentially to birds of prey before eventually using it specifically in reaction to martial eagles (Seyfarth et al. 1980; Seyfarth & Cheney 1986). Similarly, young macaques learn to use the appropriate distress calls, which differ according to the identity of the opponent and the intensity of aggression (Gouzoules & Gouzoules 1989; Gouzoules et al. 1995). Chimpanzees' social grunts are first emitted to all group members and progressively directed to several individuals (Laporte & Zuberbühler 2011). Young marmosets (Caro & Hauser 1992) and tamarins (Roush & Snowdon 2001; Joyce & Snowdon 2007) learn the appropriate usage of food calls from their social partners through food transfers from adults.

Another important aspect of social life that needs to be learnt is the rules of vocal exchanges within the group. Contact calls are frequently emitted by adults which respect turn taking rules (e.g. marmosets: Snowdon & Cleveland 1984; vervets: Hauser 1992; macaques: Hauser 1992; Sugiura & Masataka 1995; Campbell's monkeys: Lemasson et al. 2010a), but young Campbell's monkeys break this rule twelve times more often than do adults (Lemasson et al. 2011a).

1.2.3.4 – Flexibility of call usage and social contexts in adults

Adult primates are able to adjust their call rate to the context, in the presence of a predator for example. High calling rates increase the risk of detection and female Diana monkeys living in the vicinity of chimpanzees or in poaching areas have learnt to remain silent when approached by chimpanzees or humans, which can follow them in the canopy or reach them from distance, while they produce alarm calls at high rates in reaction to eagles and leopards which hunting tactic is based on surprise (Zuberbühler 2000c). This modulation of call rates has been learnt since this phenomenon is only observed in Diana monkey groups living on the territory of a chimpanzee group. Also, hierarchical ranks are reflected in the call rates (chimpanzees: 'pant hoots', Mitani & Nishida 1993) or the disappearance of loud calls emissions (male forest guenons: (Gauthier 1998).

Remarkably, call rates are also influenced by the congeners present in the audience, for example vervet monkeys emit more alarm calls when a female is nearby while females emit more alarm calls when a juvenile is nearby (Cheney & Seyfarth 1990). This phenomenon, called the audience effect, has also been evidenced for other types of calls. Females chimpanzee and bonobos emit more copulation calls when copulating with a dominant male than with subordinates (Townsend et al. 2008; Clay et al. 2011), but females emit less copulation calls when a higher ranking female is nearby (Townsend et al. 2008). Tamarins (Caine et al. 1995; Roush & Snowdon 2000), macaques (Hauser & Marler 1993) and capuchins (Di Bitetti 2005) regulate the emission of food calls together with the distance of other group members. Male chimpanzees call more after food discovery (Slocombe et al. 2010) and give more social 'pant-hoots' (Mitani & Nishida 1993) in the presence of allied males. The emission of 'greeting calls' by females chimpanzees to dominant males is enhanced or inhibited depending on the social status of the receiver as well as the number and status of eavesdroppers (Laporte & Zuberbühler 2010). Finally, the social regulation of call emissions seems to be even more complex since chimpanzees emit subtypes of distress calls depending on the intensity of aggression, and victims can use these subtypes strategically to exaggerate the gravity of their aggression if at least one eavesdropper is of equal or superior rank than the aggressor (Slocombe & Zuberbühler 2007).

Nonhuman primates are also able to adjust the temporal pattern of vocal exchanges. Intercall intervals are generally of less than one second (Sugiura 1993; Lemasson et al. 2010a) and this duration would be socially determined. Indeed, the latency to answer is group-specific (Sugiura & Masataka 1995) and within a group, the latency is shorter or the call rate is higher between highly affiliated individuals in squirrel monkeys (Biben et al. 1986) or depends on the social status of interlocutors in female Campbell's monkeys (Lemasson et al. 2010a).

1.3 – Flexibility in the perception and comprehension of vocal signals

Communication cannot be effective if the receivers cannot perceive subtle acoustic variations and decode the messages supposed to be carried by calls. Nonhuman primates also show flexibility in the perception and comprehension of conspecific but also heterospecific signals.

1.3.1 – Comprehension of conspecific calls

Within a group, nonhuman primates recognize each other by voice (e.g. Waser & Waser 1977; Cheney & Seyfarth 1999; Lemasson et al. 2008) and discriminate kin from non kin, or their mother's voice from other females' in juveniles (e.g. Masataka 1985; Rendall et al. 1996; Cheney & Seyfarth 1999). Playback experiments have shown that vervet monkeys recognize the calls of their neighbours even if they interact with them only during intergroup encounters (Cheney & Seyfarth 1982a). Group members also discriminate fine acoustic variants of social calls and are receptive to subtleties in the context of emission (baboon barks variants: Fischer et al. 2001, Campbell's monkeys contact call variants: (Lemasson et al. 2005b), chimpanzee scream variants: Slocombe et al. 2009). Spider monkeys discriminate calls that are addressed to them from calls addressed to other group members, revealing flexibility in the comprehension of directionality (Masataka 1986). Playback experiments have shown that when a primate gives alarm calls, conspecifics react to these as if the actual predator has called, showing that they attend the semantic content carried by others' alarm call subtypes (vervet monkeys: Seyfarth et al. 1980. lemurs: Macedonia 1990; Diana monkeys: Zuberbühler et al. 1997; tamarins: Kirchhof & Hammerschmidt 2006; Black & White colobus monkeys: Schel et al. 2010, see the annexed article). Chimpanzees can extract information about the nature of a food source encountered by conspecifics by listening to their calls (Slocombe & Zuberbühler 2005). In addition, nonhuman primates also infer social information about bouts of calls, for example baboons react stronger to playbacks of 'threat grunts' and 'fear bark' that call that violate the existing hierarchy than to those that do not (Cheney et al. 1995). Comprehension of the context of emission enables receivers to adapt their behaviour consequently, as revealed by the vocal alliances found in female baboons, where vocal support plays a similar role as physical support in the alliances and show the same phenomenon of kin bias (Wittig et al. 2007). This capacity to perceive and flexibly comprehend conspecific calls applies to some extent to calls from other species.

1.3.2 – Comprehension of heterospecific calls

Contrary to intra-specific communication, where both vital information such as predatory contexts and food discovery but also less vital information such as emitter identity have been found, for inter-specific communication there are only pieces of evidence in favour of vital information such as predatory contexts and food discovery. As described by Snowdon (2009), the strongest evidence for primate flexibility in comprehension of communication signals comes from studies of cross-species communication. Many nonhuman primate species understand the referential properties of other primates' alarm calls they live with (ring- tailed lemurs respond to Verraux's sifakas alarm calls: Oda & Masataka 1996; Diana monkeys respond to Campbell's monkeys alarms: ;Zuberbühler 2000a; Diana monkeys respond to chimpanzees' alarm calls (Zuberbühler 2000c). Primates can also discriminate alarm calls types of more genetically distant species such as birds (Vervet monkeys respond to super starling alarm calls: Hauser 1988; Seyfarth & Cheney 1990; Diana monkeys react to guinea fowl alarm calls: Zuberbühler 2000b). In cross-fostering experiments between Japanese macaques and rhesus macaques, mothers react to their fostered infant's calls more readily than to calls of other infants of their own species (Seyfarth & Cheney 1997). To conclude, the decoding of messages from hetero-specific vocalisations can be explained by a learning phenomenon (Snowdon 2009).

1.4 – Social life in nonhuman primates: a diversity of social and communicative needs

The abundant diversity of social systems found in nonhuman primates reflects the diversity of consequent social needs, hence the flexibility of communicative needs.

1.4.1 – Diversity of social systems and flexibility of social bonds

A striking aspect of nonhuman primates' sociality is the diversity of their social systems, which are defined by Kappeler & van Schaik (2002) as group composition (size and composition of the group as well as the spatio-temporal repartition of individuals), social relationships (nature and frequency of social interactions between individuals) and group dynamics (evolution of the social relationships and the network over time, Roeder & Anderson 1990). Rowell (1996) distinguishes four types of social structures: solitary individuals, couple with offspring, small single-male and multi-female groups and large multi-male and multi-females groups. This diversity of social structures and social organisations can be found at several phylogenetical levels. For example, among apes, orangutans have a solitary life (Rodman & Mitani 1987), gibbons form nuclear family groups consisting of a pair of adults and their offspring (Brockelman et al. 1998) while chimpanzees and bonobos form multimale multifemale groups with a male dominance in the former (Nishida & Hiraiwa-Hasegawa 1987) and a female dominance in the latter species (Vervaecke et al. 2000). Macaques, baboons and mangabeys evolve in large multi-male multi-female groups of 30 to 100 individuals (Melnick & Pearl 1987) and macaque species can by ranked along a four level scale according to the degree of their intra-group tolerance (Thierry et al. 2000). Colobus monkeys also provide a surprising variety of social structures, with red colobus monkeys composed of multi-male multi-female groups, harems of black-and-white colobus monkeys and monogamous family groups of olive colobus ((Korstjens 2001).The socio-ecological strategies are also very diverse, with very conspicuous red colobus monkeys, discreet black-and-white colobus monkeys and highly cryptic olive colobus monkeys (Korstjens 2001; Mcgraw & Zuberbühler 2008). Regarding the diversity in social networks,baboon and macaque males and females interact physically very frequently (Lemasson et al. 2008; Maestripieri 2010) and their social relationships are ruled by the Maternal Rank Inheritance system, where young individuals inherit from their mother's social status and youngest dominate the oldest (Gouzoules & Gouzoules 1987), although the strength of this system is modulated within groups depending on the general dominance status of a matriline (Kutsukake 2000). Spider monkeys (Klein & Klein 1977) and chimpanzees (Nishida 1968) form small sub-groups with a fission-fusion system. Among Old World monkeys, while the savannah-dwelling baboons and macaques have been extensively studied, data obtained from field studies at the individual level are lacking, for example for forest-dwelling species which vocal capacities are nonetheless well described.

1.4.2 – Characteristics of social life in forest-dwelling guenon species

Guenons are forest-dwelling cercopithecids of Africa and belong to the genus *Cercopithecus*. *Cercopithecini* are old world monkeys that wear a tail (Cercos = tail, pithecus=primate). They diverged from baboons, macaques and mangabeys (*Papionini*) about 10 million years ago and have greatly diversified during the last millions of years (Leakey 1988). Their taxonomy is controversial since the genus comprises more species (25) than any other genus of African primates, and speciation isolation is not entirely finished since hybridizations can be observed in the wild and in captivity (Detwiler 2004; Erhart et al. 2005).

1.4.2.1 – Geographical distribution and ecology

Guenons are endemic to sub-Saharan Africa and most species live in the forests of West and central Africa, although they range from woodlands to mangrove forests or mountain forests (Groves 2001). Each species ranges within a biogeographical zone and usually restricted to particular forest types (Lernould 1988; Glenn & Cords 2002; Colyn & Deleporte 2004). They are almost exclusively forest-dwelling species, living in the canopy or semi-terrestrial (Gautier-Hion et al. 1999). They feed mainly on fruits and seeds (43 to 85%), leaves, flowers and other plant materials (5 to 20%) but also on insects (10 to 25%) and mushrooms, the amplitude of seasonal variations of food type intake varying with the species (Gautier-Hion et al. 1988; Butynski 2004; Mcgraw & Zuberbühler 2008). Dietary overlap in guenons is very high, raising the issue of inter-species competition for food, which seems to play a role in structuring primate communities (Waser 1987). Foraging and feeding are guenons' main activity and locomotor activities are almost always related to food requirements (Fleagle 1985), but also to predator avoidance (Arnold & Zuberbühler 2008). Regarding guenon's anatomical adaptations to their life mode, although arboreality varies greatly among guenons, most of them are predominately quadrupedal and leap approximately 10% of the time (McGraw 2004). All species present a high sexual dimorphism in size and weight for adults (Glenn & Bensen 1998; Gautier-Hion et al. 1999).

1.4.2.2 – Intra-group relations

Guenon species form groups of 5 to 40 individuals, with a lot of variability between species but not within species. Groups are mostly single-male multi-female troops called "harems", although De Brazza monkeys form nuclear family groups (Gautier-Hion & Gautier 1978). Males leave their natal group when reaching adulthood (Cords 1987), while females stay in the group all their life, maintaining female philopatric groups (Wrangham 1980; Rowell & Olson 1983). Within-group behaviours such as patterns of inter-individual proximities and visual monitoring of associates are useful indicators of social organisation (Treves & Baguma 2004). Physical interactions between individuals are rare (especially agonistic ones) and inter-individual distances usually high, which can be partly due to the foraging for scattered insects habit (Gautier-Hion & Gautier 1978; Rowell 1988; Rowell et al. 1991; Treves & Baguma 2004). Group coordination is based on individuals monitoring each other's behaviour and adjusting their position accordingly to avoid agonistic encounters (Rowell 1988). These characteristics have been described as those of a 'monitor-adjust' social system (Rowell 1988). Although dominant (Mörike 1973), the adult male is most of the time in periphery of the group, surveying predators, potential rivals (Gautier & Gautier-Hion 1983) and does not seem to be involved in social activities when the females are not sexually receptive (Cords 1987; Rowell 1988; Buzzard & Eckardt 2007). Groups are female-bonded (Wrangham 1980; Lemasson et al. 2006); females hence form the core part of social life, with most affiliative interactions occurring between adult females or adult females and subadults (Mörike 1976; Oswald & Lockard 1980), including some non-vocal interactions and frequent vocal exchanges (Gautier 1974; Gautier & Gautier-Hion 1982; Lemasson et al. 2010a). There are very few studies describing the social network of females. Resting periods are favorable to grooming sessions (Höner et al. 1997). In captivity, Campbell's monkey females develop preferential social bonds stable over time and the hierarchy of dominance seems very discreet particularly within a matriline (Lemasson et al. 2006). The amount of interactions between matrilines depend on the social composition of the group (Lemasson et al. 2005a). Old females are preferred partners of vocal exchanges (Lemasson et al. 2010a). In the wild, female blue monkeys do not seem to present kin-biased grooming interactions (Rowell et al. 1991), although mothers are preferred grooming partners of offspring (Cords 2000). Sterck et al. (1997) proposed that guenons' social system is mainly resident-egalitarian given their low levels of intra-group competitions but high-level of inter-group competition (see below), female philopatry and the absence of clear dominance hierarchy.

1.4.2.3 – Inter-group relations

Being highly frugivorous, guenon groups occupy relatively small territories (less than 100 ha) and they strongly defend the territory borders (Cords 1987; Hill 1994; Buzzard 2006). Inter-group spacing seems to be regulated by males' frequent loud calls (Gautier-Hion 1975; Gautier & Gautier 1977). Inter-group encounters are not rare at territory borders; they are usually very vocal and consist of many threats but are not necessarily aggressive (Hill 1994; Glenn & Cords 2002; Buzzard & Eckardt 2007; Ouattara et al. 2009b), although they can lead to physical assaults and sometimes injuries (Pers. com.). Both adult males and adult females participate in these encounters, while mothers and young ones stay behind (Cheney 1987).

1.4.2.4 – Polyspecific associations

Interactions between species sharing the same habitat can be based on competition for food, but also on mutualism, for example to access otherwise unavailable food, or to increase safety from predators (Waser 1987). Although they do not tolerate the presence of other conspecific groups within their territory, guenons typically associate with one or several other primate species (Gautier 1969; Waser 1987; Gathua 2000; Wolters & Zuberbühler 2003). They associate with other guenons but also colobus species and mangabeys (Bshary & Noë 1997; McGraw & Bshary 2002; Buzzard 2010). The frequency of association varies greatly, with species found together on a daily basis while others intermingle more occasionally, with proportions of time spent together varying between 50% and 85% (Wolters & Zuberbühler 2003; Buzzard 2004). These polyspecific associations are supposed to reduce predation risk by augmenting the number of sentinels, each species being specialized to react to the type of predator (aerial or terrestrial) they are most exposed to (Gautier & Gautier-Hion 1983). For example, in the Taï forest of Ivory Coast, red colobus monkeys benefit from the high vigilance of Diana monkeys regarding aerial predators while Diana monkeys benefit from Campbell's monkeys' low strata occupation, which makes them more likely to detect terrestrial predators (Bshary & Noë 1997; Wolters & Zuberbühler 2003). These associations can be regarded as "supra-specific social organisations" (Gautier 1969), given that individuals not only answer other species' calls but also present affiliative interactions through occasional grooming and play (Gathua 2000), or conflicts (Buzzard 2004). During travels, there is usually a species leading travelling direction while other species merely follow (e.g. in Sierra Leone, leaders: Diana monkeys and followers: olive colobus monkeys, Oates & Whitesides 1990).

1.5 – Research questions

There is currently an increased interest in the flexibility of nonhuman primates' vocal communication. We propose to contribute to this area of research because there is a missing piece in the general scenario of the social-vocal co-evolution as well as in the origins of key properties of human language such as semanticity, syntax, conversations and plasticity. The focus on social calls of highly vocal species such as forest-dwelling old world and new world monkeys challenges the current 'phylogenetic gap' described in the evolution of vocal flexibility. Still, open questions remain such as the generality of short term plasticity, combinatorial abilities or the identity decoding. It is hence highly interesting to study the communicative needs of such species through the investigation of their sociality and the flexibility of their communication in vocal production, vocal usage and vocal comprehension.

Here, we propose to focus on two free-ranging sympatric forest guenon species, Diana monkeys and Campbell's monkeys, which are well known for the communicative properties of their alarm calls. Diana monkeys possess predator specific alarm calls which carry semantic contents labeling the predator category, while male Campbell's monkeys have proto-syntactic combinatorial abilities and female Campbell's monkeys possess long-term vocal convergence. Both species are hence good models to further search for short term acoustic flexibility and semanticity in the social calls by studying the variability either encoded in the variation of acoustic parameters or in the combinations of sounds. Although the vocal repertoire of males and females Campbell's monkeys has already been described, little is known about the vocal repertoire of female Diana monkeys at the social level. In addition, although the general characteristics of guenons' social systems have been described, no detailed study of these two species' social organisation is available in the wild. To tackle the question of flexibility in the perception and comprehension of vocalisations regarding emitter's identity, it is interesting to conduct a comparative approach in several more or less closely related *Cercopithecidae* living in polyspecific associations such as colobines, mangabeys and guenons. We will successively study the following questions:

- What are the characteristics of Diana monkeys and Campbell's monkeys' social organisation (social interactions, kin-bias, male-female differences…..)? Is the social system of guenons flexible at the level of groups or species?

- What is the vocal repertoire of female Diana monkeys' social calls? Can we differentiate based on contexts call subtypes? How is variability encoded (acoustic parameters, sound concatenation)?

- What is the level of short-term vocal flexibility in female Diana monkey social calls? What are the environmental factors influencing this variability?

- Can species living in poly-specific associations like guenons, mangabeys and colobus monkeys discriminate the voices of individuals from another primate species based on the criteria of familiarity?

CHAPTER 2 – MATERIAL AND METHODS

2.1 – Study species

We studied different old world primate species depending on the research question. The five species studied belonged to the *Cercopithecidae* family, which is divided into two subfamilies, the *Cercopithecinae* and the *Colobinae* (Grubb et al. 2003). The studied Diana monkeys (Cercopithecus diana diana), Campbell's monkeys (Cercopithecus *campbelli campbelli*), De Brazza monkeys (*Cercopithecus neglectus*) and red-capped mangabeys (*Cercocebus torquatus*) belong to the *Cercopithecinae* subfamily while black-and-white colobus monkeys (*Colobus guereza*) belong to the *Colobinae* subfamily.

2.1.1 – Forest guenons' social organisation: Campbell's monkeys *vs* Diana monkeys

2.1.1.1 – Species description and ecological traits

Diana monkeys are divided into two subspecies, *Cercopithecus diana diana* and *Cercopithecus diana roloway* (Linnaeus 1758; Groves 2001). They are very colourful, generally black or dark grey with a white throat, white underarms, white V-shaped stripe of godess Diana's bow and their lower backs are chestnut colour (figure 1). The *roloway* subspecies does not have the chesnut colour and wears a white beard. The sexual dimorphism is pronounced in adults (males: 5 kg and 55 cm, females: 4 kg and 45cm Lindenfors 2002). They can live up to 35 years in captivity (Weigl et al. 2005).

Figure 1: Diana monkeys (*Cercopithecus diana diana*) are colourful West African monkeys dwelling in the primary rainforests (©A. Candiotti).

Campbell's monkeys are *Cercopithecinae* belonging to the super-species *mona* (Lernould 1988), composed of 4 species: *C. pogonias*, *C. mona*, *C. wolfi*, and *C. campbelli* composed of 2 subspecies: *C. c. campbelli* (Waterhouse 1938) and *C. c. lowei* (Thomas & Hinton 1923). They have grey back and limbs, a dark mask on the face with pink nose and mouth as well as white eyebrows. The sexual dimorphism is pronounced in adults (males: 5 kg and females: 4 kg, Glenn & Bensen 1998) with extra-laryngeal bags developed in adult males (Gautier 1971, figure 2). Diana monkeys live in the remaining blocks of the West African rainforest, ranging from Sierra Leone to Ghana (Booth 1958; Lernould 1988; Oates & Group 1996, figure 3). *C. diana diana* subspecies is found on the western part of Sassandra river, while *C. diana roloway* occupies the eastern part of the river (Lee et al. 1988). This species lives primarily in mature rainforests (Lee et al. 1988; Kingdon & Pagel 1997). Due to habitat loss and severe hunting pressures, the species is included in the list of the most threatened African primate species (International Union for the Conservation of Nature).

Figure 2: Campbell's monkeys (*Cercopithecus campbelli campbelli*) are cryptic West African monkeys dwelling in the rainforests (© H. Bouchet & A. Candiotti).

All *mona* species are found in Western Africa, and *Cercopithecus campbelli* occupy the primary and secondary forests from Senegal to Ghana (Booth 1958). Diana monkeys are highly arboreal, occupying the highest canopy strata (McGraw 2004). Their home range is approximately of 56ha, but they share more of 50% with neighbouring conspecific groups, resulting in an adjusted home range of 38 ha (Buzzard & Eckardt 2007).

Figure 3: Geographical repartition of Diana monkeys, endemic of West African rainforests (adapted from Oates, 1996).

In contrast, Campbell's monkeys are arboreal monkeys although they occupy low strata of the canopy (McGraw 2004). Their home range is on average 40 ha or less, partly shared with conspecific neighbours (Bourliere et al. 1970; Buzzard & Eckardt 2007). Both species feed mainly on fruits (over 75%) and insects (over 15%, Galat & Galat-Luong 1985; McGraw 2004). Diana monkeys often associate with other species of primates (Galat et al. 1978; Höner et al. 1997) such as colobines, especially the red colobus (*Procolobus badius*) with which they provide mutual protection against predators (Bshary & Noë 1997). They also form poly-specific associations with other guenons such as Campbell's monkeys and lesser spot-nosed monkeys (*Cercopithecus petaurista*, Wolters & Zuberbühler 2003; Buzzard 2010), Buzzard 2010). Food competition between species is reduced by a differential use of canopy strata, while these species are reliant on each other for anti-predator benefits. Nevertheless, the inter-specific tolerance goes beyond food completion. Diana monkeys and putty nosed monkeys (*Cercopithecus nictitans*) require an ecological niche almost identical, but Diana monkeys are observed to tolerate putty-nosed monkeys' presence in their territory despite high levels of competition, because male putty-nosed monkeys play a vital role in defence against crowned eagles (Eckardt & Zuberbuhler 2004). Campbell's monkeys are also often found in association with other species such as colobines and other cercopithecinae (e.g. Diana monkeys). They are quite cryptic compared to species it associates with (Bourliere et al. 1970; Wolters & Zuberbühler 2003; Mcgraw & Zuberbühler 2008).

2.1.1.2 – Social traits

Both Diana monkeys and Campbell's monkeys form single male, multi-female harems, but Diana monkeys groups are usually composed of around 10 adult females and their offspring while Campbell's monkey groups only contain around 5 adult females and their offspring (Bourliere et al. 1970; Galat & Galat-Luong 1985; Whitesides 1989). Males leave the group when they reach sexual adulthood but females stay, hence forming female bonded groups (Cords 1987). As most guenons, the social system of both species is based on a 'monitor-adjust system' (Rowell 1988). Individuals spend 46% of their time travelling, 23% feeding, 26% resting and only 5% in social interactions in the wild (Galat & Galat-Luong 1985). Furthermore, Campbell's monkeys' social system has been classified as 'resident egalitarian' since groups are female philopatric and show high rates of inter-group but low rates of intra-group aggressions. Besides, Diana monkeys' social system has been classified as 'resident-nespotic-tolerant' by Buzzard & Eckardt (2007) because groups are female philopatric and show high rates of inter-group but also intra-group aggressions with coalitions. In captivity, males are not socially and spatially well integrated (Byrne et al. 1983; Lemasson et al. 2006; Todd et al. 2008), as it has been described in the wild (Bourliere et al. 1970; Cords 2000). Agressions between female Diana monkeys can be severe and McGraw et al. (2002) once reported the death of an adult female killed by severe lacerations from canine teeth of other females from a single troop. In captivity, the Diana monkey adult male dominates females; infants become independent after 6 months but maintain regular proximity to their mothers (Byrne et al. 1983). Adult females show differentiated relationships, they groom each other for a long time and give and receive approximately equal amounts of time in each dyad. In captive Campbell's monkeys, a female-bonded 'monitor-adjust' social system (Rowell 1988) was observed, with frequent affiliative interactions, directed gazing and avoidances rather than aggressive acts (Lemasson et al. 2006). The authors described long-term differentiated affiliative bonds between adult females, a discrete but significant hierarchy of dominance with rare reversals and an inter-matriline dominance when the situation is stable but not during groups social disturbances (Lemasson et al. 2005a).

2.1.1.3 – Social call repertoire and flexibility: focus on female Diana monkeys

Forest guenons’ vocal repertoires are highly constrained by their habitat and they are composed of discreet call types (Gautier & Gautier 1977). In addition, the sexual dimorphism is very clear in the differences of vocal repertoires between males and females. Males generally produce loud calls in reaction to a wide range of disturbances while females emit, in addition to their own alarm calls, a variety of social vocalisations (Gautier & Gautier 1977). Both male and female Diana monkeys utter predator-specific alarm calls in response to two of their predators, the crowned eagle and the leopard, named the ‘eagle alarm calls’ and the ‘leopard alarm calls’ (Zuberbühler et al. 1997). Nearby monkeys respond to these calls as if the actual predator had called, suggesting that the calls carry information about the predator type (Zuberbühler 2000b; Zuberbühler 2003). Playback experiments have shown that these alarm calls are meaningful to conspecifics (Zuberbühler 2000d) but also to other primate species (*Cercopithecus campbelli*, Zuberbühler 2000a) and to sympatric birds (Rainey et al. 2004). Females emit several other call types such as trills and ‘contact’ calls, also called ‘clear calls’, but no acoustic studies have been undertaken so far (Zuberbühler et al. 1997). These calls, which elicit vocal responses from out-of-sight group members within a few seconds, seem to maintain social cohesion and to be an essential part of the group’s mutualist system of coordinated vigilance (Uster & Zuberbühler 2001).

2.1.2 – Inter-specific auditory perception: De Brazza monkeys as emitters *vs* Campbell’s monkeys, black-and-white colobus monkeys and red-capped mangabeys as receivers

De Brazza monkeys, Campbell’s monkeys, black-and-white colobus monkeys and red-capped mangabeys originate from African tropical rain forests (Western Africa: Campbell’s monkeys, Central Africa: De Brazza monkeys, red-capped-mangabeys, Sub-saharian African belt: black-and-white colobus monkeys, figure 4). They all feed mainly on fruits (Jones & Sabater Pi 1968; Gautier-Hion & Gautier 1978; Gautier-Hion et al. 1999) and are highly territorial with male-specific loud calls regulating inter-group spacing (Marler 1972; Galat & Galat-Luong 1985). Nonetheless, several major ecological and social differences exist between these species. Colobus monkeys occupy both lowland and mountain forests, they are more arboreal than the cercopithecinae (Oates & Davies 1994), although they occasionally come to the grounds to feed on salty soils. They live in social harems in a small vital domain (20-30 ha, Oates & Davies 1994). Mangabeys are semi-terrestrial lowland forest dwelling monkeys, spending a considerable amount of time on the ground but also occupy the lowest parts of the canopy, for example as sleeping sites (Jones & Sabater Pi 1968; Mitani 1989; Gautier-Hion et al. 1999). They live in multi-male, multi-female groups in vast territories (about 250 ha, Gautier-Hion et al. 1999). De Brazza monkeys are the most terrestrial guenon species, they occupy forests bordering rivers of the Congo basin (Quris 1976; Gautier-Hion & Gautier 1978). De Brazza monkeys form nuclear families composed of the parents and their offspring in small vital domains (4-16 ha). It is the only monogamous guenon species (Gautier-Hion & Gautier 1978; Brennan 1985; Leutenegger & Lubach 1987). Campbell's monkeys are highly arboreal guenons found in primary and secondary forests, where they occupy low canopy strata (McGraw 2004). They live in harems on small territories of 40 ha or less, partly shared with neighbouring conspecific groups (Bourliere et al. 1970; Buzzard & Eckardt 2007). Importantly, the three species used as receivers in the auditory experiments form semi-permanent associations with one or several other primate species (e.g. red-capped mangabeys and Cercopithecus pogonias, Jones & Sabater Pi 1968, Campbell's monkeys and Diana monkeys, Wolters & Zuberbühler 2003, black-and-white colobus monkeys and De Brazza monkeys, (Wahome et al. 1993; Mugambi et al. 1997).

Figure 4: Left: Red-capped mangabeys (*Cercocebus torquatus*), middle: De Brazza monkeys (*Cercopithecus neglectus*), right: black-and-white colobus monkeys (*Colobus guereza*) (© H. Bouchet & A. Candiotti).

The vocal repertoire of De Brazza monkeys consists in several sound units that could be uttered alone or concatenated to form 10 call types, including only three types shared by all age-sex-classes (Bouchet et al. 2011). Both males and females emit a pulsed and low pitched contact call with high potential to encode identity (Bouchet et al. submitted). Call rates reflect age-/sex-specific degree of involvement in intra-group social networks, although these groups can stay silent for several hours (Gautier-Hion & Gautier 1978).

2.2 – Study sites

2.2.1 – Taï National park: study on vocal communication and social life in Diana monkeys and Campbell's monkeys

Due to human deforestation, Taï National Park is the last block of intact forest remaining in West Africa, from what used to be a forest belt covering a vast area from Ghana to Sierra Leone (McGraw et al. 2007, figure 5). It was declared a UNESCO World Heritage Site in 1982. The subequatorial climate shows a bimodal pluviometry, with two rain seasons from September to November and April to June, and a dry season from December to March. Annual average rainfall ranges from 1 700 mm in the north to 2 200 mm in the south and the relative humidity is constantly high, between 85 and 90% (Hoppe-Dominik 1997). Vegetation is mainly a dense ombrophilous forest with a continuous 40-60 m canopy and emergent trees (e.g. *Piptadeniastrum africanum*, *Klainedoxa gabonensis*, Riezebos et al. 1994).

Figure 5: Geographic location of Taï National Park, in the south western part of the Ivory Coast.

There are about 1300 species of plants, 150 of which are endemic. Fauna is typical of West Africa, with non-primate mammals such as forest elephants (*Loxodonta Africana*), leopards (*Panthera pardus*), pygmy hippopothamus (*Tragelaphus euryceros*) and tree hyraxes (*Dendrohyrax dorsalis*) as well as crocodiles, pythons and forest duikers (Riezebos et al. 1994; Hoppe-Dominik 1997). Over 1000 vertebrate species, amongst which 230 bird species have been identified (Thiollay 1985; Gartshore 1989). Two research projects named Taï

Chimpanzee project (TCP, founded by Pr Christophe Boesh) and Taï Monkey Project (TMP, founded by Pr Ronald Noë) have been studying the primate community of this forest for respectively 30 and 20 years. There are 12 species of nonhuman primates, three of which are nocturnal (see table 1). Taï Chimpanzees (*Pan troglodytes*) live in communities with a fission-fusion social system within a 15 to 37 km² territory (Boesch & Boesch-Achermann 2000). They feed on vegetal sources (fruits, leaves, flower, and nuts) but also little preys (termites, larvae) and sometimes hunt big preys (other primates such as red colobus). The rest of the diurnal primate community consists of three colobus species, one mangabey species and four cercopithecus species. The most arboreal are colobus monkeys, then the putty nosed monkeys, Diana monkeys, lesser spot-nosed monkeys, Campbell's monkeys and the most terrestrial species is the sooty mangabeys (McGraw 2000; McGraw 2004). All species regularly form polyspecific associations, which provide a unique opportunity to conduct comparative studies on primates that have evolved in the same habitat. The TMP established a grid system in an area with a high density of monkeys near the 'Institut d'Ecologie Tropicale' research station. This grid composed of permanent squares of 100m per 100m facilitated the daily localisation and survey of habituated primates (figure 6).

Common name	Scientific name	Conservation status
Chimpanzees	Pan troglodytes verus	Threatened
Diana monkeys	Cercopithecus diana diana	Threatened
Lesser spot-nosed monkeys	Cercopithecus petaurista	Lower risk
Putty nosed monkeys	Cercopithecus nictitans	Lower risk
Campbell's monkeys	Cercopithecus campbelli campbelli	Lower risk
Sooty mangabeys	Cercocebus atys atys	Threatened
Red colobus	Procolobus badius	Rare
King colobus	Colobus polykomos polykomos	Threatened
Olive colobus	Procolobus verus	Threatened
Potto monkeys	Perodicticus potto	Lower risk
Demidoff's dwarf bushbaby	Galago demidovii	Lower risk
Thomas' bushbaby	Galago thomasi	Rare

Table 1: List of primate species living in Taï National Park and their IUCN conservation status (adapted from Chatelain et al. 2001).

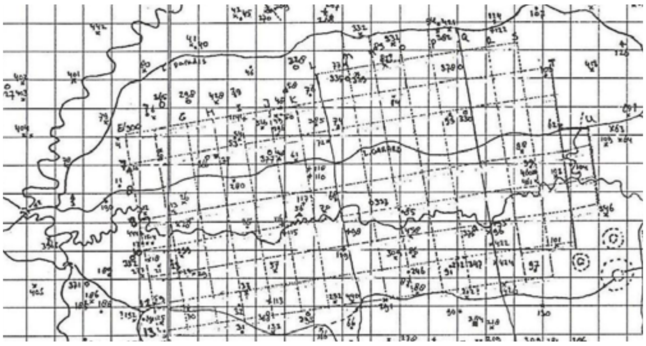


Figure 6: Grid system in the research area, consisting of 100 m² blocks.

2.2.2 – Station biologique de Paimpont: study on the auditory perception of De Brazza monkeys by Campbell’s monkeys and red-capped mangabeys

The ‘Station biologique de Paimpont’ (Université de Rennes 1, France) houses a primate facility founded in the 60s from wild caught individuals confiscated by French customs. Current species are Campbell’s monkeys, De Brazza monkeys, red-capped mangabeys and grey-cheeked mangabeys (*Cercocebus albigena*). Monkeys are kept in indoor-outdoor enclosures enriched with perches and ropes, litter (indoor) and natural vegetation (outdoor) (see table 2). Animals are fed with fresh fruit and vegetables in the morning and chow in the afternoon while water is available *ad libitum*.

2.2.3– Port Lympne Park: study on the auditory perception of De Brazza monkeys by black-and-white colobus monkeys

This wild animal zoo is located in the southern part of England (Lympne, Kentshire). It is supported by the Aspinal foundation, a charity for conservation and reintroduction of endangered species in the wild. The park houses over 600 endangered animals, amongst which many gorillas and other primates. In particular, Black-and-white Colobus monkeys and De Brazza monkeys are held together in an open-topped woodland enclosure (see table 2). Animals are fed three times a day with fresh fruit and vegetables and water is available *ad libitum*.

Species	group	subject	sex	birth year	Housing conditions
Cercopithecus neglectus	1	Fora	F	2001	Station Biologique de Paimpont (FR) outdoors: 17 m^{2}x 4 m wire netting cage enriched with perches, indoors: 11m^{2}x3 m (enriched with litter and perches)
	2	Elise	F	1988	Station Biologique de Paimpont (FR) outdoors: 17 m^{2}x 4 m wire netting cage enriched with perches, indoors: 11m^{2}x3 m (enriched with litter and perches)
		Pimprenelle	F	2004	
	3	Marjo	F	1995	Station Biologique de Paimpont (FR) outdoors: 17 m^{2}x 4 m wire netting cage enriched with perches, indoors: 11m^{2}x3 m (enriched with litter and perches)
	4	Kabinda	F	1986	Port-Lympne Zoo (UK) outdoors: 2500 m^2 open-top enclosure (enriched with perches, shrubs and trees, natural soil, pen shared with 12 Colobus monkeys), indoors: 17m^{2}x 3m (enriched with litter and perches)
		Grub	F	1999	
		Pue	F	2003	
		Cobbit	F	2005	
		Dora	F	2007	
	5	Bamboo	F	1993	Port-Lympne Zoo (UK) outdoors:78m^{2}x8m+10m^{2}x3m(wire netting cage enriched with perches) indoors: 16m^{2}x3 m (enriched with litter and perches)
		Ludo	F	2005	
	6	Bertha	F	1992	Howletts Zoo (UK) outdoors:99m^{2}x4m+9m^{2}x3m(wire netting cages enriched with perches) indoors: 26m^{2}x3 m (enriched with litter and perches)
		Hathor	F	2005	
Cercopithecus campbelli	7	Plume	F	1992	Station Biologique de Paimpont (FR) outdoors: 300m^{2}x4m wire netting cage enriched with perches, indoors 21m^{2}x3m (enriched with litter and perches)
		Maricopa	F	1995	
		Chilula	F	1996	
		Tilamook	F	1996	
		Chilie	F	2005	
		Pinsette	F	2006	
		Ecureuille	F	2006	
		Amande	F	2006	
Colobus guereza	8	Chobe	F	1998	Port-Lympne Zoo (UK) outdoors: 2500 m^2 open-top enclosure (enriched with perches, shrubs and trees, natural soil, pen shared with 6 De Brazza monkeys), indoors: 17m^{2}x3m (enriched with litter and perches)
		Sonza	F	1999	
		Tyr	M	1999	
		Anubis	M	2004	
		Horace	M	2005	
		Amun	M	2006	
		Geb	M	2008	

Cercocebus torquatus	9	Zunie	F	1987	Station Biologique de Paimpont (FR) outdoors: 17m^{2}x4 m wire netting cage enriched with perches, indoors: 11m^{2}x3m (enriched with litter and perches)
		Joly	F	2000	
		Bell	F	2002	
	10	Chipie	F	1992	Station Biologique de Paimpont (FR) outdoors: 17m^{2}x4 m wire netting cage enriched with perches, indoors: 11m^{2}x3m (enriched with litter and perches)
		Gaufrette	F	1996	
		Chipse	F	2006	

Table 2: Housing conditions of the De Brazza monkeys, Campbell's monkeys, red-capped mangabeys and black-and-white colobus groups studied in captivity.

2.3 – Study subjects

2.3.1 – Wild groups

In the research area of Taï forest, we followed two neighbouring groups of Diana monkeys that have been under human habituation since the 90s. Adult individuals were identified individually by observing the shape of the tail, overall stoutness as well as body marks or scars. The adult male was the largest individual with a conspicuous scrotum, while adult females had large nipples (Uster & Zuberbühler 2001). Adult females were DIA1 group consisted of 1 adult male and 9 adult females with their offspring. One sub-adult male became fully adult and progressively left the group during the study period. DIA2 consisted in 1 adult male and 10 adult females with their offspring. We also used the vocal and social data collected by Dr Karim Ouattara in 2006 and 2007 on two habituated groups of Campbell's monkeys living in the same area as Diana monkeys. CAM 1 group consisted in 1 adult male and 7 adult females while CAM2 group consisted in 1 adult male and 3 adult females.

2.3.2 – Captive groups

All studied animals were born in captivity and lived in the facilities for at least 4 years. We studied 8 adult females from a group of Campbell's monkeys composed of 15 individuals (1 sub-adult male, 11 adult females and 2 juveniles), 5 adult males and 2 adult females from a group of Black-and-white colobus composed of 12 individuals (6 adult males, 2 adult females, 3 juveniles and one infant), 6 adult females from two groups of red-capped mangabeys, of respectively 13 and 5 individuals (respectively 1 adult male, 5 adult females,4 juveniles and 2 infants and 3 adult females and 2 infants, see table 2). We collected vocal stimuli from 13 adult female De Brazza monkeys from 6 groups at different locations (see table 2).

2.4 – Data collection

2.4.1 – Observational data of free ranging Diana monkeys

Three sessions of data collection were conducted, the first between February and May 2009, the second between December 2009 and June 2010 and the third between June 2010 and June 2011. During the two first sessions, 10 min - focal samplings were performed on all adult females, sometimes reduced to 5 minutes if the followed individual went out of sight, between 7am and 5:30 pm. During the focal period, all focal female's behaviours were described by the observer (AC, figure 7) using a Lavallier microphone and all vocalisations of the focal female were recorded using a Seinnheiser directional microphone (K6/ME66). Both microphones were connected to a Marantz (PMD660) solid state recorder (sampling rate: 44.1 Hz, resolution: 16 bits). Behaviours (see detailed list in table 3) fell into one of the ten following categories: visually scanning the environment, foraging, feeding, walking, jumping, resting, positive social interaction, neutral social interaction, negative social interaction and state of vigilance. Given that female Diana monkeys' social calls typically trigger a vocal response by another group member within a few seconds (60% of cases; Uster & Zuberbühler 2001), calls were categorized as either isolated (no other call 3 s before nor after), exchanged (1–3 other calls separated by a less than 3 s, with no call overlap: see Lemasson et al. 2010) or chorused (at least 4 other calls with overlapping). For social interaction, the type and duration were also noted. The third session specifically consisted in focal samplings of adult females' social interactions with no sound recordings using a simpler behavioural repertoire (see table 3). The observer (Frederique Gnepa, field assistant) noted all social interactions involving the focal female, either social positive affiliative, neutral or social negative, with the duration of grooming and spatial proximity bouts. A total focal time of 32 hours was performed (mean ± sem = 96 ± 12 minutes per Diana monkey female). During all three sessions, every 30 minutes a scan sampling was performed on the following environmental variables: group's position in the territory, group's degree of scattering, group's activity, the presence of neighbourgs and the luminosity of the habitat (see chapter 3 for the detailed definitions). Luminosity level was estimated by measuring the averaged intensity (in Lux) of light received 1 m from the forest floor with a luxmeter (DVM401 Voltcraft DT8820, see details in chapter 3).

Figure 7: focal sampling of a free-ranging identified adult female Diana monkey using a directional microphone. (© F Belé)

EXPL = exploring the environment (excluding displacements)	**FORA = foraging**	**ALIM = feeding**	**LOCO = locomotion**	**SOC+ = positive social interaction**
OEI = eye glance anywhere	FOU = foraging in leaves	BOI = drink	MAR = walk alone	*EP1 = groom
SCA = scanning horizontally	TOT = touching trunc	CRA = spit food remainings	COU = run	*AP1 = approach sb
DSO = look below (>1s)	PFS = taking a fruit on the floor	FAS = rubbing food against sth	DES = going down (>1m)	*SU1 = follow
DSU = look above (>1s)	PRF = taking leave	FLU= smell fruit	MON = going up (>1m)	
POB = take object	PRI = taking an insect	LET = lick trunk	DSS = get on the floor	**SOC- = negative social interaction**
LOB= drop object	RET=looking at/inside trunc	LTF = let fruit fall	MSS = leave the floor	*BR1 = pushing back with arm
TOB = touch object	CAB= break branch	MAC = chewing on food storage		*CH1 = chasing after
REF= looking at leaves	TRB = pulling branch	MGE = eating item	**MAIN = maintenance**	*ME1 = threatening (staring at sb, showing teeth)
SCS = scanning the floor		MGF = eating leave	REP = still in resting position	*EV1 = avoid sb by changing direction
FLO = smelling object		MGI = eating insect	DFQ = defecate	*FU1 = run away from sb
		MGU = eating fruit	EPO = self-grooming	
VIG = vigilance (state of vigilance)			GRA = scratching body part	**SOCN = neutral social interaction**
FIS = stay still, staring below (>1s)			LEC = licking body part	*DP1 = leave sb
VIG = in vigilance posture			URI = urinate	*PA1 = pass by sb
PEU = scared				*RE1 =look at sb (> 1s)

Table 3: Behavioural repertoire used to describe Diana monkeys' behaviours during focal samplings performed by AC. Social behaviours were coded with a '1' if the focal individual was emitter and '2' if she was receiver. * indicates behaviours that were also used in the social focal samplings performed by FG.

2.4.2 – Observational data of free ranging Campbell’s monkeys

Between January 2006 and September 2007, Karim Ouattara performed during his PhD 15 minutes focal samplings on all adult females between 7am and 5h30 pm, describing the social interactions using a Lavallier microphone and recording the focal individual’s vocalisations with a directional Seinnheiser microphone (ME88). Both microphones were connected to a DAT recorder (SONY TCD D100, sampling rate: 44.1 Hz, resolution: 16 bits). A total focal time of 137 hours was performed (mean ± sem = 1174 ± 21 minutes per female).

2.4.3 – Fecal sampling

One to three fresh fecal samples were collected directly under the tree for all adult individuals of Diana and Campbell’s monkey species during the field sessions (between 2006 and 2007 for Campbell’s monkeys and in 2010 for Diana monkeys). They were kept in a cool place and dry conditions using silica gel until DNA extraction, which was performed by Dominique Vallet from UMR6553 Ecobio at the Station biologique de Paimpont.

2.4.4 – Experimental data

To test nonhuman primates’ capacity to discriminate familiar from non-familiar voices of other primate species, we conducted playback experiments of adult females De Brazza monkeys calls to adult female Campbell’s monkeys, adult females red-capped mangabeys and adult males and females black-and-white colobus monkeys. Campbell’s monkeys were tested in October 2011 at the Station biologique de Paimpont, black-and-white colobus monkeys were tested in November and December 2011 at Port Lympne Animal Park and red-capped mangabeys were tested in January and February 2012 at the Station biologique de Paimpont. We conducted match-paired experiments in which the targeted individuals were tested twice but not on the same day, in reaction to a single familiar voice and a single unknown voice. Stimuli were broadcast from a Marantz solid state recorder PMD660 connected to a Nagra speaker amplifier (FAC.SC.PA.71) concealed in a backpack placed on the ground. We waited until the following conditions were present: no conflict in the last 15 minutes, no De Brazza monkey call heard for the last 5 minutes, a very low ambient noise, targeted individual isolated from the rest of the group (at least 2 meters from another individual), not facing the speaker direction and in a quiet general state. Stimuli were broadcast once at the natural sound level of 60dB. Target's reaction was filmed, using a Sony DCR SR58E camera, at least 20 sec before and 20 sec after the stimulus.

2.5 – Data analysis

2.5.1 – Call analyses in Diana monkeys

We first categorised the recordings into main call types, following visual and auditory assessments (as in Lemasson & Hausberger 2011). The classification obtained was validated with a basic acoustic analysis of call structure conducted on a subset of calls from the same females to control for individual differences. The parameters measured were the total duration, minimum fundamental frequency and maximum fundamental frequency, as well as several type-specific measurements (e.g. duration of oscillations in trilled calls). To investigate the link between call types and contexts of emission, we analyzed the 'general' context based on data collected during scan sampling and 'immediate' context based on data collected during focal animal sampling. To study vocal flexibility, the most frequently emitted and highly social call subtype was then further investigated. We used customized acoustic software ANA to compare the similarity of the arched fundamental frequency contours of calls. It calculated acoustic similarity indices of pairs of Af calls based on a procedure used for frequency modulated whistle-like signals in various species. The similarity index is calculated by comparing two images pixel by pixel. Each pixel is coded, depending of the shade of grey, between 0 and 15 for a 16 colours screen (figure 9). If both pixels have the same value, a score of '2' is attributed. If both pixels have the 0 value, a score of '0' is attributed. Otherwise, a score of '1' is attributed. The final similarity index is the average score of all pixels. The software allows a temporal and frequency shift to find the best superposition. We used a 200Hz frequency shift to avoid biases due to the diminution of frequency in aging females (Gautier-Hion 1975). Comparisons of pairs of spectrograms were conducted within and between females and averaged to obtain a mean intra-individual index and a mean inter-individual index. To assess the role of context on call structure, we compared levels of intra-individual acoustic similarity in different contexts. To avoid a bias due to the "call exchange" context, we only analysed calls emitted after more than 3s of silence. Each female's mean intra-individual indexes were compared across contexts. We eventually compared the acoustic similarity of exchanged (inter-call interval <3s) and non-exchanged (inter-call interval ≥3s) calls, by calculating the mean inter-individual similarity indices of pairs of exchanged and not-exchanged calls. Focal females' calls were compared both with the call to which they responded and to the previous call to which they did not respond, provided they were all emitted within the same minute.

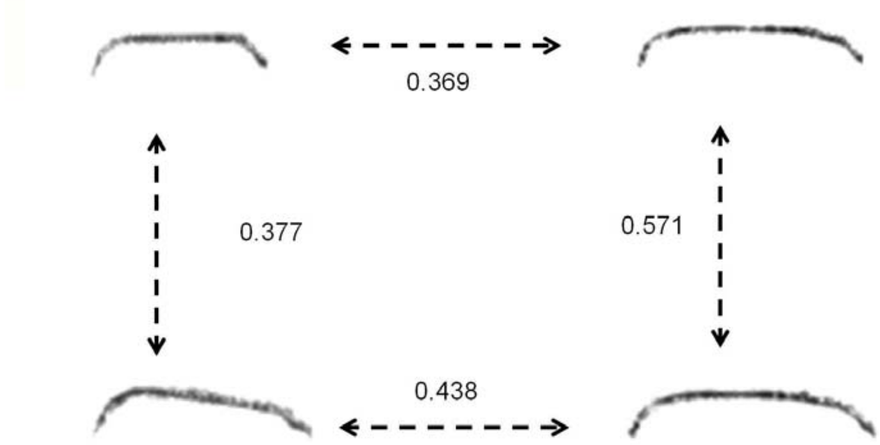


Figure 9: Examples of similarity indexes calculated between pairs of spectrograms.

2.5.2 – Social analyses

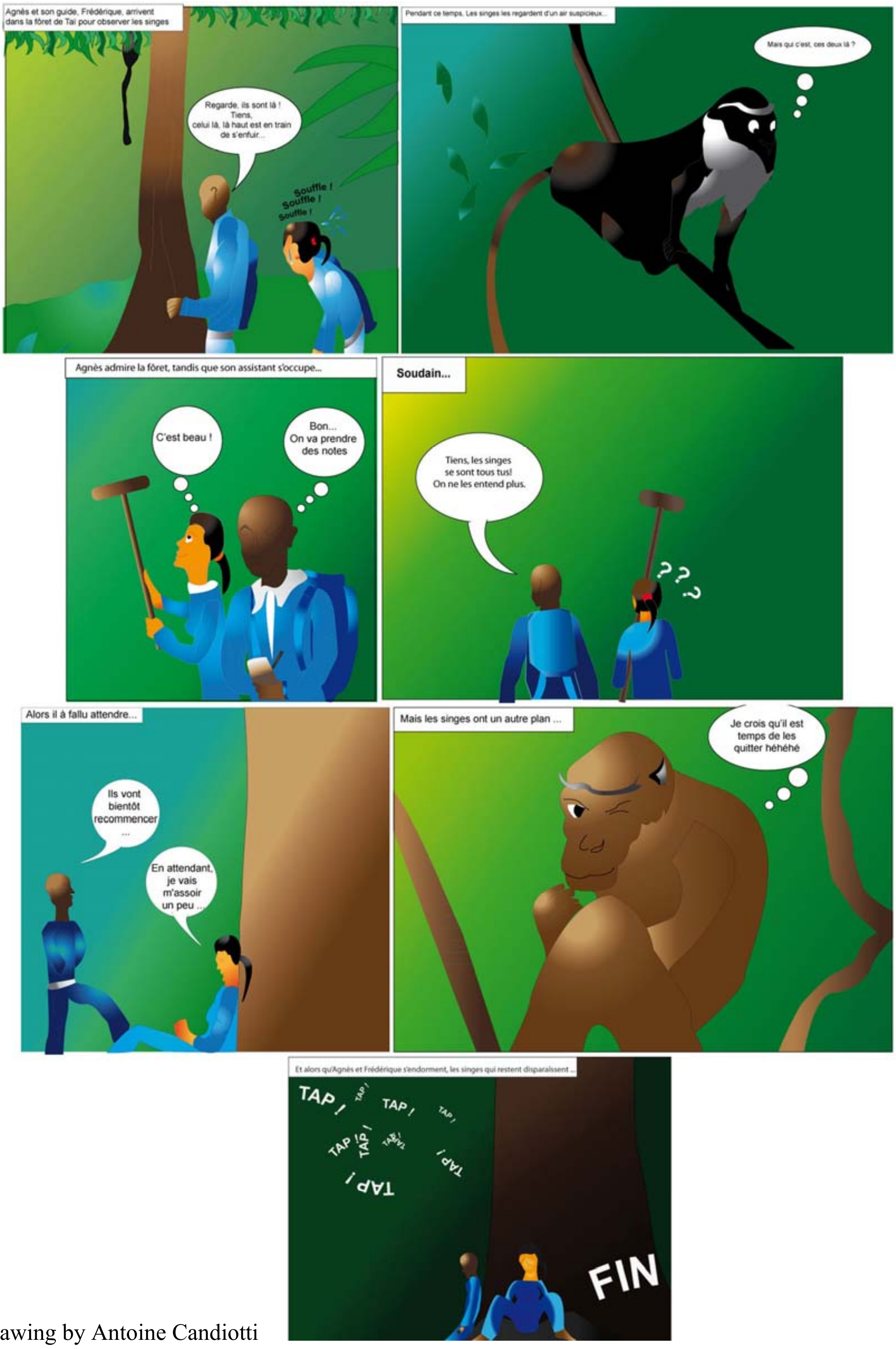
The same procedure was conducted on data from Diana monkeys and Campbell's monkeys. To study females' social time budget we specifically scored the duration of close proximity with another adult group member (distance between individuals within arm reach as defined by Lemasson et al. 2006), the duration of grooming and any occurrence of agonistic behaviours. We calculated the proportion of time each adult female (A) initiated close proximity with each other adult individual in their group (male and females), by dividing the total duration of close proximity she initiated by her total observation time. This generated dyadic scores for this female (AB, AC, AD). We then averaged the proportions obtained for female A towards all other adults (B, C, D…) to obtain female A's mean proximity index. To generate female A's mean grooming index, the same procedure was applied to grooming sessions. We also calculated the average duration of a proximity session and the average duration of a grooming session. Individual agonistic interaction rates were calculated by dividing the number of occurrences of agonistic behaviours by the total observation time. Individual contact call rates were calculated by dividing the total number of calls recorded for a given female by the total recording duration for this female. Calls could be emitted alone or be part of a vocal exchange. Here, two calls were considered as exchanged when the inter-call interval of the calls emitted successively by two individuals was inferior to 1 second (Lemasson et al. 2010a). For each female, we also calculated the proportion of exchanged calls by dividing the number of exchanged calls by the total number of calls emitted. To study the social networks of each group and each species, we generated sociograms of affiliative interactions based on the interactions that occurred more frequently than expected by chance.

2.5.3 – Genetic analyses

After extraction, DNA sequences were amplified using human autosomal microsatellite markers that were polymorphic for the species (respectively 14 for Diana monkeys and 12 for Campbell's monkeys). The microsatellite sequences were amplified using Polymerase Chain Reactions (PCR) and sized using a with an internal lane standard (GS500(-250)LIZ; Applied Biosystems) using the program genemapper version 4.0 (Applied Biosystems). Within each species and for each dyad of individuals we calculated Li's relatedness coefficient with SPAGeDi 1.3 software (Li et al. 1993; Hardy & Vekemans 2002). For Campbell's monkeys, this work had already been done (Petit et al. 2010) and for Diana monkeys, this work was performed together with Camille Coye as part of her master's internship (2011).

2.5.4 – Experiment analyses

We conducted frame by frame video analyses with VLC 20 seconds before the stimulus until 20 seconds after the stimulus (as in Lemasson et al. 2008). The angle between the monkeys' head and the speaker direction was noted for each frame all gazes that formed an angle of 45° or less with the speaker direction (left or right, above or below) were systematically counted. Several durations were calculated: the latency to react, the total duration of gazes in the speaker direction and the average gazing duration.



Drawing by Antoine Candiotti

CHAPTER 3 – SOCIAL ORGANISATION AND GENETIC RELATEDNESS IN TWO SYMPATRIC FREE-RANGING FOREST GUENONS

SUMMARY OF PAPER 1

Questions : Given their complex vocal repertoire and their acoustic plastic abilities, forest guenons such as Diana and Campbell's monkeys have a potential for complex sociality. Nevertheless, we know very little about the characteristics of their social system in the wild. It is traditionally said, from observations at the group level, that forest guenons are "more vocal" but "less social" than other old world monkeys living in much larger groups like macaques and baboons, with less physical interactions, almost no male-female bonds and a discrete dominance hierarchy. Due to the lack of studies at the individual level, almost nothing is known regarding the influence of genetic factors. What are the social characteristics of Diana and Campbell's monkeys regarding group composition, frequency of vocal and non-vocal interactions and social networks? What is the degree of genetic relatedness and what is the link between genetic relatedness and social bonding? Are those social characteristics entirely shared by both species or can inter-species or even intra-species inter-group differences be evidenced?

Methods : We conducted a comparative study of the genetic and social organisation of free ranging Diana monkeys and Campbell's monkeys, two sympatric West African guenons. We studied at the individual level four neighbouring groups, two of each species, taking into account genetic proximity (assessed with microsatellites), the frequency and duration of affiliative spatial proximity and grooming interactions, the frequency of agonistic interactions and the vocal activity of adult females. We also studied the link between females' genetic relatedness and the strength of their social bonds.

Results : Overall, our results on both species were in line with the characteristics of a female-bonded "monitor-adjust" social system, with few physical interactions, notably agonistic, an isolated single male and dyadic preferences between females. Nevertheless, Diana female monkeys were more vocally and socially active than Campbell's monkeys, a phenomenon that could not be due to differences in group sizes but maybe differences in micro-habitat or in predation pressure. Within species, group differences were also observed in the pattern of social networks. Conversely to baboons and macaques, there was no systematic correlation between genetic relatedness and social affiliations.

Conclusions: Our study provides valuable knowledge on the social characteristics of forest dwelling guenons with results comparable to what has been found in other field studies performed at the group level. This study provides a comparative case of social differences in closely related sympatric species. Differences in social complexity can drive to differences in vocal variability.

This paper has been submitted for publication to the American Journal of Primatology.

Social organisation and genetic relatedness in two sympatric forest guenons

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Abstract

Nonhuman primates are well known for their diverse and complex social systems, a potential driving force in the evolution of their communicative and cognitive abilities. Within the Old World monkeys, the social systems of forest guenons have been relatively understudied. We addressed this with a comparative study of the genetic and social organisation of two sympatric West African forest guenons, Diana monkeys and Campbell's monkeys. We assessed the genetic relatedness of two neighbouring groups of each species using microsatellites. We also described the social relationships of all group members, using measures of spatial proximity and key social behaviour of the adult females, including grooming, agonistic interactions and vocal activity. Both species revealed characteristics typical of a female-bonded social system, with few agonistic interactions, a socially isolated single male and individualised relationships between females. Diana monkey females were vocally and socially more active than Campbell's monkey females despite similar group sizes, a possible result of differences in habitat use. In contrast to other Old World monkeys, however, there was no systematic correlation between genetic relatedness and social affiliation in either species. Our study closes an important gap in the comparative study of social characteristics of a major group of Old World monkeys.

Introduction

A striking aspect of nonhuman primates is the diversity of their social systems, as assessed in terms of group composition, group dynamics (i.e. evolution of social networks) and social relationships (Kappeler & van Schaik 2002). Within the apes (genus *Pan* and *Hylobathes*), all major social systems can be found. Orang-utans are largely solitary (Rodman & Mitani 1987), gibbons form family groups with a pair of adults and their offspring (Brockelman et al. 1998), while chimpanzees and bonobos form large multi-male multi-female groups with males and females differing in relative social power (Nishida & Hiraiwa-Hasegawa 1987; Vervaecke et al. 2000). Gorillas form large groups with one or several adult males and there are social differences between western gorillas and mountain gorillas (Robbins et al. 2004).

Within the Old World monkeys (genus *Cercopithecidae*), a major distinction has been made between the social system of forest-dwelling Cercopithecids, such as guenons, and savannah-dwelling Cercopithecins, such as baboons and macaques (Melnick & Pearl 1987; Rowell 1988). The two families have separated some 30 million years ago, which has regularly led to stable differences in the average size and composition of groups, the size of their territory and the type of relationships and frequency of interactions (Smuts et al. 1987). For example, baboons and macaques form large multi-male multi-female terrestrial groups of 30-100 individuals with female philopatry (Melnick & Pearl 1987). Group members interact frequently in both affiliative and agonistic ways, within and between sexes, maintain close spatial proximity (Lemasson et al. 2008; Maestripieri 2010), with strong links between genetic relatedness and social bonds (Gouzoules & Gouzoules 1987; *Papio cynocephalus*:: Silk et al. 2006, *Cercopithecus solatus*: Charpentier et al. 2008).

In contrast, the other main group of Old World monkeys, the forest guenons, form small one-male multi-female arboreal groups of 5 to 40 individuals (Cords 1987). Most species occupy relative small home ranges, which are defended against neighbouring groups. Individuals interact less frequently with each other and inter-individual distances are higher (Rowell & Olson 1983; Treves & Baguma 2004). Social bonds are between some females (Rowell & Olson 1983; Lemasson et al. 2006), while males are spatially or socially separated from the rest of the group (Byrne et al. 1983; Rowell 1988; Cords 2000a; Lemasson et al. 2006). Individuals monitor each other’s behaviour and adjust their spatial positions accordingly, which results in low rates of aggression, a so-called "monitor-adjust" social system (Rowell 1988).

Another way of classifying primate social systems has been proposed by Sterck et al. (1997), who discriminate "resident-nepotistic" species with high rates of aggression and a strict dominance hierarchy, such as baboons, from "resident-egalitarian" species with few direct interactions and no a clear dominance hierarchy, such as the guenons. Further distinctions have been made within this general framework. For example, Buzzard & Eckardt (2007) proposed that, while Campbell's monkeys qualify as "resident-egalitarian", Diana monkeys should be described as 'resident-nepotic-tolerant", because females show relatively high levels of intra-group aggressions and form within-group coalitions.

Although these general differences are widely accepted, various aspects of the social system of forest guenons have remained unexplored. One largely unresolved question is how genetic relatedness impacts on social relationships (Cords 2000b; Lemasson et al. 2006). Also, detailed long-term behavioural data from the field are only available for blue monkeys (Cords 2000b) or from captive studies (Diana monkeys: Byrne et al. 1983; Todd et al. 2008; Campbell's monkeys: Lemasson et al. 2005; Lemasson et al. 2006 ; De Brazza monkeys: Bouchet et al. 2011).

Another striking feature of forest guenons is their propensity to form associations with other primate species (Holenweg et al. 1996; Buzzard 2010). Most guenons spend a considerable amount of their foraging and travelling time interacting peacefully with other species, which has lead some authors to describe these polyspecific associations as 'supra-social organisations' (Gautier & Gautier-Hion 1983; Wolters & Zuberbühler 2003). The primary function of these associations is thought to be in avoiding predators (Bshary & Noë 1997). This is in contrast to *Papionini*, such as baboons, that sometimes join other primate species sleeping sites, but this seems to be driven by external factors, not an active search for association with another species.

Forest guenons have experienced a major radiation during the last million of years (Leakey 1988), which has resulted in some differences in social organisation. For example, Diana monkeys and Campbell's monkeys, two sympatric species in the Taï forest, Ivory Coast, differ in average group size (20 *vs.* 10 Zuberbühler & Jenny 2002), preferred habitat (50/44/6% vs. 5/58/37% of the time occupying the highest/middle/lowest strata, McGraw

2007), and general conspicuousness (conspicuously exposed *vs* quiety concealed, McGraw 2007). In mixed species groups, Diana monkeys mostly lead during progressions while Campbell's monkeys usually follow (McGraw et al. 2007). At the same time, the two species also resemble each other in many ways, such as home range size (Buzzard & Eckardt 2007), territoriality (Zuberbühler et al. 1997; Ouattara et al. 2009), diet (Buzzard 2006a; Buzzard 2006b), and polyspecific associations (Bshary & Noë 1997).

The aim of this study is to compare two species of forest guenons, which are phylogenetically close and living in the same habitat, suggesting that they evolved under similar environmental pressures. Our goal was to provide a detailed account of the social organisation, social, and kin relationships in both species to allow more general comparisons with other Old World monkeys. To this end, we used microsatellite analyses to explore the relationship between genetic relatedness and social affinities described by spatial proximity, grooming patterns, agonistic interactions and vocal activity (Sekulic 1983; Dunbar 1988; Silk 1991; Lemasson et al. 2011a).

Material and methods

Study site and subjects

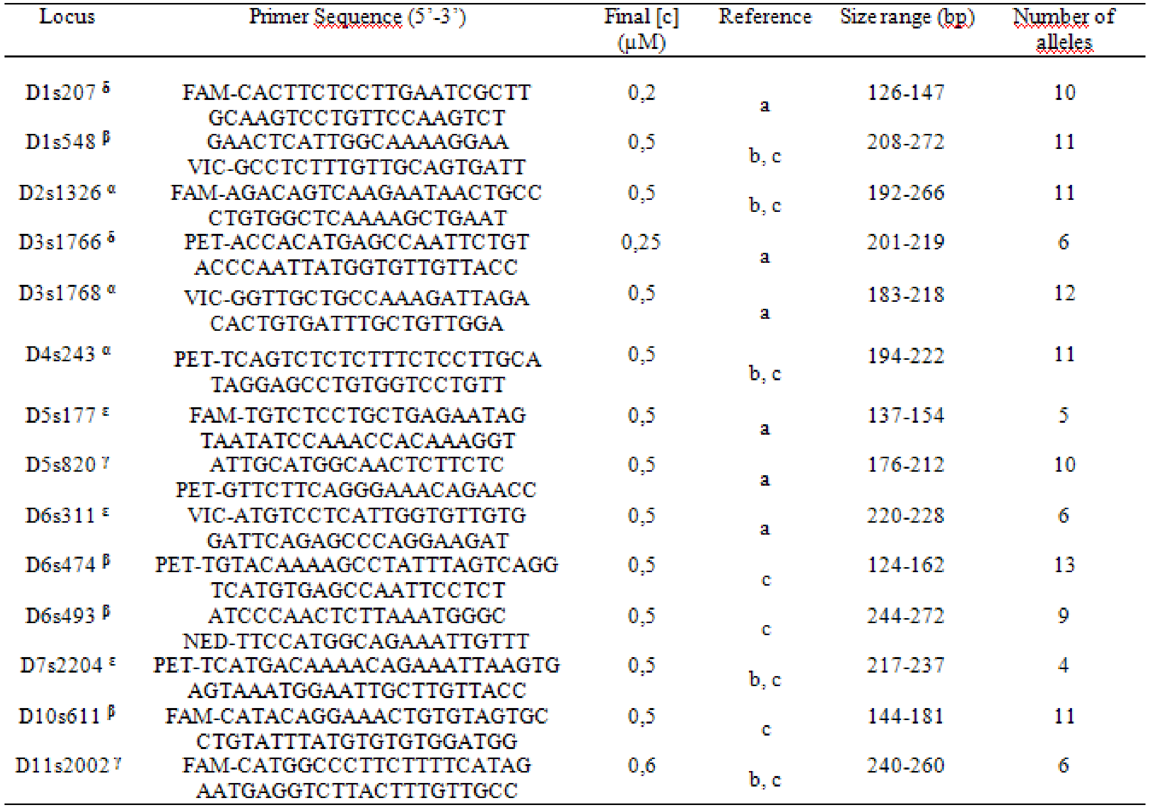
The studied groups of Diana monkeys (*Cercopithecus diana diana*) and Campbell's monkeys (*Cercopithecus campbelli campbelli*) inhabit the South-western part of Taï National Park (5°50'N, 7°21'W), a primary rainforest of the Ivory Coast. For each species, two groups were alternatively followed (DIA1, DIA2, CAM1 and CAM2). During the last 20 years, the DIA1 group has formed associations with the CAM2 group while DIA2 has associated with the CAM1 group. DIA1 and DIA2, as well as CAM1 and CAM2, have adjacent territories. Diana monkey groups were composed of one resident adult male (D1M and D2M), 9-10 adult females (D1F1 to D1F9 and D2F1 to D2F10) and their offspring. Campbell's monkey groups were composed of one resident adult male (C1M and C2M), 4-7 adult females (C1F1 to C1F7 and C2F1 to C2F4) and their offspring. All adult group members were fully habituated and individually known. The oldest female of each group (D1F1, D2F1, C1F1, and C2F1) was estimated by her scars, broken tail and body posture. Behavioural observations on these groups have started in 1991. In the meantime, the resident adult males have been replaced several times while the females have remained, apart from some disappearances, possibly due to natural deaths or predation (F. Belé and K. Ouattara, pers. com.). During this study, we observed male replacements in both CAM groups which enabled us to collect faecal samples from both new males (C1MN and C2MN).

Data were collected from Diana monkeys from December 2009 to June 2010 (AC) and from June 2010 to February 2011 by a field assistant (FG) using 10 min focal sampling (Altmann 1974), reduced to 5 min samples (42%) if the observer could not follow the focal animal anymore due to dense vegetation or a change in canopy strata. We sampled all adult females between 07:30 and 17:00 hours GMT. For Campbell's monkeys, 15 min focal sampling was carried between March 2006 and September 2007 (KO) also on all adult females and between 07:30 and 17:00 hours GMT (Altmann 1974). We recorded the contact calls (as defined by Lemasson & Hausberger 2011; Candiotti et al. 2012) of adult females and together with the type and amount of time spent interacting socially with other adults. We collected spatial proximity data, assessed by distance between individuals within arm's reach (Lemasson et al. 2006), the duration of grooming and any occurrence of agonistic behaviours (i.e. threatening, chasing, biting). For Diana monkeys, both observers had agreed on behavioural categories and had performed simultaneous observations (N = 8 x 5 min on 8 focal adult females) which confirmed the consistency in data collection and inter-rate reliability (Spearman rank–order correlation test: rs = 0.888, $P < 0.0001$).

To assess genetic relatedness, we collected faecal samples from all adult individuals provided individual identification was unambiguous. We also obtained a faecal sample from the resident male of another neighbouring group (D3M), which served as an outgroup reference for genetic relatedness comparisons. For Campbell's monkeys, the detailed procedures of the genetic analysis have been published in Petit et al. (2010). Sample collection and analyses were conducted in a similar way for Diana monkeys.

Genetic analyses on Diana monkeys

Two to four faecal samples were collected from each adult individual and samples were stored following the two-step collection method recommended by Vigilant & Guschansky (2009). DNA was extracted by DV following the 2CTAB/PCI procedure described by Vallet et al. (2007). DNA sequences were amplified using 14 human autosomal microsatellite markers that were polymorphic for Diana monkeys (Table 1). The microsatellites were amplified in 12 μL multiplex reactions containing 1 μL of DNA extract, 1 × Multiplex PCR Master 23 Mix (QIAGEN) and primer concentrations as reported in Table 1. PCR products were run on an ABI PRISM 3130 XL Genetic Analyser 16 Capillary system (Applied 3 Biosystems) and sized with an internal lane standard (GS500(-250)LIZ; Applied Biosystems) using the program gene-mapper version 4.0 (Applied Biosystems) (see Petit et al. 2010). Two individuals' genotype could not be determined due to inconsistencies in their respective faecal samples (D1F9 from DIA1 and D2F10 from DIA2). Genetic relatedness between individuals was assessed by submitting the contingency table of the consensus dataset to a correspondence analysis using the GENETIX 4.0.5.2 software. For each dyad of individuals we also calculated Li's relatedness coefficient with SPAGeDi 1.3 software (Li et al. 1993; Hardy & Vekemans 2002), in the same way that it has been done earlier with the genetic data from Campbell's monkeys (Lemasson et al. 2011b). A rarefaction curve was calculated to estimate the accuracy of our analysis (Fig. 1). The analysis included enough markers for the curve to reach a plateau, showing that information gained by adding another marker is negligible.



Locus	Primer Sequence (5'-3')	Final [c] (µM)	Reference	Size range (bp)	Number of alleles
D1s207 $^{\delta}$	FAM-CACTTCTCCTTGAATCGCTT GCAAGTCCTGTTCCAAGTCT	0,2	a	126-147	10
D1s548 $^{\beta}$	GAACTCATTGGCAAAAGGAA VIC-GCCTCTTTGTTGCAGTGATT	0,5	b, c	208-272	11
D2s1326 $^{\alpha}$	FAM-AGACAGTCAAGAATAACTGCC CTGTGGCTCAAAAGCTGAAT	0,5	b, c	192-266	11
D3s1766 $^{\delta}$	PET-ACCACATGAGCCAATTCTGT ACCCAATTATGGTGTTGTTACC	0,25	a	201-219	6
D3s1768 $^{\alpha}$	VIC-GGTTGCTGCCAAAGATTAGA CACTGTGATTTGCTGTTGGA	0,5	a	183-218	12
D4s243 $^{\alpha}$	PET-TCAGTCTCTCTTTCTCCTTGCA TAGGAGCCTGTGGTCCTGTT	0,5	b, c	194-222	11
D5s177 $^{\varepsilon}$	FAM-TGTCTCCTGCTGAGAATAG TAATATCCAAACCACAAAGGT	0,5	a	137-154	5
D5s820 $^{\gamma}$	ATTGCATGGCAACTCTTCTC PET-GTTCTTCAGGGAAACAGAACC	0,5	a	176-212	10
D6s311 $^{\varepsilon}$	VIC-ATGTCCTCATTGGTGTTGTG GATTCAGAGCCCAGGAAGAT	0,5	a	220-228	6
D6s474 $^{\beta}$	PET-TGTACAAAAGCCTATTTAGTCAGG TCATGTGAGCCAATTCCTCT	0,5	c	124-162	13
D6s493 $^{\beta}$	ATCCCAACTCTTAAATGGGC NED-TTCCATGGCAGAAATTGTTT	0,5	c	244-272	9
D7s2204 $^{\varepsilon}$	PET-TCATGACAAAACAGAAATTAAGTG AGTAAATGGAATTGCTTGTTACC	0,5	b, c	217-237	4
D10s611 $^{\beta}$	FAM-CATACAGGAAACTGTGTAGTGC CTGTATTTATGTGTGTGGATGG	0,5	c	144-181	11
D11s2002 $^{\gamma}$	FAM-CATGGCCCTTCTTTTCATAG AATGAGGTCTTACTTTGTTGCC	0,6	b, c	240-260	6

Table 1: Human microsatellites identified as polymorphic in Diana monkeys. $^{\alpha}$, $^{\beta}$, $^{\gamma}$, $^{\delta}$ and $^{\varepsilon}$ designate the five multiplexes used, for which we give the final primer concentration in the PCR mix. The hybridization temperature used during PCR was 55°c for $^{\alpha}$ and $^{\beta}$ multiplexes and 57°C for multiplexes $^{\gamma}$, $^{\delta}$ and $^{\varepsilon}$. References: a : Petit et al. 2010, b : Roeder et al. 2009, c : Vallet D. Personal Communication. Amplification conditions were as follows: 15 min at 95 °C; 45 cycles of 95 °C for 45 s, X°C (depending on the multiplexes, see table 1 for corresponding temperature) for 45 s, 72 °C for 60 s; 60 min at 72 °C.

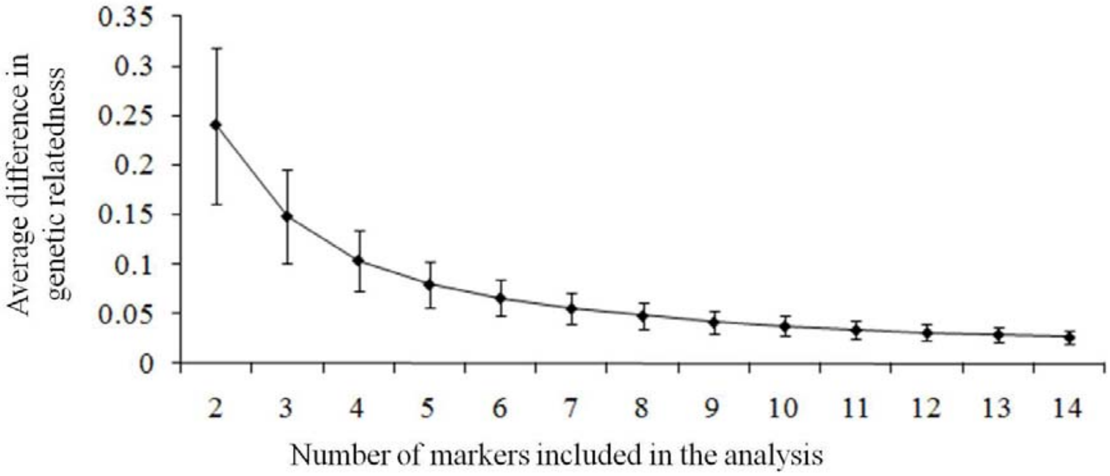


Figure 1: Rarefaction curve. Graph shows the mean difference in genetic relatedness obtained for the number of markers used in the analysis for Diana monkeys population studied. Error bars show SD.

Vocal analyses in Campbell's and Diana monkeys

Individual contact call rates were calculated by dividing the total number of calls recorded for a given female by the total recording duration for this female. Calls could be emitted alone or as part of a vocal exchange. Two calls were considered as exchanged when the inter-call interval of successive calls was less than one second (Lemasson et al. 2010). For each female, we also calculated the proportion of exchanged calls by dividing the number of exchanged call by the total number of calls emitted. It was not possible to identify the partners of a vocal exchange due to poor visibility in the forest.

Social bond analyses in Campbell's and Diana monkeys

We calculated the proportion of time that each adult female (A) maintained close proximity with another adult individual in her group, relative to her total observation time, which yielded dyadic scores for each focal female (A) with all other females in the group. We then averaged the proportions obtained for one female relative to all other adults to obtain her mean proximity index. To generate her mean grooming index, the same procedure was applied to grooming sessions. We also calculated, for each female, the average duration of a proximity session and the average duration of a grooming session. Individual agonistic interaction rates were calculated by dividing the number of occurrences of agonistic behaviours by the total observation time.

Statistical analyses

To compare rates of contact call rate, call exchange rate, spatial proximity (Proximity rate and Proximity duration), allogrooming (Grooming rate and Grooming duration) and agonism (Agonistic rate) across groups and species, we carried out nested ANOVAS. We checked for normality using Shapiro Wilk tests, and performed log transformations or used Generalized Linear Models ($GLM_{negative\text{-}binomial}$ type III analysis on the likelihood-ratio chi-square $LR\chi^2$) if the normality assumption was violated. We used Mantel's tests to compare dyadic scores of genetic relatedness and spatial proximity or grooming rates (see Lemasson et al. 2011b). We calculated sociograms using all possible dyads, based on interactions occurring more frequently than expected by chance in one dyad than in others. To do so, we calculated for each dyad A=>B the ratio of behaviours emitted from female A to individual B divided by the mean duration of behaviours emitted by female A towards all adult individuals. Since we did not perform focal samplings on males, it was not possible to assess males' social initiations. We calculated the expected ratio under the null hypothesis that female A did not have preferential partners, i.e. distributed her behaviours equally to all other adult individuals (male and females). We then compared both the observed and the theoretical ratios, and considered that A significantly emitted her behaviours towards B if the observed ratio was higher than expected by chance. All tests were two tailed and we used SPSS.18 as well as R.2.14 software.

Results

During the study period, DIA1 and CAM2 were observed intermingled in a polyspecific association 45.6% of the time (N= 724 scans) while DIA2 and CAM1 were observed together 89.3% of the time (N= 656 scans). A total focal time of 32 hours was performed for Diana monkeys (mean ± sem = 96 ± 12 minutes per female). For Campbell's monkeys, a total focal time of 137 hours was performed (mean ± sem = 1174 ± 21 minutes per female).

Genetic relatedness within and between groups

We first carried out a Factorial Correspondence Analysis (FCA) on all genetic markers for both species combined, which explained at least 17% of the variance on the first two axes (Fig. 2). For Diana monkeys, the first axis accounted for 9.3% of the variance and the second one for an additional 8.4%. For Campbell's monkeys, the first axis accounted for 13.6% of the variance and the second for an additional 11.1%. In both species, females were generically more closely related to each other within than between groups (Fig. 2 and 3) but this effect was stronger for Diana monkeys. In addition, there seems to be a negative relationship between genetic relatedness and group size with larger groups containing individuals that are genetically more scattered than smaller groups. Interestingly, in both species the supposed oldest adult females of each group (as estimated by the scars, broken tail and frail general shape) were genetically very close to each other. Regarding adult resident males (former and new males), Campbell's monkeys were clearly genetically distant from females of both groups while all Diana monkey males including the D3M out-group male were not distant from females of DIA2 group because their genetic position overlapped with the ranging of females' genetic distribution (Fig. 2).

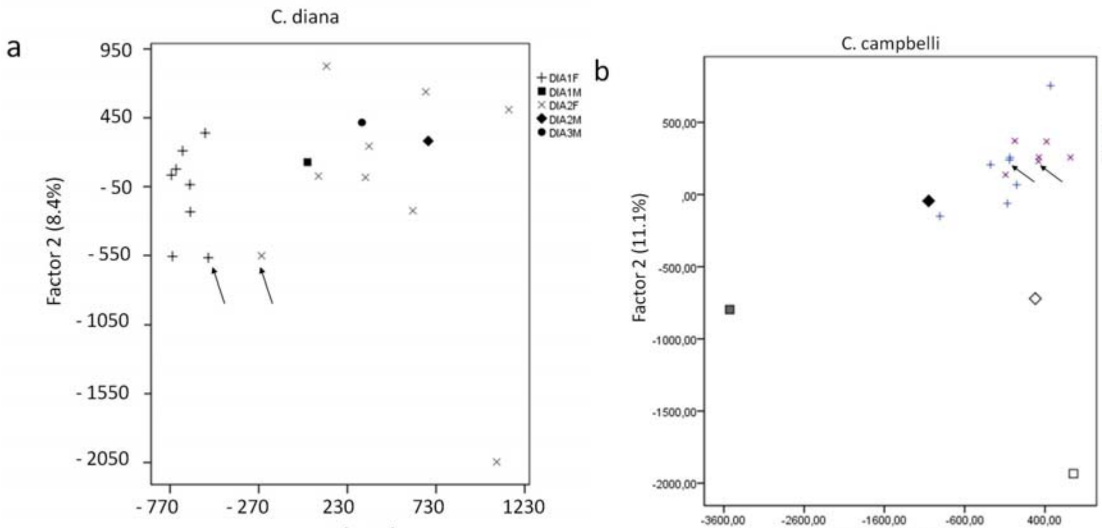


Figure 2: Genetic relatedness between adult individuals of Diana monkey neighbouring groups (a) and Campbell's monkey neighbouring groups (b). Arrows show the eldest females of each group. DIA1 corresponds to the first group of Diana monkeys, DIA2 to the second one and DIA3 to another neighbouring group, CAM1 corresponds to the first group of Campbell's monkeys and CAM2 to the second one, F to adult females, M to adult males and MN to the replacing males.

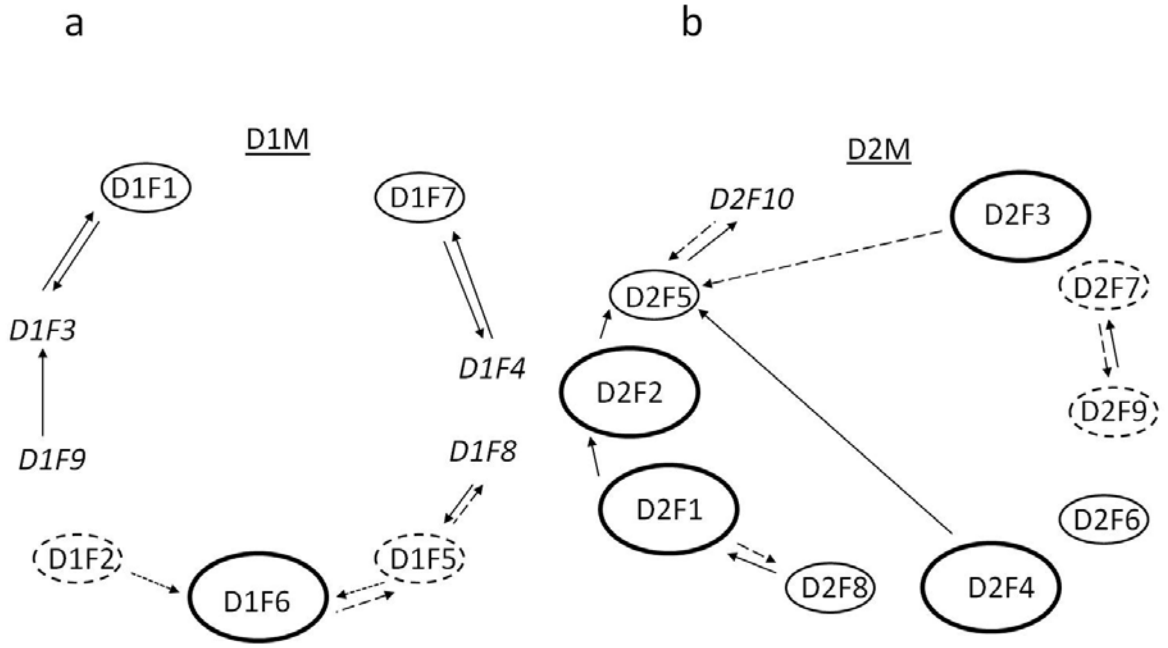


Figure 3: Diana monkeys vocal and social networks. Sociograms represent all adult individuals, with males' names underlined. For DIA1 (a) and DIA2 (b) groups, sociograms show proximity interactions as well as grooming interactions occurring more often than expected by chance (ratio tests described in the methods section). Arrows are directed from emitters to receivers, with dotted lines indicating preferential proximity only, hyphen lines representing preferential grooming only and plain lines representing both preferential proximity and grooming. For females, the proportion of exchanged calls is represented with black circles, with firm line thick circles indicating an average proportion >70%, firm line thin circles an average proportion >60%, dotted line circles an average proportion >50% and no circle an average proportion <50%. This variable was not calculated for males. Importantly, it was not possible to calculate the proportion of exchanged calls for females *D1F3, D1F4, D1F8, D1F9, and D2F9* due to small call samples (less than 30 calls).

Frequency and duration of social interactions

Durations of sitting in proximity and grooming showed no significant differences between species or between groups (Table 2). Diana monkeys' proximity, grooming and agonistic rates were higher than Campbell’s monkeys’ while there were no significant group differences within species (GLM, Table 2a and 2c). Regarding females’ vocal activity, Diana monkeys showed higher call rates and higher proportions of exchange rates than Campbell’s monkeys, while there were also no significant group differences within species (ANOVA, Table 2a and 2b).

A	groups			
	CAM2*	CAM1^{+}	DIA1*	DIA2^{+}
number adult females	4	7	9	10
call rate (per min)	0.30±0.09	0.18±0.06	0.45±0.61	0.78±0.35
exchange rate (%)	60.7±15.8	49.8±9.0%	63.8±6.2	68.2±8.1
proximity duration (s)	131±59	238±146	67±108	67±69
grooming duration (s)	110±27	140±121	95±29	90±58
agonistic rate (per hour)	0.001±0.001	0.001±0.001	0.004±0.013	0.006±0.006
proximity rate (%)	0.5±0.6	1.1±0.6	1.6±7.2	0.9±2.6
grooming rate (%)	0.9±0.3	0.4±0.5	2.1±8.9	1.7±4.5

B		Shapiro-wilk test	species effect	groups effect
callrate (per min)	ANOVA (log)	W=0.957 p=0.396	F_1=30.345 p=0.031	F_2=1.141 p=0.340
call exchanges (%)		W=0.968 p=0.629	F_1=218.665 p=0.004	F_2=0.238 p=0.791
proximity duration (s)	ANOVA	W=0.981 p=0.850	F_1=3.985 p=0.184	F_2=1.630 p=0.216
grooming duration (s)		W=0.941 p=0.109	F_1=4.279 p=0.175	F_2=1.901 p=0.170

C				
agonistic rate (per hour)	GLM		$LR\chi^2_1$=33.12 P<0,001	$LR\chi^2_2$=0.862 P=0.650
proximity rate (%)			$LR\chi^2_1$=5.274 P=0.022	$LR\chi^2_2$=3.214 P=0.200
grooming rate (%)			$LR\chi^2_1$=8.714 P=0.003	$LR\chi^2_2$=1.203 P=0.548

Table 2: Results of the statistical tests. A. For each variable and each group, the Mean ± SD are presented in the first raw as well as the minimum and maximum for each variable and each species in the second raw. B. We ran nested analyses of variance (ANOVA type III), with ‘‘species’’ and “species(group)” as the fixed factors. When necessary, the variables were transformed to obtain a normal distribution (verified with the Shapiro-Wilk normality test). C. We performed Generalized Linear Model analyses with ‘‘species’’ and “species(group)” as

the fixed factors on the variables that did not fit a normal distribution even after transformation.

Social network analyses

In Diana monkeys, the resident male was never approached or groomed by any of the females, although this happened a few times in Campbell's monkeys, but not enough to indicate a significant preference towards the male (Fig. 3 and 4). Between females, we were able to identify preferential dyads in all four groups (Fig. 3 and 4). First, there was overlap between proximity and grooming preferences in DIA1 and CAM2, but not DIA2 and CAM1. Second, half of the preferential dyads were bidirectional in both species. Third, females presenting preferential partners had generally only one (excepted from D2F5 and C1F2). Nevertheless, there was a species difference in terms of the number of females with no preferential partner (DIA1: 0/9, DIA2: 1/10, CAM1: 3/7, CAM2: 2/4). Unlike Diana monkeys, female Campbell's monkeys appeared to direct their behaviours more homogeneously towards all group members. In both species, females' vocal activity varied given their heterogeneity to contribute to vocal exchanges (e.g. only 50.5% for D2F9 but 77.1% for D2F4), but there was no obvious link between females' social popularity and their vocal activity (Fig. 3 and 4). Interestingly, the oldest female of each group (D1F1, D2F1, C1F1, and C2F1) in both species was involved in preferential dyadic relationships, but no specific vocal pattern emerged for these females.

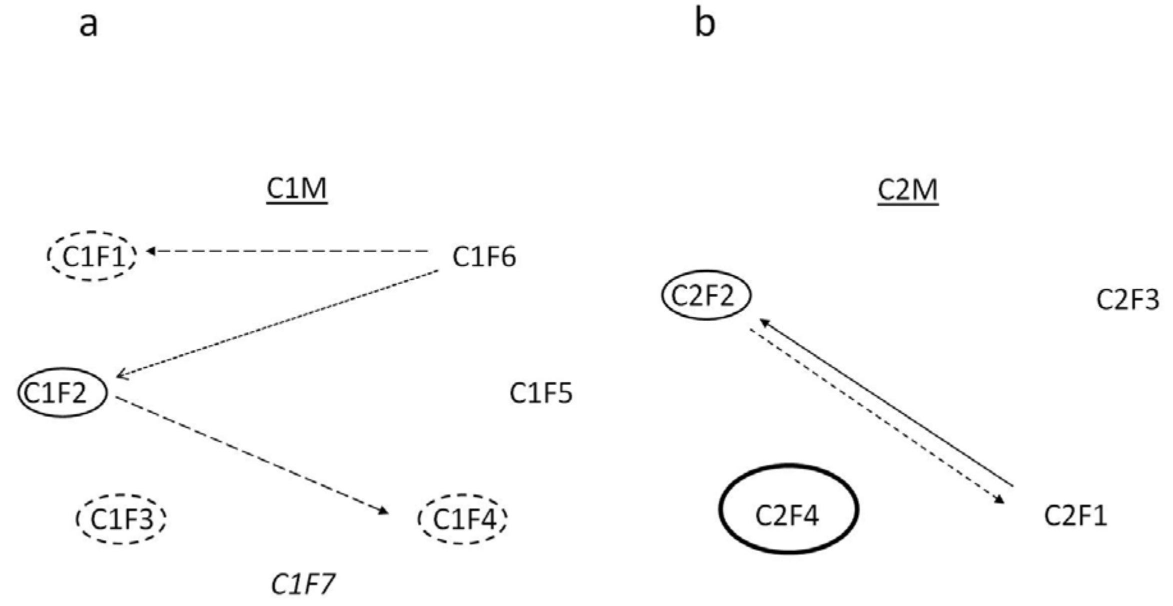


Figure 4: Campbell' monkeys vocal and social networks. Sociograms represent all adult individuals, with males' names underlined. For CAM1 (a) and CAM2 (b) groups, sociograms show proximity interactions as well as grooming interactions occurring more often than expected by chance (ratio test described in the methods section). Arrows are directed from emitters to receivers, with dotted lines indicating preferential proximity only, hyphen lines representing preferential grooming only and plain lines representing both preferential proximity and grooming. For females, the proportion of exchanged calls is represented with black circles, with firm line thick circles indicating an average proportion >70%, firm line thin circles an average proportion >60%, dotted line circles an average proportion >50% and no circle an average proportion <50%. This variable was not calculated for males. Importantly, it was not possible to calculate the proportion of exchanged calls for the female *C1F7* due to small call samples (less than 30 calls).

Genetic relatedness and social life

We found no link between genetic relatedness and social affinities in Diana monkeys, as assessed in terms of proximity and grooming rates (Mantel tests, genetic *vs.* proximity DIA1 r = 0.024, p = 0.448 and DIA2 r = -0.023, p = 0.542, Fig. 5a and genetic *vs.* grooming DIA1 r = 0.018, p = 0.432 and DIA2 r = 0.033, p = 0.334, Fig. 5c). In contrast, there was a significant relation between genetic relatedness and proximity in CAM1, but no correlation between genetic relatedness and grooming (Mantel tests, genetic *vs*. proximity CAM1 r = 0.480, p = 0.016 and CAM2 r = 0.307, p = 0.354, Fig. 5b and genetic *vs*. grooming CAM1 r = 0.154, p = 0.272 and CAM2 r = 0.291, p = 0.343, Fig. d), showing that in CAM1, females maintained proximity preferentially with genetically related group members.

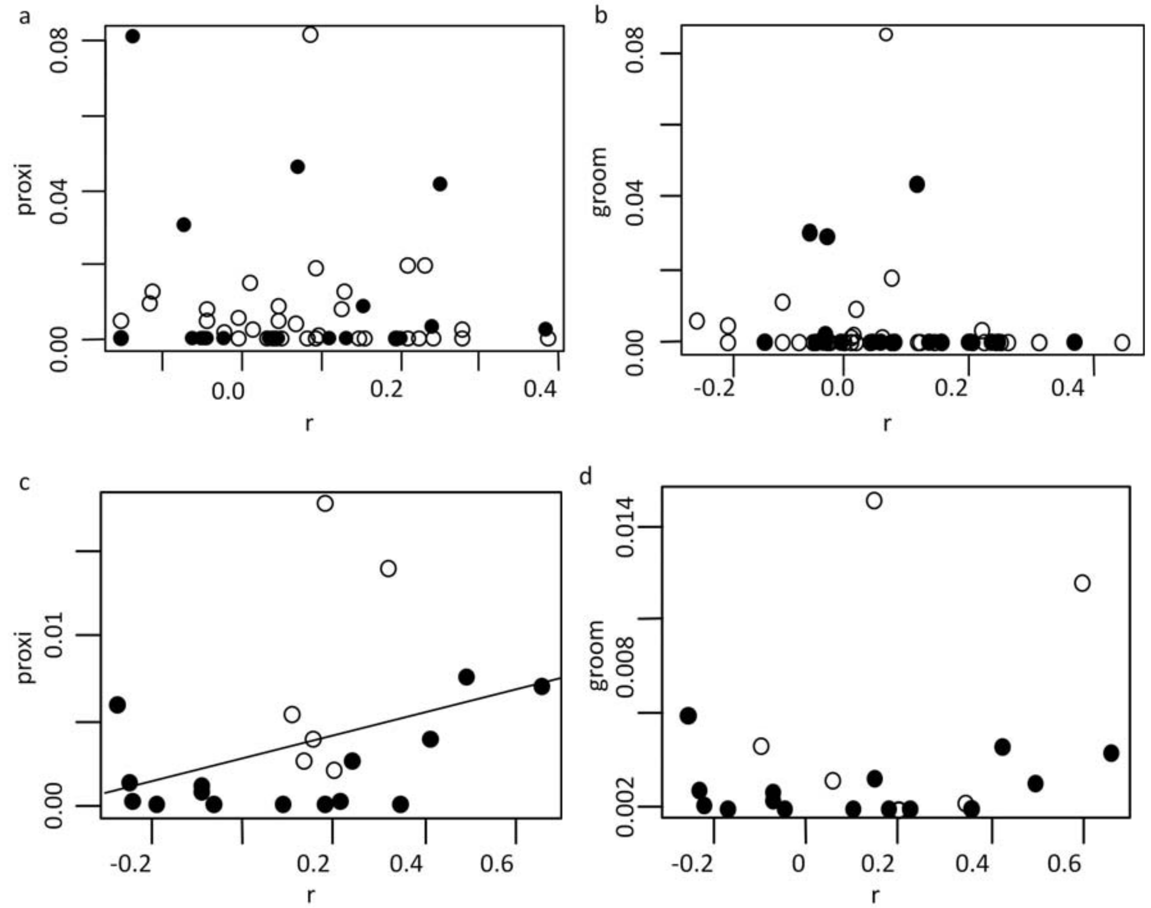


Figure 5: Relationship between genetic relatedness and social affinities in Diana monkeys (a,c) and Campbell's monkeys (b,d). Graphs show the relationship between the proximity (a,b) index (proxi) or the grooming index (c,d) and Li's genetic relatedness coefficient (r) for both groups (group 1 : black dots, group 2 : white dots).

Discussion

Our study on Diana and Campbell's monkeys revealed that the social system of these forest guenons is characterised by very few physical interactions. We also found that, in contrast to the other cercopithecids, there was no strong and systematic link between genetic relatedness and social bonding in our study groups.

However, our analyses also showed that, in both species, females were more closely related within than between groups, most likely the result of female philopatry (Wrangham 1980; Rowell & Olson 1983). Genetic diversity was bigger in larger groups, which indicated the possible presence of several matrilines. In line with earlier observations of male migration (Cords 1987), we observed two young Diana monkey males to leave their natal group in a gradual manner, by disappearing from their native group for several weeks and reappearing again but remaining in the periphery only (AC, pers. obs.), a phenomenon that has also been described in Campbell's monkeys (Pusey & Packer 1987). Despite strong female philopatry, female migration can happen in guenons (Moore 1984; Pusey & Packer 1987; Rowell 1988). In both species, we observed that what appeared to be the oldest female of both groups were genetically closely related to each other, suggesting that they were born in the same group, which then split into two or one of them left their native group. Group fission has been observed in other guenon species, with both subgroups sharing the original territory (Cords & Rowell 1986). There were also some potential species differences in the genetic structure of the groups. While in Diana monkey groups, there was no genetic overlap between the two groups, this was not the case for the two Campbell's monkeys groups, which might be explained by a greater genetic heterogeneity in Diana monkeys due to a higher number of females with possibly several matrilines, which could have, during a fission event, formed subgroups depending on the existing matrilines, as has been observed in other species (Koyama 1970; Nash 1976; Ménard & Vallet 1993; Lefebvre et al. 2003). Another species difference concerned the observation that male Campbell's monkeys were genetically more distant to their females than male Diana monkeys were to their females. This may have to do with the more frequent turnover of resident male Campbell's monkeys or with differences in migration distances. Male Diana monkeys may not disperse very far compared to Campbell's monkeys; hence all three males could originate from neighbouring groups.

In line with earlier observations, we found that resident males were spatially and socially not well integrated. We also found that social interactions between all group members were relatively rare (Cords 1987; Rowell 1988; Lemasson et al. 2006). In our study, females spent less than 2% of the observed time in close proximity to each other and agonistic interactions were extremely rare. Both affiliative and agonistic behaviours occurred at much lower frequency than what has been observed in baboons (Seyfarth 1976; Barton et al. 1996; Lemasson et al. 2008) and macaques (Sterck & Steenbeek 1997). Nevertheless, species differences were observed, with Diana monkeys showing higher rates of intra-group aggression, affiliation and vocal behaviour than Campbell's monkeys. Sterck et al. (1997) hypothesized that the strength of inter- and intragroup competition is a strong determinant of the nature of females' relationships. Diana monkeys' higher agonistic rates could be due to bigger group size resulting in higher within-group food competition (Buzzard & Eckardt 2007) or to the fact that Diana monkeys feed on better quality food than Campbell's monkeys, suggesting higher levels of competition in Diana monkeys (McGraw et al. 2007). While the mean duration of proximity bouts and grooming bouts did not differ between species, female Diana monkeys showed higher proximity rates and higher grooming rates than Campbell's monkeys as well as higher vocal exchange rates. Since Diana monkey groups are usually bigger than Campbell's monkey groups (Whitesides 1989; Mcgraw & Zuberbühler 2008), an explanation could be that the former need to dedicate a higher part of their budget time to social interactions than the latter to cope with daily needs of group's social life. This hypothesis could also explain the greater vocal activity of female Diana monkeys, which showed higher call rates and exchanged more calls than female Campbell's monkeys. Another possibility is a difference in predation pressure, with smaller cryptic Campbell's monkeys (average body size 2.7 kg, Zuberbühler & Jenny 2002) foraging in the lower strata and being more exposed to terrestrial threats than bigger conspicuous Diana monkeys (average body size 3.9 kg, Zuberbühler & Jenny 2002) foraging in the upper strata. Chimpanzees occasionally hunt on these monkeys, and this type of predation where preys are chased in the canopy, which is very different from the surprise technique of eagles and leopards, has a major impact on call rates (Zuberbühler 2000). A third explanation could be a difference in the micro-habitat, with a difference of visibility between higher strata occupied by Diana monkeys and lower strata occupied by Campbell's monkeys. In both species, groups were clearly female bonded and females had developed preferred dyadic bonds. Nevertheless, species also differed in the pattern of the group's social network. Female Campbell's monkeys directed their proximity and grooming acts more equally towards all adult females, resulting in less dyadic preferences than in Diana monkeys. This difference could be due to higher degrees of feeding competition generating more conflicts where coalitions within group occur (Wrangham 1980; Buzzard & Eckardt 2007).

We could not conclude in favour of a strong influence of genetic relatedness on social preferences. Indeed, there was no social bias towards genetically related females in 3 out of the 4 studied groups. Only one group of Campbell's monkeys showed a positive correlation between relatedness and the proportion of time spent in proximity, but not the proportion of time spent grooming. In captivity, kin bias depends on the social stability of the group (Lemasson et al 2005). In addition, in guenons genetic relatedness is not a major factor of influence on vocal convergence, another reliable marker of social affinities (Lemasson & Hausberger 2004; Lemasson et al. 2011b). Our study shows that kin bias is much less present in guenons than what has been described in baboons and macaques (Leinfelder et al. 2001; Silk 2002).

To conclude, social diversity in primates is interesting from an evolutionary perspective because sociality is considered as preponderant factor in the evolution of animal communication and the emergence of human language (Dunbar 1998). In the guenon species studied here, environmental pressures have favoured a "monitor-adjust" system within a female bonded network with a "Resident-Egalitarian" (Campbell's monkeys) or a "Resident-Nepotistic-Tolerant" (Diana monkeys) organisation (Sterck et al. 1997; Buzzard & Eckardt 2007). Further species comparisons at several phylogenetic levels would be necessary to gain a better overview of social systems and communicative abilities in our closest relatives, the nonhuman primates.

Acknowledgments

This research was funded by the French Ministry of Research, IUF, PICS-CNRS, ANR 'Orilang' with additional support by the Wissenschaftskolleg zu Berlin as well as grants from the European Union (FP6 programme: "What it means to be human" and ESF-Eurocores: "The Origin of Man Language and Languages"), from the French Ministry of Foreign Affairs (Egide) and from the Centre Suisse de Recherches Scientifiques (CSRS). In Côte d'Ivoire, we thank the minister of scientific research and the 'Office Ivoirien des Parcs et Réserves' (OIPR) for permission to conduct research in Taï National Park. We also thank A. Bitty and the CSRS for logistic support. We are very thankful to our field assistants B. Diero, F. Belé and F. Gnepa for their invaluable help with data collection and to members of the Taï Chimpanzee Project (TCP) and the 'Centre de Recherche en Ecologie' (CRE) for their support in the field. We are grateful for comments and thoughts by V. Biquand and M. Laparie.

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CHAPTER 4 – VOCAL REPERTOIRE OF FEMALE DIANA MONKEYS: FLEXIBILITY IN ACOUSTIC STRUCTURES AND CALL COMBINATIONS

SUMMARY OF PAPER 2

Questions : Adult female Diana monkeys are known to possess referential alarm call types, but the organization of the vocal repertoire regarding intra-group social communication remains unknown. Can social calls also be classified into several structurally and contextually distinctive call types? How do call types acoustically vary from one another? Are combinatorial abilities limited to loud male calls in guenons?

Methods : We conducted 10 minutes focal sampling on identified adult females of two groups of free ranging Diana monkeys in Taï forest, Ivory Coast. We also performed scan samplings every 30 A preliminary classification of call strminutes to sample the general group activity and environmental context. Calls were classified according to their temporal, frequency and combinatorial patterns. We thejn verified whether the identified call types also varied contextually.

Results : We identified 4 units differing in their acoustic structure. They could be emitted alone or be non-randomly combined, with the most frequent call type divided into two subtypes used as a "suffix" and several introductory units used as "prefixes. These combinations resulted in a repertoire of 11 types of calls. Although patterns of context of emission were largely overlapping, contextual profiles between call types emerged.

Conclusions : Diana monkey adult females increased the effective size of their "social vocal repertoire" by varying the acoustic structure of the basic call types but also by combining them into more complex structures. These two non exclusive strategies of vocal flexibility may have enables nonhuman primates to enlarge their communicative potential.

This paper has been published in Animal Cognition and presented to the 2010 Congress of the International Primatological Society (IPS).

Context-related call combinations in female Diana monkeys

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Key words social calls, call combination, vocal flexibility, nonhuman primates

Abstract

Nonhuman primates possess species-specific repertoires of acoustically distinct call types that can be found in adults in predictable ways. Evidence for vocal flexibility is generally rare and typically restricted to acoustic variants within the main call types or sequential production of multiple calls. So far, evidence for context-specific call sequences has been mainly in relation to external disturbances, particularly predation. In this study, we investigated extensively the vocal behaviour of free-ranging and individually identified Diana monkeys in non-predatory contexts. We found that adult females produced four vocal structures alone (‘H’, ‘L’, ‘R’ and ‘A’ calls, the latter consisting of two subtypes) or combined in non-random ways (‘HA’, ‘LA’, ‘RA’ call combinations) in relation to ongoing behaviour or external events. Specifically, the concatenation of an introductory call with the

most frequently emitted and contextually neutral 'A' call seems to function as a contextual refiner of this potential individual identifier. Our results demonstrate that some non-human primates are able to increase the effective size of their small vocal repertoire by varying the acoustic structure of basic call types but also by combining them into more complex structures. We have demonstrated this phenomenon for a category of vocalisations with a purely social function and discuss the implications of these findings for evolutionary theories of primate vocal communication.

Introduction

One widespread mechanism of increasing acoustic flexibility in animal communication is to concatenate sounds into more complex vocal sequences. This phenomenon is common in songbirds and other species that produce utterances composed of a series of notes or 'syllables' (e.g. Passeri: Catchpole & Slater 1995, quacking frog *Crinia georgiana:* Gerhardt et al. 2000, Humpback whales: *Megaptera novaeangliae*: Payne & McVay 1971). Although there have been repeated efforts to compare such animal communication systems with syntax in human language (e.g. Marler 1977) the gulf has remained vast with major differences in terms of generativity and semanticity (Chomsky 1981, Hauser et al. 2002). For example, animal syntax is typically based on elements with little or no independent meaning that could be linked to the organisational principles of the sequence. Moreover, there is no clear evidence for generative use of sound combinations, and as a consequence the debate on the phylogenetic origins of human language has not yet made much progress (Bickerton & Szathmáry 2009).

However, due to their close phylogenetic proximity to humans, the vocal behaviour of non-human primates is relevant to investigate the evolutionary pathways of human language (Lemasson 2011). The mainstream hypothesis here is that human speech has emerged as an evolutionary derivative of a gesture-based communication system, with a subsequent transition from the visual to the vocal domain (Corballis 2003). One alternative view is that ancestral humans initially relied on a primate-like vocal communication system, perhaps complemented by gestural signals, but then experienced an evolutionary process of gaining increasing motor control over their vocal apparatus which eventually enabled them to imitate sound patterns and produce arbitrary vocal patterns (e.g. Enard et al. 2002). Social complexity may have favoured this process (Dunbar 1998). One prediction of the vocal transition hypothesis therefore is that enhanced acoustic flexibility should be found, to various degrees, in primate call types that are primarily used while interacting socially.

There are a growing number of primate studies that have demonstrated acoustic flexibility within some of the species-specific (i.e. “genetically” predetermined) call types (*Cebuella pygmaea*: Elowson & Snowdon 1994, Snowdon & Elowson 1999; *Macaca fuscata*: Koda et al. 2008; *Papio anubis*: Ey et al. 2009; *Cercopithecus campbelli:* Lemasson & Hausberger 2004; *Pan troglodytes:* Slocombe et al. 2010). A second source of acoustic flexibility is in the form of combinations of existing calls (*Pan troglodytes*: Crockford & Boesch 2005; *Pan paniscus*: Clay & Zuberbühler 2009; *Hylobates lar*: Clarke et al. 2006; *Colobus guereza*: Schel et al. 2009; *Cercopithecus nictitans*: Arnold & Zuberbühler 2006; *Cercopithecus campbelli*: Ouattara et al. 2009a,b; *Sanguinus oedipus*: Cleveland & Snowdon 1982; *Cebus olivaceus*: Robinson 1984) with evidence that some of these sequences can be ‘meaningful’ to others (*Cercopithecus nictitans:* Arnold & Zuberbühler 2008; *Cercopithecus diana*: Zuberbühler 2002; *Colobus guereza:* Schel et al. 2010; *Pan paniscus*: Clay & Zuberbühler 2011).

One drawback is that studies of call combinations in primates have focused on long-distance communication or calls to predators. For example, male putty-nosed monkeys (*Cercopithecus nictitans*) combine two types of loud calls into sequences that reliably predict forthcoming group progression (Arnold & Zuberbühler 2008). Similarly, male Campbell’s monkeys (*Cercopithecus campbelli*) transform highly specific alarm calls into general alert calls by an affixation mechanism (Ouattara et al. 2009a) and concatenate individual calls into sequences that are context-specific and related to external events (Ouattara et al. 2009b). However, a largely unaddressed question is whether close-range social calls in primates show similar or even increased flexibility in terms of acoustic properties and sequential structure, as hypothesised by Lemasson and Hausberger (2011).

Many primate species produce short-distance social calls, usually referred to as ‘clear calls’ or ‘contact calls’ (e.g. Uster & Zuberbühler 2001). They tend to be amongst the most frequently emitted calls of the vocal repertoire and can encode information on the caller’s identity, social affinities, or spatial positioning (Harcourt & Stewart 1996; Gautier-Hion 1988; Lemasson & Hausberger 2004 and 2011). For example, Seyfarth & Cheney (1984) showed that vervets monkeys give acoustically distinct grunts in different social contexts, such as when approaching a dominant or subordinate group member, and that these acoustic differences are ‘meaningful’ to conspecifics. In terms of acoustic flexibility, various studies have found subtle contact call subtypes, and in some cases there is evidence for semantic content (e.g. Japanese macaque ‘coo’ calls: Green 1975; Pygmy marmoset ‘trill’ calls: Pola & Snowdon 1975; Baboon ‘grunts’: Owren et al 1997; Campbell’s monkey ‘CH’ calls: Lemasson et al. 2004; Lemasson & Hausberger 2011; review by Snowdon 2009). Further evidence for socially-determined acoustic flexibility is in the form of converging acoustic structure of contact calls between affiliated females (Pygmy marmosets: Snowdon & Elowson 1999; Campbell’s monkeys: Lemasson & Hausberger 2004, Lemasson et al. 2005). Here, we define ‘social’ calls broadly as vocalisations to communicate with other group members over short distances in non-predatory contexts.

To address this possibility that primate social calls also have combinatorial properties, we carried out a study on wild Diana monkeys, *Cercopithecus diana diana*, a guenon species closely related to Campbell’s and putty-nosed monkeys (Gautier 1988). Although Diana monkeys’ alarm calls have been extensively studied (Zuberbühler et al 1997, Zuberbühler et al 1999, Zuberbühler 2000a, Zuberbühler 2000b), little attention has been paid to females’ other types of vocalisations (Gautier 1988, Hill 1994, Zuberbühler et al 1997, Uster & Zuberbühler 2001). This was partly due to the difficulties in identifying and describing these animals’ behaviour in details, because they spend much of their time in the upper forest canopy (McGraw 2007). Unlike savannah dwelling primates, forest guenons are often out of sight from each other. Social interactions are much less common because they spend more effort monitoring each other’s behaviour and adjusting their own spatial position accordingly (Rowel & Olson 1983; Rowell 1988). Instead, guenons typically emit social calls to overcome the constraints of poor visibility in the forest and maintain group cohesion (e.g. Gautier & Gautier 1977; Uster & Zuberbühler 2001). Calling tends to be contagious and call rates are increased when visibility is poor. Still, the specific contexts of emission of these social calls remain unknown. It is hence both interesting and challenging to try and better understand these females' social communicative system.

We were interested in the influence of social and environmental factors on the acoustic structure of female Diana monkey's vocalisations at several organisational levels of their repertoire. Given the complexity of their alarm calling system and the importance of indirect social interactions via vocal communication, we hypothesized that their social calls contained similar or even greater levels of acoustic diversity in relation to contextual variables.

Methods

Study site and subjects

Data were collected from February to May 2009 and from January to June 2010 from two groups (DIA1 and DIA2) of free-ranging Diana monkeys (*Cercopithecus diana diana*) in Taï National Park, Ivory Coast. The study area is located in the South-western part of the park, adjacent to the CRE (Centre de Recherche en Ecologie) research station (5°50'N, 7°21'W). Both groups had been under observation since the early 1990s and were fully habituated to the presence of human observers. Both groups consisted of about 20–25 individuals, including one adult male, 9-10 adult females (individuals with visible nipples and at least one offspring), several sub-adults, juveniles and infants.

Data collection

DIA1 and DIA2 groups were followed alternatively. Data were collected between 07:30 and 17:00 hours GMT. Every 30 minutes, a scan sample (Altmann 1974) was taken on a number of variables that, according to previous studies, had the potential to influence the monkeys' vocal behaviour (Ouattara et al. 2009a). Specifically, we scored the location of the group within its territory (using a map and a grid system), the degree of group scattering, the group's main activity, general luminosity and the presence of a neighbouring Diana monkey group (table 1).

	Name	Definition
Scan variables	territory	The group is located in a grid cell in the core part of the territory, which represents about 30% of the surface explored (center), or the group is visiting grid cells at the periphery of their usual home range, which represents about 60% of the surface explored (periphery), or the group is out of its usual home range, next to a never visited area, which represents about 10% of the surface explored (outside)
	scattering	The majority of the individuals, i.e. more than 50% of the adults, is (yes) or is not (no) dispersed over an area of more than 25 m^2
	activity	The majority of the individuals, i.e. more than 50% of the adults is moving around, foraging for food or feeding on insects/leaves/fruits (foraging), or resting as well as interacting socially (resting) or has initiated a group movement of at least 100 meters in the last 10 minutes (travelling)
	neighbours	A neighbouring group can (present) or cannot (absent) be heard at less than 200 meters
	luminosity	Illumination of the observation area is very bright (bright) or very dark (dark). Luminosity level was estimated by measuring the intensity (in Lux) of light received 1m from the forest floor with a luxmeter (DVM401 Voltcraft DT8820). For a given scan, 9 points of measurements were equally spaced within a 10 m² and then averaged. There was a significant difference between both conditions (N= 36 scans, Mean +/- sem, M_{bright}= 645.7 +/- 45.3 Lux, M_{dark} = 256.6 +/- 18.2 Lux , Mann Whitney test, U= 1647, p<0.001)
Focal variables	scanning	female is exploring the environment visually
	foraging	female is searching for food in the leaves, on the trunk or on the floor
	feeding	female is feeding on fruits, leaves or insects
	walking	female is walking
	jumping	female is jumping
	resting	female is resting or grooming herself
	friendly social	female is involved in a positive social interaction such as grooming

agonistic social	female is involved in an aggressive social interaction such as threatening another individual
neutral social	female is involved in a neutral social interaction, *e.g.* another individual passes by
vigilance	female is in a general state of alertness

Table 1: Definition of the scan and focal variables

Between scans, adult females were monitored alternatively following a 10-min focal animal sampling procedure (Altmann 1974). We systematically described the female's behaviour, according to the behavioural categories described in table 1. Efforts were made to equalize the amount of observation effort for each female.

Recordings were made 5 to 25 metres from the focal female (depending on her elevation in the canopy) with a Sennheiser K6/ME66 directional microphone and a Marantz PMD660 solid-state recorder (sampling rate 44.1 kHz; resolution 16 bits). The observer (AC) complemented her observations with a running commentary on the behaviour of focal individuals, recorded with a Lavallier microphone to the recorder's second channel and later transcribed.

Acoustic analyses

Spectrograms were generated with RAVEN 1.3 software (Cornell Laboratory of Ornithology, Ithaca, New York). Poor quality recordings were discarded (3.7%). From the remaining sample, we first categorised the recordings according to the main call types, following visual and auditory assessments and taking into accounts previous findings from work on Campbell's monkeys' vocal behaviour (Lemasson & Hausberger 2011; fig. 1a). We then validated our classification with a basic acoustic analysis of call structure conducted on a sub-set of calls from the same females to control for individual differences (fig. 1b; table 2). It was based on total duration, minimum fundamental frequency ($F0_{min}$) and maximum fundamental frequency ($F0_{max}$). We also took a number of measurements that were more suited to some call types, such as amplitude and duration of frequency modulation in trilled calls and the number of units and duration of the first unit in the multi-units calls.

Contextual analyses

Our goal was to investigate the link between a given call type and its context of emission. Consequently, behaviours not associated with a vocalisation by the focal individual were not further considered. The influence of context on call production was investigated at two levels. ‘General’ context was based on data collected during scan sampling while ‘immediate’ context was based on data collected during focal animal sampling. Continuous observations from focal sampling were divided into 30s intervals to determine which of the ten aforementioned behavioural categories were produced by the focal animal when calling (see Lemasson et al. 2004). Our prospective analysis on detailed behavioural categories showed trends that brought us to lump the different behaviours into more general biologically relevant categories, as follows: (a) socio-positive or relaxed situations (‘resting’, ‘foraging’, ‘feeding’, ‘positive social interaction’), (b) neutral situations (‘scanning’, ‘walking’ and ‘neutral social interaction’), or (c) socio-negative or potentially dangerous situations (‘jumping’, ‘negative social interaction’ and ‘vigilance’).

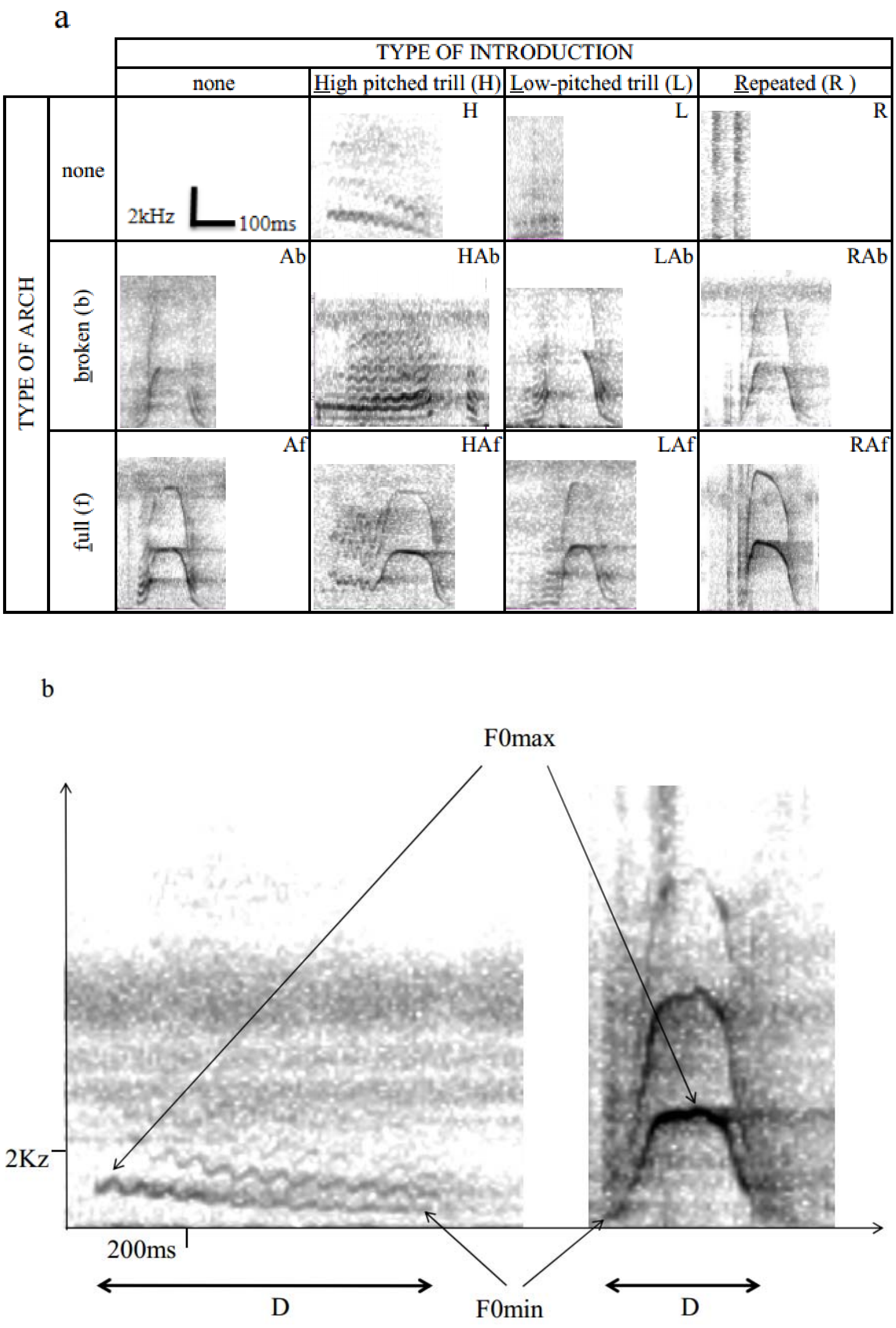

Fig.1: Spectrographic representation of the calls and acoustic parameters measured. Spectrograms were produced using a Hanning window function; filter bandwidth: 124 Hz; frequency resolution: 86.1 Hz; grid time resolution: 5.80 ms. a: Calls were classified according to two criteria: in columns the presence and type of arched frequency modulation

and in lines the presence and type of introductory unit. b: Figure shows the total duration (D), minimum (F0min) and maximum (F0max) of fundamental frequency measured

In Diana monkeys, social calls typically trigger a vocal response by another group member within a few seconds ((> 60% of cases; Uster & Zuberbühler 2001). We thus counted the number of calls emitted 3s prior and after a focal animal's call to determine whether the call was (a) isolated (no other call 3s before nor after), (b) exchanged (1-3 other calls separated by a less than 3s, with no call overlap: see Lemasson et al. 2010), or (c) chorused (at least 4 other calls with overlapping).

Statistical analyses

To test for morphological differences between the call types we performed a Discriminant Function Analysis (DFA) based on the three basic acoustic variables that were measurable on every call type: total duration and the minimum and the maximum fundamental frequency. To control for individual differences, we used the same number of calls per call type from each female. The classification results were based on equal probabilities of class (call type) membership. After generating the discriminant function, we used the leave-one-out classification procedure to verify our subjective classification. In this cross-validation procedure, each call is classified by the functions derived from all other calls. The ideal procedure to investigate the influence of context on call structure would have been to conduct a multivariate analysis including all possible contexts of emission. Unfortunately, this was not possible due to insufficient sample size. Instead, we conducted separate tests for each contextual variable while avoiding multiple comparisons on the same dataset. The relations between call types and context of emission were examined at the individual level, except for rare call types where small sample size precluded this level of analysis. Although less rigorous, we decided to carry out analyses at the level because this provided us with a crucial basis for comparisons with combined calls. We performed G-tests of independence on contingency tables of call types vs. contextual categories to assess which associations were the strongest (see Bouchet et al. 2010). When the expected values were small we corrected the

G-statistics for continuity, according to Williams (1976). For the analyses at the individual level, all females were included, provided we had recordings of their calls in the respective context, and subjected them to Wilcoxon signed-rank tests. Statistical analyses were performed using SPSS 17.0 software. All tests were two-tailed and significance was set at $\alpha = 0.05$.

Results

A Acoustic morphology analysis

Call types

A total of N=2,129 vocalisations were collected during 58 hours of focal sampling. We found four different calls types referred to as 'H' (high-pitched trilled calls), 'L' (low-pitched trilled calls), 'R' (repeated-unit calls), and 'A' (arched frequency modulation calls). 'H' calls were continuous high-pitched quavered structures with a descending frequency modulation, ranging from 1,237±616 to 358±87 Hz (table 2). 'L' calls were continuous low-pitched quavered structures with a general ascending frequency modulation ranging from 247±84 to 664±354 Hz. Importantly, 'H' and 'L' call were structurally discrete, not variants of a graded continuum. Although both types of call structure were trilled, we found no intermediate forms, suggesting they were separate types. 'R' calls were composed of one to four brief (25-34 ms), generally atonal sounds, separated by short (40–57 ms) periods of silence. 'A' calls were characterised by a tonal arched-shape frequency modulation of 3,047±774 Hz. We were able to distinguish two subtypes of 'A' call, based on whether the arch was continuous ('Af': full arch) or broken ('Ab': broken arch).

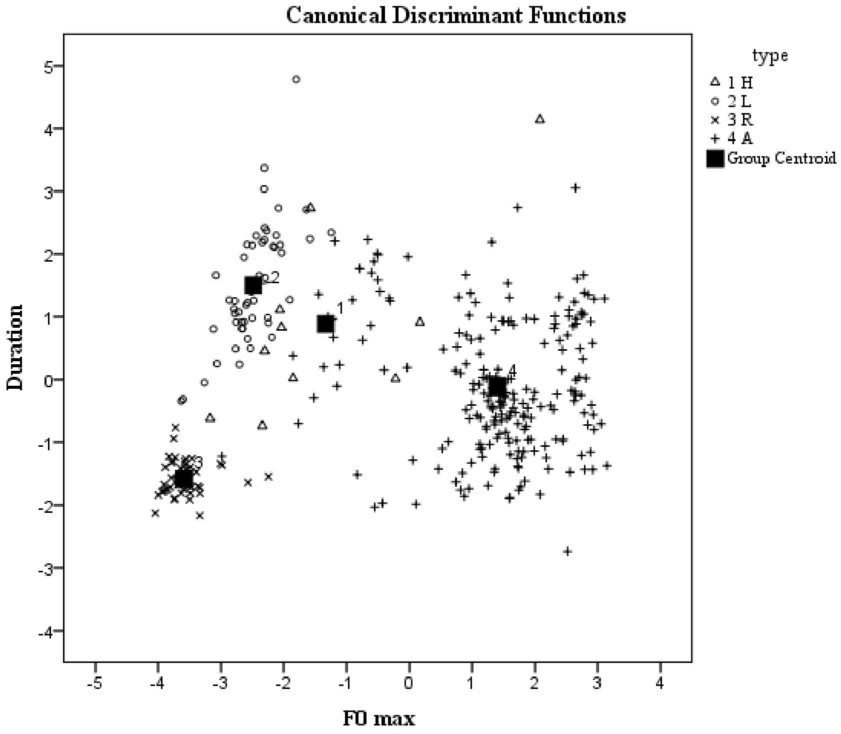

Fig.2: Results of the Discriminant Function Analysis

Three acoustic parameters (D, F0min and F0max) were sufficient to discriminate significantly between the four call types (DFA: Wilk's λ= 0.111, χ_2=707.295, Df = 6, P<0.001, fig. 2). The discriminant analysis derived three functions (one less than the number of categories) with the first accounting for 84.7% of the variance and the second for an additional 15.3%. The success rate of classification was higher than expected from a random assignment, both in the original (88.9%, N= 323) and in the leave-one-out cross-validation procedure (88.0%). In addition, 'Ab' subtypes differed from 'Af' subtypes by the presence of a long silence gap in the arched modulation, representing on average 37% of the total duration (mean ± SD = 114±65 ms, N = 119 calls from 6 females, range: 87-142 ms).

We further confirmed the generality of our classification by showing that each type and subtype was present in at least two adult females of both habituated groups (table 3).

	Calls			
	H	L	R	A
N females	2	6	5	6
N calls	8	56	43	216
D (ms)	288 ± 76 (241 : 410)	409 ± 106 (326 : 499)	82 ± 29 (68 : 99)	298 ± 105 (241 : 410)
F0max (Hertz)	1237 ± 616 (530 : 2865)	664 ± 354 (223: 1327)	429 ± 199 (169: 1189)	3090 ± 696 (604 : 4282)
F0min (Hertz)	358 ± 87 (197 : 633)	247 ± 84 (105 : 535)	331 ± 170 (144 : 500)	324 ± 233 (105 : 2865)
Amfosc (Hertz)	379 ± 67 (364 : 394)	184 ± 44 (167 : 202)	/	/
Dfosc (Hertz)	26 ± 9 (20 : 33)	28 ± 8 (23 : 35)	/	/
NbU	/	/	1.83 ± 0.98 (1 : 2.85)	/
DU1(ms)	/	/	28 ± 11 (25 : 34)	/
DiU (ms)	/	/	46 ± 18 (40 : 57)	/

Table 2: Acoustic parameters. First row shows the number of calls measured and the number of females contributing to the data set selected for acoustic analyses. In each cell: first line shows mean +- standard deviation and second line shows minimal and maximal values in brackets. D is total duration in ms, F0min is minimum of Fundamental frequency in Hertz, F0max is maximum of Fundamental frequency in Hertz, Amfosc is the amplitude of a quavering oscillation in Hertz, Dosc is the duration of a quavering oscillation in ms, NbU is the number of subunits contained in a 'R' unit, DU1 is the duration of the first subunit in ms, and DiU is the duration between two subunits in ms

individuals		call type (number of calls per hour)											
	(time in hours)	H	L	R	Ab	Af	HAb	HAf	LAb	LAf	RAb	RAf	**total**
i1	(7.00 h)	1 (0.1)			54 (7.7)	3 (1.4)			45 (6.4)	12 (1.7)	8 (1.1)	7 (1)	**130 (18.6)**
i2	(3.66 h)	3 (0.8)		1 (0.3)	35 (9.6)	12 (3.3)		1 (0.3)	25 (6.8)	20 (5.5)	2 (0.5)	4 (1.1)	**103 (28.2)**
i3	(1.65 h)				21 (12.8)			1 (0.6)	2 (1.2)	3 (1.8)			**27 (16.4)**
i4	(0.48 h)	2 (4.2)			3 (6.3)				1 (2.1)	1 (2.1)			**7 (14.6)**
i5	(2.00 h)	3 (1.5)			2 (1)	29 (14.5)		2 (1)	1 (0.5)	17 (8.5)		5 (2.5)	**59 (29.5)**
i6	(0.54 h)				3 (5.5)				5 (9.2)	1 (8.1)			**9 (16.6)**
i7	(0.64 h)				7 (10.9)	14 (21.7)			2 (3.1)	12 (18.6)			**35 (54.3)**
i8	(1.35 h)	1 (0.7)	1 (0.7)	2 (1.5)		12 (8.9)			1 (0.7)	156 (105.2)			**173 (127.8)**
i9	(0.56 h)		3 (5.4)			9 (16.2)				1 (1.8)		1 (1.8)	**14 (25.1)**
i10	(0.48 h)		8 (16.7)		10 (20.8)	1 (2.1)				1 (2.1)			**20 (41.7)**
i11	(2.91 h)	5 (1.7)			17 (5.6)	92 (31.6)			3 (1)	67 (23)		17 (5.8)	**201 (69)**
i12	(4.94 h)	1 (0.2)		6 (1.2)	57 (11.5)	33 (6.7)			50 (10.1)	49 (9.9)		18 (3.6)	**214 (43.3)**
i13	(4.55 h)	2 (0.4)	12 (2.6)		44 (9.7)	10 (2.2)	1 (0.2)	1 (0.2)	90 (19.8)	47 10.3)	4 (0.9)	4 (0.9)	**215 (47.2)**
i14	(4.73 h)				49 (10.4)	53 (11.2)		1 (0.2)	2 (0.4)	23 (4.9)		26 (5.5)	**154 (32.5)**
i15	(1.68 h)	3 (1.8)			6 (3.6)	7 (4.2)	1 (0.6)			1 (0.6)		10 (6)	**28 (16.7)**
i16	(4.64 h)	1 (0.2)		3 (0.6)	46 (9.9)	19 (4.1)			5 (1.1)	11 (2.4)	5 (1.1)	14 (3.0)	**104 (22.4)**

i17 (3.63 h)	3 (0.8)	1 (0.3)		53 (14.6)	77 (21.2)			28 (7.7)	131 (36.1)		3 (0.8)	**296 (81.5)**
i18 (2.09 h)	3 (1.4)		1 (0.5)	3 (1.4)	35 (16.7)			12 (5.7)	103 (49.2)		2 (1)	**159 (75.9)**
i19 (1.42 h)	34 (23.9)			8 (5.6)	9 (6.3)		4 (2.8)		47 (33.1)			**102 (71.8)**
total (49 h)	**62 (1.3)**	**25 (0.5)**	**13 (0.3)**	**418 (8.5)**	**415 (8.5)**	**2 (<0.1)**	**10 (0.2)**	**272 (5.5)**	**703 (14.3)**	**19 (0.4)**	**111 (2.3)**	**2050 (41.8)**

Table 3 Female's individual vocal repertoires. For each type of call and each female (DIA1 group: females i1 to i9, DIA2 group: females i10 to i19), the number of calls and call combinations emitted is given. For each female the total time of recording is given in brackets in the first column, and for each call type the corresponding call rate is given in brackets

Call combinations

Our results showed that females could produce four call types ('H', 'L', 'R' and 'A') either alone or combined in the following three ways (fig. 1a). We found combinations of 'H' and 'A' calls ('HA' combination), 'L' and 'A' calls ('LA' combinations) and 'R' and 'A' calls ('RA' combinations), with either full ('Af') or broken ('Ab') arched components. Although other combinations would have been possible, we did not find them. Instead combined calls were always introduced by 'H', 'L' or 'R' call type followed by one of the two arched call subtypes. The most common utterances were uncombined 'A' calls and 'LA' combinations (respectively 17 calls per hour and almost 20 calls per hour), while all other structures were much more rare ('RA': 2.7 calls per hour; 'H': 1.3 calls per hour; 'HA', 'L' and 'R': less than 1 call per hour; table 3).

B <u>Contextual analyses</u>

Call types

Call types could be discriminated by their context of emission. 'H' calls were significantly associated with high mobility, high spatial cohesion, being outside of the territory, high luminosity and with the presence of neighbours (G-tests of independence, table 4). 'H' calls were also significantly associated with socio-positive or relaxed situations and were often uttered in isolation. 'L' calls were significantly associated with high mobility, low spatial cohesion, being in the centre of the territory, high luminosity and vocal chorusing (table 4). 'R' calls were significantly associated with being in the centre of the territory, high spatial cohesion, low luminosity and socio-negative situations. 'R' calls were uttered mainly in isolation of other vocal behaviour. 'A' calls finally were associated with group resting, being in the core area of the territory, low spatial cohesion, low luminosity, neutral situations and vocal exchanges (table 4). Although 'L' was the only type to show no association with an immediate non-vocal context, it was significantly different from the 'R' type ('R' associated with socio-negative situations and 'L' with neutral situations, G-test of independence, G =

8.9, Df = 2, P = 0.0115), while it did not differ significantly from ‘H’ or ‘A’ type (G-tests of independence, G = 2.2, Df = 2, P = 0.3357 and G = 2.2, Df = 2, P = 0.3368, respectively). In sum, each call type had a particular contextual profile. Specifically, ‘A’ call type was contextually more neutral than the other calls and was the only type preferentially used during vocal exchanges.

Variable	Parameters	Calls			
		H	L	R	A
territory	outside	**27**	4	3	106
	periphery	28	0	1	**353**
	center	7	**21**	**9**	**372**
group spread	No	**32**	4	**11**	259
	Yes	29	**21**	2	**558**
group activity	foraging	**52**	**25**	10	544
	travelling	7	0	0	69
	resting	3	0	3	**212**
neighbours	absent	40	22	10	**725**
	present	**22**	3	3	106
luminosity	dark	5	0	**7**	**125**
	bright	**24**	**12**	2	224
immediate non vocal	positive	**36**	10	12	292
	negative	11	6	**8**	94
	neutral	53	14	13	**508**
immediate vocal	isolated	**28**	3	**8**	106
	exchanged	34	17	3	**363**
	chorus	0	**5**	1	25

Table 4: Contextual analyses of call types. The total number of ‘H’, ‘L’,’R’ and ‘A’ calls recorded in each context is given. For each contextual variable a G-test of independence was performed. Variable names are in bold when the G test was significant (P_{exact}<0.05), and occurrences are in bold when $G_{partial}$> 4

Arched call subtypes

The arched call type ‘A’ occupies a key position in the vocal repertoire of female Diana monkeys (>95% of all calls; table 3) with the two subtypes ‘Af’ and ‘Ab’ differing in contextual use. The ‘Af’ subtype was emitted significantly more frequently than the ‘Ab’ if neighbours were nearby (Wilcoxon two-tailed test: N=14, Z=2.229, P_{exact}=0.026), the luminosity was low (N=14, Z=2.103, P_{exact}=0.035), the caller jumped (N=15, Z=2.045, P_{exact}=0.041) or was engaged in an agonistic interaction (N=15, Z=2.032, P_{exact}=0.047). The ‘Af’ subtype was also significantly more frequent than the ‘Ab’ during choruses (N=15, Z=2.480, P_{exact}=0.01). Conversely, the ‘Ab’ subtype was more frequent when the neighbours were absent (Wilcoxon two-tailed test: N=14, Z=2.229, P_{exact}=0.026) and when the caller was resting (N=15, Z=2.556, P_{exact}=0.008). ‘Ab’ subtypes were also more frequent, though not significantly, when calls were uttered in isolation (N=15, Z=1.915, P_{exact}=0.058). Table 5 summarises the main effects. In sum, there were significant differences in the contextual use of the two arched subtypes, with ‘Af’ subtype preferentially used in situations when providing identity cues was important.

Call combinations

Both ‘L’ and ‘R’ calls were found in combination with ‘A’ calls (i.e. ‘LA’ and ‘RA’ combinations), depending on the context of emission. ‘LA’ combinations were emitted significantly more often than ‘RA’ combinations when the group was foraging (Wilcoxon two-tailed test, N=15 females, Z=2.954, P_{exact}=0.002), during call exchanges (N=15 females, Z=2.124, P_{exact}=0.001), when the caller was resting (N=15, Z=2.271, P_{exact}=0.021), involved in a friendly social interaction (N=15, Z=2.201, P_{exact}=0.031) and more generally during positive situations (N=15, Z=1.978, P_{exact}=0.047). ‘LA’ combinations were more frequent, though not significantly, when the groups were at the periphery of their territory (Wilcoxon two-tailed test, N=10, Z=1.955, P_{exact}=0.055) and when individuals were scattered (N=15, Z=1,867, P_{exact}=0.067). Conversely, ‘RA’ combinations were uttered significantly more in isolation than ‘LA’ calls (N=15, Z=2.354, P_{exact}=0.017) and were more frequent, though not significantly, when the group was not scattered (N=15, Z=1.956, P_{exact}=0.054). ‘HA’ combinations also existed but were too rare to be included in this analysis. Table 5 summarises the main effects obtained when conducting the analysis at the individual level. Interestingly, at the population level, ‘LA’ combinations were still significantly associated with positive situations, while ‘RA’ combinations were significantly associated with negative situations (G-test, G = 13.5, Df = 2, P_{exact}= 0.0012). In sum, there were significant differences in the contextual use of ‘LA’ and ‘RA’ call combinations.

Variable	Parameters	N females	LA		RA	N females	Ab		Af
			% of calls				% of calls		
territory	outside	10	18.5 ± 6.1		19.5 ± 7.4	15	11.9 ± 4		17.8 ± 5.8
	periphery		45.4 ± 7.5		28.6 ± 5.8		39.1 ± 8.2		38.8 ± 4
	center		36.1 ± 9.2		33.8 ± 7.8		49 ± 8.4		43.5 ± 7.3
group spread	No		30.2 ± 6		47.9 ± 9.8		60.6 ± 6		61.2 ± 4.4
	Yes	15	69 ± 6		46 ± 9.9	15	34.2 ± 6.2		36.8 ± 4.8
group activity	foraging	15	84.9 ± 2.9	**	48.9 ± 10	15	71.0 ± 5.7		76.6 ± 4
	travelling		6.4 ± 2.5		5.5 ± 3.5		16.1 ± 7.8		8.1 ± 3.4
	resting		9.9 ± 2.5		16.8 ± 5.8		19.2 ± 5.3		14.4 ± 3.3
neighbours	absent	11	79.7 ± 6.9		87.8 ± 4.8	14	87.1 ± 4.5	*	76.3 ± 5.8
	present		20.3 ± 6.9		12.2 ± 4.8		12.9 ± 4.5	*	23.4 ± 5.8
luminosity	dark	12	13.4 ± 4		13.1 ± 4.3		26.6 ± 7.4	*	43.9 ± 8.4
	bright		22.6 ± 5.2		19.7 ± 5.2	14	63.9 ± 9.3		56.1 ± 8.4
immediate non vocal (detailed)	scanning	15	61.1 ± 6.1		57 ± 0.8	15	58.8 ± 7		69.1 ± 4.1
	foraging		38.3 ± 6.1		31.8 ± 7.4		27.3 ± 5.2		35.5 ± 2.3

	feeding		29.5 ± 3.7		27.9 ± 0.9		27.8 ± 4.4		30 ± 3.4
	jumping		26 ± 6.2		29.3 ± 0.2		18.5 ± 6.1	*	24.7 ± 3.9
	walking		49.9 ± 5.9		49 ± 10		56.4 ± 5.4		58.1 ± 4.6
	resting		14 ± 3.1	*	4 ± 1.8		21.3 ± 3.3	**	10.6 ± 1.9
	friendly interaction		3.6 ± 1.7	*	0 ± 0		6.8 ± 5.7		2 ± 0.8
	agonistic interaction		1.1 ± 0.6		2.2 ± 2.2		0.5 ± 0.4	*	2 ± 0.7
	neutral interaction		3.8 ± 1.6		2.4 ± 1.8		5.2 ± 1.7		4 ± 1
	vigilance		2 ± 0.7		3.2 ± 1.8		4.6 ± 2.1		4.7 ± 1.4
immediate non vocal (lumped)	positive	15	84.2 ± 4.6	*	62 ±14.4	15	28.7 ± 3.1		24.3 ± 1.2
	negative		27.6 ± 5.8		30.4 ± 8.7		7.6 ± 2		9.7 ± 1.3
	neutral		126.1 ± 11.9		111.2 ± 19.2		40 ± 1.9		40.8 ± 1.1
immediate vocal	isolated	15	8.7 ± 1.8	*	27.5 ± 5.6	15	22.5 ± 4.8		12.7 ± 1.7
	exchanged		83.6 ± 3	**	37.7 ± 8.3		73.6 ± 4.9		77.6 ± 1.3
	chorus		7.6 ± 1.7		8.1 ± 3.9		3.9 ± 1.3	**	9.7 ± 2

Table 5: Contextual profiles of arched calls depending on the introduction (‘LA’ vs ‘RA’) or the subtype of arch (‘Ab’ vs ‘Af’). Table shows females’ mean proportion of ‘LA’ combinations and ‘RA’ combinations, as well as the mean proportion of ‘Ab’ and ‘Af’ calls emitted in each contextual category. We calculated the proportion of calls emitted for each call type in each context (e.g. $\%LA_{travelling}$= number of ‘LA’ combinations emitted in the travelling context / total number of ‘LA’ combinations emitted). Two-tailed Wilcoxon signed-rank tests were performed to compare the contextual profiles of ‘LA’ vs RA’ calls and ‘Ab’ vs ‘Af’ subtypes. Table shows: “blank cell” for $P_{exact} > 0.05$, * for $P_{exact} \leq 0.05$ and ** for $P_{exact} \leq 0.01$

Discussion

We carried out an observational study to investigate the levels of flexibility in female Diana monkey's social calls. We found flexibility at two levels, variability in acoustic structures and combinations of these structures into more complex utterances. Both mechanisms significantly enlarged females' vocal repertoire that consisted of only four basic call types ('H', 'R', 'L', 'A'). First, we observed non-random combinations of the four basic calls, which increased the repertoire to seven types of utterances ('H', 'L', 'R', 'A', 'HA', 'LA', 'RA'). Second, we found that, within the most frequently emitted call type ('A'), females produced two subtypes characterised by differences in the frequency modulation, which in turn increased the repertoire to eleven utterances.

The shape of the frequency modulation of 'A' calls (arch broken or full) is a pattern also seen in the calls of other guenon species (Gautier 1988). For instance, female Campbell's monkeys produce six subtypes of 'CH' calls, which seem to be the structural and contextual analogue of the 'LA' combinations of Diana monkeys. Campbell's monkeys also produce broken and full arches in relation to different contexts, regardless of the caller's age (Lemasson & Hausberger 2004 and 2011). In individuals raised in captivity, the full arch encoded information about caller's identity and affiliative bonds. Call structure changed across years in adult females and playback experiments showed that females reacted differently to current and to no longer produced variants of familiar females (Lemasson et al. 2005). Although presumably other calls are also individually distinctive, we found that Diana females preferentially used the full arched calls when revealing identity was particularly important, such as during periods of low visibility, when facing an opponent and during auditory confusing environments such as call choruses. The full arched frequency modulation is an acoustic structure that has a high potential for individual coding (Candiotti et al, in prep).

Although the contextual variables used in this study were somewhat crude, especially if compared with studies on the social calls of savannah-dwelling-primates, they generated biologically relevant links to the observed vocal patterns. Indeed, both levels of flexibility -

acoustic modulation and combination- turned out to be context-related in this species, showing that the cohesion-contact calls system of Diana monkeys contains subtleties that go beyond a simple function of individual identification and spatial positioning, as originally proposed by early studies (Gautier 1988). When uttered alone, ‘H’ and ‘R’ types were associated with social activities and contexts relating to high group spatial cohesion, and were uttered in isolation. ‘H’ calls were given when in the outer parts of the home range, in the presence of neighbours and when luminosity was high, while ‘R’ calls were given in the centre of the territory and when luminosity was poor. ‘L’ and ‘A’ types were more typically associated with neutral contexts, when the group was scattered and when the vocal activity was high. Importantly, ‘H’ calls were emitted in situations that were “socially positive or relaxed” for the emitter while ‘R’ calls were emitted in “socially negative or potentially dangerous situations”. The majority of ‘L’ calls uttered alone were emitted during a “neutral situation”, although this result was not statistically significant. It is hence possible that these three call types form a gradient reflecting the general motivational state of the caller. In contrast ‘A’ calls uttered alone differed from the previous call types in several ways. They were emitted much more frequently, were contextually neutral and were typically used during vocal exchanges.

Call combinations were optional and always in the form of a two-compound utterance with the first call used as an introductory unit followed by one of two subtypes of arched calls. In addition, when females produced call combinations, their contexts of emission were not fundamentally different from the contextual profile of the same calls emitted alone (either the introductory unit or the arched call). Instead, call combination seemed to modulate the utterance of an ‘A’ call with a contextual value regarding the immediate situation faced by the emitter in terms of “positive or relaxed”, “negative or potentially dangerous” or “neutral” situation. One hypothesis is that the ‘A’ call could function as an individual identifier combined with or without contextual situation. A similar finding has recently been reported in Campbell’s monkeys, where females emit ‘LA’-like combinations in which the ‘L’-like part reveals something about the caller’s kin relatedness and the ‘A’-like part the caller’s social bonds (Lemasson & Hausberger 2011). For Diana monkeys, further work is needed to explore the kind of information conveyed by differences in arch structures.

Combinatorial properties may be more widespread in primate communication than previously reported, although very little is still known about the informational content of these combinations if compared to the single units (Zuberbühler 2002; Crockford & Boesch 2005; Ouattara et al. 2009a; Ouattara et al. 2009b). Traditionally, analyses of primate vocal behaviour have been carried out at the level of the individual call type, but as stated by Hauser (2000), sequences may also be communicatively relevant (see Bouchet et al 2010). In non-primate taxa, sequence-based investigations are more common (e.g. songbirds: Kroodsma (1982), killer whales *Orcinus orca*: Shapiro et al. 2010), although this has not generated much progress in terms of context-specific production.

When compared to previous studies in closely related species, the combinatorial system of social calls in Diana monkeys showed some parallels with the affixation system in Campbell's monkeys (Ouattara 2009a), although a number of important differences were also present. Specifically, there was no evidence that Diana monkeys' combinations of social calls carried strong semantic content relating to specific events, such as a falling tree, the approach of a neighbouring group (Ouattara et al 2009b) or a signal for group progression (Arnold & Zuberbühler 2006). Instead, the combinations of social calls seen in Diana monkeys appear to convey the individual identity of the caller (most likely, though not exclusively, to be found in the arched frequency modulation) and something about the immediate motivational state the caller finds herself in, i.e. whether she assesses the current situation as positive, negative or neutral (found in the introductory call). A particularly interesting case is the rare 'HA' combinations whose communicative function will require more investigations.

Whatever the function of non-random concatenation of calls is, it is clear that this behaviour can significantly enlarge the vocal repertoire of a species and expand the functional use of calls, which may be particularly relevant for species that have little control over call morphology. Similar arguments have been made for male Campbell's monkeys, where affixation broadens the 'meaning' from predator-specific alarm calls to calls given to a broader class of disturbances (Ouattara et al. 2009a). In male putty nosed monkeys, 'pyow-hack' combinations carry different 'meanings' than pure 'pyow' or 'hack' series (Arnold & Zuberbühler 2006). In Diana monkeys, the concatenation of one of several possible introductory calls to the arched call unit seems to function as a contextual refiner of this contextually neutral call. The degree to which these subtleties are intentionally produced, mere reflections of a caller's motivational state (Owings & Morton 1998; Owren & Rendall 2001) or both has not been addressed by this study and will require further investigation.

To conclude, we evidenced optional and potentially partially redundant combinatorial properties in the social calling system of female Diana monkeys, the first evidence of this kind for short distance vocalisations used in social contexts. This study brings new insights into the mechanism by which non-human primates can achieve enhanced acoustic flexibility, something that may be especially important during social interactions. The degree to which this and other nonhuman primate combinatorial calling systems are relevant for understanding the early biological roots of human language is currently unclear and much debated. The outcome of this debate will also largely depend on whether similar properties can be found in the calling systems of our closest relatives, the chimpanzees and bonobos.

Acknowledgments

This research was funded by the French Ministry of Research, IUF, PICS-CNRS and ANR "Orilang". In Côte d'Ivoire, we thank the minister of scientific research and the "Office Ivoirien des Parcs et Réserves" (OIPR) for permission to conduct research in Taï National Park. We also thank the Centre Suisse de Recherches Scientifiques en Côte d'Ivoire (CSRS) for logistic support. We are very thankful to our field assistants F Belé and F Gnepa for their invaluable help with data collection, and to members of the Taï Chimpanzee Project (TCP) and the "Centre de Recherche en Ecologie" (CRE) for their support in the field. We are grateful for comments and thoughts by K Ouattara, K Arnold, T Aubin and H Bouchet as well as for the referees' valuable comments on the manuscript. We thank the Wissenschaftskolleg zu Berlin as well as the Institut Universitaire de France for additional support.

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SUMMARY OF PAPER 3

Questions : We now know that adult female Diana monkeys present a complex vocal repertoire for intra-group communication, including the frequently emitted, highly modulated and highly social so-called Af call type. Can the arched frequency pattern encode caller's identity? Is the level of acoustic variability contextually dependent? Do callers vocally converge towards or diverge from other group members according to the social context?

Methods : We used an acoustic software comparing fundamental frequency contours to generate a similarity index between pairs of Af calls. The arched frequency contours were compared within and between females, within and between contexts of emission.

Results : Overall, frequency contours showed higher levels of variability between than within individuals. Nevertheless, the degree of individuality also varied with the social context of emission. Callers increased the level of vocal divergence when social cohesion was needed due to poor visibility or to the presence of a neighbouring group. Still, callers converged vocally during vocal interactions.

Conclusions : Adult female Diana monkeys show some level of control over the acoustic fine structure of their most important social vocalisation. Vocal convergence and divergence are complementary processes that enable callers to ensure spatial proximity and social cohesion. We suggest this phenomenon presents similarities with the vocal accommodation phenomenon described in humans.

This paper has been published in Biology letters, was presented at the 2011 IBAC (International Bioacoustic congress) and at the 2012 SFECA (Société Française de l'étude du comportement animal) conference.

CONVERGENCE AND DIVERGENCE IN DIANA MONKEY VOCALISATIONS

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Key words: vocal flexibility; individual signatures; call matching; nonhuman primates

Individually distinct vocalisations are widespread amongst social animals, presumably caused by variation in vocal tract anatomy. A less explored source of individual variation is due to learned movement patterns of the vocal tract, which can lead to vocal convergence or divergence in social groups. We studied patterns of acoustic similarity in a social call produced by 14 female Diana monkeys in two free-ranging groups. Calls showed variability in fundamental frequency contours, due to individual identity and external context. Vocal divergence increased significantly between females during poor visibility and tended to increase in the presence of neighbours. In contrast, vocal convergence increased significantly between females during vocal interactions, because females matched the frequency contour of their own call to another female's preceding call. Our findings demonstrate that these primates have some control over the acoustic fine structure of their most important social vocalisation. Vocal convergence and divergence are two opposing processes that enable callers to ensure spatial proximity and social cohesion with other group members.

1. INTRODUCTION

In human communication, acoustic features of voice and speech signals serve as reliable indicators of individual identity and other important social variables [1]. However, these markers are not fixed but vary with social context and composition of the audience [2]. In socio-linguistics, the ‘communication accommodation theory’ describes the ability of humans to adjust social distance during interactions through a process of vocal convergence and divergence [3]. Although animal communication plays an important role in understanding the evolution of human communication, such processes of vocal accommodation have not received much empirical attention.

This is despite the fact that some animal species possess highly flexible vocal abilities. One frequent consequence is vocal convergence, a process during which individually distinct acoustic features are reduced. The phenomenon is typically observed during group formation, reproductive pair bonding and non-reproductive social bonding [4–7]. In contrast, vocal divergence, a process during which individually distinct acoustic features are highlighted, has been observed in group living species after separation and during inter-group encounters [8,9]. Thus, callers appear to alternate between the need to differ from others by advertising individual identity and the need to conform to others to secure social bonding.

Non-human primates are famously limited in the amount of control they have over their vocal output, with only limited degrees of plasticity (see [10] for review). Temporary acoustic modification has been documented in reaction to ambient noise, social isolation and habitat [11–13]. Acoustic convergence has been documented in terms of callers matching some of each others’ acoustic features during vocal exchanges or as part of social bonding [14,15]. Vocal divergence has been documented between neighbouring groups of chimpanzees [16].

We investigated the presence of vocal convergence and divergence in free-ranging Diana monkeys (*Cercopithecus diana*), an arboreal, forest-dwelling West African primate species. Females regularly emit close-range vocalisations (‘contact calls’) that function in maintaining social and spatial cohesion and callers often, but not always, respond to each other’s calls. We investigated acoustic variability within and between females of two free-ranging groups. In general, we predicted lower acoustic similarity between than within females’ calls. More specifically, we predicted increased divergence when individual identification is crucial, such as during low visibility, travel episodes, presence of neighbours and high group dispersion, while we expected increased convergence during social interactions, such as call exchanges.

2. METHODS

Data were collected from February to May 2009 and from January to June 2010, from two groups of Diana monkeys in Taï Forest, Ivory Coast (5°50'N, 7°21'W). Both groups were fully habituated to human observers, consisting each of 1 adult male and 9-10 individually identified adult females with their offspring. Groups were followed alternatively with data collection between 07:30 and 17:00 hours GMT for 46 and 38 days, respectively. Scan samples [17] were taken every 30 minutes to score the group's main activity, the degree of group dispersion, the presence of a neighbouring group and general luminosity (see supplementary data for definitions). Individual females were observed and all vocalisations recorded during 10-min focal animal sampling [17]. Females produce various social calls, but the most common one is the 'contact call' ('Af' call, see supplementary data for spectrogram). Recordings were made with a Sennheiser K6/ME66 directional microphone and Marantz PMD660 recorder (sampling rate 44.1 kHz; resolution 16 bits).

We calculated acoustic similarity indices of Af calls, based on a procedure used for frequency modulated whistle-like signals in various species [15,18]. We used customised acoustic software ANA [19] to compare the similarity of the arched fundamental frequency contours of pairs of calls within and between females. First, we calculated, for each female, her mean intra-individual similarity index for all her calls. We also calculated the mean similarity index for all calls given by pairs of females. Second, to assess the role of context on call structure we compared levels of intra-individual acoustic similarity in different contexts for non-responding calls. As responding calls, we considered any Af call given within 3s of a preceding call by another female [20]. Conversely, non-responding calls were emitted after at least 3s of silence. Call context was determined by the previous scan sample. We then compared, for each female, her mean intra-individual similarity index within each context. Only females that contributed with at least two focal samples per context of emission with a maximum of five Af calls per sample were included. Third, we compared the acoustic similarity of exchanged (inter-call interval<3s) and non-exchanged (inter-call interval>3s) calls, by calculating the mean inter-individual similarity indices of pairs of exchanged and not exchanged calls. Focal females' calls were compared both with the call they responded to and the previous call they did not respond to. Owing to the small sample size, we used non-parametric Wilcoxon tests to compare similarity indices with SPSS 17.0 software. Tests were two-tailed and significance levels set at $\alpha = 0.05$.

3. RESULTS

We recorded 1,091 Af calls from 14 adult females (group 1: n=6; group 2: n=8) during 44 focal observation hours (mean±se = 3.1±0.5h per female) and 789 calls were of sufficient quality for acoustic analysis (mean±se = 56.4±9.5 calls per female). First, we found that Af calls reliably conveyed individual identity, as intra-individual similarity indices were significantly higher than inter-individual ones (n=14 females, Z=-3.408, p<0.001; figure 1a). Second, we found that intra-individual acoustic variability varied within some but not all contexts of emission in which we expected increased levels of individual identity. In particular, we found that similarity indexes were significantly higher in dark compared to bright habitats (n=5 females, Z=-2.023, p=0.043; figure 1b). Similarity indexes were also higher in the presence than the absence of a neighbouring group, but not significantly so (n=6 females, Z=-1.782, p=0.075; figure 1c). We failed to find significant effects between group travel and foraging (n=5 females, Z=-0.135, p=0.893) and during high versus low group spread (n=12 females, Z=-0.941, p=0.347). Finally, we compared pairs of exchanged and not exchanged calls, provided they were emitted within the same minute. We found that pairs of exchanged calls resembled each other significantly more than not exchanged calls (n=13 females, Z= -2.411, p=0.006; figure 2).

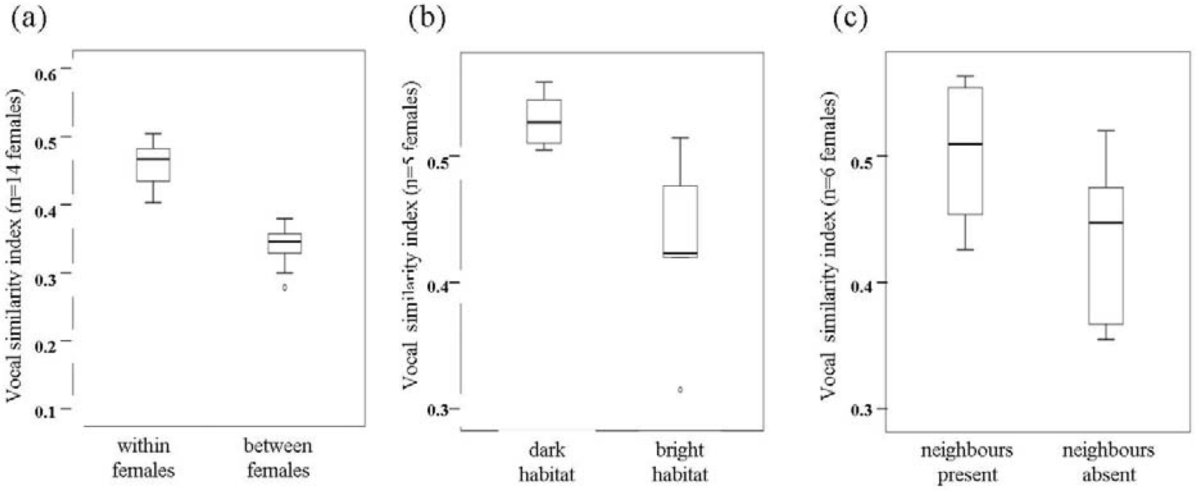

Figure 1. (a) Box plots illustrate the intra-individual (within females) and the inter-individual (between females) vocal similarity. Similarity of calls within females varied with the presence of neighbouring groups (b) and habitat luminosity (c).

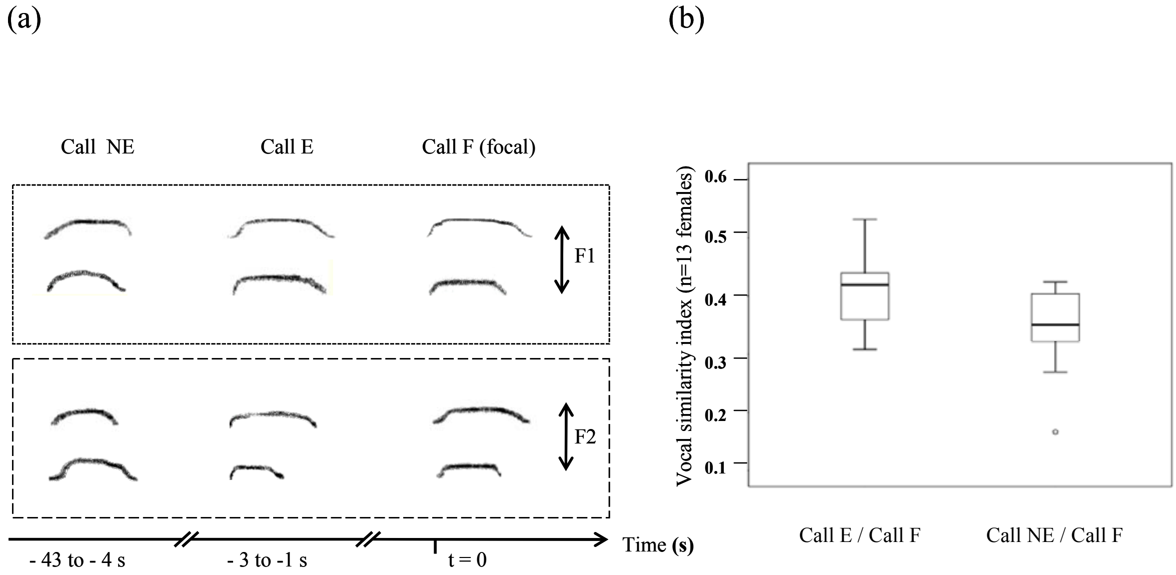

Figure 2. (a) Illustration of exchanged and non-exchanged call sequences from two focal females (F1, F2). Call F (Focal) was emitted in response to call E (Exchanged) but not to call NE (Non Exchanged). (b) Box plots illustrate vocal similarity of F calls with E and NE calls.

4. DISCUSSION

We have documented that the main social call of free-ranging female Diana monkeys contains sufficiently stable acoustic variation across individuals to convey individual identity. However, these individual differences in acoustic structure were not fixed, but varied systematically in relation to a number of external factors including social context. We observed significant vocal divergence when the habitat illumination is low, most likely due to individuals highlighting individual identity. In contrast, we observed significant vocal convergence during peaceful vocal exchanges. This was due to the fact that exchanged calls were acoustically more similar than non-exchanged calls, i.e. vocalisations given during the same narrow time period that were not part of a vocal exchange. To our knowledge, this study thus presents some of the first evidence of context-specific vocal accommodation, i.e. convergence or divergence, in a nonhuman primate.

Individual vocal signatures seem to be particularly important in species where individuals depend on each other socially. Diana monkeys form tightly bonded social groups, with individuals cooperating during inter- and intra-group conflicts [21]. In forest primates, signalling individual identity by acoustic means is crucial, due to the danger of losing contact with others, especially during periods of darkness or during conflicts. Further research, including playback experiments, will be required to confirm that listeners are able to infer individual identity from these calls, although this has partly been demonstrated with the homologous call type of female Campbell's monkeys [22].

In many animal species, including nonhuman primates, call exchanges show a number of properties that resemble aspects of human communication [23]. For example, callers adhere to rules that determine the patterns of turn-taking [24]. Another phenomenon found in humans is acoustic convergence during conversations, an effect that is particularly common amongst closely bonded individuals. In nonhuman primates, similar effects appear to exist, both long-term [months and years: 15,25] and short-term, as shown by patterns of coo call exchanges in Japanese macaques [14]. In our study, females produced calls that were more similar to calls they responded than to calls they did not respond to, suggesting that females were not just similarly motivated but adjusted the acoustic structure of their calls in relation to specific social motivations. As we only considered calls given within the same very narrow time limit (less than 60s), it is not likely that response patterns could be explained with general states of arousal. To conclude, some nonhuman primates can temporarily alter the acoustic fine structure of their social calls, to both increase or decrease individual distinctiveness, depending on whether highlighting individual identity or social affiliation takes communicative priority.

We thank the Ivorian ministery of scientific research and the 'Office Ivoirien des Parcs et Réserves' for permission to conduct research, the 'Centre Suisse de Recherches Scientifiques en Côte d'Ivoire' for logistic support, F. Belé and F. Gnepa for help with data collection. We thank Robert Seyfarth and an anonymous referee for helpful comments on the manuscript. Funding was from the French Ministry of Research, PICS-CNRS, ANR 'Orilang', Wissenschaftskolleg zu Berlin, Leverhulme Trust, and Institut Universitaire de France.

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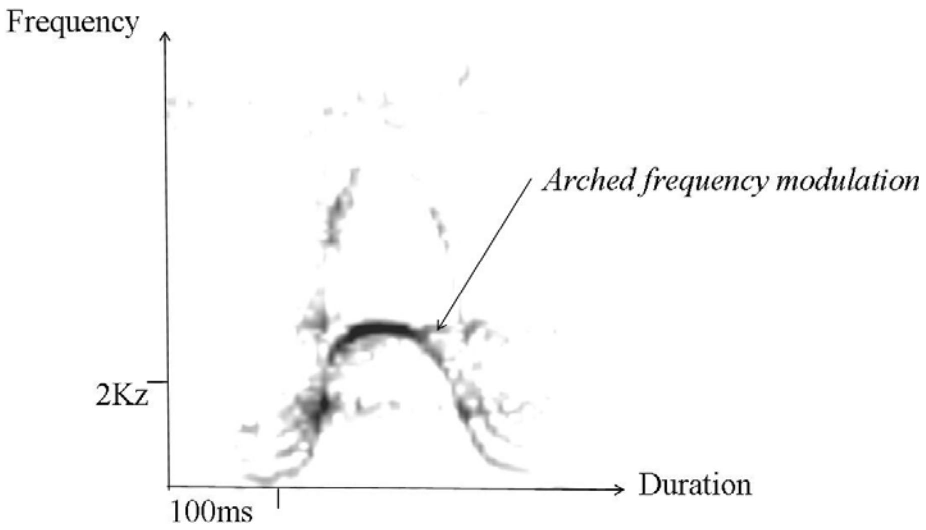
Variable	Definition
Activity	The majority of the individuals, i.e. more than 50% of the adults is moving around, foraging for food or feeding on insects/leaves/fruits (foraging) or has initiated a group movement of at least 100 meters in the last 10 minutes (travelling)
Neighbours	A neighbouring group can (present) or cannot (absent) be heard at less than 200 meters
Scattering	The majority of the individuals, i.e. more than 50% of the adults, is (scattered) or is not (not scattered) dispersed over an area of more than 25 m^2
Luminosity	Illumination of the observation area is very bright (bright) or very dark (dark). Luminosity level was estimated by measuring the intensity (in Lux) of light received 1m from the forest floor with a luxmeter (DVM401 Voltcraft DT8820). For a given scan, 9 points of measurements were equally spaced within a 10 m² and then averaged. There was a significant difference between both conditions (N= 36 scans, Mean +/- sem, M_{bright}= 645.7 +/- 45.3 Lux, M_{dark} = 256.6 +/- 18.2 Lux , Mann Whitney test, U= 1647, p<0.001)

Supplementary Electronic Material 1



Supplementary Electronic Material 2

CHAPTER 5 – PERCEPTION AT THE INTER-SPECIFIC LEVEL: INTERSPECIES DISCRIMINATION OF VOICES FAMILIARITY

SUMMARY OF PAPER 4

Questions : Forest guenon's calls can carry information about emitter identity and it has been shown that this type of information is perceived by conspecifics.Given the abundance of polyspecific associations amongst African forest *Cercopithecinae* and the affiliative vocal and non-vocal interactions occurring between species, we wondered whether individuals were able to discriminate familiar and unfamiliar voices of other species they live with.

Methods : We conducted a playback experiment in captivity to test the ability of three primate species forming polyspecific associations in the wild (Campbell's monkeys, Black and white colobus monkeys and Red-capped mangabeys), to discriminate familiar and unfamiliar female voices of a fourth species, De Brazza monkeys.

Results : Individuals from all species analyzed together gave significantly more gazes in the speaker direction in reaction to unfamiliar stimuli than to familiar stimuli but showed no difference in the latency to turn the head, the total and the mean gaze durations.

Conclusions : At the population level, individuals were able to discriminate the familiarity of voices from another species, but the reactions were not as strong as what could be expected at the conspecific level. Future research will say whether this is due to a general lack of interest for other species' social vocalisations or to a lack of redundancy of identity information contained in the De Brazza's contact calls.

This paper has been submitted for publication in the Journal of Zoology.

Inter-specific recognition of familiar individual voices in nonhuman primates

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Abstract

An important function of animal vocal behaviour is to convey identity, with abundant evidence that animals recognise each other by voice. However, in natural habitats, individuals not only interact with conspecifics but also with members of other species. This is particularly well documented for African forest monkeys, which form semi-permanent mixed species groups that can persist for decades. Individuals of such poly-specific groups usually interact with each other on a daily basis, both physically and vocally. However, whether poly-specific group members are able to identify each other individually, based on their voices, is currently unknown. We addressed this problem with research on three primate species that are known to form polyspecific associations in the wild; red-capped mangabeys, Campbell's monkeys and black-and-white Colobus monkeys. In playback experiments, we tested for discrimination abilities of contact calls given by familiar and unfamiliar female De Brazza monkeys (*Cercopithecus neglectus*). When analysing each species separately, no significant difference between conditions emerged. When pooling all species, subjects produced significantly more gazes in the speaker direction in reaction to contact calls of unfamiliar than familiar individuals, suggesting that they discriminated De Brazza monkeys based on their voices.

Keywords: Old World monkeys- vocal recognition-heterospecific-playback-

Introduction

One powerful way of studying the communicative abilities of animals has been to discriminate between communication processes relating to the production, usage and perception of signals (Seyfarth et al. 2010). In terms of perception, there is good evidence that some vocal signals, notably alarm calls, can have referential properties, for instance by carrying information about the predator type (Seyfarth et al. 1980; Macedonia 1990; Zuberbühler et al. 1999; Schel et al. 2010). Other vocal signals, such as contact calls, often show strong individual variation in acoustic structure and thus appear to be especially adapted to convey a signaller's identity (Lemasson & Hausberger 2011). Individually distinct calls have been demonstrated widely, including by studies on birds (Charrier et al. 2001), cetaceans (Janik & Slater 1998; Kremers et al. 2012), monkeys (Seyfarth & Cheney 2003; Egnor et al. 2004;) and apes (Bauer & Philip 1983; Kojima et al. 2003). Other relevant information that can be conveyed by vocal signals concerns the signaller's sex (birds: Ballintijn & Cate 1997; Vicario et al. 2001, primates: Green 1981; Rendall et al. 2004; Bouchet et al. 2010), body size (horses: Lemasson et al. 2009, monkeys: Ey et al. 2007), age (yellow-bellied marmot:Blumstein & Munos 2005 ; monkeys: Fischer et al. 2002; Bouchet et al. 2011) social position (monkeys: Fischer et al. 2004, hyenas: Mathevon et al. 2010) and social affiliations (birds: Hausberger et al. 1995, monkeys: Lemasson et al. 2005).

There is little doubt that animals can take advantage of some of the available acoustic information in calls to discriminate different conspecific group members (e.g. birds: Brooks & Falls 1975; McGregor & Avery 1986; Weary & Krebs 1992, bullfrogs: Bee & Gerhardt 2002, sea lions: Gwilliam et al. 2008, horses: Lemasson et al. 2009, monkeys: Cheney & Seyfarth 1980; Lemasson et al. 2008; Wittig et al. 2007; Price et al. 2009). This is perhaps unsurprising because individual recognition is a prerequisite for the maintenance of social relations and may further help spatial cohesion, notably for species travelling as social groups in visually dense habitats (Marler 1965).

In the wild, many animals live in communities with other species, sometimes involving phylogenetically closely related species. In such mixed species associations, individuals can eavesdrop on hetero-specific calls, which is particularly useful with alarm calls. For several species, it has been shown that individuals react to hetero-specific alarm calls with enhanced vigilance. For example dik-dik antelopes react to the alarm calls of white-bellied go-away birds (Lea et al. 2008) while yellow-bellied marmots and golden-mantled ground squirrels react to each other's alarm calls (Shriner 1998). Another interesting example is the Galápagos marine iguana, a non-vocal reptile that eavesdrops on the alarm call of the Galápagos mockingbird (Vitousek et al. 2007). Other common responses are escaping or responding with their own alarm calls. This has been shown for sympatric red-fronted lemurs and Verreaux's sifakas of Madagascar, which react to each other's alarm calls but not to unfamiliar baboons' alarm calls (Fichtel 2004). In other work, it has been shown that individuals can be sensitive to the referential specificity of other species' alarm calls. A typical finding is that one call type is given to aerial predators while another call type is given to a broad range of disturbances on the ground (superb starlings: Seyfarth & Cheney 1990; Black-casqued hornbills: Rainey et al. 2004, Campbell's monkeys: (Zuberbühler 2001). There is evidence that the external referents of hetero-specific are learned (Oda & Masataka 1996; Ramakrishnan & Coss 2000; Zuberbühler 2000; Carrasco & Blumstein 2012).

A particularly well-studied example is the poly-specific associations formed by many African forest monkeys (e.g. Taï *Cercopithecinae* community: McGraw et al. 2007). These mixed species groups go far beyond mere sympatry but are usually of a semi-permanent nature, in which the same groups seek each other out, mingle, and live together for substantial periods each day (Holenweg et al. 1996), most likely for purposes of anti-predator avoidance (Bshary & Noë 1997). Individuals from different species regularly interact with each other socially, both agonistically and affiliatively, which can include grooming and contact call exchanges (Fleury & Gautier-Hion 1997, K. Ouattara, pers. com.), foraging in the same tree and travelling together (McGraw et al. 2007), which has led to the term "supra-social" organisation (Gautier & Gautier-Hion 1983).

Given the level of individual interactions that can take place between members of different primate species and given the importance of these relationships for survival, it seems reasonable to ask whether primates are able to discriminate individuals of other species by their voices. It has been shown that domestic dogs can discriminate the voice of their owners from the voices of strangers (Adachi et al. 2007). To our knowledge, however, there is no study showing similar capacities in non-human primates in the wild. To address this question we have tested three species of *Cercopithecinae* that form poly-specific associations in the wild, Campbell's monkeys (Wolters & Zuberbühler 2003), black-and-white Colobus monkeys (Chapman & Chapman 2000) and red-capped mangabeys (Jones & Sabater Pi 1968), for their capacity to discriminate the contact calls of another species, De Brazza monkeys. We have focussed on female contact calls, which have high levels of acoustic variation both within and between individuals (Bouchet et al. 2011).

Methods

Subjects and housing conditions

We used contact calls from female adult De Brazza monkeys from recorded in three facilities, the 'Station biologique de Paimpont' (France), 'Howlett's animal park', and 'Port Lympne animal park' (United Kingdom). We generated playback stimuli from the different recordings and carried out playback experiments with female adult Campbell's monkeys (*Cercopithecus campbelli*), female and male adult Guereza Colobus monkeys (*Colobus guereza*) and female adult red-capped mangabeys (*Cercocebus torquatus*). All individuals lived in various facilities with indoor-outdoor enclosures (table 1). Subjects were provided with fruit, vegetables, and commercial monkey chow daily. Water was available *ad libitum*.

Stimuli collection

In the weeks preceding the experimental sessions, contact calls by female De Brazza monkeys were recorded outdoors by A.C. at a maximum distance of 5 meters from subjects, using a Sennheiser K6/ME66 directional microphone connected to a Marantz PMD660 solid-state recorder (sampling rate 44.1 kHz, resolution 16 bits). On some occasions (4 of 42), recordings were made indoors, but then we made sure that the recording quality was the same as for the recordings made outdoors. We also added four recordings made by H. Bouchet in October 2008 at Howlett's Park with the same recording equipment and settings.

All playback stimuli consisted of a single contact call (“On”), emitted by an adult female De Brazza monkey, a vocal signal with considerable individual variation, especially in terms of call duration (fig. 1; Bouchet et al. 2011). When selecting playback stimuli, we thus verified that there was no significant difference in call duration of familiar stimuli (FS) and unfamiliar stimuli (US), to prevent discrimination biases (FS: mean ± SD = 191±98 ms, US: mean ± SD = 198±109 ms, Mann Whitney U test N=40, Z=-0.054, P=0.963). To assess the amplitude of De Brazza monkeys’ contact calls, we placed a sound pressure metre (DVM401 Voltcraft DT8820) at a distance of 1 m from two calling females. All naturally produced calls were around 60 dB (N=10), which allowed us to adjust the amplitude of playbacks in the same way.

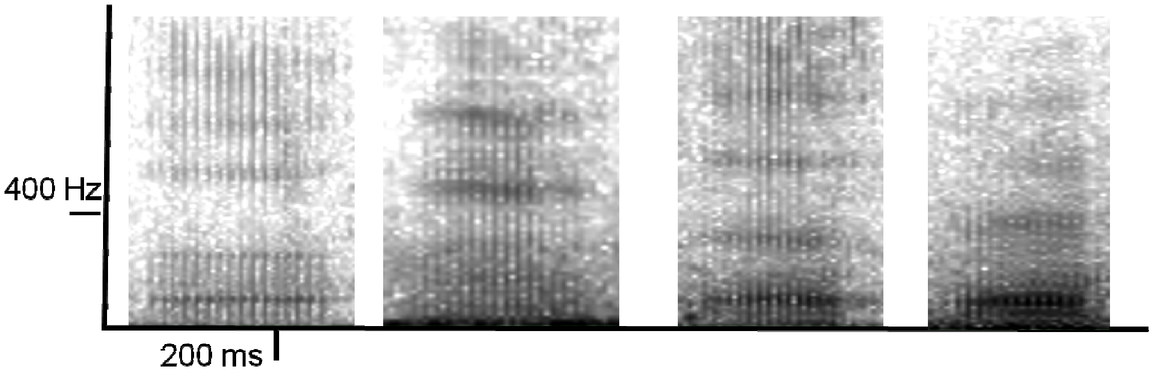

Figure 1: Spectrograms of stimuli. Spectrograms of ‘On’ calls from four different adult females (Hanning window function; filter bandwidth: 124 Hz; frequency resolution: 86.1 Hz; grid time resolution: 5.80 ms)

Experimental design

For each subject, sets of FS and US were distributed randomly. FS consisted of calls recorded from neighbouring individuals that were housed at the same place for the previous four or more years. US were recorded from individuals housed in another captive facility that had never been in contact with the subjects and that were not related to the individuals that contributed the FS. For all the experiments, FS and US came from individuals of about the same age (range: 5-20 years). Each subject was tested with one FS and one US. Because other group members could also hear each experimental trial, we never played the same stimulus more than once. To avoid habituation, we limited the total exposure to three trials per day, separated by at least 30 minutes. The playback apparatus (see below) was placed in its final position at least 30 minutes before each trial, and left for at least 3 hours afterwards, so that individuals could not form associations between the presence of the speaker and the unusual events simulated by an US. Campbell's monkeys were tested in October 2011, Guereza colobus monkeys were tested from November to December 2011 and red-capped mangabeys were tested from January to February 2012.

Experimental protocol

Stimuli were broadcast from a Marantz solid-state recorder PMD660 connected to a Nagra DS speaker amplifier (FAC.SC.PA.71) that was concealed in a backpack placed on the ground. To make the experience as plausible as possible for the monkeys, the backpack was placed near the outdoor enclosure of one of the De Brazza monkey cages, so that the distance between the speaker and the subject varied from 10 to 25 meters. For each subject this distance was the same for both conditions (FS and US). Monkeys from the targeted group and the neighbouring De Brazza group were free to move in their indoor-outdoor enclosures. We ensured that (a) no conflict has occurred in the 15 minutes prior to each trial, (b) no De Brazza monkey call had been produced in the 5 minutes prior to each trial and (c) the ambient noise was low. In addition, before each trial, we waited for the subject (d) to be at least 2 m from another individual, (e) to not face the speaker direction and (f) to be in a relaxed general state, such as during resting or chewing food. All subjects were tested under the same conditions (posture: sitting or on four legs, orientation: not facing the speaker and activity: resting, self grooming or chewing food) for FS and US tests. Subjects' responses were filmed using a Sony DCR SR58E camera, from at least 20 s before to 20 s after the playback stimulus was broadcast.

Data analysis

Using VLC software, we conducted frame-by-frame video analyses of each 40 s video recording, a time period that had turned out to be relevant in comparable studies (Palombit et al 1997, Lemasson et al 2008). For each frame, we noted the angle between the subject's head relative to the speaker direction. We systematically counted all gazes that formed an angle of

45° or less with the speaker direction (left or right, above or below) as “looking in the speaker direction”. Latency to gazing at the speaker area was the duration between the beginning of the playback and the beginning of the target’s first head movement towards the speaker direction. We also measured the total duration of all gazing at the speaker per 20 s before playback (and 20 s after playback) for each trial. As final variables, we subtracted to these measurements the value obtained for the 20 seconds before the playback to the value obtained for the 20 seconds after the playback.

Statistical analysis

We first performed analyses within each species, then pooled all individuals into a single analysis. To test for species differences, we conducted Kruskall & Wallis tests on the three species for each variable and each condition. We performed non-parametrical matched-pair Wilcoxon tests with SPSS 17.0 software and two-sample tests for equality of proportions with R 2.14. Statistical tests were two-tailed and significance levels were set at $\alpha = 0.05$.

Results

We performed a total of 42 trials (Campbell’s monkeys: N= 16; Colobus monkeys: N= 14; mangabeys: N= 12). Overall, subjects reacted to 60% of FS trials (Campbell’s monkeys: 100%; Colobus monkeys: 71%; mangabeys: 50%) and 73% of US trials (Campbell’s monkeys: 50%; Colobus monkeys: 71%; mangabeys: 67%). If comparing response proportions, no significant differences were found between the two conditions (two-sample tests: Campbell’s monkeys P=0.083, Colobus monkeys P=1; mangabeys P=0.830).

When comparing the different response variables within each species, none of the variables were statistically significant in either species (table 1).

species	variable	N	Z	P	FS (mean SD)	US (mean SD)
C.campbelli	latency (ms)	8	-1.483	0.188	4785 ± 2002	465 ± 224
	number of gazes	8	-1.496	0.188	0.8 ± 0.5	1.5 ± 0.5
	total gazing duration (ms)	8	-0.912	0.414	430 ± 247	555 ± 199
	mean gazing duration (ms)	8	-0.420	0.742	234 ± 121	159 ± 47
C. guereza	latency (ms)	7	-1.214	0.313	1371 ± 497	389 ± 112
	number of gazes	7	-1.511	0.250	0.3 ± 0.2	2.0 ± 0.8
	total gazing duration (ms)	7	-0.507	0.688	2429 ± 1135	2849 ± 1292
	mean gazing duration (ms)	7	-0.676	0.578	1290 ± 644	980 ± 794
C. torquatus	latency (ms)	6	-0.948	0.375	1827 ± 1112	3233 ± 2146
	number of gazes	6	-0.816	0.688	0.3 ± 0.3	0.7 ± 0.2
	total gazing duration (ms)	6	-0.314	0.844	253 ± 267	980 ± 794
	mean gazing duration (ms)	6	-0.734	0.563	89 ± 200	447 ± 166

Table 1: Reaction to the FS and the US for each species. Results of the matched-pair two-tailed Wilcoxon tests performed for each species.

In order to run the tests with more subjects and given the fact that no significant effects were found when comparing the different response variables between species (table 2), we pooled all subjects to conduct one global analysis across all three species. Across conditions, we found no significant difference in the latency to react, or in the total gazing duration towards the or in the mean number of gazes (table 3). However, we found that monkeys gave significantly more gazes in the speaker direction in reaction to US than to FS (figure 2).

variable	stimulus	Df	χ^2	P
latency	FS	2	2.28	0.320
	US	2	1.10	0.570
number of gazes	FS	2	0.51	0.770
	US	2	2.01	0.370
total gazing duration	FS	2	2.82	0.870
	US	2	1.76	0.430
mean gazing duration	FS	2	0.31	0.860
	US	2	1.35	0.510

Table 2: Species comparisons of the reactions to FFS and US stimuli. Results of the matched-pair two-tailed Kruskall & Wallis tests performed on each variable.

variable	N	Z	P	FS (mean SD)	US (mean SD)
latency	21	-1.307	0.202	2802 ± 1345	1230 ± 205
number of gazes	21	-2.262	0.026	0.5 ± 0.4	1.4 ± 0.6
total gazing duration	21	-1.026	0.320	1046 ± 666	1289 ± 768
mean gazing duration	21	-1.167	0.254	545 ± 425	515 ± 508

Table 3: Overall reaction to the FS and the US. Results of the matched-pair two-tailed Wilcoxon tests performed on each variables.

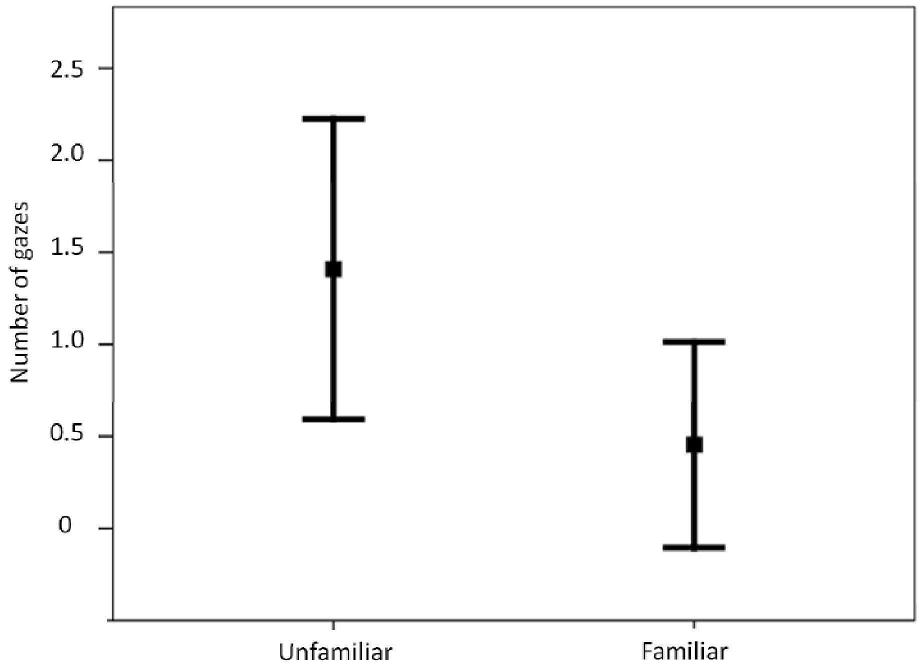

Figure 2: Discrimination of another species' voice familiarity. Mean number of looks in the speaker direction, in reaction to an unfamiliar and to a familiar stimulus. Error bars represent the 95% confidence interval (CI).

Discussion

When analysing each species separately, we found we failed to find a significant difference in the reaction of either species. Of the three tested species, red-capped mangabeys is the one presenting the lowest score of polyspecific association given that their home range size is considerably larger than those of arboreal monkeys (McGraw & Bshary 2002). It is hence likely that this species is less sensitive to other species' individual voices. Nonetheless, small sample sizes were very small for each species, suggesting that statistical power was low. When pooling the data across the three species, we found evidence for the ability to discriminate familiar from unfamiliar heterospecific voices. Of all the variables studied, the effect was strongest for the number of gazes towards the speaker, which showed a significant effect, with a higher number of gazes after the playback of unfamiliar voices as predicted. Consequently, individuals from various other species seem to have, to some extent, been able to discriminate between individual hetero-specific voices they are used to hear and voices they have never heard. Hence, nonhuman primate species frequently forming polyspecific associations seem to be able to extract information from other species' vocalisations that go beyond predator labelling. Nonhuman primates often form poly-specific associations, especially in tropical rain forests. Consequently, the possibility of inter-specific confusion of vocal signals is increased (Marler 1965). Several authors insist on the important influence of interspecies competition on communication system, leading to species-specific vocal repertoires (Gautier 1988). In our study, several explanations could account for the lack of strong results in terms of gaze latencies and durations. Although statistically significant, the subjects' responses were not as strong as what could be expected at the conspecific level. Indeed, the mean gaze durations were very short which revealed a general lack of interest for other species' vocalisations when compared to reactions to conspecific vocalisations (baboons: 2-20s, Lemasson et al. 2008; meerkats: 2s, Townsend et al. 2011). In an inter-specific discrimination task testing birds, Dooling et al. (1992) found that all four tested species showed clear evidence of several perceptual categories corresponding to the calls of the several species, but showed that three of them presented an enhanced ability to discriminate among calls of their own species over the calls of the others. A second explanation could be that the Campbell's monkeys and red-capped mangabeys tested are merely cage neighbourgs of De Brazza monkeys, which implies that cannot develop strong individual relationships but merely exchange calls. The black-and-white colobus monkeys tested did live in a mixed open top enclosure together with De Brazza monkeys, but during the observational period, their interactions were limited to conflicts over food and sometimes play between youngsters (Pers. Com.). Third, perhaps we did not choose a type of call adapted to our experiment. Since "On" calls are very short, it is possible that they do not carry enough information about the emitter's identity for other species to detect a difference. Longer calls would potentially carry information redundancy suppressing identification ambiguities. Further investigations, with other acoustic structures and other useful signals such as food calls, are hence required to confirm or infirm this preliminary hypothesis of a weaker interest for heterospecific neighbours' voices.

Acknowledgments

This study was funded by the French Ministry of Research, IUF, PICS-CNRS and ANR 'Orilang'. We are thankful to C. Blois-Heulin for permission to conduct research in Paimpont and to M. Kingston Jones for permission to conduct research in Port-Lympne Wild Animal Park. We thank all the keepers for their help with individual identification. We are grateful to H. Bouchet for her comments and thoughts as well as for providing some of the playback stimuli. Our research protocol was approved by the ethical committee of the School of Psychology from the University of St Andrews, in lines with the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

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CHAPTER 6 – DISCUSSION – CONCLUSIONS

In this section, the main results will be compared with current theories of nonhuman primate sociality and communication and I will discuss how the findings confirm or differ from these theories. My empirical contributions to current theories are in terms of understanding the evolution of primate social systems, vocal flexibility and comprehension.

First, the general model for guenons' social system is the 'monitor-adjust' system proposed by Rowell (1988), in which individuals of a group rarely interact physically but monitor each other's spatial position visually and vocally to adjust their own accordingly. The results obtained for Diana and Campbell's monkeys were overall in line with this interpretation. Nonetheless, there were several qualitative and quantitative differences in the social interactions between these two phylogenetically closely related guenon species.

Regarding vocal communication, the currently most widely accepted framework states that nonhuman primates' vocal repertoires are largely fixed with very little acoustic flexibility in the production of calls. In Diana monkeys, females showed some acoustic flexibility in the production of their contact calls, both in terms of modifications of the arched frequency contour and in terms of combining basic call elements in non-random ways. Hence, the results are in line with a growing literature that has demonstrated limited degrees of flexibility in the production of nonhuman primate calls. Structural modifications and combinations are two non-exclusive vocal strategies that can lead to increased communicative flexibility. These findings are also important in relation to a number of questions regarding the communicative function of calls given in social contexts, functions that will need to be further explored.

Finally, it has long been known that primates not only understand the calls of their own but also of other species. Within social groups individuals recognise each other individually, but it is currently unknown whether this is also the case for mixed species groups. To this end, I wanted to test the extent to which primates living in poly-specific communities recognize hetero-specific individuals through their voice. Although responses to other species' contact calls were generally weak, the results revealed an ability to differentiate voices of strangers from voices of familiar individuals, across species. This finding opens the door towards more investigations on the cognitive representation of individuals from another species, especially for those living in so-called "supra-social" poly-specific communities.

6.1 – Social functioning and communication in two sympatric forest guenon species

6.1.1 – The consequences of social organisation for communication

First, I found that female Diana monkeys and female Campbell's monkeys were genetically more closely related within than between groups, as predicted by their female philopatric social system (Wrangham 1980; Rowell & Olson 1983). Second, I found that males were genetically not very distant from each other or from the local females, suggesting that they do not migrate very far. Third, there was no strong relation between the genetic relatedness of female group members and their preferences for each other as social partners, while a study on Cercopithecus solatus revealed that individuals biased some of their behavior according to relatedness (Charpentier et al. 2008).

There were several lines of evidence which suggested that both species should be classified as having a 'monitor adjust' social system, as proposed for guenons more generally by Rowell (1988). Indeed, the four study groups were all female-bonded with young males emigrating. Physical interactions were rare between females and very rare between the male and the females. Females developed preferential social bonds with one another, especially in Diana monkeys. Dominance relationships could not be studied, partly because agonistic interactions were very rare, as expected for this type of social system.

Despite many similarities, there were several differences between the two species, such as a greater number of individuals per group and higher rates of intra-group aggression and affiliative interactions in Diana monkeys than Campbell's monkeys. Moreover, female Diana monkeys, whose groups contained more adult females than Campbell's monkey groups, called significantly more than female Campbell's monkeys. Indeed, females' individual call rates were significantly different betweens species. Consequently, Campbell's monkeys are more cryptic and less implied in poly-specific associations than Diana monkeys. Several hypotheses could explain these distinctions, such as differences in predation pressure due to differences in canopy use, with Campbell's monkeys more exposed to leopard predation than Diana monkeys (Zuberbühler & Jenny 2002) or differences in the quality of consumed food items, with Diana monkeys feeding on better quality food than Campbell's monkeys, which can provoke higher rates of intra-group conflicts (Buzzard & Eckardt 2007).

Amongst the Old World monkeys, the social system of forest dwelling guenons is usually contrasted with the social system of open habitat species, such as baboons or macaques. The latter tend to live in large multi-male multi-female groups, interact physically very frequently and have a maternal rank inheritance system (Melnick & Pearl 1987; Rowell 1988). Apart from this main difference, there is important variation within both types of social system. Indeed, savannah baboons and hamadryas baboons show striking differences in their social organisation such as male-female 'friendships' and the difference in female social power (Wrangham 1987). Also, in the macaque radiation that consists of 22 species, many differences in social behaviour and organisation have been attributed to ecological differences (Thierry et al. 2000). Macaques display varying degrees of dominance asymmetry and preference for kin, with affiliative behaviours prominent in some species but limited in others, as well as contrasts in patterns of conflict resolution (Thierry 2000; Thierry 2007). Thierry (2000) hence suggested a four-grade scaling of social styles, from very intolerant species, such as rhesus macaques, to highly tolerant species, such as Tonkean macaques. It is highly possible that, within the guenon radiation (consisting of 24 species, Butynski 2002), not all species can be classified as having a 'monitor adjust' social system but they may show gradients in some of their social characteristics.

In my study, I found variations in the social organisation of Diana monkeys and Campbell's monkeys, with species more or less bonded and more or less cryptic. Although both species do not bias their social behaviours towards kin in the wild, this is not the case for other guenon species, such as *Cercopithecus solatus* (Charpentier et al. 2008). In the simplest form of guenon social systems found in the nuclear groups of De Brazza monkeys, individuals also display high inter-individual distances with few interactions (Gautier-Hion & Gautier 1978b). In addition to the detailed studies of blue monkeys' social relationships (Cords 2000a; Cords 2000b; Glenn & Cords 2002), a comparative study of the social characteristics, such as the frequency of physical contacts, the frequency and intensity of agonistic interactions and the presence of kin biases would be necessary across all guenon species to further investigate the social variations. For example, Sterck et al. (1997) emphasised the combined importance of ecological factors, habitat saturation and infanticide avoidance to explain variations in the social relationships of female primates. The radiation of African guenons being much more recent than the radiation of baboons or macaques (Raaum et al. 2005), a diversification of guenon social systems is likely to be in process together with the guenon radiation.

The social differences observed between baboons and macaques on one hand and guenons on the other hand parallel the differences in their communication behaviour. The main mode of communication in guenons is vocal (Gautier 1988). However, there is a large sexual dimorphism in the vocal repertoires (Gautier & Gautier 1977) which are composed of discrete call types, which may lower the risks of communication confusion in their visually dense habitats (Marler 1965). In comparison, the larger number of potential social partners in macaques and baboons is somehow compensated by their multimodal communication system involving additional visual clues. To search for vocal flexibility in the vocal communication of nonhuman primates, it seems promising to further study female guenons, especially their social calls that are likely to show degrees of flexibility with social contexts ('social function hypothesis', (Snowdon & Hausberger 1997; Griebel & Oller 2008). Within guenons, social variations are also likely to be reflected in vocal differences.

6.1.2- The social vocal repertoire of Diana and Campbell's monkey females

When compared to alarm calls which have little social function, calls used during social interactions should be more complex both in the number and the variability of calls. This hypothesis named the 'social function hypothesis' (Snowdon & Hausberger 1997; Griebel & Oller 2008), was supported in Diana and Campbell's monkeys when comparing the number of females' social calls to the number of alarm calls (Zuberbühler et al. 1997; Ouattara et al. 2009c). In both species, females possess a variety of social calls that have been classified as belonging to the 'cohesion-contact' calling system of the guenons (Gautier 1988). Also, both species present a key structural element in females' vocal repertoire, which is an arched frequency modulation that is also found in several other guenon species as a result of their recent phylogenetic diversification (Gautier 1988).

In Diana monkeys, this arched frequency modulation (A) was emitted very frequently, mostly in combination with a preceding low-pitched trill (LA). The A unit in Diana monkeys structurally resembles the arched frequency modulation of Campbell's monkeys, the CH call. I was able to distinguish two subtypes of the A unit: the Af call, characterised by a full arched frequency modulation and the Ab calls, characterised by a broken arched frequency modulation. In Campbell's monkeys, it was possible to divide the social CH calls into six subtypes, with CH1 to CH5 subtypes consisting of broken arched frequency modulations and a CH6 subtype with an unbroken modulation (Lemasson & Hausberger 2011). These subtypes have been described in a captive study with fine telemetry recording, which ensured recordings of very good quality that can normally not be obtained in the wild, but they have also all been found in the wild (Ouattara et al. in prep). In lower quality recordings obtained from free-ranging Diana monkeys, the Ab subtype appeared structurally heterogeneous, suggesting that it also contained several broken subtypes (fig. 10 a). Further investigations, including telemetry recordings from captive socially housed Diana monkeys would be necessary to test this hypothesis. Another important finding was that, in both species, inter-individual variability of the full arched frequency modulation was higher than intra-individual variability, suggesting a good potential for individual coding (see chapter 4, paper 3 and Lemasson & Hausberger 2011).

Despite this acoustic variability within this social call type, the overall repertoire of different call types is remarkably low in both species, possibly because of a general lack of motor control of the vocal tract that appears to characterise the vocal behaviour of all non-human primates. One potential evolutionary solution to this constrain in communication is to combine calls into larger units. In Diana monkeys, I found three types of combined units, the HA, LA and RA combinations. Similarly, female Campbell's monkeys also emit three types of combinations, the CH calls or 'OnHi' calls composed of a SH followed by a ST, the CT call or 'Ion' call composed of a ST followed by a SH and the RST calls or 'UnI' calls composed of several repetitions of the same unit (Lemasson & Hausberger 2011, Bouchet et al submitted, fig. 10 b). In both cases, combinations consisted in two-compound calls with, most of the time, the arched frequency modulation introduced by a short introductive note.

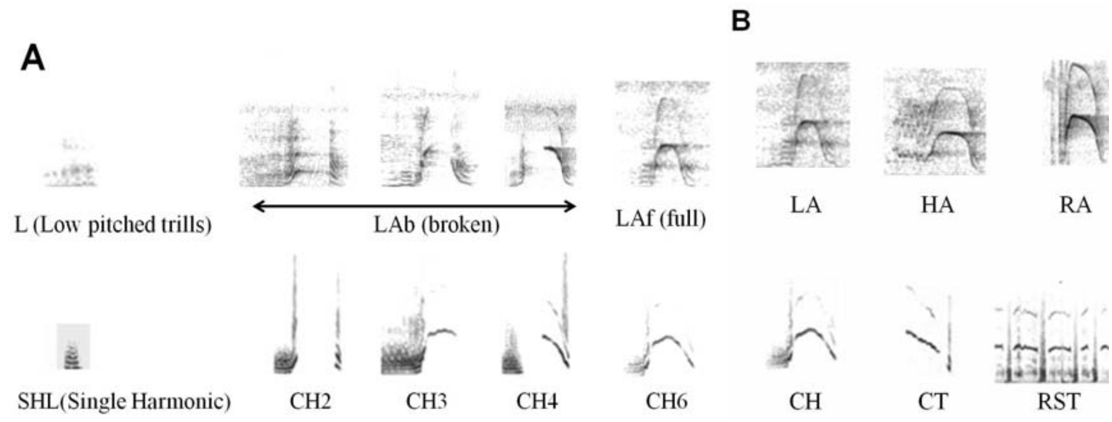

Fig 10. A. Comparative elements of Diana monkeys (upper row) and Campbell's moneys (lower row) vocal repertoires. Both species present calls with structural analogies suggesting a possible common origin. B. Diana monkeys (upper row) and Campbell's moneys (lower row) also present combined structures.

Several authors hypothesized that vocal and social complexity may have evolved together, predicting that species living in harems could emit a number of vocal combinations that is intermediate between monogamous species and multi-male multi-female species ('social-vocal hypothesis', (McComb & Semple 2005; Freeberg & Harvey 2008). Indeed, a comparative study between three species that have different levels of social complexity has shown that red-capped mangabeys, who lived in the most complex social groups, were the ones who produced the highest number of combinations, with over 16 'unit assembling patterns' (units emitted singly, repeated of combined) against 10 in Campbell's monkeys and 9 in De Brazza monkeys (Bouchet et al submitted). Hence, the hypothesis of a 'social-vocal co-evolution' of complexity suggests that increased quality and quantity of combinations are more likely to be found in species with complex social systems.

Despite these similarities in structural patterning, the social vocal repertoire of Diana and Campbell's monkeys diverged in several ways. First, in addition to the diversity of CH subtypes in Campbell's monkeys, the CH6 subtype consisted of variants that differed in the general shape of the full frequency modulation (Lemasson et al. 2003). An important finding was that, within a group, socially bonded females shared one or several variants while females that were not socially close did not, suggesting that these vocal variants reflected the females' social affiliations (Lemasson et al. 2003; Lemasson & Hausberger 2004). Importantly, the authors found a significantly positive relation between bond strength and acoustic similarity that was independent of genetic relatedness, suggesting a mechanism of vocal learning. I did not find the same pattern in the Diana monkeys' Af calls, although it is possible that this was partly due to the inferior recording conditions in the field. Overall, the intra-similarity indices of Diana monkeys were lower than those of Campbell's monkeys (intra-individual indices ranging from 0.60 to 0.77 in Campbell's monkeys and from 0.40 to 0.51 in Diana monkeys, see chapter 4, paper 3, fig. 1). Diana calls seemed to be composed of one main Af variant, which showed gradations in the duration and frequency modulation. Females preferentially used the full arched calls when revealing their identity was particularly important, such as during periods of low visibility, when facing an opponent and in acoustically difficult environments, such as during call choruses (chapter 4, paper 2, table 5). Also, the variability of the arched structure changed in relation to a number of external factors. Calls diverged when females needed to enhance their identity but converged during peaceful vocal exchanges. Campbell's monkeys seemed to use the full arched frequency modulation in a different way. Here, only 15.3% of the CH emitted were fully arched CH6 calls (data from Lemasson & Hausberger 2011) while 63.5% of Diana monkeys' A calls were Af (data from chapter 4, paper 3, table 3). To further understand the differential use of this phylogenetically shared acoustic structure, it would be now necessary to carry out analyses of the emission contexts in wild Campbell's females, similar to the ones performed on Diana monkeys.

Second, the introductory part of the various call combinations also seemed to function differently. One finding was that Campbell's CH introduction duration differed significantly between the matrilines, suggesting a possible role in identity coding (Lemasson & Hausberger 2011). In contrast, the introductive note of Diana monkey calls (H, L or R) seemed to carry information about the basic arousal state of the emitter (positive, neutral or negative), although this type of information does not exclude additional identity coding. In Diana monkeys, we hypothesized that the 'A' call could function as an individual identifier combined with or without contextual situation. In addition, we found no evidence that Diana monkeys' combinations of social calls neither carried strong semantic content relating to specific events, such as a falling tree, the approach of a neighbouring group (Ouattara et al. 2009b) or a signal for group progression (Arnold & Zuberbühler 2006a), nor broadened the 'meaning' of units emitted singly, as found in the affixation system of Campbell's monkeys (Ouattara et al. 2009a). Instead, Diana monkey's calls appeared to convey the individual identity of the caller (likely to be found in the arched frequency modulation) and information about the immediate motivational state of the caller (plausibly found in the introductory call).

From an evolutionary perspective, it is relevant to point out that two closely related species with very similar vocal repertoires, identical habitats, and a very similar evolutionary history have evolved significant differences in call use and functions. Campbell's monkeys are cryptic; they emit few full arched modulations but advertise their social bonds by sharing call variants. Diana monkeys are more conspicuous, they are more frequently in close proximity with their preferential social partners and emit very often full arched modulations which converge during vocal exchanges. We hence described two different systems in closely related species. It would be interesting to compare this diversification in acoustic communication with the diversification found in the visual communicative signals of macaque species (Petit & Thierry 1994), or in diversification of use in copulation calls in bonobos and chimpanzees (Townsend et al. 2008; Clay et al. 2011; Clay & Zuberbühler 2012).

6.2 – Perception of vocal signals

As described earlier, nonhuman primates emit a variety of social calls that can carry information such as a caller's identity, sex and social status (e.g. Fischer et al. 2002; Fischer et al. 2004; Rendall et al. 2004; Lemasson et al. 2005b). Amongst the multiple types of information that receivers can potentially perceive, identity of the emitter is a fundamental one. Individual recognition of the voice is a widespread phenomenon in the animal kingdom (frogs: Bee & Gerhardt 2002; seal pups: Charrier et al. 2001; sea lions: Gwilliam et al. 2008; King penguins: Jouventin et al. 1999; horses: Proops et al. 2009; meerkats: Townsend et al. 2011; Old World monkeys: Cheney & Seyfarth 1980; Masataka 1985; Rendall et al. 1996; Lemasson et al. 2008). This capacity has been described within species in cercopithecidae, with female putty-nosed monkeys answering the calls of their own male only (Arnold & Zuberbühler 2008) and female Campbell monkeys perceiving the frequency modulation of their arched calls (Lemasson et al. 2005b). In poly-specific associations of primates, one species attends the alarm calls of another species but whether the attentional process extends to less vital vocalisations is currently unknown. Given the frequency and strength of poly-specific associations in African primate communities as well as the inter-individual variability found in most calls, it is plausible that monkeys might also discriminate voices of individuals from other species.

To test this hypothesis, I chose to examine the capacity of three species of Old World monkeys to discriminate the voices of individuals from another species. The basic paradigm was to expose subjects to the calls of individuals that lived in the same facility, or individuals they had never heard before. I found that the subjects were able to recognise these differences, but their responses were not as strong as what would have been expected at the conspecific level (Lemasson et al. 2008; Townsend et al. 2011). It is possible that receivers simply lacked interest for other species' vocalisations and other vocal signals, such as food calls, might be more likely to generate interest from other species due to their general relevance.

Cross-fostering experiments in which the mother and the infant react to each other's calls provide indirect evidence for hetero-specific voice recognition (Masataka & Fujita 1989; Owren et al. 1993). In poly-specific primate communities, it has been shown that some groups actively search out groups of another species to associate with them (Holenweg et al. 1996). Groups of saddle-back tamarins and emperor tamarins, for example, respond to the playback of long calls from other tamarin species they associate with (Windfelder 2001). Playbacks elicited long calls and approaches towards the speaker, suggesting that long calls serve as inter-specific signals between different species. It would be highly interesting to test whether a given group reacts more strongly to the long calls of hetero-specific group it usually associates with than to the long calls of another unknown hetero-specific group.

Generally speaking, primates eavesdrop very effectively from other sympatric species. While this capacity is likely to increase the fitness of eavesdroppers, especially if they understand another species' alarm calls, there does not seem to be a direct benefit to the capacity to identify hetero-specific individual's voices. Nonetheless, if such a capacity exists in primates, it may be due to open-ended call comprehension and would stress the underlying cognitive abilities. Mixed species groups interact in a variety of ways, for example to avoid predation or to compete over food. The fact that many of these associations are very stable over time suggests that there are reciprocal benefits to maintain such associations. In primate communities, the main benefit seems to be the reduction of predation (e.g. Bshary & Noë 1997). Other potential benefits are foraging advantages, for example through increased flushing of insects (Waser 1987).

Although most examples of comprehension of hetero-specific calls seem to be phenomena of mere eavesdropping, it may be premature to rule out the possibility of inter-species communication *sensus stricto*, as observed in the vocal exchanges between female guenons of different species and the vocal duos of male loud calls in the Taï forest. The extent to which individuals know each other individually remains a largely open question and further investigations would be required. Ideally, further studies should be carried out in the wild, for example on the Taï primate community that provides spectacular examples of poly-specific associations with an apparent ‘supra-social’ organisation (McGraw et al. 2007).

6.3 – Vocal flexibility in nonhuman primates and the roots of human language

How has human speech evolved from earlier forms of primate communication? The vocal origins theory proposes that some features of human language have deep biological roots in the vocal communication of animals (Masataka 2008; Lemasson 2011). Among the key properties are structurally flexible and psychologically intentional communication that can refer to external events, properties that all have been described in nonhuman primates. Vocal plasticity has been defined as the ability to actively modify the acoustic structure (production) or the emission rate (usage) of a vocal signal, depending on the social and environmental conditions (McCowan & Reiss 1997). The difference with vocal flexibility (defined in the first chapter as a qualitative -flexibility in production- or quantitative -flexibility in usage- modulation of a vocal signal over time), is the fact that a variation is actively controlled, so there is intentionality involved in the process. Vocal plasticity under social influence has been well described in some mammals (cetaceans: Janik 2000; Noad et al. 2000; pinnipeds: Schusterman 2008; elephants: Poole et al. 2005). A typical manifestation of vocal plasticity is vocal production learning (Janik & Slater 2000), a capacity that has also been documented in a recent study on goats, which have a very small vocal repertoire (Briefer & McElligott 2012). Further work in other mammal species might reveal that socially-driven vocal plasticity is more ubiquitous than currently assumed. This would represent a key step in the emergence of human language.

6.3.1 – Flexibility in the acoustic structure

In this thesis, I have documented that the main social call of free-ranging female Diana monkeys contains sufficiently stable acoustic variation across individuals to convey individual identity. Nonetheless, the acoustic structure of this call also varies according to the context of emission. The balance between the needs to advertise identity and the need to bond with others is a paradox that is widespread in the animal kingdom (e.g. Snowdon & Hausberger 1997; Kremers et al. 2012). Bonding is usually seen in terms of vocal convergence between closely affiliated individuals, a phenomenon that can occur both on a long term (e.g. Smolker & Pepper 1999; Hile & Striedter 2000) or short term scale (e.g. (Sugiura 1998; Pardo 2006).

First, in several primates species, the acoustic structure of vocalisations can converge between individuals on a long-term scale, encompassing weeks, months or years. This is usually a consequence of changes in social relationships (e.g. marmosets: Snowdon & Elowson 1999, Campbell's monkeys: Lemasson & Hausberger 2004, chimpanzees: Crockford et al. 2004). However, convergence is never complete, and even if two individuals share some kind of vocal structure as a result of social bonding, a minimum of individual distinctiveness remains present, probably to ensure individual identification in the absence of visual contact. This process has been refer to as the 'optimal vocal sharing' hypothesis (Snowdon & Hausberger 1997) and it has been found in several species of birds (e.g. Australian magpie: (Brown & Farabaugh 1997), Indigo buntings: Payne & Payne 19977, nightingales: Grie\ssmann & Naguib 2002, European starlings: Hausberger et al. 1995) and some marine mammals (bottlenose dolphins: McCowan & Reiss 1997, killer whales: Miller & Bain 2000; Kremers et al. 2012). Further investigations are required to confirm this hypothesis in nonhuman primates.

Second, short term modifications in acoustic structure have also been observed, usually within vocal exchanges. This phenomenon has been found during exchanges of the social coo calls of Japanese macaques (Sugiura 1998) and described in the pant hoot chorusing of chimpanzees (Mitani & Brandt 1994), although in this case the mechanism might be a vocal matching and not a convergence. My study thus provides another example of short term vocal changes in nonhuman primates, with female Diana monkeys producing calls that resemble more the call of a female they are responding to than the call of another female they are not responding to, despite similar inter-call intervals. In humans, short-term vocal changes is common from early infancy and present throughout adulthood and psycholinguists have referred to this phenomenon as a 'vocal accommodation', by which interlocutors change one or several speech parameters in response to specific contexts and relative to each other (Giles et al. 1991; Locke & Snow 1997; Giles & Ogay T 2006). Humans can achieve vocal accommodation through modification of acoustic features, similar to what has been found in nonhuman primates, or through the choice of vocabulary or changes in prosody and intonation. How humans have evolved their capacity to generate this large degree of flexibility and enhanced control over their vocal apparatus remains an unresolved question.

Vocal exchanges play a major role in nonhuman primates, and several conversation-like properties such as turn-taking and the attention to elder's voice have already been highlighted (Snowdon & Cleveland 1984; Sugiura & Masataka 1995; Lemasson et al. 2010a). This highly social context could involve some degrees of control on the vocal production by cortical structures of the brain, as recently evidenced in Japanese macaque coo calls (Coudé et al. 2011). The extend to which these vocal exchanges can be considered as intentional communication is still debated. Intentional communication will be defined here as the emission of a signal where the emitter intends to influence the receiver in a certain way (Leavens 2004). Although intentional communication has been documented repeatedly in the gestural communication of nonhuman primates (Corballis 2002; Pollick & de Waal 2007; Call & Tomasello 2008), the evidence in vocal communication is less strong. Evidence for intentional communication in the vocal domain in nonhuman primates is usually in terms of adjusting call production to the social context, as documented in studies of audience effects (Hauser et al. 1993; Di Bitetti 2005) and conversation-like vocal interactions (Snowdon & Cleveland 1984; Hauser 1992). Intentional communication can also be inferred if callers take into account the social context during emission, as has been shown in baboon grunts macaque girneys (Silk 2002) and baboon threat calls (Wittig et al. 2007a). In these instances, calls are socially directional in that they target a particular individual whose behaviour is sought to be changed.

6.3.2 – Combinatorial abilities and the evolution of language

As mentioned earlier, one way of dealing with the constraints of limited vocal control is by combining based call units into more complex structures. In this study, I found that Diana monkeys could produce non random combinations of social calls (chapter 4, paper 2). In several guenon species, males combine calls into sequences (Arnold & Zuberbühler 2006a; Ouattara et al. 2009b). Arnold & Zuberbühler (2011) studied the call combinations of male putty-nosed monkeys by questioning whether they were compositional or idiomatic expressions. In this species, males produce series of 'Pyow' and 'Hack' calls which can be combined into so-called 'P-H' sequences, which specifically trigger group progression

(Arnold & Zuberbühler 2006b). Pyow-hack (P-H) sequences are not stereotypic but vary in the number and proportion of constituent calls. Playback experiments have shown that the number of constituent calls within P-H sequences had no significant effect on listeners' responses, suggesting that the sequence functioned as an idiomatic expression (Arnold & Zuberbühler 2011). Therefore, there is at the moment no evidence that animal communication systems possess anything like the generative power of syntax. Nevertheless, these communication systems have a great potential for increasing the number of messages that can be conveyed by a small call repertoire and thus contain some of the combinatorial features also found in linguistic systems.

Complex signal combinations have also been described in the gestural communication of great apes (Liebal et al. 2004; Pika et al. 2005). This has been interpreted as being in line with an increased tendency for multi-modal signalling, which eventually led to the origins of language (Arbib et al. 2008; Lemasson 2011; Taglialatela et al. 2011). Importantly, Crockford & Boesch (2005) described non-random combinations of calls and gestures (drums) in the communication of wild chimpanzees, illustrating a case of communicative multi-modal combinations.

Another relevant topic in the context of signal combinations and the emergence of language is the issue of recursion. Recursion is usually defined as a 'computational procedure that calls itself or that calls an equivalent kind of procedure' (Corballis 2007), a process that requires complex combinatorial abilities. Hauser et al. (2002) first drew attention to this by distinguishing the faculty of language in the broad sense (FLB), which is shared between humans and other species, and the faculty of language in the narrow sense (FLN), which is uniquely human. According to these authors, the main characteristic that distinguishes FLN from FLB is recursion. This procedure allows us to create sentences of any desired length and complexity. According to Corballis (2007), there is a distinction between mere iteration called 'tail recursion' and the 'centre-embedded recursion', in which the procedure invokes an instance of itself or of an equivalent procedure in the middle of the computation. Fitch & Hauser (2004) investigated the ability of tamarins to deal with centre-embedded recursivity (results were negative), with similar attempts by Gentner et al. (2006) in starlings (results were positive). However, Corballis (2007) argued that the paradigms chosen in these studies were not cases of true centre-embedded recursion and that therefore there is no evidence for recursion in the processing of sequences in any species other than humans. Still, Rey et al.

(2012) recently showed that, with sufficient training, baboons respond to visual shapes organised in recursive, centre-embedded structures, suggesting that the human ability for recursion might originate from fundamental processing abilities already present in non-human primates. A reasonable explanation of these recent findings is that recursive abilities might be closely tied to working memory capacities (Rey et al. 2012).

General conclusion

This research was carried out with the specific aim of obtaining a better understanding of the relationship between the sociality and communication in a group of primates that are not well understood, the forest guenons, and the more general aim of gaining knowledge about vocal flexibility in nonhuman primates' vocalisations when compared to human communication. I provide detailed insights into the social organisation and vocal communication of two free-ranging species. To my knowledge, this represents the first comparative study of its kind, conducted largely by focussing at the individual level in two sympatric species with groups sharing the same territory. In line with previous findings, I found that adult females form the social core of the group and that they interact according to a 'monitor-adjust' system, with little influence of the genetic relatedness. The originality of my study also lays in the fact that all aspects of vocal communication were investigated, from emitters to receivers, and from production, usage and the comprehension of calls. Given that most African primate species form stable poly-specific associations in primate communities, I further predicted that they should be able to identify the voice of individuals they live with, even if they are from a different species. My results suggest that this is the case, at least in captivity, which opens new possibilities for the study of 'supra-social' cognition and its impacts on the evolution of each species within such associations. Regarding the production and usage of calls, I focused on the social calls which have been understudied in Old World monkeys, especially if compared with the alarm calls, and if compared with the communication of baboons or macaques. My results confirmed that nonhuman primates have some limited capacity of flexible call production both via modification of acoustic structures and via combinatorial abilities. This finding provides a significant extension of the current literature, which has been limited to the loud calls of adult males. Results from the short distance 'cohesion-contact' calling system of adult females contribute to a reassessment of the phylogenetic gap in the evolution of vocal flexibility. Results are in line with the hypothesis that human language has a partially vocal origin, in line with recent reviews which tend to favour a multimodal origin of language (Arbib et al. 2008; Meguerditchian et al. 2011; Lemasson 2011).

Finally, my work has raised several new questions. The dynamic of the social networks of free-ranging forest guenons remains largely unexplored, and a long-term study of several years would be necessary to understand the evolution of the current social system. A particular concern would be to confirm the absence of kin-biased social relations, which is unusual for primates. It would be interesting to conduct additional research on other guenon species to have a better view on the social structure-social organisation- ecology co-evolution. Regarding vocal flexibility, the function of a short term convergence needs to be further explored, by studying notably the influence of vocal partners' social affinities for example. The extend to which a flexible vocal production is ubiquitous in nonhuman primates is not certain and other investigations about the complexity of vocal repertoires, the existence of structural flexibility or combinations and the contextual use of such flexibility should be carried out in other Old World monkey species but also New World monkeys species and Apes, to better understand the phylogenetic gap between humans and the rest of the primates.

Another point that will require further research is to test Diana monkeys' abilities to decode the information potentially carried through their vocalisations, such as the individuals signatures encoded in the arched frequency modulation but also the general arousal state potentially encoded in the introductory part of call combinations. Eventually, monkeys' ability to identify the voice of individuals from another species requires additional playback experiments in the field, testing the capacity of a given species to discriminate the voice of individuals from another sympatric species they usually associate with *versus* the voice of individuals that live further in the forest.

To conclude, the study of nonhuman primates' vocal communication is a field of research that opens promising perspectives for the quest of human language origins.

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ANNEXES

Flexibilité vocale sous influences sociales chez les primates non-humains

Vocal flexibility under social influences in nonhuman primates

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Résumé

La communication vocale animale, tout comme le langage humain, est avant tout un acte social. Il est donc logique de défendre l'idée d'une coévolution entre socialité et complexité vocale. Pourtant, à l'inverse du langage humain, la communication vocale des singes, nos plus proches cousins vivants, a longtemps était décrite comme rigide et fortement déterminée génétiquement. Cet article se propose de passer en revue les différentes preuves de flexibilité vocale sous influences sociales chez les primates non-humains. Tout d'abord, une approche multi-niveaux de la structure organisationnelle du répertoire vocal révèle un encodage complexe de messages dans les signaux vocaux. Ensuite, l'étude du contexte social de l'interaction de communication atteste de son rôle dans l'émergence de variabilité vocale chez le jeune et l'adulte, tant en termes de production que d'utilisation. Nous concluons en soulignant le besoin d'effectuer à l'avenir des études comparatives évaluant l'influence des caractéristiques du système social sur le degré de complexité communicative observé au niveau de l'espèce.

Abstract

Animal vocal communication, as human language, is primarily a social act. It is therefore legitimate to argue in favor of a coevolution between sociality and vocal complexity. However, in contrast with human language, vocal communication in monkeys and apes, our closest living relatives, has long been described as rigid and strongly genetically determined. We review recent evidence of vocal flexibility under social influences in nonhuman primates. First, a multi-level approach of the organisational structure of vocal repertoire reveals a complex encoding of messages in vocal signals. Then, the analysis of the social context of communicative interaction demonstrates its role in the emergence of vocal variability in juveniles and adults, both in terms of production and usage. We conclude by emphasizing the need, in the future, for comparative studies to assess the influence of the characteristics of social system on the degree of communicative complexity observed at the species level.

Mots clefs : communication vocale, primates non-humains, flexibilité vocale, variabilité acoustique, contexte, rôle social.

Key words : vocal communication, nonhuman primates, vocal flexibility, acoustic variability, context, social role.

1 **Introduction**

Le langage humain constitue le système de communication le plus élaboré du monde animal. Comme tout comportement, il n'a laissé que peu de traces directes de ses origines ce qui rend l'étude de sa phylogénèse complexe. De récentes études théoriques et empiriques ont souligné l'intérêt d'opter pour une approche interdisciplinaire de la question de l'origine du langage. L'un des moyens d'y répondre serait alors de comparer les mécanismes de communication et les capacités cognitives sous-jacentes chez l'homme et chez d'autres espèces animales plus ou moins proches phylogénétiquement (Zuberbühler et al., 2009 ; Fitch, 2010 ; Lemasson et al., sous presse).

Les facteurs ayant conduit à l'émergence du langage font l'objet d'un débat important. Le langage humain (Locke & Snow, 1997), tout comme la communication animale (Marler & Tenaza, 1977), constitue avant tout un acte social. Il semble donc logique que la socialité ait pu influencer l'évolution de la communication (Marler, 1977 ; Waser, 1982). Les hypothèses invoquant une influence majeure des pressions sociales sur l'évolution des capacités communicatives, notamment vocales, se sont multipliées et précisées ces dernières années (Snowdon & Hausberger, 1997 ; Oller & Griebel, 2008 ; Lemasson, 2011). Ainsi, le rôle social d'un individu, le contexte social de l'interaction de communication, ou encore la complexité du système social de l'espèce pourraient influencer le degré de complexité communicative observé tant au niveau de l'individu que de l'espèce.

Cet article se propose de passer en revue les récentes études ayant mis en évidence des capacités de flexibilité vocale (définie ici comme une modulation qualitative [production] ou quantitative [utilisation] d'un signal sonore au cours du temps) jusque là sous-estimées chez les primates non-humains. Dans un premier temps, nous traiterons de la variabilité acoustique (définie ici comme le fait qu'un signal acoustique ait une structure plus ou moins variable au niveau intra- ou inter-individuel) permettant un encodage complexe de messages dans les signaux vocaux. Dans un second temps, nous traiterons des influences du contexte social sur la flexibilité vocale, en termes de production et d'utilisation, chez le jeune et l'adulte. En conclusion, nous établirons les parallèles possibles entre langage humain et communication vocale animale, et nous discuterons de l'influence des facteurs sociaux sur l'évolution de la communication dans la lignée primates.

2 **L'encodage de messages**

Les primates non-humains émettent des signaux vocaux dont la structure acoustique varie en fonction du contexte biotique ou abiotique, et à partir desquels les individus récepteurs sont capables d'extraire un certain nombre d'informations (Smith, 1965 ; Egnor et al., 2005). Traditionnellement, les auteurs définissent le répertoire vocal, propre à chaque espèce, en cataloguant les types de cris structurellement et contextuellement distincts qu'elle produit. Cette classification, et donc la variabilité des signaux vocaux des primates non-humains, a longtemps été considérée comme fortement contrainte par les propriétés de propagation du son dans l'habitat (Brown et al., 1995), par la phylogénie (Gautier, 1988 ; Oates & Trocco, 1983) et par un contrôle limité de l'émetteur sur son appareil phonatoire (Jürgens, 2002). Néanmoins, une approche multi-niveaux de la structure organisationnelle du répertoire vocal des primates non-humains (unité sonore – type de cri – séquence vocale), par analogie avec la littérature concernant les oiseaux chanteurs (notes – syllabes – phrases – chant) ou l'homme (voyelles/consonnes – syllabes – mots – phrases) (Hauser, 2000), ainsi que l'étude systématique de la variabilité acoustique, tant au niveau intra- qu'inter-individuel, ont permis de mettre en évidence un encodage de messages plus complexe que ce qui avait été décrit jusqu'alors. Ici, nous allons illustrer les différentes formes de variabilité acoustique observées chez les primates non-humains.

2.1 De la variabilité acoustique à différents niveaux du répertoire vocal : sous-types de cris, concaténations d'unités sonores et séquences vocales

Les catégories fonctionnelles auxquelles sont attribuées les types de cris sont souvent peu nombreuses (e.g. interactions affiliatives, interactions agonistiques, découverte de nourriture, alarme, territorialité ou encore sexualité). Cela contraste avec la grande variabilité des structures acoustiques parfois observée à l'intérieur d'un type de cri donné. Dans un tel cas, de fines variations structurales dans les domaines temporel ou fréquentiel peuvent permettre de distinguer des sous-types de cri. L'étude détaillée du contexte d'émission de ces sous-types et, dans certains cas, des expériences de repasses testant la réaction des individus récepteurs ont permis de mettre en évidence qu'ils encodaient un supplément d'information au sein d'une catégorie fonctionnelle donnée. Depuis les fameux travaux de Seyfarth, Cheney et Marler (1980) qui furent les premiers à révéler l'existence de sous-types de cris d'alarme associés à différentes espèces de prédateurs chez les vervets, des découvertes similaires ont été faites chez de nombreuses espèces de primates non-humains à différents niveaux phylogénétiques (prosimiens : Macedonia, 1990 – singes du nouveau monde : Wheeler, 2010 – singes de l'ancien monde : Cheney & Seyfarth, 1990 ; Zuberbühler et al., 1997). Par exemple, les femelles mones de Campbell émettent différents sous-types de cris d'alarme ('RRA') en fonction de la nature du danger et du type de prédateur détecté (Lemasson et al., 2004 ; Ouattara et al., 2009c), tandis que les chimpanzés produisent différents sous-types de cris alimentaires ('rough grunts') liés à la qualité de la nourriture découverte (Slocombe & Zuberbühler, 2005). Concernant les cris émis lors des interactions sociales agonistiques et affiliatives, des sous-types de cris de détresse ('screams') liés à l'intensité de l'agression ou à l'identité de l'opposant ont pu être identifiés chez les macaques (Gouzoules et al., 1984) et les chimpanzés (Slocombe & Zuberbühler, 2007 ; Slocombe et al., 2009), tandis que des sous-types de cris de contact (cris 'CH' et 'A', respectivement) liés à l'activité du groupe ou de l'individu émetteur ont été observés chez les mones de Campbell (Lemasson & Hausberger, 2011) et les cercopithèques Diane (Candiotti et al. 2012).

L’étude des structures acoustiques à un niveau d’organisation inférieur, c’est-à-dire au niveau de l’unité sonore, a permis de mettre en évidence que les primates non-humains étaient capables d’émettre une grande variété de signaux à partir de quelques unités discrètes en les concaténant selon diverses configurations. Un exemple remarquable est celui de la mone de Campbell. Les mâles produisent des cris d’alarmes spécifiques au type de danger détecté. Ainsi, les mâles émettent des cris ‘Krak’ lorsqu’un léopard est détecté et des cris ‘Hok’ lorsqu’un aigle est repéré (Ouattara et al., 2009a). La valeur sémantique des ‘Krak’ et des ‘Hok’ a été confirmée expérimentalement. Lorsqu’ils entendent des repasses de ces cris, les cercopithèques Diane qui vivent en sympatrie avec les mones de Campbell se comportent comme si le prédateur avait été réellement détecté (Zuberbühler, 2000). Les mâles mones de Campbell produisent également des variantes de ces cris auxquels ils ajoutent un suffixe ‘oo’. Les ‘Krak-oo’ et ‘Hok-oo’ sont émis dans un contexte plus large de perturbation, respectivement au sol et dans la canopée. Ainsi, l’affixation d’une unité ‘oo’ permet d’élargir le sens du message porté par les cris sans suffixe ‘Krak’ et ‘Hok’ (Ouattara et al., 2009a). Les femelles mones de Campbell produisent quant à elles quatre types de cris affiliatifs : deux constitués d’une seule unité (‘ST’ et ‘SH’), un résultant de la combinaison de ces deux unités (‘CT’), et un dernier résultant de la combinaison de l’unité ‘SH’ avec une seconde unité en forme d’arche (‘CH’) (Lemasson & Hausberger, 2011). Là encore, ces quatre types de cris encodent des variations subtiles quant au contexte social d’émission. Par exemple, le cri ‘CH’ est composé d’un préfixe (‘SH’) encodant l’appartenance à une matriligne et d’un suffixe (modulation de fréquence en forme d’arche) encodant l’appartenance à un réseau social affinitaire (Lemasson & Hausberger, 2004 ; Lemasson & Hausberger, 2011). Un phénomène similaire a pu être observé chez les cercopithèques Diane. Leur répertoire vocal inclut sept types de cris de contact : quatre sont constitués d’une seule unité (‘A’, ‘R’, ‘L’ ou ‘H’) et trois correspondent à la combinaison entre une unité préfixe (‘R’, ‘L’ ou ‘H’) et l’unité ‘A’ qui occupe la position de suffixe. Ici aussi, l’utilisation de ces sept types de cris varie en fonction du contexte social d’émission, notamment l’activité et la cohésion spatiale du groupe (Candiotti et al. 2012). Enfin, un autre exemple est celui des mangabés à collier. Leur répertoire vocal comprend, entre autres, quatre types de cris fonctionnellement distincts (découverte de nourriture : ‘Ti+(Uh)’, compétition alimentaire : ‘A+(Uh)’, menace : ‘Un+(Uh)’ et affiliation : ‘Ro+(Uh)’) (Bouchet et al., 2010). Ces cris peuvent être constitués d'une seule unité (respectivement 'Ti', 'A', 'Un' et 'Ro'), de cette même unité émise de manière répétée (e.g. 'TiTi' ou 'TiTiTi'), ou bien de cette (ces) unité(s) concaténée(s) à une unité suffixe ('Uh') (e.g. 'TiUh' ou 'TiTiUh'). Les cris comprenant ce suffixe 'Uh' sont tous émis plus souvent lors d'échanges vocaux impliquant de multiples partenaires que lors d'émissions vocales isolées (Bouchet et al., 2010).

L'étude des structures acoustiques à un niveau d'organisation supérieur, c'est-à-dire au niveau de la séquence de cris, a permis de mettre en évidence que la structure organisationnelle des séquences vocales pouvait elle aussi être porteuse d'informations contextuelles. Ainsi, les cris alimentaires sont émis en séquences dont la composition, en termes de types de cris chez les bonobos (Clay & Zuberbühler, 2009 ; Clay & Zuberbühler, 2011) et en termes de nombre de répétitions d'un type de cri unique chez les macaques (Dittus, 1984) et les tamarins (Elowson et al., 1991 ; Caine et al., 1995), varie en fonction de la qualité ou de la quantité de nourriture découverte. Un autre exemple remarquable est celui des mâles mones de Campbell qui produisent six types de cris d'alarme ('Boom', 'Krak', 'Krak-oo', 'Hok', 'Hok-oo' et 'Wak-oo') qu'ils émettent généralement en séquences comptant de 2 à 40 cris émis à la suite. L'analyse de la structure de ces séquences a révélé un système de combinaisons complexe, reposant sur des associations et des transitions (ordre de succession des cris) non-aléatoires entre les différents cris. Ce système encode des informations aussi diverses que la nature et l'imminence du danger, le type de prédateur et l'activité du mâle (Ouattara et al., 2009a). Par exemple, une séquence composée de cris 'Boom' suivis de cris 'Krak-oo' est émise suite à la chute d'un arbre. Lorsqu'un groupe voisin est détecté, des cris 'Hok-oo' sont ajoutés à l'intérieur de la séquence « chute d'arbre » qui porte alors un nouveau message (territorial). De la même manière, une séquence composée de cris 'Krak-oo' est émise lorsqu'un prédateur est détecté. L'ajout de cris 'Krak' ou l'ajout de cris 'Wak-oo' (et optionnellement 'Hok' et 'Hok-oo') au sein d'une séquence « alerte générale au prédateur » spécifie le type de prédateur détecté (respectivement léopard ou aigle). Les mâles mones de Campbell sont également capables de combiner les séquences vocales entre elles. Par exemple, la séquence « chute d'arbre » résulte de la combinaison entre une séquence « rassemblement et déplacement du groupe » (série de cris 'Boom') et une séquence « alerte générale au prédateur » (série de cris 'Krak-oo'). En outre, il est apparu que l'organisation des séquences vocales est prévisible puisque les informations cruciales sont données dès le début de la série de cris (Ouattara et al., 2009a). Par exemple, les cris ‘Boom’ produits dans un contexte de non-prédation sont émis en premier. Les cris simples (‘Krak’ et ‘Hok’) informant sur le type de prédateur détecté sont également émis avant les cris suffixés au sein d’une séquence. Des repasses de séquences vocales liées à la détection d’un prédateur auxquelles des cris ‘Boom’ avaient été artificiellement ajoutés ne provoquent d’ailleurs pas de réaction anti-prédatrice chez les individus récepteurs (Zuberbühler, 2002). Enfin, le rythme d’émission des cris au sein de la séquence s’est également avéré être porteur d’informations. Le débit d’émission des cris ‘Krak’ et ‘Krak-oo’ augmente en fonction de l’imminence du danger (léopard vu *versus* entendu), tandis que le rythme d’émission des ‘Hok’ augmente lorsque le mâle s’apprête à contre-attaquer l’aigle détecté (Lemasson et al., 2010b). Les exemples indiquant que l’émission de cris en séquences permet d’affiner le message ou bien de créer de nouveaux messages se sont multipliés ces dernières années (e.g. chimpanzés : Crockford & Boesch, 2005 – gibbons : Clarke et al., 2006 – singes hocheurs : Arnold & Zuberbühler, 2006 ; Arnold & Zuberbühler, 2008 – capucins : Wheeler, 2010).

Toutes ces études démontrent l’importance d’analyser le répertoire vocal des primates non-humains à différents niveaux (Hauser, 2000). Il en ressort qu’ils possèdent deux moyens de générer de la variabilité acoustique pour augmenter le nombre ou la précision des messages transmis. Le premier repose sur des structures acoustiques dont les paramètres (temporels ou fréquentiels) ne sont pas fixés donnant ainsi lieu à un système gradué ou permettant la subdivision d’un type en sous-types. Le second repose sur la concaténation d’éléments discrets en des structures d’ordre supérieur (unités vocales en cris ou cris en séquences) permettant à des espèces présentant un répertoire vocal simple de l’enrichir de manière significative.

2.2 Valeur sociale du cri et degré de variabilité acoustique

Les exemples présentés jusqu’ici traitent de variabilité acoustique intra-individuelle liée au contexte d’émission. Simultanément, un signal vocal peut également présenter de la variabilité acoustique inter-individuelle porteuse d’un message identitaire (encodant des informations relatives aux caractéristiques physiques ou sociales de l'individu émetteur) (Seyfarth & Cheney, 2003 ; Egnor et al., 2005). Une hypothèse a été émise suggérant l'existence d'un lien entre le degré de variabilité structurale d'un signal vocal et la valeur sociale de son contexte d'émission (Snowdon et al., 1997 ; Griebel & Oller, 2008). Les cris impliqués dans la médiation des relations intra-groupe et dirigés vers un partenaire social particulier (par exemple les cris affiliatifs), pourraient ainsi être sujets à des pressions (sociales) de sélection en faveur d'un degré important de variabilité. Cela permettrait notamment l'encodage d'informations relatives à l'identité de l'émetteur (variabilité inter-individuelle), à son état émotionnel ou encore à ses « intentions » en termes de stratégies sociales (variabilité intra-individuelle). Au contraire, les cris émis dans un contexte moins social et dirigés vers l'ensemble du groupe (par exemple les cris d'alarmes) seraient sujets à des pressions de sélection en faveur d'une plus grande stéréotypie permettant d'éviter tout risque de confusion du signal. Cette hypothèse a été validée récemment grâce à des études évaluant le degré de variabilité acoustique dans tout ou partie du répertoire vocal chez plusieurs espèces. En effet, les cris affiliatifs sont ceux qui présentent le degré de variabilité des paramètres acoustiques le plus élevé et qui encodent l'identité de la manière la plus fiable (e.g. macaques : Rendall et al., 1998 – babouins : Rendall et al., 2009 – mones de Campbell : Lemasson & Hausberger, 2011 – mangabés à collier : Bouchet et al., sous presse). En revanche, chez ces mêmes espèces, les cris d'alarme ou les cris alimentaires ont une structure comparativement plus stéréotypée (e.g. mones de Campbell : Lemasson & Hausberger, 2011 – mangabés à collier : Bouchet et al., sous presse), la variabilité prenant plutôt la forme de sous-types ou de concaténations d'éléments discrets comme on a pu le voir précédemment.

3 **Influences sociales sur le comportement vocal du jeune et de l'adulte**

Dans les années 1970-1980, les premières études concernant l'ontogénie de la communication vocale chez les primates non-humains ont conclu à un fort déterminisme génétique. Les vocalisations des juvéniles apparaissaient comme structurellement comparables à celles des adultes dès la naissance et peu variables par la suite (revues :

Newman & Symmes, 1982 ; Seyfarth & Cheney, 1997 ; Hammerschmidt & Fischer, 2008). Néanmoins, le débat autour de l'ontogénie de la production vocale reste ouvert car les résultats disponibles à l'heure actuelle diffèrent d'une espèce à l'autre (Egnor & Hauser, 2004). De plus, peu d'auteurs se sont penchés sur cette question depuis ces premiers travaux. En revanche, les études concernant l'ontogénie de l'utilisation vocale ont révélé que le développement de cette autre facette de la communication était pour sa part bien dépendant de l'expérience (Seyfarth & Cheney, 1997 ; Naguib et al., 2009). Enfin, des études récentes sur la communication vocale chez les primates non-humains à l'âge adulte ont révélé une flexibilité vocale conséquente, tant en termes de production que d'utilisation vocale, notamment pour les cris impliqués dans les interactions sociales (Snowdon, 1997 ; Egnor & Hauser, 2004 ; Naguib et al., 2009). Ici, nous allons passer en revue les études ayant mis en évidence de la flexibilité vocale sous influences sociales chez le jeune et l'adulte.

3.1 Développement des structures acoustiques chez le jeune

L'idée que les vocalisations des primates non-humains sont déterminées uniquement génétiquement s'est appuyée sur des expériences d'isolement social ou d'assourdissement à la naissance (e.g. macaques : Harlow, 1958 – saïmiris : Winter et al., 1973 – Newman & Symmes, 1974), ou encore sur des expériences d'hybridation et d'adoption croisée (e.g. gibbons : Brockelman & Schilling, 1984 ; Geissmann, 1984 – macaques : Owren et al., 1992). Ces expériences peuvent cependant être critiquées car le juvénile ne peut jamais être totalement privé d'expérience sociale (notamment au stade prénatal). De plus, les expériences d'hybridation et d'adoption croisée ont été réalisées avec des espèces proches phylogénétiquement ce qui empêche toute conclusion définitive en termes de déterminisme génétique (Geissmann, 1984 – Owren et al., 1992). En outre, des expériences similaires apportent parfois des résultats contradictoires. L'adoption croisée entre macaques rhésus et macaques japonais a amené Masataka & Fujita (1989) à conclure en faveur d'un phénomène d'apprentissage vocal tandis que Owren et al. (1992) ont conclu en faveur d'un déterminisme génétique. Récemment, des réplications de l'expérience d'élevage en isolement social de Newman & Symmes (Newman & Symmes, 1974) réalisées par

Hammerschmidt et al. chez des macaques rhésus (2000) et des saïmiris (2001) ont pour leur part révélé un certain degré de variabilité acoustique au cours du développement qui serait, en partie seulement, expliqué par des changements morpho-anatomiques maturationnels. Le développement des techniques de mesures acoustiques à la fin des années 1980 pourrait expliquer pourquoi ces études récentes ont détecté dans les vocalisations des primates non-humains juvéniles un degré de variabilité acoustique supérieur à ce qui avait été rapporté jusqu'alors (Seyfarth & Cheney, 1997 ; Snowdon et al., 1997). Enfin, un cas exceptionnel de flexibilité vocale au cours du développement a été rapporté chez les ouistitis pygmées (Snowdon & Elowson, 2001). Un phénomène de « babillage » (i.e. production de longues séquences de cris de structures variées ressemblant plus ou moins aux structures adultes) a été observé chez les juvéniles. Au cours de leur développement, les jeunes ouistitis pygmées émettent des séquences de cris de plus en plus courtes, et la fréquence des cris « juvéniles » diminue au profit des cris structurellement identiques à ceux des adultes. Quoiqu'il en soit, il demeure à l'heure actuelle toujours difficile de distinguer les influences respectives de la maturation et de l'apprentissage social sur le développement vocal du jeune.

3.2 Flexibilité vocale et rôle social chez l'adulte

A l'âge adulte, l'existence d'une flexibilité vocale liée au rôle social de l'individu émetteur a été rapportée chez diverses espèces de primates non-humains. Ainsi, l'appartenance à une entité sociale donnée, le statut social, ou encore le sexe, sont autant de messages identitaires qui peuvent être portés par les signaux vocaux. C'est le cas en particulier pour les cris impliqués dans la cohésion sociale intra-groupe et cet encodage d'informations identitaires leur confère une fonction de 'badge social' (Snowdon, 1997).

Des comparaisons inter-groupes ont révélé que l'appartenance de l'émetteur à une population donnée se reflétait dans la structure acoustique de certains types de cris (e.g. chimpanzés : Mitani et al., 1999 ; Crockford et al., 2004 – lémurs : Hafen et al., 2000 ; Braune et al., 2005 – macaques : Tanaka et al., 2006 – marmosets : De la Torre & Snowdon, 2009). Cet encodage se traduit par la présence, à un moment donné, de structures acoustiques similaires dans le répertoire de congénères appartenant à une même entité. Une hypothèse serait que ces dialectes sont le résultat d'une dérive génétique entre les populations ou bien de différences liées à l'acoustique de l'habitat occupé (e.g. macaques : Sugiura et al., 2006 – babouins : Ey et al., 2009). Néanmoins, l'hypothèse d'un phénomène d'apprentissage social semble souvent la plus plausible. En effet, il a pu être prouvé que les dialectes ne sont pas liés à une divergence génétique inter-groupes chez les lémurs (Hafen et al., 2000) et les macaques (Tanaka et al., 2006). Les dialectes ne seraient pas non plus liés aux facteurs environnementaux puisque même des groupes voisins de chimpanzés et de lémurs présentent des structures acoustiques distinctes alors qu'ils occupent le même habitat (Crockford et al., 2004 ; Hafen et al., 2000 ; Braune et al., 2005). De plus, les différences acoustiques relevées chez différentes populations de marmosets éloignées géographiquement n'ont pu être entièrement expliquées par les caractéristiques acoustiques de l'habitat occupé (De la Torre & Snowdon, 2009). Enfin, une étude longitudinale chez les macaques a révélé que les différences inter-populations n'apparaissaient chez les juvéniles qu'après l'âge de 6 ou 7 mois (Tanaka et al., 2006), ce qui nous conforte dans l'idée que l'expérience joue un rôle prépondérant dans l'acquisition des dialectes. Par ailleurs, des différences entre populations captives et sauvages d'une même espèce ont été rapportées. Les femelles mones de Campbell sauvages produisent, dans un contexte de danger, trois sous-types de cris 'RRA' ('RRA1' : dangers divers autres que prédation, 'RRA3' : détection d'un aigle, 'RRA4' : détection d'un léopard) (Ouattara et al., 2009c). En revanche, les femelles mones de Campbell captives ne produisent pas les cris d'alarmes liés aux prédateurs, mais émettent le cri 'RRA1' (dangers divers) ainsi qu'un cri 'RRA2' lors du passage de certains humains (e.g. vétérinaire, personne non familière) à proximité de l'enclos (Lemasson et al., 2004). Ce cri 'RRA2' n'a jamais été enregistré dans des groupes sauvages (Ouattara et al., 2009c). Ainsi, les individus captifs présentent un répertoire de cris d'alarme plus restreint, probablement du fait de la rareté des évènements dangereux dans leur environnement. En revanche, il est intéressant de constater qu'ils ont développé leur propre version de cri d'alarme liée à leur environnement immédiat (associée à la présence humaine) (Lemasson et al., 2004). Ce phénomène s'apparenterait à de l'innovation vocale, la captivité pouvant être vue comme une nouvelle niche écologique propice au développement de nouvelles capacités vocales (Snowdon, 2009). Deux exemples anecdotiques soutiennent cette idée d'innovation : l'observation chez des chimpanzés (‘extended grunt’ et ‘raspberry’ – Hopkins et al., 2007) et des orangs-outangs (sifflement – Wich et al., 2009) de signaux nouveaux produits uniquement en captivité, respectivement destinés à attirer l’attention des humains ou produits par imitation de ces derniers.

Au sein d’un même groupe, des différences inter-individuelles liées au statut social de l’émetteur ont également été constatées. Ainsi, l’appartenance à un réseau affinitaire au sein du groupe peut transparaître dans les vocalisations. Cet équivalent des dialectes à plus petite échelle a été qualifié de partage vocal. Il a été notamment mis en évidence chez les mones de Campbell : les femelles ayant des liens sociaux privilégiés émettent les mêmes variantes de cris de contact (caractérisées par la forme de la modulation de fréquence) alors que les femelles isolées socialement ont des cris divergeant des autres individus (Lemasson et al., 2003). De plus, le répertoire d’une femelle (i.e. la structure acoustique et le nombre de ses variantes) et ses partenaires de partage vocal évoluent au cours du temps, en parallèle de la dynamique de ses affinités au sein du groupe social (Lemasson & Hausberger, 2004). Cette réorganisation des répertoires vocaux individuels et des réseaux de partage est particulièrement importante suite à une perturbation sociale (e.g. remplacement du mâle du harem : Lemasson & Hausberger, 2004). En outre, des expériences de repasse de ces variantes de cris de contact ont permis de confirmer que les individus récepteurs percevaient ce degré de variabilité acoustique et qu’ils répondaient différemment à une variante présente (faisant partie du répertoire de partage actuel du groupe), une variante passée (n’étant plus utilisée dans le groupe depuis 4 ans) et une variante inconnue (Lemasson et al., 2005b). D’autres cas de convergence de certains paramètres acoustiques entre membres d’un même groupe ont été observés. Le suivi de la formation de nouveaux groupes sociaux (e.g. mise en couple d’individus non-familiers, introduction d’un nouvel individu dans un groupe) a révélé que les individus étaient capables d’ajuster les paramètres acoustiques de leurs cris en fonction de ceux de leur nouveau partenaire chez les marmosets (Snowdon & Elowson, 1999), les gibbons (Geissmann, 1999) et les chimpanzés (Marshall et al., 1999). De plus, il a été observé que ce type de perturbation sociale pouvait également engendrer une augmentation de l’activité vocale chez les sakis (Di Fiore et al., 2007), et plus particulièrement une augmentation de la fréquence des échanges vocaux chez les gibbons (Geissmann, 1986 ; Dooley & Judge, 2007) et les mones de Campbell (Lemasson et al., 2005a). Cela pourrait faciliter l’ajustement vocal au nouveau partenaire ainsi que la mise en place des relations sociales. Par ailleurs, dans le cadre d'un d'échange vocal, un individu est capable de sélectionner dans son répertoire le cri le plus proche structurellement de celui utilisé par son partenaire. Ce phénomène dit de « call matching » a été décrit chez les chimpanzés (Mitani & Brandt, 1994) et les macaques japonais (Sugiura, 1998). Outre cette flexibilité vocale liée aux relations affinitaires entretenues par l'individu émetteur au sein de son groupe, son rang hiérarchique peut également transparaître dans la structure acoustique de ses cris. Ainsi, un babouin dominant émet des cris 'wahoo' plus aigus et plus longs qu'un subordonné (Fischer et al., 2004), tandis qu'un chimpanzé dominant émet plus souvent des cris 'pant-hoots' qu'un dominé (Mitani & Nishida, 1993). Il est intéressant de noter qu'en cas de changement de statut hiérarchique, on observe un ajustement des paramètres acoustiques de telle manière que le message contenu dans les signaux vocaux de l'individu émetteur demeure fiable. Chez les babouins, une chute dans la hiérarchie se traduit par un raccourcissement et un déclin de la fréquence fondamentale des cris (Fischer et al., 2004), tandis que chez les mâles cercopithèques, elle se traduit par la disparition des émissions de cris forts (Gautier, 1998).

Enfin, les caractéristiques identitaires comme le sexe de l'émetteur peuvent aussi être encodées dans la structure des cris. Qu'elles soient de l'ordre d'une phonation particulière ou de types de cris propres à un sexe, ces différences sont généralement expliquées par des différences morphologiques et physiologiques. En effet, certains paramètres acoustiques dépendent des propriétés physiques de l'appareil phonatoire (Riede, 2010), elles-mêmes corrélées à la taille et au poids de l'individu (Fitch & Hauser, 1995 ; Ey et al., 2007). Les cris forts chez les cercopithèques et les mangabés seraient spécifiques aux mâles adultes car les sacs vocaux sont particulièrement développés chez ces individus (Gautier, 1971 ; Gautier & Gautier, 1977 ; Waser, 1982). Néanmoins, des découvertes anecdotiques récentes suggèrent que certains de ces cris dits spécifiques à un sexe ne seraient pas toujours le reflet de l'incapacité des individus de l'autre sexe à les produire. Cela a pu être prouvé expérimentalement chez les saïmiris (Jürgens, 1979 ; Smith et al., 1982), les mâles étant capables de produire des cris dits spécifiques aux femelles suite à une stimulation électrique cérébrale. Cela a également été observé dans un contexte de perturbation sociale chez les gibbons (i.e. mise en couple d'individus non-familiers) (Geissmann, 1983) et de danger imminent chez les cercopithèques (Ouattara et al., 2009c ; Bouchet et al., en révision) : dans ces trois exemples, les femelles ont produit des cris dits spécifiques aux mâles lorsque celui-ci demeurait anormalement silencieux. Une hypothèse permettant d'expliquer ces observations serait que les différences entre les répertoires des mâles et des femelles adultes reflèteraient plutôt la préférence des individus pour certains types de cris. Cette préférence serait en accord d'un point de vue fonctionnel avec le rôle social du sexe correspondant (i.e. protection du groupe pour les mâles adultes *versus* maintien de la cohésion sociale intra-groupe pour les femelles adultes) (e.g. saïmiris : Smith et al., 1982 – macaques et langurs : Hohmann, 1991 – mangabés : Bouchet et al., 2010 – cercopithèques de Brazza : Bouchet et al., en révision).

3.3 Apprentissage du contexte d'émission des vocalisations chez le jeune

Si l'on s'intéresse à un autre aspect de la communication qu'est l'utilisation des vocalisations, il existe chez les primates non-humains un certain nombre de preuves d'apprentissage social du contexte d'émission approprié (Seyfarth & Cheney, 1997 ; Snowdon, 1997 ; Naguib et al., 2009). L'importance de l'expérience et des influences sociales sur l'ontogénie de cette facette de la communication est donc moins débattue. Ainsi, il y a un affinement progressif du contexte d'utilisation des différents types de cris au cours du développement, notamment par observation du comportement des adultes. Les jeunes vervets apprennent à sélectionner le cri d'alarme approprié en fonction du prédateur détecté : par exemple, le cri d'alarme spécifique à la détection d'un aigle martial est d'abord émis envers tout objet volant (y compris une feuille d'arbre) par les enfants, puis envers toutes les espèces d'oiseaux par les juvéniles, et enfin préférentiellement envers les espèces de rapaces et surtout l'aigle martial par les adultes (Seyfarth et al., 1980 ; Seyfarth & Cheney, 1986). De même, les jeunes macaques apprennent à émettre dans le contexte approprié les différents sous-types de cris de détresse (liés à l'intensité de l'agression ou à l'identité de l'opposant) au cours de leur développement (Gouzoules & Gouzoules, 1989 ; Gouzoules & Gouzoules, 1995). Chez les chimpanzés, l'utilisation des grunts sociaux (connus sous le nom de 'pant-grunts' à l'âge adulte) ne suit pas une progression asymptotique simple pendant le développement et l'on observe la mise en place progressive d'un choix sélectif des individus vers lesquels ces grunts sont dirigés (Laporte & Zuberbühler, sous presse). Enfin, une influence des partenaires sociaux sur l'apprentissage de l'utilisation des cris alimentaires par les jeunes marmosets a été mise en évidence dans le contexte d'un transfert de nourriture (de l'adulte vers le jeune). Cela pourrait constituer un cas de « coaching » (Caro & Hauser, 1992) où les cris des adultes fournissent un modèle pour le juvénile et le partage de nourriture constituent l'encouragement (le renforcement positif) (Roush & Snowdon, 2001). Enfin, une étude récente chez les mones de Campbell a révélé que les règles d'échange vocal se mettaient en place au cours du développement (Lemasson et al., 2011). Chez les primates non-humains, les cris de contact sont fréquemment émis par les adultes lors d'échanges vocaux caractérisés par l'alternance d'émissions vocales entre les émetteurs ; on parle, comme chez l'homme, de tours de parole (e.g. marmosets : Snowdon & Cleveland, 1984 – vervets : Hauser, 1992 – macaques : Hauser, 1992 ; Sugiura & Masataka, 1995). Les cas de rupture de ces tours de parole, lorsqu'un individu crie deux fois de suite sans laisser le temps à son interlocuteur de répondre, sont extrêmement rares chez l'adulte mone de Campbell (moins de 1%), alors qu'ils sont douze fois plus fréquents chez les juvéniles (Lemasson et al., 2010a ; Lemasson et al., 2011). De plus, les adultes présentent un niveau d'intérêt différent pour des repasses d'échanges vocaux (entre deux interlocuteurs A et B) respectant (type ABA) ou non (type BAA) la règle des tours de parole, mais ce n'est pas le cas des juvéniles. Ces résultats confirment que cette règle est perçue par les individus et suggèrent qu'elle est apprise socialement (Lemasson et al., 2011).

3.4 Utilisation vocale en fonction du contexte d'émission chez l'adulte

A l'âge adulte, les primates non-humains sont capables d'ajuster leur comportement vocal au contexte d'émission, qu'il soit social ou non. C'est notamment le cas dans les contextes de prédation. L'émission d'un signal vocal augmentant le risque de se faire détecter par le prédateur, l'individu a tout intérêt à en limiter la production. Il a été observé que l'émission de cris d'alarme peut dépendre de l'identité des congénères présents à proximité ; on parle alors d'effet d'audience. Par exemple, les mâles vervets émettent plus fréquemment des cris d'alarmes si une femelle est à proximité, tandis que les femelles en émettent préférentiellement si des juvéniles sont à proximité (Cheney & Seyfarth, 1990). Ce phénomène d'effet d'audience a également été mis en évidence pour plusieurs autres catégories de cris. Dans le cas des cris de copulations, les femelles chimpanzés et bonobos en émettent plus en présence de mâles dominants *versus* subordonnées (Townsend et al., 2008 ; Clay et al., 2011), mais les femelles chimpanzés en émettent moins si une femelle de rang supérieur est également présente (Townsend et al., 2008). Concernant les cris alimentaires, leur émission est fonction de la distance séparant l'émetteur des congénères chez les tamarins (Caine et al., 1995 ; Roush & Snowdon, 2000) et les capucins (Di Bitetti, 2005). Les mâles chimpanzés quant à eux émettent plus fréquemment leurs cris alimentaires suite à la découverte de nourriture (Slocombe et al., 2010) et leurs cris de cohésion 'pant-hoots' (Mitani & Nishida, 1993) lorsqu'ils sont en présence de partenaires avec lesquelles ils forment des alliances. L'émission de cris de « salutation » émis en direction des mâles dominants ('pant-grunts') par les femelles chimpanzés peut quant à elle être favorisée ou inhibée selon l'identité et le statut social du receveur ainsi que selon le nombre et le statut des congénères présents (Laporte & Zuberbühler, 2010). Enfin, un dernier exemple a révélé que les primates non-humains étaient capables d'ajuster leur comportement vocal de manière plus complexe que le simple choix d'émettre ou non des cris en fonction de l'audience. Les chimpanzés émettent différents sous-type de cris de détresse en fonction de l'intensité de l'agression ou du statut hiérarchique de l'opposant (Slocombe & Zuberbühler, 2007), mais ils utilisent également ces sous-types de cris stratégiquement. Les victimes d'attaques sévères exagèrent la gravité de l'agression qu'elles subissent si au moins un congénère dans l'audience est de rang égal ou supérieur à l'agresseur (Slocombe & Zuberbühler, 2007).

Les primates non-humains sont également capables d'ajuster leur comportement vocal lors des échanges vocaux. Nous avons vu précédemment que les échanges vocaux sont caractérisés par le respect de règles temporelles chez l'adulte (tours de paroles), néanmoins ce pattern présente un certain degré de flexibilité en fonction de facteurs sociaux. Les échanges vocaux chez les macaques japonais et les mones de Campbell se caractérisent par la succession de cris émis par différents individus à intervalles réguliers dont la durée a été déterminée à environ une seconde (Sugiura, 1993 ; Lemasson et al., 2010a). Ce délai de réponse serait déterminé socialement. En effet, la latence à répondre est plus courte chez les partenaires les plus affiliés chez les saïmiris (Biben et al., 1986). La fréquence de réponse reçue dépend également du degré d'affinité avec l'interlocuteur chez les saïmiris (Biben et al., 1986) ou de son statut social chez les mones de Campbell (les femelles les plus âgées sont des interlocutrices préférentielles) (Lemasson et al., 2010a). Inversement, un individu est capable de moduler son comportement vocal afin d'attirer l'attention d'un partenaire quand celui-ci reste silencieux. Ainsi, les macaques émettent des cris « exagérés » (i.e. augmentation de la modulation de fréquence, cris plus longs et plus aigus) de manière à augmenter la probabilité de recevoir une réponse (Masataka, 1992 ; Koda, 2004).

4 **Théorie d'une coévolution social-vocal**

Dans une première partie, nous avons souligné l'importance d'adopter une approche multi-niveaux de la structure organisationnelle du répertoire vocal des primates non-humains. Celle-ci a permis de révéler un degré conséquent de variabilité acoustique, au sein et entre les signaux vocaux, permettant un encodage complexe de messages. Parmi les résultats remarquables, nous avons relevé que les primates non-humains étaient capables de combiner des éléments discrets en structures d'ordre supérieur dont la composition, l'agencement ou encore le rythme encodent un supplément d'information. En outre, nous avons souligné l'influence de la fonction sociale du cri sur son degré de variabilité acoustique. Dans une seconde partie, nous avons répertorié les preuves de flexibilité vocale sous influences sociales chez le jeune et l'adulte. Si l'apprentissage social ne semble pas avoir un rôle prépondérant dans l'ontogénie de la production vocale, son implication dans l'ontogénie de l'utilisation vocale (contexte et règles d'émission des cris) est évidente. Chez l'adulte, le statut social de l'individu, dynamique dans le temps, est un facteur favorisant l'émergence de flexibilité vocale, tant en termes de production que d'utilisation. Parmi les résultats remarquables, nous avons noté l'existence de convergence vocale entre congénères (dialecte, partage vocal, call matching), d'échanges vocaux structurés ainsi que d'un effet d'audience sur le comportement de l'individu émetteur.

D'un point de vue évolutif, la communication vocale des primates non-humains a longtemps été placée à l'écart de celle des autres espèces, homme compris, car elle était décrite comme fortement contrainte par l'habitat, la phylogénie et les facteurs génétiques. Les preuves de plasticité vocale tout au long de la vie de l'individu étaient bien plus nombreuses chez les oiseaux, les cétacés et l'homme (Snowdon & Hausberger, 1997). Ce n'est que récemment qu'elles se sont multipliées pour les primates non-humains, en grande partie grâce à l'intérêt croissant porté aux cris impliqués dans la médiation des relations sociales intra-groupe (Masataka, 2003 ; Snowdon, 2009). Il est de moins en moins contestable aujourd'hui qu'il soit possible de trouver des formes primitives d'un certain nombre de caractéristiques du langage humain dans la communication animale et ce à différents niveaux phylogénétiques (Oller & Griebel, 2008 ; Naguib et al., 2009), primates non-humains compris (Zuberbühler et al., 2009 ; Lemasson, 2011). Ainsi, le caractère référentiel des signaux vocaux (e.g. mammifères et oiseaux : Evans et al., 1997) se rapproche du caractère sémantique des mots chez l'homme. La structure organisationnelle complexe des émissions sonores (composition, agencement, rythme) portant un message référentiel (i.e. relatif à un stimulus extérieur) (e.g. mones de Campbell : Ouattara et al., 2009a ; Ouattara et al., 2009b ; Lemasson et al., 2010b) pourrait quant à elle correspondre à une forme primitive des propriétés syntaxiques et prosodiques du langage humain (Hauser et al., 2002 ; Scherer, 2003). L'encodage plus ou moins important d'informations identitaires dans les signaux vocaux en fonction de leur fonction sociale (e.g. primates non-humains : Lemasson & Hausberger, 2011 ; Bouchet et al., sous presse – oiseaux : Charrier et al., 2001) s'apparente à l'observation faite chez l'homme de la présence plus ou moins prononcée d'indices identitaires dans le discours en fonction du contexte et de la composition de l'audience (Bell, 1984) et au phénomène d'accommodation vocale chez l'homme (Giles et al., 1991). La mise en évidence de convergence vocale liée à la dynamique des réseaux sociaux (e.g. mammifères : Tyack, 2008 – oiseaux : Snowdon & Hausberger, 1997) peut être mise en parallèle avec le fait que, chez l'homme, les amis ou les apparentés font correspondre leur façon de parler (Locke & Snow, 1997). L'utilisation flexible des signaux vocaux en fonction du contexte social, notamment révélée avec l'effet d'audience (e.g. primates non-humains : Zuberbühler et al., 2011 – oiseaux : Evans & Marler, 1994), serait quant à elle une preuve du caractère intentionnel et directionnel de la communication animale (Tomasello & Call, 1997). Enfin, les échanges vocaux structurés s'apparenteraient à des formes primitives de conversations (e.g. primates non-humains : Snowdon & Cleveland, 1984 ; Hauser, 1992 ; Sugiura & Masataka, 1995 ; Lemasson, 2011 – oiseaux : Hausberger et al., 2008) puisqu'ils sont caractérisés par des règles similaires à celles observées chez l'homme (Ghiglione, 1986 ; Stivers et al., 2009).

Il est incontestable que des différences majeures existent entre le langage humain et la communication vocale animale. Néanmoins, ces résultats révèlent que des parallèles peuvent être établis, y compris entre l'homme et les primates non-humains. Il est difficile à l'heure actuelle de statuer si ces formes primitives chez l'animal des caractéristiques du langage humain sont héritées d'un ancêtre commun (caractères homologues) ou bien si elles sont le reflet d'une évolution convergente soumise à des pressions sélectives similaires (caractères analogues). A l'avenir, une multiplication des études comparatives, notamment dans la lignée primates à laquelle l'homme appartient, est nécessaire pour tenter de répondre à cette question.

Quoiqu'il en soit, identifier les pressions évolutives ayant favorisé l'émergence d'une complexité vocale chez les espèces animales apporterait des éléments de réflexion quant aux pressions de sélection ayant conduit jusqu'à l'émergence du langage chez l'homme. Au cours de cette revue, nous avons mis l'accent sur le lien existant entre vie sociale et flexibilité vocale au niveau individuel. De la même manière, il a été suggéré qu'à l'échelle de l'espèce le degré de complexité du système social pourrait être à l'origine d'une complexification des capacités communicatives. Quelques hypothèses en faveur d'une coévolution social-vocal ont été testées par le biais de revues de la littérature existante. Chez les sciuridés, un lien entre la taille du répertoire de cris d'alarme et la complexité de la structure sociale a été mis en évidence (Blumstein & Armitage, 1997). Chez les odontocètes (baleines à dents), un lien entre la complexité structurale des signaux vocaux et le degré de socialité a été trouvé (May-Collado et al., 2007). Enfin, chez les primates non-humains, un lien fut identifié entre la taille du répertoire vocal et la taille moyenne du groupe social ainsi que le temps moyen consacré à l'épouillage (i.e. une mesure de la force des liens sociaux) (McComb & Semple, 2005). Ces études suggèrent donc qu'il est fort probable que des pressions sociales puissent être à l'origine de la complexification des systèmes de communication vocale animale au cours de l'évolution. A l'avenir, il est crucial que ces hypothèses soient testées conjointement de manière empirique par le biais d'études comparatives d'espèces proches phylogénétiquement et issues d'un habitat similaire mais présentant des différences marquées entre leurs systèmes sociaux. De telles études dans la lignée primates, notamment chez les grands singes qui sont les plus apparentés à l'homme, serait particulièrement informatives pour les théories d'évolution du langage. Il est intéressant de noter qu'une telle approche chez trois espèces de macaques a permis de révéler une influence de l'organisation sociale sur la taille du répertoire de gestes ainsi que sur la complexité de la dynamique de communication gestuelle (Maestripieri, 2007). Cela suggère que la théorie d'une coévolution social-vocal pourrait s'étendre à d'autre modes de communication que l'acoustique.

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Animal Behaviour 80 (2010) 799–808

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Predator-deterring alarm call sequences in Guereza colobus monkeys are meaningful to conspecifics

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ARTICLE INFO

Article history:
Received 11 January 2010
Initial acceptance 4 March 2010
Final acceptance 9 July 2010
Available online 15 September 2010
MS. number: 10-00027R

Keywords:
alarm call
Budongo Forest
Colobus guereza
Guereza colobus
perception advertisement
predation
predator deterrence
primate communication
semantic
syntax

Guereza colobus monkeys, *Colobus guereza*, produce acoustically conspicuous vocalizations, the roars, in response to their main predators, leopards, *Panthera pardus*, and crowned eagles, *Stephanoaetus coronatus*. Roaring alarm utterances generally consist of the same basic call types but differ in overall structural composition. Leopards trigger roaring alarms containing many roaring sequences of only a few calls each, while eagles trigger few sequences with many calls each. To investigate whether conspecifics extract meaning from these structural differences, we played back leopard and eagle alarm call sequences and compared the monkeys' responses in terms of their locomotor, gaze and vocal behaviour with their responses to the corresponding predator vocalizations. Locomotor responses did not differ between playback conditions; movement was always towards the simulated caller with no clear patterns in the vertical plane. Gaze direction, however, was highly predator specific. When hearing leopard-related stimuli, monkeys were significantly more likely to scan the area beneath them than when hearing eagle-related stimuli, which caused more scanning above. Vocal response rates to conspecific alarms were generally low but comparable with rates to the corresponding predators. If monkeys called, however, they produced the matching call sequences. Overall, our results showed that Guerezas discriminated between predator alarm call sequences produced by unfamiliar conspecifics and responded to them in predator-specific ways. Since the sequences were composed of the same basic call types, we concluded that the monkeys attended to the compositional aspects of these utterances.

One view in animal communication studies is that the vocalizations produced during predator encounters merely reflect location, identity, sex, body size or internal state of the caller, but nothing about the experienced event (e.g. Morton 1977; Owren & Rendall 2001). Yet, a number of studies have challenged this stance by showing that alarm calling in primates and other animal species can be the product of more complicated cognitive processing, sometimes as part of specific biological functions such as conspecific warning or predator deterrence (e.g. Seyfarth et al. 1980; Woodland et al. 1980; Zuberbühler et al. 1997, 1999; Manser et al. 2002; Zuberbühler 2003, 2009).

Conspecific warning has been observed in different degrees of contextual specificity. Some prey species respond with distinct alarm calls to the behaviour of the predator, such as the speed of its approach (Griesser 2008). As a consequence, identical signals can be produced in response to a variety of predators, allowing recipients to make inferences about the degree of danger and urgency of response (Robinson 1980; Macedonia & Evans 1993; Blumstein 1995). In contrast, some other species, such as East African vervet monkeys, *Cercopithecus aethiops*, produce discrete alarm calls to distinct predator types. Here, recipients can infer the predator category from the calls alone even in the predator's physical absence (e.g. Seyfarth et al. 1980; Cheney & Seyfarth 1990; Macedonia 1990; Marler et al. 1992; Zuberbühler et al. 1997; Zuberbühler 2000a, b, 2001; Fichtel & Kappeler 2002; Manser et al. 2002; Seyfarth & Cheney 2003; Kirchhof & Hammerschmidt 2006). Such observations are interesting from an evolutionary perspective because of the parallels with symbolic reference in human language (e.g. Seyfarth et al. 1980; Macedonia & Evans 1993).

However, the debate about referential signals in animal communication is far from settled. An alternative explanation is that such findings are the result of receiver biases, caused by the mere acoustic characteristics of a signal, not by any mental representations or memories associated with them (e.g. Morton 1977; Fichtel et al. 2001; Owren & Rendall 2001; Rendall 2003). An extreme version of this position is that receivers are mere

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doi:10.1016/j.anbehav.2010.07.012

automatons whose responses can be triggered by specific physical stimuli. A less extreme version is that different acoustic morphologies have different effects on the psychology of the receivers, and that calls merely induce different degrees of arousal rather than mental representations of the event usually associated with the different calls (Rendall et al. 2009). Another point is that conspecific warning may not be the evolved function of alarm calls, and that signallers may be targeting the predator, while conspecifics are mere eavesdroppers of such interactions (e.g. Zuberbühler et al. 1999). In this view, the form and patterning of alarm signals are determined by the sensory bias of the predator, regardless of conspecific receivers (e.g. Marler 1965, 1967; Rundus et al. 2007). Under this hypothesis, signals are arbitrary for conspecifics in terms of their morphology, although receivers can form associations with specific contexts, that is, they can become meaningful to them. This is especially well illustrated by various cases of interspecies communication. For instance, African hornbills, such as *Ceratogymma elata* or *C. atrata*, are capable of discriminating the alarm calls of Diana monkeys, *Cercopithecus diana*, to crowned eagles, *Stephanoaetus coronatus*, and leopards, *Panthera pardus*, even though monkeys clearly have no intention of informing them (Rainey et al. 2004a, b).

Much of the current literature on alarm calling in primates is based on research with Cercopithecines (Zuberbühler 2009), while the alarm call behaviour of the other major group of Old World monkeys, the Colobines, has not received much attention. This is surprising because the vocal behaviour of some colobine monkeys is particularly remarkable and has been a major research focus for other reasons (e.g. Hill & Booth 1957; Davies & Oates 1994; Oates et al. 2000; *Colobus guereza*: Marler 1969, 1972; Gautier & Gautier 1977; Oates & Trocco 1983; *Colobus angolensis*: Groves 1973; Walek 1978). In recent studies, we have shown that black-and-white colobus monkeys in both East (*Colobus guereza*) and West (*Colobus polykomos*) Africa produced vocal alarms ('roaring') to two of their major predators, leopards and crowned eagles. In response to chimpanzees, *Pan troglodytes*, another serious predator in many parts of Africa, black-and-white colobus monkeys usually remain vocally and visually inconspicuous (Schel & Zuberbühler 2009). Predator roars consist of a variable number of roaring sequences, which are composed of acoustically uniform call units, the roaring phrases. To leopards, individual sequences are generally short, while to crowned eagles they are significantly longer, suggesting that callers potentially convey information about the predatory event at the level of the sequence, rather than at the level of individual calls (Fig. 1).

In Guereza colobus monkeys (further called Guerezas), alarm calling is usually performed by the single adult male of the group, although, occasionally, other animals join in, presumably the caller's subadult sons. In general, however, monkeys are reluctant to respond with alarm calls to predator models, although other forms of antipredator behaviour occur in age-, sex- and predator-specific ways (see Schel & Zuberbühler 2009 for locomotor data in the Kaniyo Pabidi Guereza population in Uganda). In response to acoustic leopard models, adult males usually approach while moving up and down in the vertical plane. Other group members typically move higher up or they remain seated, although sometimes the male is accompanied in his approach by other group members. In response to acoustic eagle models, the males also

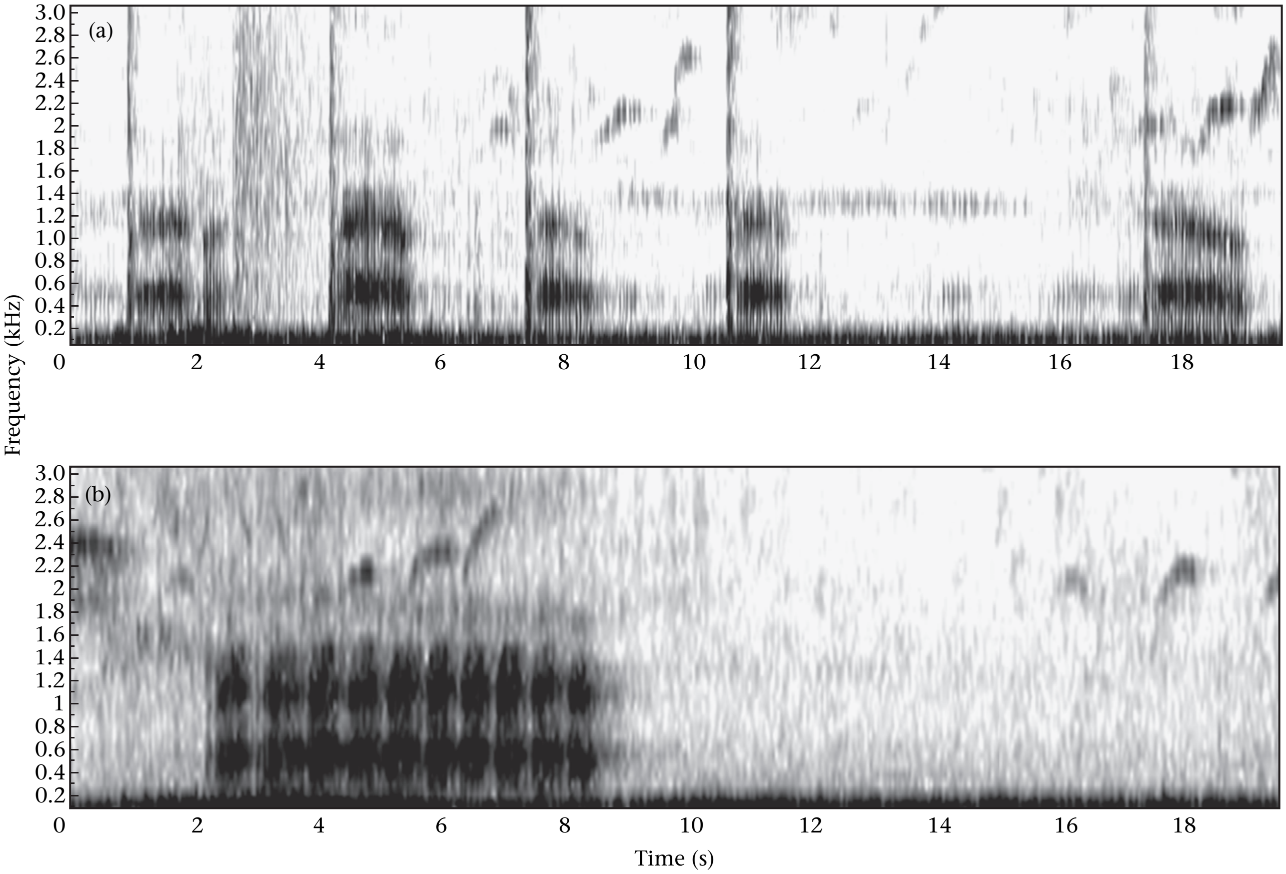

Figure 1. Spectrographic representation of the vocal responses of (a) a Guereza male responding to a leopard model with an utterance consisting of five snort-introduced short roaring sequences, and (b) a Guereza male responding to an eagle model with an utterance consisting of one non-snort-introduced long roaring sequence.

approach but mainly move upwards in the canopy, again sometimes accompanied by one or more individuals, while other group members typically move down into dense cover or they remain seated.

To test whether the alarm call sequences of Guerezas are meaningful to conspecifics and inform them about predator type, we played back Guerezas' leopard and eagle alarm sequences, originally recorded at the Sonso study area of Budongo Forest Reserve, Uganda, to naïve monkey groups. We compared their responses with those to the corresponding predators, simulated by playbacks of leopard growls and crowned eagle shrieks. Following the protocol of a previous study (Schel & Zuberbühler 2009), we recorded the Guerezas' horizontal locomotor and vocal antipredator responses, which we expected to be adaptive to the predator type for which the alarms are normally produced. Yet, because horizontal locomotor responses of the adult males are largely identical to both predators and because of the different antipredator strategies of the two sexes, we decided to add vertical locomotor responses and the direction of gaze as additional variables. Vertical movements and gaze have traditionally been used in experimental primate field studies as a measure of call discrimination (Seyfarth et al. 1980; Fichtel & Kappeler 2002; Fichtel 2004; Kirchhof & Hammerschmidt 2006). In our case, we assumed that initial gaze responses were consistent across all group members, irrespective of age/sex class, as the different hunting behaviours of eagles and leopards are likely to generate different expectations in the monkeys (cf. Macedonia & Evans 1993). We expected that eagle-related stimuli would trigger a higher proportion of upward gazes than leopard-related stimuli, and vice versa, in line with the predators' most likely direction of attack. We scored the monkeys' locomotor responses in the vertical plane as an additional measure of their expectations (see Schel & Zuberbühler 2009).

METHODS

Study Sites and Subjects

Data were collected at the Sonso study site of Budongo Forest Reserve, Uganda (01°42′–01°44N, 31°31′–31°33′E), in the vicinity of the Budongo Conservation Field Station. We mainly operated within the grid system of the study site, an approximately 9 km^2 area of secondary tropical moist semideciduous rainforest. We occasionally visited areas outside the grid system by following an old logging road or smaller forest transects. Guerezas are highly arboreal medium-sized colobine monkeys, living in groups generally consisting of 8–10 individuals, including one adult male, approximately four adult females, and their subadult, juvenile and infant offspring (Marler 1969; Davies & Oates 1994).

Monkey predators at Sonso include chimpanzees and crowned eagles, but not leopards, which became locally extinct a few decades ago. In previous work we have shown that, despite having no experience with leopards, the Guerezas at Sonso show appropriate antipredator behaviour to leopards, indistinguishable from a neighbouring population that continues to be exposed to leopards (Schel & Zuberbühler 2009).

Between 2005 and 2009, we conducted playback experiments with predator vocalizations and conspecific alarm calls. In 2005, we conducted 26 trials with leopard growls and 17 trials with eagle shrieks, allowing us to record the Guerezas' horizontal locomotor and vocal responses (reported in Schel & Zuberbühler 2009). In 2008 (September–December: A.C.), we additionally filmed the monkeys' vertical locomotor behaviour and gaze directions in response to these stimuli, by targeting groups that had not been tested before. Finally, in 2009 (March–May: A.S.) we collected further data on locomotor and vocal behaviour, but not on gaze directions. In 2007 (March–September: A.S.) and 2008 (September–December: A.C.), we tested a large number of Guereza groups on their responses to their own alarm calls, focusing on vocal behaviour in 2007 and also on horizontal and vertical locomotor behaviour and gaze direction in 2008. We adhered to a minimum distance criterion of 200 m between trials conducted in the two successive study periods (see below) to keep trials independent from each other.

The Minimum Distance Method

Group densities in Sonso are very high, reaching 6–10 Guereza groups per square kilometre (Plumptre & Reynolds 1994; Plumptre 2000). At the start of our studies in 2005, we systematically mapped all groups encountered. Separate groups, consisting of an adult male and several females with their offspring, could be found as close as 150–200 m apart from each other (A. M. Schel, unpublished data). In line with previous density estimates (Plumptre 2000), we discriminated approximately 60 different Guereza groups in the entire study area (equivalent to about 500–1000 individuals: Marler 1972). In 2008 and 2009, we chose a minimum distance of 200 m from any of the previous 2005 and 2007 test locations. The minimum distance method is a standard procedure that has been used successfully by many other playback studies with unhabituated groups of unknown home ranges (e.g. Zuberbühler et al. 1997). Furthermore, within a specific year (i.e. 2005, 2007, 2008 and 2009), we kept a distance of at least 750 m between adjacent trials conducted on the same day, since some of our stimuli could carry over considerable distances through the forest. On consecutive test days with one particular stimulus type (e.g. leopard growls), we only tested groups that inhabited a different part of the forest relative to the ones tested the day before. These precautions ensured that only a very small fraction of the 500–1000 tested individuals could have heard a particular playback stimulus more than once (for instance young males that migrated to another group). Although the number of potentially affected individuals was very small, the more crucial point is that it is very unlikely that such single experiences will have lasting effects over a period of one to several years, especially considering the large number of predator-related sounds monkeys are exposed to on a daily basis in tropical forest habitats. We therefore concluded that trials conducted across the different study periods could be treated as independent events.

Terminology of Vocal Responses

As mentioned, male Guerezas produce loud and low-pitched vocalizations, 'roaring', in response to predators and as part of spontaneous dawn choruses (Marler 1972; Oates & Trocco 1983; Oates et al. 2000; Schel et al. 2009). Roaring responses consist of either a large or small number of roaring sequences, which are composed of either 'few' or 'many' individual call units, the roaring phrases. The acoustic energy of roaring phrases is concentrated in two discrete frequency bands around 600 and 1300 Hz, representing two formant frequencies (Harris et al. 2006). The first roaring phrase in a sequence can be preceded by one or more snorts, which consist of broadband acoustic energy with a sudden onset, ranging in frequency up to about 4 kHz with the main frequency at around 1 kHz. As described before, the roaring sequences vary in the number of roaring phrases they consist of between predator types (Schel et al. 2009; Schel & Zuberbühler 2009; Fig. 1), whereas acoustic structures of individual roaring phrases are very similar (Schel et al. 2009; Schel & Zuberbühler 2009).

Experimental Protocol

We systematically searched for Guereza groups throughout the study area, usually by looking for their conspicuous tail tufts or by hearing their soft intragroup vocalizations. When found, we determined their geographical location using a Garmin GPS 76 and a detailed map to ensure that the group had not been tested before (see minimum distance method described earlier). We then monitored the monkeys' vocal behaviour for at least 15 min to ensure they were unaware of our presence. A trial was conducted only if during this period (1) no other animal in the group's surroundings had produced any alarm calls, (2) no predator vocalizations were heard, (3) no predator was seen, (4) the monkeys were unaware of the observers and playback equipment, and (5) no other humans were present in the experimental area. Using Leica Trinovid 10 × 42 binoculars, we determined the sex of all clearly visible focal individuals during each trial, which was possible in about 70% of trials.

Presentation of playback stimuli

Playback stimuli of leopard growls were edited from a master recording from the British Library of Wildlife Sounds, London (African leopard; BBC master tape number MM 35 © South African Broadcasting Corporation). Eagle shrieks were recorded by K.Z. in the Taï Forest, Ivory Coast, with a Sony Professional Walkman WMD6C and Sennheiser 70 mm microphone (K3U + ME88). We edited playback stimuli of conspecific alarms from original recordings of Guerezas giving alarm calls to leopard growls and eagle shrieks (Fig. 1). All playback stimuli were edited such that they consisted of 5 min of silence followed by approximately 15 s of vocalizations (three different recordings of eagle shrieks, six different recordings of leopard growls, four different recordings of conspecific leopard alarms and four different recordings of conspecific eagle alarms). Methodologically, it would have been ideal to use a unique playback stimulus for every trial, but given the large number of groups tested in this study, this was simply not feasible. Obtaining high-quality recordings from free-ranging crowned eagles, leopards and Guerezas is not a trivial task (see Schel & Zuberbühler 2009; Schel et al. 2009), so that we opted for the next best strategy, that is, to use a smaller number of high-quality recordings that could be used for several groups. For each stimulus type, we were able to use at least three different recordings, which we used to test the different groups in random ways.

In 2005 and 2007, we broadcast all playback stimuli with an Apple IPod Nano mp3 player connected to a Nagra DSM speaker-amplifier. In 2008 and 2009, we broadcast the playback stimuli with an Archos Gmini XS100 mp3 player connected to a Kenwood KAC-52-03 amplifier and a Bose 151 speaker. All playback stimuli were uncompressed. We adjusted the amplitude of the playback stimuli so that they were all broadcast within their natural amplitude range (eagle shrieks within 80–100 dB, leopard growls within 70–90 dB and conspecific playbacks within 60–70 dB). Stimulus amplitude was calibrated with a Radioshack Sound Pressure Level Meter at 1 m from the source in the natural environment. The playback equipment was placed at a distance of ca. 25–40 m from the group, outside their visual range. All stimuli were played back from beneath the monkeys' location in the trees (i.e. either from the ground or from a height of 0–15 m, with the speaker hanging from a branch).

Locomotor behaviour

In the horizontal plane, we scored whether any of the focal animals moved at least 5 m away from, or closer to, the speaker. In the vertical plane, we scored whether the monkeys moved at least 1 m upwards or downwards from their initial position. These observations were made with a pair of Leica Trinovid 10 × 42 binoculars and, if conditions allowed, a Panasonic NV-GS17 video recorder with 24× optical/800× digital zoom. Our previous observations had revealed that females showed a more differentiated locomotor response than males (see also Schel & Zuberbühler 2009), suggesting that it would have been appropriate to conduct comparisons within the sexes. As mentioned earlier, however, it was not always possible to identify the sex of the focal individual, but this made it simply more difficult to reject the null hypothesis (no locomotor differences). Statistical comparisons were made with two-tailed Fisher's exact tests, using a Bonferroni-corrected significance level of alpha = 0.025 (Siegel & Castellan 1988).

Gaze orientation

We aimed to film one individual of each focal group 1 min before and at least 1 min after playback to determine its vertical gaze orientation to the different stimuli. Video clips were transferred onto a laptop using Windows Movie Maker software. We conducted a frame-by-frame analysis to determine the direction of the first and second look in the vertical plane following each playback. The second look was relevant because it was likely to reveal something about the monkey's expectation after being surprised by alarm calls. Looking directions were separated into 'downwards' and 'upwards' relative to the monkey's horizontal gaze. We could think of no a priori reason to assume sex differences in this variable. As post hoc scoring of video material can be ambiguous, we performed interobserver reliability tests, which generated high Cohen's kappa coefficients (first and second look: 0.80 and 0.92, respectively; Cohen 1960). Comparisons were made with two-tailed Fisher's exact tests, using a Bonferroni-corrected significance level of alpha = 0.025 (Siegel & Castellan 1988).

Vocal responses

Vocal responses to the playback stimuli were recorded using a Sony TCD D8 DAT recorder connected to a Sennheiser K6/ME66 directional microphone. Vocalizations were transferred onto a PC at a sampling rate of 48 kHz, 16 bits accuracy using Cool Edit 2000 (Syntrillium Software, Scottsdale, AZ, U.S.A.). Acoustic analyses were performed with Raven 1.2 (Cornell Laboratory of Ornithology, Ithaca, New York) and Praat 4.3.12 (Boersma & Weenink 2005). If more than one individual called in response to the stimulus (e.g. the adolescent son of the adult male), we used the vocal response of the individual that called first for subsequent analyses. To allow for comparisons with previous studies (Schel et al. 2009; Schel & Zuberbühler 2009), we measured the following temporal variables: (1) total duration of the vocal response (s); (2) total number of roaring sequences; (3) total number of roaring phrases; (4) mean number of roaring phrases per roaring sequence; (5) number of snorts; and (6) call rate (phrases/s). The following spectral variables were measured for individual roaring phrases: (1) phrase duration (ms); (2) number of combined pulses per phrase; (3) fundamental frequency (Hz); (4) harmonics to noise ratio (dB); (5) first formant (Hz); (6) second formant (Hz); and (7) peak frequency (Hz). If possible, we conducted all spectral analyses on the first and last phrases of the first two roaring sequences (i.e. four roaring phrases per vocal response). We used two-tailed Wilcoxon signed-ranks tests to compare the spectral characteristics of first and last roaring phrases produced within roaring sequences. For the comparison of spectral and temporal parameters between the predator alarm contexts and between alarm contexts and predator vocalization contexts we used two-tailed Mann–Whitney *U* tests. For all comparisons we used a Bonferroni-corrected critical significance level of alpha = 0.017 (Siegel & Castellan 1988). Apart from the roaring sequences, we also collected data on other calls produced, especially grunts, tongue-clicks and snorts (Marler 1972; Oates 1977).

RESULTS

Between 2005 and 2009, we tested 66 different Guereza groups with playbacks of leopard growls and 53 different groups with playbacks of eagle shrieks. The full data set was used to determine the monkeys' locomotor responses in the horizontal domain, although seven leopard and four eagle trials had to be excluded owing to poor visibility. Data on vertical movements were collected in 2008–2009, yielding a final data set of 37 trials for leopard growls and 33 for eagle shrieks, after excluding three leopard and three eagle trials owing to poor visibility. Orienting and gaze responses were collected in 2008, with a final data set of 14 for leopard growls and 13 for eagle shrieks, after excluding three leopard and seven eagle trials owing to poor visibility. Vocal responses to the two predator types were rare (2005: $N = 11$ groups to leopard growls; $N = 12$ groups to eagle shrieks; 2008: $N = 5$ groups to leopard growls; $N = 1$ group to eagle shrieks). The vocal recordings of the 2009 data set ($N = 6$ leopard and $N = 2$ eagle responses) had to be excluded from acoustic analyses owing to a technical problem, yielding a final data set of 16 vocal responses to leopard growls and 13 to eagle shrieks for acoustic analyses.

Between 2007 and 2008, we also conducted 45 valid trials using leopard alarm sequences and 51 valid trials using eagle alarm sequences to determine the Guerezas' responses to their own alarm vocalizations. Data on vocal responses were collected in both 2007 and 2008 ($N = 11$ vocal responses to leopard alarms and $N = 5$ vocal responses to eagle shrieks). Data on locomotor behaviour and gaze direction, however, were only collected in 2008, leading to a final data set of 18 responses to leopard alarms and 18 to eagle alarms, after excluding one eagle trial owing to poor visibility. Table 1 summarizes the composition of the full data set.

Locomotor Responses

After hearing both types of leopard-related stimuli (L growls or L alarms), the focal individuals either remained seated or approached the stimuli in the horizontal plane (binomial test: L growls: $N_{\text{Move}} = 37$, $N_{\text{Not move}} = 22$, $P = 0.067$; $N_{\text{Further}} = 6$, $N_{\text{Closer}} = 31$, $P = 0.001$; L alarms: $N_{\text{Move}} = 9$, $N_{\text{Not move}} = 9$, exact $P = 1.000$; $N_{\text{Further}} = 0$, $N_{\text{Closer}} = 9$, $P = 0.004$). In the vertical plane, they either remained seated or they moved up or down (binomial test: L growls: $N_{\text{Move}} = 22$, $N_{\text{Not move}} = 15$, exact $P = 0.405$; $N_{\text{Up}} = 16$, $N_{\text{Down}} = 6$, $P = 0.052$; L alarms: $N_{\text{Move}} = 12$, $N_{\text{Not move}} = 5$, $P = 0.143$; $N_{\text{Up}} = 7$, $N_{\text{Down}} = 5$, $P = 0.774$; Table 1, Fig. 2).

After hearing both types of eagle-related stimuli (E shrieks or E alarms), the focal individuals either remained seated or they approached the stimulus in the horizontal plane (binomial test: E shrieks: $N_{\text{Move}} = 18$, $N_{\text{Not move}} = 31$, exact $P = 0.085$; $N_{\text{Further}} = 0$, $N_{\text{Closer}} = 18$, $P = 0.001$; E alarms: $N_{\text{Move}} = 8$, $N_{\text{Not move}} = 10$, $P = 0.815$; $N_{\text{Further}} = 0$, $N_{\text{Closer}} = 8$, $P = 0.008$). In the vertical plane, the monkeys either remained seated or they moved up or down (binomial test: E shrieks: $N_{\text{Move}} = 19$, $N_{\text{Not move}} = 14$, exact $P = 0.487$; $N_{\text{Up}} = 6$, $N_{\text{Down}} = 13$, $P = 0.167$; E alarms: $N_{\text{Move}} = 5$, $N_{\text{Not move}} = 8$, $P = 1.000$; $N_{\text{Up}} = 4$, $N_{\text{Down}} = 1$, $P = 0.375$; Table 1, Fig. 2).

Comparing the Guerezas' locomotor responses to conspecific alarms with those to the corresponding predators revealed no significant differences, implying that the response patterns were largely identical (all P values > 0.122; Table 1, Fig. 2). However, across predator conditions, Guerezas were more likely to start approaching leopard growls than eagle shrieks (Fisher's exact test, two-tailed: $P = 0.012$) and moved more often down in response to eagle shrieks than leopard growls (Fisher's exact test, two-tailed: $P = 0.013$), something that was not observed as strongly in response to the conspecific alarm trials (Table 1, Fig. 2).

Gaze Orientation

In response to both types of leopard-related stimuli, the focal individuals usually turned their head in the horizontal plane towards the speaker (binomial test: L growls: 15/17 trials, 88.2%, $P = 0.002$; L alarms: 15/18 trials, 83.3%, $P = 0.008$). We were able to determine the first vertical gaze direction of at least one individual in 14/17 trials with leopard growls and in 12/18 trials with leopard alarms, and the second vertical gaze in 12/17 trials with leopard growls and in 12/18 trials with leopard alarms. In both contexts, the first and second gazes were usually downwards (binomial test: 1st gaze L growls: downwards: 12/14 trials, 85.7%; upwards: 2/14 trials, 14.3%, $P = 0.013$; 1st gaze L alarms: downwards: 9/12 trials, 75.0%; upwards: 3/12 trials, 25.0%, exact $P = 0.146$; 2nd gaze L growls: downwards: 11/12 trials, 91.7%; upwards: 1/12 trials, 8.3%, exact $P = 0.006$; L alarms: downwards: 9/12 trials, 75.0%; upwards: 3/12 trials, 25%, exact $P = 0.146$; Table 1, Fig. 3).

In response to eagle-related stimuli, the focal individuals usually turned their head in the horizontal direction towards the speaker (binomial test: E shrieks: 17/20 trials, 85.0%, $P = 0.003$; E alarms: 19/19 trials, 100%, $P = 0.001$). We were able to determine both the first and second vertical gaze directions of at least one individual in 13/20 trials with eagle shrieks and in 14/19 trials with eagle alarms. In response to eagle shrieks, the monkeys' first gaze was upwards in 7/13 trials (53.8%) and downwards in 6/13 trials (46.2%; binomial test:

Table 1
Overview of results of all playback experiments

Year	Stimulus	*N*	Call	Orient	Approach	Retreat	0	Move up	Move down	0	1st Gaze up	1st Gaze down	2nd Gaze up	2nd Gaze down
2005	L growl	26	11/26	—	15/22	2/22	5/22	—	—		—	—	—	—
2008	L growl	17	5/17	15/17	8/15	0/15	7/15	7/15	2/15	6/15	2/14	12/14	1/12	11/12
2009	L growl	23	6/23	—	8/22	4/22	10/22	9/22	4/22	9/22	—	—	—	—
Overall	L growl	66	0.324	0.882	0.525	0.09	0.383	0.438	0.157	0.405	0.143	0.857	0.083	0.917
2005	E shriek	17	12/17	—	10/15	0/15	5/15	—	—	—	—	—	—	—
2008	E shriek	20	1/20	17/20	5/19	0/19	14/19	3/18	3/18	12/18	7/13	6/13	9/13	4/13
2009	E shriek	16	2/16	—	3/15	0/15	12/15	3/15	10/15	2/15	—	—	—	—
Overall	E shriek	53	0.294	0.850	0.367	0.000	0.623	0.183	0.416	0.400	0.538	0.462	0.692	0.308
2007	L alarms	27	6/27	—	—	—	—	—	—	—	—	—	—	—
2008	L alarms	18	5/18	15/18	9/18	0/18	9/18	7/17	5/17	5/17	3/12	9/12	3/12	9/12
Overall	L alarms	45	0.249	0.833	0.500	0.000	0.500	0.412	0.294	0.294	0.250	0.750	0.250	0.750
2007	E alarms	32	3/32	—	—	—	—	—	—	—	—	—	—	—
2008	E alarms	19	2/19	19/19	8/18	0/18	10/18	4/13	1/13	8/13	11/14	3/14	9/14	5/14
Overall	E alarms	51	0.099	1.000	0.444	0.000	0.556	0.308	0.077	0.615	0.786	0.214	0.643	0.357

L: leopard; E: eagle. 0: no movement in horizontal or vertical plane.

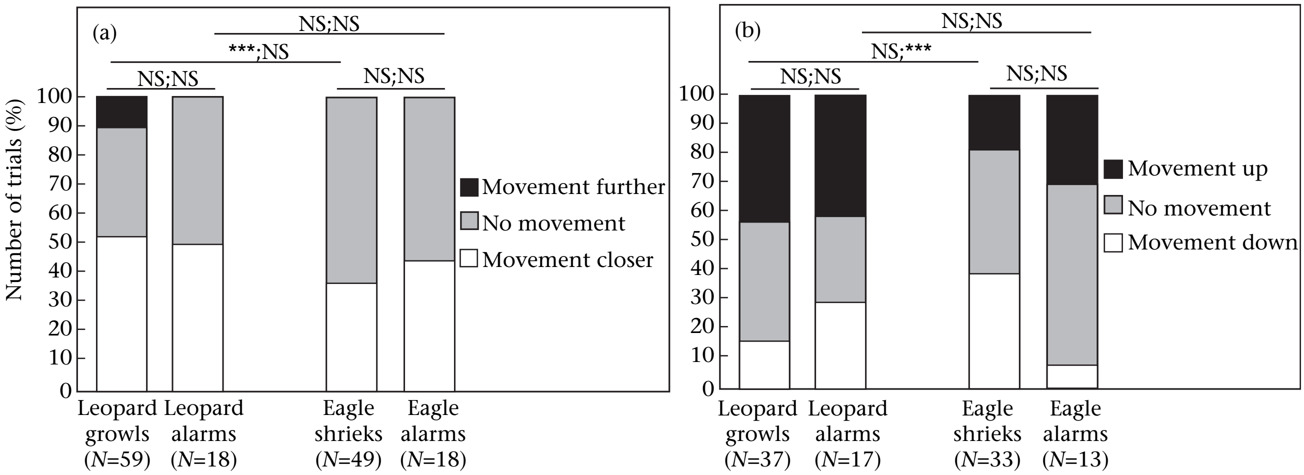

Figure 2. Locomotor responses in the (a) horizontal and (b) vertical plane to the different playback stimuli. The first set of asterisks refers to the difference in occurrence of movement between contexts, the second set to the difference in direction of movements between contexts. $^{***}P < 0.001$ (Fisher's exact tests, two tailed).

exact $P = 1.000$), whereas their second gaze was upwards in 9/13 trials (69.2%) and downwards in 4/13 trials (30.8%; binomial test: exact $P = 0.267$; Table 1, Fig. 3). In response to eagle alarms, the monkeys' first gaze was upwards in 11/14 trials (78.6%) and downwards in 3/14 trials (21.4%; binomial test: exact $P = 0.057$), and their second gaze upwards in 9/14 trials (64.3%) and downwards in 5/14 trials (35.7%; binomial test: exact $P = 0.424$; Table 1, Fig. 3).

Comparing the Guerezas' gaze responses to conspecific alarms with those to the corresponding predators revealed no significant differences, implying once more that the response patterns were largely identical (all P values > 0.24; Table 1, Fig. 3). Crucially, across all conditions, monkeys generally looked up in a significantly higher proportion of eagle-related trials compared to leopard-related trials (Fisher's exact test, two-tailed: 1st gaze: L growls versus E shrieks: $P = 0.046$; L alarms versus E alarms: $P = 0.016$; 2nd gaze: L growls versus E shrieks: $P = 0.004$; L alarms versus E alarms: $P = 0.062$; Fig. 3).

Vocal Responses

Individuals were reluctant to respond with alarm sequences to all four types of playback stimuli. Response rates to eagle alarm sequences were lowest (5/51 trials, 9.8%) and significantly different from those to the corresponding predators (15/53 trials, 28.3%; Fisher's exact test, two-tailed: $P = 0.024$). Response rates to leopard alarms were 11/45 trials (24.4%), similar to the response rates to the corresponding predators (22/66 trials, 33.3%; Fisher's exact test, two-tailed: $P = 0.399$; Fig. 4). Grunts, but not tongue-clicks, were produced in 9/51 trials (17.6%) conducted with eagle alarms, and in 8/45 trials (17.8%) conducted with leopard alarms. These proportions were comparable to those in response to actual predator vocalizations (E shrieks: 13.2%, $N = 7/53$; L growls: 9.1%, $N = 6/66$; Fisher's exact tests, two-tailed: L growls versus L alarms: $P = 0.245$; E shrieks versus E alarms: $P = 0.594$).

Acoustic Measurements of Vocal Responses

Predator vocalizations

Adding the vocal responses to predator vocalizations collected in 2008 (three leopard responses; two leopard alarms and one eagle alarm recorded in 2008 were discarded owing to background noise) to the 2005 data set (Schel & Zuberbühler 2009) did not change the overall vocal response patterns as described in our earlier reports (Schel et al. 2009; Schel & Zuberbühler 2009). Thus,

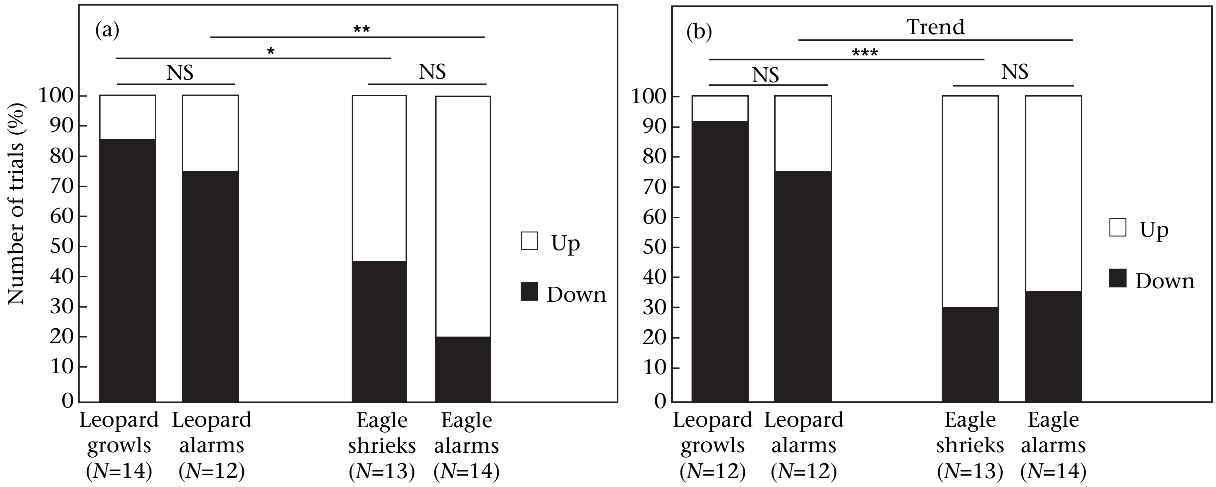

Figure 3. Gaze direction of the (a) first and (b) second look after playback of the different stimuli. Asterisks refer to the significance of differences between contexts. Trend: $P < 0.08$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$ (Fisher's exact tests, two tailed).

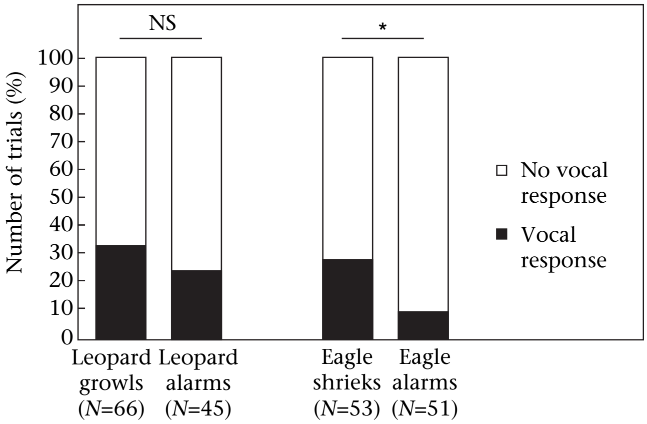

Figure 4. Vocal response rates to the different playback stimuli. Asterisks refer to the significance of differences between contexts. $^*P < 0.05$ (Fisher's exact tests, two tailed).

between the two different predator contexts, there were no consistent spectral differences in roaring phrases produced, but we found consistent differences within predator contexts when comparing the first and last phrases produced in a roaring sequence (Table 2). Furthermore, the structural composition of roars differed significantly between predator contexts, with a large number of short roaring sequences consisting of only a few phrases each produced to leopard growls and a small number of long roaring sequences consisting of many phrases each produced to eagle shrieks (Fig. 1).

Conspecific predator alarms

Three of the 11 vocal responses to conspecific leopard alarms only contained snorts, and were discarded from further acoustic analyses. One of the 11 vocal responses to leopard alarms only contained roaring sequences consisting of a snort followed by one roaring phrase. Two of the five vocal responses to conspecific eagle alarms just contained one roaring sequence. Because we were interested in measuring both first and last phrases of the first two roaring sequences for reasons outlined before, our final data set consisted of seven responses to conspecific leopard trials, five containing a first roaring sequence, and three containing a second roaring sequence to conspecific eagle trials.

Table 3

Comparison of acoustic measurements of roaring sequences between contexts

Acoustic variable	LG and ES		LA and EA		LG and LA		ES and EA	
	FP	LP	FP	LP	FP	LP	FP	LP
First roaring sequence								
Phrase duration (ms)	0.288	0.104	0.030	0.639	0.650	0.773	0.743	0.027
Harmonics to noise ratio (dB)	0.960	0.853	0.476	0.886	0.820	0.863	0.613	0.733
First formant (Hz)	0.695	0.379	0.073	0.876	0.142	0.650	0.827	0.267
Second formant (Hz)	0.449	0.288	0.106	0.755	0.028	0.167	0.115	0.320
Peak frequency (Hz)	0.382	0.033	0.500	0.343	0.756	0.695	0.769	0.108
Number of pulses	0.356	0.026	0.116	0.782	0.827	0.670	0.309	0.052
Fundamental frequency (Hz)	**0.008**	0.065	0.149	0.755	0.270	0.375	0.872	0.601
Second roaring sequence								
Phrase duration (ms)	0.381	0.314	1.000	0.267	0.902	0.592	0.469	0.371
Harmonics to noise ratio (dB)	0.974	0.129	0.262	0.250	0.682	0.913	0.371	0.776
First formant (Hz)	0.107	0.973	0.833	0.833	0.536	0.126	0.077	0.077
Second formant (Hz)	0.456	0.705	0.833	0.183	0.142	0.211	0.161	**0.014**
Peak frequency (Hz)	0.022	0.709	0.142	0.475	0.821	0.058	0.804	0.773
Number of pulses	0.355	0.173	0.325	0.475	0.950	0.489	0.127	0.605
Fundamental frequency (Hz)	0.080	0.159	0.117	0.367	0.724	0.577	0.373	0.811

The table shows statistical output of comparisons between acoustic measurements of first (FP) and last (LP) phrases of the first and second roaring sequences produced across different experimental contexts (leopard growls (LG), eagle shrieks (ES), leopard alarms (LA) and eagle alarms (EA); Mann–Whitney *U* test, $\alpha = 0.017$). Significant *P* values are shown in bold.

Similar to the responses to predator vocalizations, we found consistent differences in the acoustic structure between the first and last roaring phrases produced within a context. These differences were significant in vocal responses to leopard alarms, and they showed a comparable trend in responses to eagle alarms (Table 2). There were no consistent differences in acoustic characteristics between individual roaring phrases produced to eagle and leopard alarm sequences (Table 3). Apart from this, there were a number of minor differences between calls given in response to actual predator vocalizations and corresponding alarm calls (Table 3).

Composition of roaring sequences

A key finding of our previous study was that, in response to their predators, callers produced roars composed of a large number of

Table 2

Comparison of acoustic measurements of roaring sequences within contexts

Acoustic variable	Leopard growls			Leopard alarms			Eagle shrieks			Eagle alarms		
	FP	LP	*P*	FP	LP	*P*	FP	LP	*P*	FP	LP	*P*
First roaring sequence												
Phrase duration (ms)	930	274	**0.001**	1067	281	**0.016**	757	320	**0.001**	802	262	0.063
Harmonics to noise ratio (dB)	2.29	2.91	0.090	1.9	2.8	0.250	3.13	2.85	0.820	3.34	2.86	0.625
First formant (Hz)	643	592	0.519	557	584	0.579	659	686	0.465	645	570	0.438
Second formant (Hz)	1401	1510	0.151	1268	1234	0.938	1338	1327	0.413	1236	1249	1.000
Peak frequency (Hz)	524	430	0.226	500	390	0.297	547	522	0.969	576	437	0.125
Number of pulses	17	4	**0.002**	16	5	**0.016**	15	6	**0.002**	13	5	0.063
Fundamental frequency (Hz)	13	16	0.049	15	17	0.047	18	19	0.320	18	18	0.813
Second roaring sequence												
Phrase duration (ms)	898	353	**0.001**	909	372	**0.016**	766	417	**0.002**	934	161	0.250
Harmonics to noise ratio (dB)	3.83	1.68	0.102	2.32	1.19	0.313	2.77	3.7	0.383	4.71	3.1	0.250
First formant (Hz)	597	734	0.206	583	617	0.938	658	727	0.770	589	565	1.000
Second formant (Hz)	1332	1533	0.320	1263	1238	0.469	1422	1445	0.557	1206	1145	0.500
Peak frequency (Hz)	522	471	0.566	537	437	**0.016**	572	496	0.098	616	597	0.250
Number of pulses	16	6	**0.001**	13	6	**0.016**	13	8	**0.004**	18	3	0.250
Fundamental frequency (Hz)	16	16	0.086	16	18	1.000	18	17	0.301	18	19	1.000

The table shows measurements (medians) and statistical output (exact *P* values) of comparisons between acoustic measurements of first (FP) and last (LP) phrases of the first and second roaring sequences produced within predator and conspecific alarm contexts (Wilcoxon signed-ranks test, $\alpha = 0.017$). Significant *P* values are shown in bold.

roaring sequences containing few phrases each to leopards and roars composed of a small number of roaring sequences containing many phrases each to crowned eagles (Schel et al. 2009). In this study, we found the same pattern in the monkeys' responses to conspecific alarm calls. Responses to other monkeys' leopard alarms were composed of roaring sequences consisting of a few roaring phrases, whereas responses to monkeys' eagle alarms consisted of roaring sequences containing many roaring phrases per sequence (Mann–Whitney *U* test, two-tailed: $U = 2.0$, exact $P = 0.003$). All other temporal parameters of Guerezas' vocal responses did not differ between alarm contexts (Mann–Whitney *U* test, two-tailed: total calling duration: $U = 20.0$, exact $P = 0.572$; total number of roaring sequences: $U = 19.0$, exact $P = 0.495$; total number of phrases: $U = 19.0$, exact $P = 0.493$; call delivery rate: $U = 10.0$, exact $P = 0.074$; number of snorts: $U = 9.5$, exact $P = 0.059$). In addition, we found no significant statistical differences when comparing the responses to conspecific alarms with responses to predator vocalizations (Mann–Whitney *U* test, two-tailed: leopard context: total calling duration: $U = 21.0$, exact $P = 0.052$; total number of roaring sequences: $U = 22.5$, exact $P = 0.068$; total number of phrases: $U = 27.0$, exact $P = 0.149$; number of phrases per roaring sequence: $U = 41.0$, exact $P = 0.780$; call delivery rate: $U = 42.0$, exact $P = 0.842$; number of snorts: $U = 20.5$, exact $P = 0.046$; eagle context: total calling duration: $U = 22.0$, exact $P = 0.583$; total number of roaring sequences: $U = 23.0$, exact $P = 0.638$; total number of phrases: $U = 24.0$, exact $P = 0.723$; number of phrases per roaring sequence: $U = 21.5$, exact $P = 0.526$; call delivery rate: $U = 12.0$, exact $P = 0.09$; number of snorts: $U = 15.5$, exact $P = 0.163$), except for the production of snorts accompanying roaring sequences in the different contexts. Our raw data revealed that 80.0% (4/5 trials) of vocal responses to eagle alarms were accompanied by snorts, something that was not generally observed in response to eagle shrieks (5/12 trials). Snorts were common in response to leopard growls (13/13 trials) and also in response to leopard alarm sequences (10/10 trials).

DISCUSSION

A key methodological advance in the study of animal communication has been to compare subjects' responses to their own alarm calls with their responses to the corresponding predators (Seyfarth et al. 1980). If the responses are identical, and adaptive in relation to the predator, then this is usually taken as evidence that the calls convey something about the external event encountered by the caller. Gaze orientation is a particularly useful measure in such studies because it reveals something about the subjects' anticipation of the forthcoming event. In our study, individuals confronted with leopard-related stimuli, either leopard growls or conspecific leopard alarm sequences, were more likely to look downwards during their first two looks than individuals confronted with eagle-related trials, which caused more upward gazes. There were some interesting differences in gaze orientation to conspecific eagle alarms and eagle shrieks. To conspecific eagle alarms, the monkeys mainly looked up as a first response, while looking down was only observed in 21.4% of trials, as expected. To eagle shrieks, looking down as a first response was more common (46.2% of trials) but still less than to leopard growls, although both predator vocalizations were broadcast from below. This difference may have to do with the fact that crowned eagles sometimes hunt in pairs, with one eagle flying through the canopy and another flying overhead (Gautier-Hion & Tutin 1988). Hearing one eagle's shrieks may thus be indicative of a second eagle's presence so that scanning both above and below becomes an adaptive strategy.

Guerezas were generally reluctant to respond with alarm calls to any of the playback stimuli, both predator calls and conspecific alarm call sequences. Yet, if they responded, they did so in a higher proportion of predator vocalization trials than conspecific alarm trials, especially in the eagle context. Furthermore, if the monkeys responded, the vocal responses to alarm sequences were identical to the ones made by monkeys responding to the corresponding predators in all major variables. The only exception concerned the production of a nonvocal signal, the snorts, which were produced more often in response to playbacks of eagle alarms than eagle shrieks.

In terms of general locomotor responses, we did not observe any significant deviation between the monkeys' standard response to the two predators and the corresponding alarm call sequences. It is also relevant that, even though the alarm calls were essentially given by an unfamiliar male intruder, the callers did not show any of their highly conspicuous display behaviour usually observed during intergroup encounters, such as stiff leg posturing, yawning or bouncing around noisily (Marler 1972; Oates 1977). Because their gaze responses differed between conditions, we rejected the idea that males were simply responding to the presence of a conspecific intruder. More likely, the males reacted to the predator information conveyed by the stimuli.

Why do eagle- and leopard-related stimuli cause these differences in alarm sequences? As mentioned earlier, one explanation is that the calls have evolved as (honest) signals to communicate aggressive motivation to the predator (Zahavi 1977; Zuberbühler et al. 1999). Guerezas actively chase away eagles while producing their impressive roars. In visual predator model experiments, they usually approach and follow a leopard while roaring at it until it is out of sight (A. M. Schel, unpublished data). The long eagle alarm sequences could then function as an indicator of fighting ability and aggressive intent (cf. Harris 2006), while the shorter leopard alarm sequences might primarily function in detection advertisement. Additionally, under this hypothesis the somewhat higher response rates to predator vocalizations (compared to conspecific predator alarms) can be explained with the fact that in such cases predator localization has already taken place. In response to conspecific alarms, it may be adaptive for Guerezas to remain silent and to look for additional cues to locate the predator before giving away one's own position during predator deterrence displays (Searcy & Caine 2003). Nevertheless, although the primary function of these alarm sequences may be in communicating to the predator, our results also show that recipients eavesdrop on these signals and associate them with the predator type for which they are normally produced, as demonstrated by predator-specific gaze direction responses.

An alternative view is that the monkeys' calling behaviour is a mere reflection of the perceived dangerousness of the situation. For example, crowned eagles may be perceived as a more serious threat than leopards, which have been absent from the Sonso area for a considerable time period (Schel & Zuberbühler 2009) and are generally less of a danger for arboreal primates. Under this hypothesis, the long roaring sequences given to eagles are a reflection of perceived high threat, whereas short sequences, given to leopards, are a reflection of low threat. Observations relevant to this question have been made on chimpanzees hunting for colobus monkeys. During a hunt, the chimpanzees usually single out one monkey, which they surround and follow through the treetops. Male Guerezas often attempt to protect their females by chasing away the chimpanzees during direct confrontations in which they actively approach the chimpanzees, while typically producing short roaring sequences (A. M. Schel, personal observation). On two occasions, we observed how an adult male Guereza, captured, wounded and about to be killed by the chimpanzees, also produced short roaring sequences. Although these observations may not be representative for the entire species, it is difficult to argue that such events could not be perceived as the highest possible degree of danger during a predator encounter. The hypothesis that long roaring sequences indicate high ‘perceived threat’, therefore, is not supported by these observations. More likely, short roaring sequences refer to significant events on or from the ground, while the long roaring sequences refer to eagle-related events.

We also recorded a number of other sounds produced by the monkeys, notably grunts, tongue-clicks and snorts. Earlier reports have suggested that snorts function as an alarm call in response to ground predators, that is, mainly if given in isolation (e.g. Hill & Booth 1957; Marler 1972). In our study, callers produced snorts to leopard growls, to leopard alarms and to eagle alarms, but usually not consistently to eagle shrieks, even though all four stimuli were played from the ground. In all eagle-related cases, the snorts preceded roaring sequences and were never produced alone, whereas in leopard-related responses snorts were also often produced singly. The function of snorts preceding roaring sequences currently remains unclear. One possibility is that snorts are produced in response to any disturbance coming from below, sometimes including eagles, which are not typical ground predators. By introducing roaring sequences with snorts, callers may indicate to their group members that a specific event is taking place below the group. The prediction here is that alarm sequences (to eagles or leopards) played from above will not elicit any snorts. Testing these possibilities will require further playback experiments, which may be difficult to carry out in light of the Guerezas' highly arboreal lifestyle in the treetops.

Although the default response to conspecific alarms was to remain silent, individuals sometimes produced alarms. When comparing the acoustic structure of these vocal responses with vocal responses to actual predator vocalizations, we found no consistent differences in the major variables, although there were a few subtle acoustic differences, most notably in the details of the second formant frequency of individual calls. It is unclear which kind of psychological factors experienced by the callers could explain these differences (Rendall 2003). One possibility is that, within the same predator class, some situations are perceived as more dangerous than others, but unfortunately we did not measure any suitable independent variables that would allow us to address this hypothesis more systematically. Whether or not these subtle acoustic differences are communicatively important is also unclear and will require further work. Despite this, our key finding was that callers reproduced the alarm call sequences that they heard, suggesting that these were meaningful to them.

In sum, based on the lower vocal response rates to conspecific alarms compared to the corresponding predator vocalizations, we suggest that Guerezas' vocal predator responses have evolved as predator deterrence signals, a function further illustrated by the fact that Guerezas often approach their predators while calling. Natural observations of interactions with predatory chimpanzees argue against the hypothesis that the observed differences in sequence organization are a mere side-product of perceived threat. Our results also show that recipients attribute meaning to these compositional differences. Thus, although not necessarily produced for this purpose, Guerezas' alarm sequences refer to two different external events, the presence of a disturbance on the ground or an eagle. In this species, meaning is conveyed by the call sequences, not the individual calls, a possibly underestimated feature of animal communication (e.g. Zuberbühler 2002; Templeton et al. 2005; Arnold & Zuberbühler 2006, 2008; Clarke et al. 2006). We conclude that Guerezas' alarm sequences evolved to deter predators and function as referential signals by providing vital information to eavesdropping conspecifics.

Acknowledgments

We thank the Royal Zoological Society of Scotland for providing core funding for the Budongo Conservation Field Station. We are grateful to Gophine Erickson, James Kakura and Steven Amati for assistance in the field. This research was funded by the European Commission (FP6 ‘what it means to be human’), the Leverhulme Trust, the Wenner-Gren Foundation, and the Schure Beijerinck Poppink Fonds and Dobberke Stichting from the Koninklijke Nederlandse Akademie van Wetenschappen (KNAW). We thank the Wissenschaftskolleg zu Berlin for additional support. R. Wittig, C. Crockford, M. Laporte, C. Hobaiter, T. Gruber and A. Dye contributed with stimulating discussion, help with the analyses and photographic material.

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VIE SOCIALE ET FLEXIBILITE DU COMPORTEMENT VOCAL CHEZ LE SINGE DIANE ET AUTRES CERCOPITHECIDES

CHAPITRE 1 –INTRODUCTION GENERALE

1.1 –Communication vocale et vie sociale

1.1.1 – La communication est un besoin social

La communication est un processus qui nécessite un émetteur, un receveur et un signal qui peut véhiculer différents messages (Smith 1969). Ce processus essentiel aux fonctions vitales et inhérent à toute vie sociale (Goldberg 1998), peut s'effectuer via divers signaux (électriques, chimiques, tactiles, visuels ou acoustiques). Ceux-ci sont à la fois contraints par l'anatomie de l'émetteur et par l'environnement de propagation. Les vertébrés vivant dans un environnement visuellement dense utilisent prioritairement des signaux vocaux (Catchpole & Slater 1995, Tyack & Sayigh 1997, Marler 1965, Gautier 1988). Tout mode de communication implique plusieurs composantes qui sont la production du signal (la structure acoustique pour un signal vocal), l'utilisation (son mode et son contexte d'émission), la perception (la capacité à discriminer des signaux) et la compréhension (le décodage des messages). Une co-évolution des systèmes sociaux et des capacités vocales semble logique en raison des forts liens entre besoins communicatifs et vie sociale. L'hypothèse du "cerveau social" va dans ce sens et suggère que le cerveau des primates non humains n'a pas évolué pour faire face à des problèmes d'ordre écologique mais que leur large taille reflète la demande d'intégration des données sociales traduisant la complexité des systèmes sociaux de cette branche (Dunbar 1988; Whiten & Byrne 1988). Des besoins sociaux accrus auraient donc engendré de plus grandes capacités cognitives (Zuberbühler & Byrne 2006) et communicatives (Lemasson 2011).

1.1.2 – La flexibilité vocale, un fossé phylogénétique?

La variabilité acoustique est le fait qu'un signal vocal ait une structure plus ou moins variable tandis que la flexibilité vocale est une modulation qualitative (flexibilité de production) ou quantitative (flexibilité d'usage) du signal vocal au cours du temps. Ce phénomène, bien connu chez les oiseaux chanteurs (Hausberger et al. 1995; Brown & Farabaugh 1997), les cétacés (McCowan & Reiss 1995; Miller & Bain 2000) et les chauves souris (Boughman 1998) semble limité chez les primates non humains. Des expériences d'hybridations (Geissmann 1984; Brockelman & Schilling 1984), d'adoptions croisées (Owren et al. 1992), d'assourdissement (Talmage-Riggs et al. 1972) et de privation sociale (Winter et al. 1973; Newman & Symmes 1974) ont mené à la conclusion que le répertoire vocal des singes et singes humanoïdes était fixe et déterminé génétiquement (Seyfarth et al. 1997; Hammerschmidt & Fischer 2008). De plus, des études neurologiques ont révélé que la production de vocalisations des singes était dépendante du système limbique et des aires sub-corticales associées aux émotions, alors que les humains avaient une connexion directe entre le cortex moteur et le larynx, leur permettant un contrôle subtil de la production vocale (Ploog 1981; Jürgens 2002). Il semble donc y avoir un fossé phylogénétique du point de vue de la flexibilité de production vocale entre les humains, les autres primates et les oiseaux ou cétacés (Lemasson 2011).

1.1.3 – Théories de l'origine du langage humain

Deux théories s'opposent quant à l'origine du langage humain : la théorie de l'origine vocale et la théorie de l'origine gestuelle. La théorie de l'origine vocale du langage avance qu'il existe des précurseurs du langage dans les cris des primates non humains (Masataka 2003; Snowdon 2009; Zuberbühler et al. 2009; Lemasson et al. 2012). En effet, plusieurs caractéristiques fondamentales du langage se retrouvent sous des formes primitives dans la communication vocale des primates non humains comme la sémantique (Zuberbühler et al. 1999, Seyfarth & Cheney 2003) , la syntaxe (Clarke et al. 2006, Arnold & Zuberbühler 2006), l'adaptation à l'audience sociale (Roush & Snowdon 2000,Slocombe & Zuberbühler 2007) ou les conversations (Snowdon & Cleveland 1984, Symmes & Biben 1988). Certains auteurs affirment cependant que le langage humain possède des caractéristiques uniques, notamment une grammaire générative et récursive (Chomsky 1981; Corballis 2002) ou un symbolisme (Deacon 1997), impliquant une théorie de l'esprit qui ne semble pas exister chez les autres espèces animales (Cheney & Seyfarth 2010). D'autres défendent la théorie d'une origine gestuelle du langage (Corballis 2002; Vauclair 2004). Ils avancent pour arguments le fait que le langage ne soit pas uniquement oral, que les gestes se développent avant les sons chez les jeunes humains et que la communication gestuelle des grands singes est latéralisée et associée à l'activation d'une région du cerveau homologue à l'aire de Broca, qui contrôle la production du langage chez l'homme (Corballis 2002; Taglialatela et al. 2006). Cependant, des avancées récentes suggèrent que les théories des origines vocale et gestuelle ne sont pas nécessairement exclusives et tendent vers une origine multimodale du langage (Meguerditchian et al. 2011; Lemasson 2011; Taglialatela et al. 2011).

1.2 –Flexibilité vocale sous influences sociales chez les primates non humains

1.2.1 – Avancées neurologiques récentes

Contrairement aux conclusions tirées des premières études neuro-anatomiques, le contrôle de la production et de l'utilisation vocale ne serait pas limité au système limbique et aux aires sub-corticales. Des études comportementales et neurobiologiques ont confirmé l'existence d'un certain contrôle chez plusieurs espèces de primates (Miller et al. 2003, Koda et al. 2007, Taglialatela et al. 2011, Coudé et al. 2011).

1.2.2 –Une approche multi-niveaux des répertoires vocaux

La variation des paramètres acoustiques au sein du signal permet la distinction de sous-types de cris classifiables en catégories structurales et fonctionnelles comme des cris d'alarme codant pour les types de prédateurs (e.g. Macedonia 1990, Wheeler 2010, Cheney & Seyfarth 2010, Zuberbühler et al. 1997, Slocombe et al. 2008), les cris liés à la nourriture codant pour la quantité ou la qualité de l'aliment découvert (Benz 1993, Hauser & Marler 1993, Slocombe & Zuberbühler 2006; Clay & Zuberbühler 2009), des cris de détresse codant le rôle des protagonistes du conflit (Gouzoules et al. 1984, Slocombe & Zuberbühler 2007; Slocombe et al. 2009), les cris de copulation codant la présence ou non de l'éjaculation (Pfefferle et al. 2008) ou encore des sous-types de cris de contact codant pour le degré d'affinité sociale(Green 1975, Lemasson & Hausberger 2011).

De plus, de nombreux cris sont composés d'unités sonores discrètes concaténées de diverses façons (i.e. répétition, affixation, combinaison) et ils peuvent également être concaténés en séquences. Des cris complexes peuvent être produits en répétant de manière optionnelle une même unité (e.g. Bouchet et al. 2010). Les cris peuvent aussi résulter d'un processus d'affixation où différentes racines sont suivies d'un suffixe unique invariant (Ouattara et al. 2009a). Les cris peuvent à leur tour être combinés en séquences (Arnold & Zuberbühler 2006) qui sont potentiellement porteuses d'informations encodées dans la nature et l'ordre de succession des composants mais aussi dans leur rythme d'émission (Ouattara et al. 2009a, Lemasson et al. 2010b).

Plusieurs auteurs ont émis l'hypothèse d'un lien entre le degré de variabilité structurelle des cris et leur valeur sociale, avec plus de variabilité attendue dans les cris à forte valeur sociale (Snowdon & Hausberger 1997; Griebel & Oller 2008). Cette hypothèse a été validée chez plusieurs espèces de singes (Rendall et al. 1998, Rendall et al. 2009, Lemasson & Hausberger 2011, Bouchet et al. 2012)

1.2.3 – Contexte social de l'interaction communicative

La flexibilité vocale s'observe à divers niveaux de production. Tout d'abord, plusieurs espèces émettent des cris spécifiques au sexe à cause de différences morphologiques et hormonales. Néanmoins, des constats anecdotiques rapportent que ces cris spécifiques au sexe ne reflètent pas nécessairement une incapacité de l'autre sexe à les émettre mais plutôt des préférences pour certains types de cris, en accord avec le rôle du sexe correspondant (Smith et al. 1982; Geissmann 1983; Hohmann 1991; Ouattara et al. 2009b; Bouchet et al. 2010). De plus, les liens sociaux intra-groupes orientent la structuration des répertoires vocaux individuels, car les préférences sociales peuvent se refléter dans un phénomène de partage vocal dynamique où la dynamique des relations sociales influence les convergences vocales entre individus (Marshall et al. 1999, Snowdon & Elowson 1999, Lemasson & Hausberger 2004). Les interactions vocales révèlent quant à elles une convergence acoustique à court terme où les receveurs répondent vocalement à un émetteur en produisant une vocalisation dont la structure converge pour un ou plusieurs des paramètres acoustiques (Mitani & Brandt 1994, Mitani & Gros-Louis 1998, Sugiura 1998, Geissmann 1999). D'autre part, la flexibilité peut être observée en réponse à un changement dans l'habitat, comme le niveau sonore (Brumm et al. 2004) et la visibilité (Koda et al. 2008, Ey et al. 2009). L'appartenance à un groupe influence également la flexibilité des cris, faisant émerger des signatures au sein des groupes (Hafen et al. 1998) et entre groupes (e.g. Mitani et al. 1999; Mitani et al. 1999; Crockford et al. 2004; Crockford et al. 2004; Braune et al. 2005, Tanaka et al. 2006, de la Torre & Snowdon 2009). Enfin des différences (présence/absence de types de cris)ont été décrites dans les répertoires vocaux des primates sauvages et captifs (Lemasson & Hausberger 2004; Ouattara et al. 2009b, Lemasson et al. 2004, Hopkins et al. 2007).

Il existe un apprentissage social des contextes d'émission appropriés par les juvéniles (Seyfarth et al. 1997; Snowdon & Hausberger 1997; Naguib et al. 2009), ainsi que des règles d'échange vocal au sein du groupe (e.g. Snowdon & Cleveland 1984, Hauser 1992, Sugiura & Masataka 1995, Lemasson et al. 2010a). Chez les adultes, la flexibilité d'utilisation des cris en fonction du contexte existe, par exemple dans l'ajustement des taux d'émission de cris en présence d'un prédateur (Zuberbühler 2000c), selon le rang hiérarchique des interlocuteurs (Mitani & Nishida 1993) ou selon l'audience présente (Townsend et al. 2008; Clay et al. 2011, Laporte & Zuberbühler 2010).

1.3 – Flexibilité de la perception et de la compréhension des signaux vocaux

Au sein d'un groupe, les primates non humains se reconnaissent entre eux individuellement grâce à leur voix (e.g. Waser & Waser 1977; Cheney & Seyfarth 1999; Wittig et al. 2007; Lemasson et al. 2008). Les membres du groupe sont également capable de discriminer des variantes dans les cris sociaux et sont sensibles aux subtilités des contextes d'émission (Fischer et al. 2001, Lemasson et al. 2005b, Slocombe et al. 2009). Il peuvent également déduire des informations sociales à partir de séquences de cris, comme les babouins qui réagissent plus fortement à des repasses de cris de menace et cris de détresse ne respectant pas la hiérarchie existante qu'à des cris respectant la hiérarchie (Cheney et al. 1995).

Au niveau hétéro-spécifique, de nombreuses espèces de primates non humains comprennent les propriétés référentielles des cris d'alarme émis par d'autres espèces de primates sympatriques (Oda & Masataka 1996, Zuberbühler 2000a, Zuberbühler 2000c). Il peuvent également discriminer des messages d'alarme d'espèces génétiquement plus éloignées comme certains oiseaux (Hauser 1988; Seyfarth & Cheney 1990, Zuberbühler 2000b).

1.4 – Vie sociale chez les primates non humains: une diversité de besoins sociaux et communicatifs

1.4.1 – Diversité des systèmes sociaux et flexibilité des liens sociaux

Kappeler & van Schaik (2002) ont défini les systèmes sociaux par la composition du groupe, les relations sociales et la dynamique des réseaux sociaux, présentent une grande diversité chez les primates. [orang-outans: vie solitaire (Rodman & Mitani 1987), gibbons : groupes familiaux (Brockelman et al. 1998), chimpanzés, bonobos, macaques et babouins: groupes multimâles multifemelles (Nishida & Hiraiwa-Hasegawa 1987, Vervaecke et al. 2000,, Melnick & Pearl 1987)]. Au sein des singes de l'ancien monde, macaques et babouins convergent néanmoins sur certains paramètres sociaux. Les mâles et les femelles interagissent physiquement très fréquemment (Lemasson et al. 2008; Maestripieri 2010) et leurs relations sociales sont guidées par le système d'héritage maternel du rang, selon lequel les jeunes individus ont le même statut social que leur mère et où les plus jeunes dominent les plus âgés (Gouzoules & Gouzoules 1987).

1.4.2 – Caractéristiques de la vie sociale chez les espèces de cercopithèques forestières

Les cercopithèques, appartenant au genre *Cercopithecus*, sont des singes de l'ancien monde qui portent une queue. Leur taxonomie est controversée puisque ce genre contient plus d'espèces (25) que tous les autres genres de primates d'Afrique et que les spéciations ne sont pas entièrement finies et des hybrides existent (Detwiler 2004; Erhart et al. 2005). Ils sont quasiment exclusivement forestiers et vivent dans la canopée ou sont semi-terrestres (Gautier-Hion et al. 1999). Leurs activités principales sont l'alimentation et les déplacements en lien avec la recherche de nourriture (Fleagle 1985) ou l'évitement des prédateurs (Arnold & Zuberbühler 2008). Ces espèces forment des groupes de 5 à 40 individus et comportent de la variabilité entre espèces mais aussi au sein des espèces. Les groupes sont majoritairement uni-mâle et multi-femelles (formant des "harems"), même si les singes de Brazza forment des groupes familiaux (Gautier-Hion & Gautier 1978). Les jeunes mâles quittent le groupe natal à l'âge adulte (Cords 1987) et les femelles y restent toute leur vie (Wrangham 1980; Rowell & Olson 1983). Les interactions physiques sont rares, surtout les agressions, et les distances inter-individuelles sont importantes (Gautier-Hion & Gautier 1978; Rowell 1988; Rowell et al. 1991; Treves & Baguma 2004). La coordination du groupe est basée sur une surveillance des comportements des congénères et un ajustement des positions évitant les rencontres conflictuelles (Rowell 1988). Ces caractéristiques ont été définies comme typiques d'un système social 'monitor-adjust' (Rowell 1988). Les femelles et les sub-adultes effectuent la majorité des interactions affiliatives (Mörike 1976; Oswald & Lockard 1980), dont de nombreuses interactions vocales via des échanges de cris réguliers (Gautier 1974; Gautier & Gautier-Hion 1982; Lemasson et al. 2010). A l'état sauvage, les séances de toilettage des femelles cercopithèque à diadème ne présentent pas de biais en faveur des individus affiliés (Rowell et al. 1991). Les cercopithèques occupent de petits territoires (moins de 100 ha) qu'ils défendent vigoureusement (Cords 1987; Hill 1994; Buzzard 2006). Les rencontres entre groupes ne sont cependant pas rares et consistent en de nombreuses vocalisations et postures de menaces (Hill 1994; Glenn & Cords 2002; Buzzard & Eckardt 2007; Ouattara et al. 2009b). En revanche, ces espèces s'associent volontiers à d'autres espèces de primates présentes sur leur territoire (Gautier 1969; Waser 1987; Gathua 2000; Wolters & Zuberbühler 2003) comme d'autres cercopithèques, des colobes ou des mangabés (Bshary & Noë 1997; McGraw & Bshary 2002; Buzzard 2010). Ces associations sont parfois considérées comme des "organisations sociales supra-spécifiques" (Gautier 1969), où les individus répondent aux vocalisations d'autres espèces et interagissent occasionnellement à travers des séances de toilettage et de jeu (Gathua 2000), voire de conflits (Buzzard 2004).

1.5 – Problématique

Ces travaux de recherche ont pour but précis de mieux comprendre le lien entre socialité et communication chez un groupe de primates peu connu, les cercopithèques forestiers, ainsi qu'un objectif plus large d'approfondir les connaissances sur la capacité de flexibilité vocale des primates non humaines par rapport à la communication orale humaine. Nous proposons ici de contribuer aux travaux portant sur la communication vocale des primates non humains pour mieux étudier le scénario d'une co-évolution sociale-vocale ainsi que les origines de propriétés clés du langage humain comme la sémantique, la syntaxe, les conversations et la plasticité vocale. L'intérêt pour les cris sociaux d'espèces hautement vocales comme les singes forestiers de l'ancien et du nouveau monde permet de remettre en cause le fossé phylogénétique décrit dans l'évolution de la flexibilité vocale. Cependant, des questions restent ouvertes comme la généralité du phénomène de plasticité à court terme, les capacités combinatoires ou le décodage de l'identité hétérospécifique. Ici, nous proposons de nous focaliser sur deux espèces sympatriques de cercopithèques forestiers, le singe Diane et la mone de Campbell, bien connues pour les propriétés référentielles de leurs cris d'alarme. Ces deux espèces sont de bons modèles pour chercher de la flexibilité acoustique à court terme et de la référentialité dans les cris sociaux en étudiant la variabilité des paramètres acoustiques et les combinaisons de sons. Le répertoire vocal des femelles Diane est très peu connu sur le volet social. De plus, aucune étude n'a été menée à ce jour sur l'organisation sociale de ces deux espèces à l'état sauvage. Afin d'approfondir la question de la flexibilité de perception et de compréhension des vocalisations notamment l'identité de l'émetteur, il est intéressant d'adopter une approche comparative chez plusieurs espèces de *Cercopithecidae* plus ou moins phylogénétiquement proches et vivant en associations poly-spécifiques. Nous nous pencherons successivement sur les questions suivantes :

- Quelles sont les caractéristiques de l'organisation sociale des singes Diane et des mones de Campbell? Le système social des cercopithèques est-il flexible au niveau du groupe ou de l'espèce?

- Quel est le répertoire de cris sociaux des femelles Dianes? Des sous-types de cris sont-ils structurellement et contextuellement différentiables? Comment la variabilité est-elle encodée?

- Quel est le niveau de flexibilité acoustique à court terme des cris sociaux des femelles Diane? Quels sont les facteurs environnementaux influençant cette variabilité?

- Des espèces vivant en associations poly-spécifiques comme les cercopithèques, les mangabés et les colobes discriminent-elles les voix d'individus issus d'une autre espèce de primate sur la base du degré de familiarité?

CHAPITRE 2 – METHODOLOGIE GENERALE

2.1 – Espèces étudiées

2.1.1 – L'organisation sociale des cercopithèques forestiers: mone de Campbell *vs* singe Diane

Les singes Diane sont divisés en deux sous-espèces, *Cercopithecus diana diana* et *Cercopithecus diana roloway* (Linnaeus 1758; Groves 2001). Les mones de Campbell appartiennent à la super-espèce des *mona* (Lernould 1988). La sous-espèce *C. diana diana*, qui vit sur la rive ouest de la rivière Sassandra, occupe principalement des forêts tropicales primaires (Lee et al. 1988; Kingdon & Pagel 1997). L'espèce *Cercopithecus campbelli* occupe des forêts primaires et secondaires du Sénégal au Ghana (Booth 1958). Les singes Diane sont hautement arboricoles, occupant les strates hautes de la canopée (McGraw 2004). En revanche, les mones de Campbell sont arboricoles mais occupent les strates basses de la forêt (McGraw 2004). Les deux espèces se nourrissent principalement de fruits (plus de 75%) et d'insectes (plus de 15%, Galat & Galat-Luong 1985; McGraw 2004). Elles sont souvent en association avec d'autres espèces de singes comme les colobes et autres cercopithèques (Galat et al. 1978; Höner et al. 1997, Wolters & Zuberbühler 2003). Les groupes de singes Diane sont composés d'environ dix femelles adultes et leur progéniture alors que les groupes de mone de Campbell ont environ cinq femelles adultes et leur progéniture (Bourliere et al. 1970; Galat & Galat-Luong 1985; Whitesides 1989). En captivité, les femelles adultes ont développé des relations préférentielles (Byrne et al. 1983, Lemasson et al. 2006).

2.1.2 – Répertoire des cris sociaux et flexibilité: focus sur les singes Diane femelles

Les mâles et les femelles Diane émettent des cris d'alarme spécifiques en réponse à deux types de leurs prédateurs, l'aigle couronné et le léopard (Zuberbühler et al. 1997). Des expériences de repasse de cris ont montré que ces alarmes ont du sens pour les congénères

(Zuberbühler 2000d) mais aussi pour d'autres espèces de primates (*Cercopithecus campbelli*, Zuberbühler 2000a) et certains oiseaux sympatriques (Rainey et al. 2004). Les femelles émettent plusieurs autres types de cris comme les trilles et les cris de contact, mais aucune étude acoustique approfondie n'a été menée (Zuberbühler et al. 1997). Ces cris suscitent des réponses vocales de la part de congénères hors de vue en quelques secondes, qui semblent maintenir la cohésion sociale et participent au système de vigilance coordonnée (Uster & Zuberbühler 2001).

2.1.3 – Perception auditive inter-spécifique: les singes de Brazza émetteurs *vs* les mones de Campbell, les colobes noirs et blancs et les mangabés à collier receveurs

Les singes Brazza, les mones de Campbell, les colobes noir et blanc et les mangabés à collier viennent des forêts tropicales Africaines et forment des associations poly-spécifiques (Jones & Sabater Pi 1968; Gautier-Hion & Gautier 1978; Gautier-Hion et al. 1999). Ces espèces diffèrent cependant dans la composition de leurs groupes et leur degré de terrestrialité. Les mâles et femelles singes Brazza ont un cris de contact pulsé et de basse fréquence, à haut potentiel pour encoder l'identité (Bouchet et al. 2011).

2.2 – Sites d'étude

, Une étude de la communication vocale et de la vie sociale chez le singe Diane et la mone de Campbell a été menée dans le parc national de Taï. Ce bloc forestier est le plus grand d'Afrique de l'Ouest, vestige de l'ancienne ceinture forestière qui s'étalait du Ghana à la Sierra Leone (McGraw et al. 2007, figure 5). Il a été déclaré patrimoine mondial de l'UNESCO en 1982. La végétation est une forêt dense ombrophile dont la canopée se situe entre 40 et 60 mètres avec des arbres émergeants (Riezebos et al. 1994). La communauté de primates diurnes consiste en trois espèces de colobes, une espèce de mangabés et quatre espèces de cercopithèques. Le Taï Monkey Project a établi un système de grille facilitant les déplacements et la localisation dans une zone à forte densité de singes près de la station de recherche de l'Institut d'Ecologie Tropicale.

Une étude de la perception auditive des singes de Brazza par des mones de Campbell et des mangabés à collier a été menée à la Station biologique de Paimpont. Les singes sont logés dans des enclos intérieurs et extérieurs enrichis avec des perchoirs, de l'herbe naturelle ou de la litière. Les animaux y sont nourris le matin avec des fruits et légumes frais, et des granulés l'après midi. L'eau est disponible à volonté.

Une étude de la perception auditive des singes de Brazza par des colobes noirs et blancs a également été menée au parc animalier de Port Lympne. Les colobes et les singes Brazza sont logés ensemble dans un enclos à ciel ouvert naturellement boisé. Ils sont nourris trois fois par jours avec des fruits et légumes frais et l'eau est disponible à volonté.

2.3 – Sujets d'étude

Dans la forêt de Taï, nous avons suivi deux groups de singes Diane voisins. Les individus adultes étaient reconnaissables individuellement grâce à des détails anatomiques (forme de la queue, cicatrices…). Les données sociales et vocales collectées par Dr Karim Ouattara en 2006 et 2007 ont porté sur deux groupes de mones de Campbell vivant dans la même zone. Concernant les animaux captifs, ils étaient tous nés en captivité et vivaient sur le lieu d'étude depuis au moins quatre ans. Huit femelles adultes ont été étudiées dans un groupe de mones de Campbell, ainsi que 5 mâles adultes et 2 femelles adultes d'un groupe de colobes noirs et blancs et 6 femelles adultes de deux groupes de mangabés à collier. Les stimuli ont été collectés en enregistrant 13 femelles adultes Brazza appartenant à 6 groupes dans 3 lieux différents.

2.4 – Collecte des données

Les données d'observation des singes Diane ont été récoltées en trois sessions: de février à mai 2009, de décembre 2009 à juin 2010 et de juin 2010 à juin 2011. Des focus de dix minutes, parfois réduits à cinq si l'animal n'était plus visible, ont été effectués sur toutes les femelles adultes entre 7h et 17h30. Durant les deux premières sessions, les comportements de la femelle suivie étaient décrits par l'observatrice (AC) à l'aide d'un microphone Lavallier et les vocalisations de l'animal suivi étaient enregistrées grâce à un microphone Seinnheiser directionnel (K6/ME66). Les micros étaient connectés à un enregistreur Marantz (PMD660, taux d'échantillonnage: 44.1 Hz, résolution: 16 bits). La troisième session a consisté plus spécifiquement en des focus prenant en compte les interactions sociales grâce à un répertoire comportemental simplifié. L'observateur (FG, assistant de terrain) écrivait toutes les interactions physiques impliquant la femelle focus, qu'elles soient positives, neutres ou négatives. En particulier, les durées de proximité et de toilettage ont été calculées. Pour les trois sessions, des scans toutes les 30 minutes ont permis de relever les variables environnementales suivantes: la position du groupe dans son territoire, son degré de dispersion, son activité, la présence de voisins et la luminosité de l'habitat. Entre janvier 2006 et septembre 2007, Karim Ouattara a effectué au cours de sa thèse des focus de 15 minutes sur toutes les femelles adultes, grâce à un microphone Lavallier et enregistrait les cris de l'individu suivi à l'aide d'un microphone Seinnheiser directionel (ME88). Les deux micros étaient connectés à un enregistreur DAT (SONY TCD D100, taux d'échantillonnage: 44.1 Hz, résolution : 16 bits). Un à trois échantillons de fèces fraîches ont été collectés pour tous les individus adultes Dianes et Campbells (entre 2006 et 2007 pour les Campbells et en 2010 pour les Dianes). Ces échantillons ont été conservés au sec grâce à du gel de silice en attendant l'extraction d'ADN. Concernant les données expérimentales, des expériences de repasse de cris de contact des femelles Brazza ont été effectuées à des femelles Campbell, des femelles mangabé à collier et des mâles et femelles colobe noir et blanc. Les expériences étaient appariées et chaque individu a été testé une fois avec une voix familière et une voix non familière à des jours différents. Les stimuli étaient diffusés avec un Marantz PMD660 connecté à un haut parleur amplificateur Nagra (FAC.SC.PA.71) caché dans un sac à dos posé au sol. L'expérience n'était effectuée que si les conditions suivantes étaient remplies : aucun conflit dans les quinze dernières minutes, aucun cri de singe Brazza émis dans les cinq dernières minutes, le bruit ambiant était très bas, l'individu cible était à l'écart du groupe, dans un état peu actif et ne regardait pas dans la direction du haut parleur. Les stimuli étaient diffusés une seule fois à l'intensité naturelle de 60dB. La réaction de la cible était filmée à l'aide d'une caméra Sony DCR SR58E au moins 20 secondes avant et 20 secondes après le stimulus.

2.5 – Analyse des données

Les cris des singes Diane ont été catégorisés en types de cris principaux validés par une analyse des paramètres acoustiques. Le contexte général d'émission a été analysé d'après les données de scans et le contexte immédiat d'après les données de focus. Le logiciel acoustique ANA a été utilisé pour comparer la similarité des contours de fréquence fondamentale. Ce logiciel calcule un indice de similarité pour une paire de cris en comparant les images pixel par pixel. Les comparaisons ont été conduites au sein et entre les femelles, et moyennées pour obtenir un indice moyen intra-individuel et inter-individuel. La variabilité intra-individuelle a été évaluée dans différents contextes. Les cris des femelles focus ont également été comparés à la fois au cri auquel elles répondaient ainsi qu'à un cri auquel elles ne répondaient pas mais émis dans la minute précédente. Pour les analyses sociales, nous avons calculé les durées de proximité avec un autre membre adulte du groupe, la durée des sessions de toilettage et toutes les occurrences de comportements agonistiques. La proportion de temps où les femelles ont initié une proximité avec chaque autre individu adulte a été calculée pour toutes les femelles. Le même calcul a été effectué pour les sessions de toilettage. Les taux individuels d'interactions agonistiques ont également été calculés, ainsi que les taux d'émissions individuels et les proportions de cris échangés. Des sociogrammes d'interactions affiliatives ont été générés à partir des interactions qui avaient lieu plus fréquemment que par chance. Au niveau des analyses génétiques, les séquences d'ADN ont été amplifiées en utilisant des marqueurs microsatellites humains. Les séquences de microsatellites ont été amplifiées avec des Polymerase Chain Reactions (PCR) et leur taille a été estimée. Au sein de chaque espèce et pour chaque dyade d'individus, nous avons calculé le coefficient de Li avec le logiciel SPAGeDi 1.3 (Li et al. 1993; Hardy & Vekemans 2002). Pour les mones de Campbells, ce travail avait déjà été effectué (Petit et al. 2010). Enfin, concernant les expériences de repasse, une analyse image par image a été effectuée avec le logiciel VLC vingt secondes avant et vingt secondes après le stimulus (Lemasson et al. 2008). L'angle entre la tête du singe et le haut parleur était relevé pour chaque image et tous les regards formant un angle de 45° ou plus avec la direction du haut parleur étaient systématiquement comptés. Plusieurs paramètres ont été calculées: la latence à réagir, le nombre total de regards dans la direction du haut parleur ainsi que la durée moyenne et la durée totale des regards.

CHAPITRE 3 – ORGANISATION SOCIALE ET LIEN GENETIQUE CHEZ DEUX ESPECES DE CERCOPITHEQUES FORESTIERS SYMPATRIQUES

RESUME DE L'ARTICLE 1

Questions : Vu la complexité du répertoire vocal et les capacités de flexibilité acoustique des cercopithèques africains tels que le singe Diane ou la mone de Campbell, ces espèces ont potentiellement une structure sociale complexe. Néanmoins, très peu de choses sont connues sur les caractéristiques de leur système social dans la nature. D'après les observations menées au niveau du groupe, il est traditionnellement reconnu que les cercopithèques forestiers sont "plus vocaux" mais "moins sociaux" que d'autres espèces de singes de l'ancien monde comme les macaques et les babouins, avec des interactions physiques moins nombreuses, quasiment aucun lien mâle-femelle et une hiérarchie de dominance peu marquée. Etant donné le manque d'études au niveau individuel nous ne savons pratiquement rien sur l'influence de facteurs génétiques. Quelles sont les caractéristiques sociales des singes Diane et des mones de Campbell en termes de composition du groupe, de fréquence des interactions vocales et non vocales et au niveau des réseaux? Quel est le degré de proximité génétique entre les individus et quel est le lien avec la proximité sociale? Les caractéristiques sociales sont-elles entièrement partagées ou des différences inter-espèces voire inter-groupes émergent-elles?

Méthodologie : Nous avons effectué une étude comparative de la génétique et de l'organisation sociale chez deux espèces de cercopithèques forestières sympatriques de l'Afrique de l'ouest, les singes Diane et les mones de Campbell sauvages. Nous avons étudié quatre groupes au niveau individuel, deux de chaque espèce, en prenant en considération la proximité génétique (estimée à l'aide de marqueurs microsatellites), la fréquence et la durée des interactions affiliatives à la fois en terme de proximité physique et en terme de toilettage, la fréquence des interactions agonistiques, et l'activité vocale des femelles adultes. Chez les femelles, nous avons également estimé le rapport entre la proximité génétique et la force du lien social.

Résultats : Dans l'ensemble, nos résultats chez les deux espèces sont en accord avec les caractéristiques du système social de type "monitor-adjust", comprenant des interactions physiques rares, un seul mâle adulte isolé et des préférences dyadiques entre femelles. Néanmoins, les femelles Diane se sont révélées plus vocales et plus actives socialement que les mones de Cambpell, un phénomène qui ne peut pas être attribué à la différence de taille des groupes mais possiblement à des différences du micro-habitat et de la pression de prédation. Au sein des espèces, des différences entre groupes ont également été observées dans les motifs de réseaux sociaux. Contrairement aux babouins et aux macaques, il n'y avait pas de corrélation systématique entre lien génétique et affiliation sociale.

Conclusions : Cette étude apporte des connaissances non négligeables sur les caractéristiques sociales à l'échelle individuelle de deux espèces de cercopithèques forestières, avec des résultats comparables à ce qui a été précédemment décrit au niveau du groupe sur d'autres sites d'étude. Cette étude est un cas comparatif de différences sociales chez deux espèces proches et sympatriques. Des différences de complexité sociale peuvent conduire à des différences de variabilité vocale.

Cet article a été soumis pour publication dans le journal American Journal of Primatology.

CHAPITRE 4 – REPERTOIRE VOCAL DES SINGES DIANE FEMELLES: FLEXIBILITE DES STRUCTURES ACOUSTIQUES ET COMBINAISONS DE CRIS

RESUME DE L'ARTICLE 2

Questions : Les singes Diane femelles sont connus pour leurs types de cris d'alarme à valeur référentielle, mais l'organisation de leur répertoire vocal au niveau de la communication sociale intra-groupe reste méconnue. Les cris sociaux peuvent-ils être également classés en types de cris structurellement et contextuellement distincts ? Quelles sont les variations acoustiques entre types de cris? Chez les cercopithèques, les capacités combinatoires sont-elles limitées aux cris forts des mâles?

Méthodologie : Nous avons effectué des focus de dix minutes sur des femelles identifiées dans deux groupes de singes Diane sauvages du parc national de Taï, en Côte d'Ivoire. Nous avons également effectué des scans toutes les trente minutes pour relever l'activité du groupe et certaines variables environnementales. Une classification préliminaire des cris enregistrés a été effectuée selon leurs motifs temporels, fréquentiels et combinatoires. Nous avons ensuite vérifié que les types de cris identifiés variaient contextuellement.

Résultats : Nous avons identifié quatre types de cris unitaires qui se différenciaient par leur structure acoustique. Ils étaient émis seuls ou en combinaisons non aléatoires, avec le type de cri le plus fréquent divisé en deux sous-types et utilisé comme « suffixe » ainsi que plusieurs unités introductives utilisées comme « préfixes ». Ces combinaisons constituent un répertoire de onze types de cris. Même si les contextes d'émission se recouvraient grandement, des profiles de contexte d'émission ont émergé entre types de cris.

Conclusions : Les femelles Diane augmentent la taille effective de leur répertoire vocal social en variant la structure acoustique des types de cris unitaires mais également en les combinant pour former des structures plus complexes. Ces deux stratégies de flexibilité vocale non exclusives ont peut-être permis aux primates non humains d'élargir leur potentiel communicatif.

Cet article a été publié dans le journal Animal Cognition et présenté au congrès international de la société de primatologie (IPS) en 2010.

RESUME DE L'ARTICLE 3

Questions : Il est connu que les singes Diane femelles ont un répertoire vocal complexe de communication intra-groupe, dont le type de cri Af émis très fréquemment, fortement modulé et à forte valeur sociale. Les motifs de modulation de fréquence peuvent-ils encoder l'identité de l'émetteur? Les niveaux de variabilité acoustique dépendent-ils du contexte d'émission? Sur le plan vocal, les émetteurs convergent-ils ou divergent-ils des autres membres du groupe en fonction du contexte social?

Méthodologie : Nous avons utilisé un logiciel de traitement acoustique afin de comparer les modulations de fréquence fondamentale et de générer un indice de similarité entre paires de cris Af. Les modulations de fréquence en forme d'arche ont été comparées au sein et entre les femelles, ainsi qu'au sein et entre les contextes d'émission.

Résultats : Dans l'ensemble, les contours de fréquence ont révélé un niveau de variabilité moindre an sein des femelles qu'entre elles. Néanmoins, le degré d'individualité variait avec le contexte social d'émission du cri. Les émettrices augmentaient la divergence vocale lorsque la cohésion sociale était nécessaire à cause d'une visibilité moindre ou de la présence d'un groupe voisin. Toutefois, elles convergeaient vocalement lors des interactions vocales.

Conclusions : Les femelles Diane adultes montrent un certain degré de contrôle de la structure acoustique fine de leur vocalisation, la plus importante socialement parlant. Une convergence et une divergence vocales sont des processus complémentaires qui permettent aux émettrices d'assurer une proximité spatiale ainsi qu'une cohésion sociale. Nous soulignons le fait que ce phénomène présente des similarités avec celui de l'accommodation vocale décrit chez l'Homme.

Cet article a été publié dans le journal Biology letters et présenté au congrès international de Bioacoustique (IBAC) en 2011 ainsi qu'au congrès de la Société Française de l'étude du comportement animal (SFECA) en 2012.

CHAPITRE 5 – PERCEPTION AU NIVEAU INTER-SPECIFIQUE:

DISCRIMINATION INTER-ESPECES DE LA FAMILIARITE DES VOIX

RESUME DE L'ARTICLE 4

Questions : Les vocalisations des cercopithèques forestiers peuvent transmettre des informations comme l'identité de l'émetteur et il a été montré que ce type d'information est décodé par les congénères. Etant donné l'abondance des associations poly-spécifiques existant au sein des primates forestiers africains ainsi que les interactions affiliatives vocales et non vocales observables entre les espèces, nous nous sommes demandés si les individus d'une espèce étaient capables de discriminer des voix familières de voix non familières d'une autre espèce avec laquelle ils cohabitent.

Méthodologie: Nous avons effectué des expériences de repasse de cris en captivité afin de tester la capacité de trois espèces de primates non humains formant des associations poly-spécifiques dans la nature (mones de Campbell, colobes noir et blancs, mangabés à collier), à discriminer des voix familières de voix inconnues chez une quatrième espèce, le singe de Brazza.

Résultats : Analysés ensemble, les individus de toutes les espèces ont regardé significativement plus de fois en direction du haut parleur après la repasse d'un stimulus non familier qu'après un stimulus familier mais n'ont pas montré de différence dans la latence pour tourner la tête, la durée totale ni la durée moyenne des regards.

Conclusions : Au niveau populationnel, les individus étaient capables de discriminer les voix d'une autre espèce, mais les réactions ne furent pas aussi fortes que ce qui serait attendu au niveau conspécifique. D'autres études permettront de conclure si cela est dû à un manque général d'intérêt pour les vocalisations sociales d'autres espèces de primates, ou un manque de redondance de l'information identitaire contenue dans les cris de contact des singes Brazza.

Cet article a été soumis pour publication dans le Journal of Zoology.

CHAPITRE 6 – DISCUSSION –CONCLUSION GENERALE

6.1 – Fonctionnement social et communication chez deux espèces de cercopithèques forestières sympatriques

6.1.1 – Conséquences de l'organisation sociale sur la communication

Le modèle général du système social chez les cercopithèques est le 'monitor-adjust' proposé par Rowell (1988), où les individus d'un groupe interagissent rarement physiquement mais surveillent la position des congénères visuellement et vocalement pour ajuster leur positionnement. Les résultats obtenus pour les singes Diane et les mones de Campbells vont globalement dans ce sens. Néanmoins, nous avons trouvé plusieurs différences qualitatives et quantitatives dans les interactions sociales entre ces deux espèces. Les singes Diane passent plus de temps à proximité, se toilettent plus souvent et échangent plus de cris que les mones de Campbell. Les variations du système de 'monitor-adjust' trouvées entre ces espèces peuvent refléter des gradations entre espèces de cercopithèques comme cela a été décrit chez les macaques (Thierry et al. 2000).

6.1.2 –Le répertoire vocal social des femelles Diane et mones de Campbell

Concernant la communication vocale des primates non humains, le consensus actuel il est actuellement considéré que leur répertoire vocal est fixe et qu'il y a très peu de flexibilité dans la production des cris. Chez les singes Diane, les femelles ont révélé une flexibilité de production de leurs cris de contact, à la fois en termes de modifications du contour de fréquence ainsi qu'en terme de combinaison d'éléments basiques de façon non aléatoire. Ainsi, ces résultats vont dans le sens de la littérature grandissante qui démontre un certain degré de flexibilité dans la production des cris des primates non humains. La modification structurelle et les combinaisons sont deux stratégies non exclusives pouvant augmenter les capacités communicatives. Ces résultats ont une importance pour les questions de fonction communicative des cris émis dans des contextes sociaux, fonctions qui nécessitent d'autres recherches. Chez les singes Diane et les mones de Campbells, les femelles possèdent une variété de cris sociaux appartenant à la classe des cris de 'cohésion-contact' des cercopithèques (Gautier 1988). Aussi, les répertoires des femelles des deux espèces ont un élément clé qui est la modulation de fréquence en arche, également présente chez d'autres espèces de cercopithèques suite à leur divergence phylogénétique récente (Gautier 1988). Les Campbells possèdent plusieurs sous-types de cris avec une arche incomplète et un sous-type avec une arche complète présentant de nombreuses variantes (Lemasson & Hausberger 2011).

La qualité des enregistrements plus basse pour les cris des Dianes en milieu naturel a malgré tout révélé de l'hétérogénéité dans les arches ce qui suggère qu'il existe également plusieurs sous-types. Dans les deux espèces, la variabilité inter-individuelle de l'arche était plus forte que la variabilité intra, suggérant un bon potentiel pour l'encodage de l'identité. Chez le singe Diane femelle, comme chez la mone de Campbell femelle, trois types de combinaisons d'unités ont été trouvés (Lemasson & Hausberger 2011). Dans les deux cas, les combinaisons forment des cris à deux composantes où la modulation en arche est précédée d'une unité introductive. Plusieurs auteurs ont émis l'hypothèse que les complexités vocale et sociale ont pu co-évoluer, prédisant ainsi que les espèces vivant en harem pourraient émettre un nombre de combinaisons intermédiaire entre une espèce monogame et une espèce à groupe multi-mâles et multi-femelles (McComb & Semple 2005; Freeberg & Harvey 2008). Le répertoire vocal des singes Diane et des mones de Campbells présente également certaines divergences. Au sein d'un groupe de singes Campbells, les femelles affiliées socialement partagent des variantes vocales (Lemasson et al. 2003; Lemasson & Hausberger 2004). Les cris Af des femelles singe Diane semblent être composés d'une seule variante, qui présente des gradations dans la durée et la modulation de fréquence mais sont flexibles dans le cadre de changements de contexte d'émission, par exemple lors d'un échange vocal. De plus les deux espèces semblent utiliser l'arche complète de manières différentes, et la partie introductive des combinaisons semble aussi fonctionner différemment. Nous avons décrit le cas de deux espèces proches avec des répertoires vocaux similaires et des habitats identiques, qui ont développé des différences importantes dans l'utilisation et la fonction des cris. Cela ouvre des perspectives intéressantes pour comprendre la diversification de l'utilisation et de la fonction des vocalisations avec les contraintes évolutives.

6.2 – Perception des signaux vocaux

Il est bien connu que les primates comprennent non seulement les cris de leur propre espèce mais aussi ceux d'autres espèces. Dans un groupe, les individus reconnaissent les cris des autres, mais nous ne savons actuellement pas si cette capacité s'applique aux groupes d'espèces mélangées. Les expériences d'adoption croisée où la mère et l'enfant d'une autre espèce reconnaissent le cri de l'autre sont une source de preuve indirecte d'une reconnaissance hétéro-spécifique de la voix (Masataka & Fujita 1989; Owren et al. 1993). Dans les communautés poly-spécifiques de primates, il a été montré que certains groupes cherchent activement à s'associer à une autre espèce (Holenweg et al. 1996, Windfelder 2001). Nous avons donc testé la capacité de singes vivant en associations poly-spécifiques à reconnaître la voix d'individus d'une autre espèce. Même si les réponses obtenues étaient faibles et variables, les résultats ont montré une capacité à différentier des voix étrangères de voix d'individus familiers. Cela ouvre de nouvelles perspectives nécessitant d'autres études sur la représentation cognitive des individus d'autres espèces. Même si la plupart des exemples de compréhension de cris hétéro-spécifiques semblent être un simple phénomène de déduction, il semble prématuré d'éliminer toute possibilité de communication entre espèces *sensus stricto*, comme cela semble être le cas lors des échanges vocaux entre femelles cercopithèques ou lors des duos de cris forts des mâles d'espèces différentes dans la forêt de Taï.

6.3 –Flexibilité vocale chez les primates non humains et racines du langage humain

6.3.1 – Flexibilité des structures acoustiques

La théorie d'une origine vocale du langage humain propose que certains aspects trouvent leurs racines biologiques dans la communication vocale des animaux (Masataka 2008; Lemasson 2011). Premièrement, chez plusieurs espèces de primates non humains, la structure acoustique des vocalisations peut converger entre individus à long terme (mois, années), en conséquence de changements dans les relations sociales (Mitani & Brandt 1994, Snowdon & Elowson 1999, Lemasson & Hausberger 2004, Crockford et al. 2004). Deuxièmement, des modifications à court terme ont été décrites, au sein d'échanges vocaux au cours desquels d'autres propriétés proches de conversations humaines ont déjà été décrites (Snowdon & Cleveland 1984; Sugiura & Masataka 1995; Lemasson et al. 2010).

6.3.2 – Capacités combinatoires et évolution du langage

A l'heure actuelle il n'y a aucune preuve consensuelle que les systèmes de communication animale possèdent une propriété de syntaxe générative. Cependant, des combinaisons de signaux complexes ont été décrits dans la communication gestuelle des grands singes (Liebal et al. 2004; Pika et al. 2005). Cela semble cohérent avec une tendance grandissante pour l'étude de la communication multimodale qui aurait conduit à l'émergence du langage (Arbib et al. 2008; Lemasson 2011; Taglialatela et al. 2011).

Conclusion générale

L’originalité de cette étude réside dans le fait que tous les aspects de la communication ont été successivement abordés, de l’émetteur au receveur, de la production à la perception en passant par l’utilisation des cris. Ce travail a soulevé une nouvelle série de questions. En effet, la dynamique des réseaux sociaux chez les cercopithèques sauvages reste méconnue, la fonction d’une flexibilité à court terme doit être étudiée en détail chez les cercopithèques. L’existence d’une flexibilité structurale et de combinaisons ainsi que l’utilisation contextuelle d’une telle flexibilité devrait être cherchée chez d’autres espèces de singes et de grands singes afin de résoudre l’énigme du fossé phylogénétique chez les primates non humains. La question de la capacité des primates à identifier la voix d’individus issus d’une autre espèce nécessite des expériences supplémentaires, notamment sur le terrain. En conclusion, l’étude de la communication vocale des primates non humains est un vaste champ de recherche avec des perspectives nombreuses et prometteuses pour la quête des origines du langage humain.