Vocal communication in a tolerant multi-level society: insights from signallers and receivers in Guinea baboons

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SUMMARY

When studying the evolution of animal communication it is important to consider both, the signaller (i.e. signal structure and signal usage) and the receiver (i.e. signal response). While in primates the structure of sounds is supposed to be largely innate, the usage of calls is more malleable and modifiable by experience. The perception and response to calls is highly flexible in primates and, in contrast to signal production, depend strongly on developmental and cognitive mechanisms. Accordingly, the three aspects are expected to be differently affected by evolutionary constrains and selective pressures.

The major goal of my thesis was to investigate primate vocal communication from an evolutionary perspective. I examined the vocal communication of free ranging Guinea baboons (*Papio papio*) and assessed how the characteristics of their social relationships might have contributed to the specifics of their vocal behaviour. To clarify the impact of the Guinea baboons' social system on their vocal communication, I separately studied the structure and usage of their vocal signals as well as their response behaviour, and compared my results to studies conducted on other closely related baboon taxa. Guinea baboons differ in their social system from the well-known savannah baboons (i.e. chacma baboons (*P. ursinus*), olive baboons (*P. anubis*), yellow baboons (*P. cynocephalus*)), which makes them ideal candidates to study the social impact on the characteristics of vocal communication, in general. While savannah baboons live in stable multi-male, multi-female groups with rather hostile male-male relationships, Guinea baboons live in a complex multi-level society with a much less competitive and more tolerant social style among males.

To assess the reliability and validity of acoustic parameters, firstly, I conducted sound transmission experiments, before I used them for acoustic analysis. By re-recording different baboon vocalizations under various broadcasting conditions (i.e. various heights, distances and habitat types) I investigated which parameters where particularly susceptible to degradation. Acoustic parameters, such as start- or end- parameters, where not reliable; i.e. they were highly variable even when recorded under the same conditions. Almost all measured parameters were strongly affected by degradation over distance, which could mainly be attributed to amplitude based attenuation effects. Tonal parameters were only marginally affected by different broadcasting conditions and remained highly valid even when calls were recorded from larger distances. Based on the outcomes of my transmission experiments, I adjusted the recording conditions in the field. Furthermore, I could systematically justify the parameter selection for the following acoustic analyses of the Guinea baboons' vocal repertoire.

In the second part of my project I examined the vocal repertoire of Guinea baboons and analysed their call structure as well as their call usage. I found important differences and similarities of the Guinea baboons' vocal behaviour in comparison to other taxa. While the structure of their vocal repertoire largely coincided with call structures found in other baboons, i.e. the same call types occurred; the usage of calls differed and corresponded to the less competitive and rather affiliative social style of Guinea baboons. Males showed only a diminished usage of contest or display vocalizations (a common vocal pattern observed in the competitive chacma baboons), while they frequently used vocal signals during affiliative and greeting interactions. My results suggest that the use of calls is adapted to the requirements of the specific social system and that competition and cooperation affect animal signalling behaviour to regulate social interactions.

Finally, I conducted playback experiments to investigate how the response behaviour of male Guinea baboons was influenced by the characteristics of their social relationships. Specifically, I played back male calls from individuals of different social units (i.e. their own social unit, a neighbouring unit or a stranger unit) and examined how subjects differentiated among their conspecifics. In correspondence with their highly tolerant social style, males largely ignored any male outside their own unit, irrespective whether the caller was a neighbour or a complete stranger, a response pattern that stands in stark contrast to numerous group living primates. On the other hand, males responded strongly to calls of their own unit members, with whom they are socially related, which indicates that they are strongly motivated to monitor the social manoeuvres of their associates. My findings suggest that the quality and consistency of social interactions appear to be important for the response behaviour in primates and that the allocation of social attention is tuned to the specifics of a species’ social organization.

In sum, the evolution of primate vocal communication appears to be driven by a species’ social system, although the different aspects of communication (i.e. structure, usage and response) are differentially affected. While phylogenetic constrains play an important role by limiting the variation in the structure of nonhuman primate vocalizations, the use of calls as well as the way primates respond, can be flexibly adapted to the requirements of the specific social structure and social organisation. Hence, to understand the overall influence of the determining factors (i.e. phylogeny, social system) on the evolution of animal communication it is important to elucidate the differences and similarities of both, signal production and receivers’ responses.

ZUSAMMENFASSUNG

Wenn man die Evolution tierischer Kommunikation studieren möchte, ist es wichtig sowohl den Signalgeber (d.h. die Signalstruktur und den Signalgebrauch) als auch den Signalempfänger (d.h. die Signalantwort) zu betrachten. Während bei Primaten die Rufstruktur stark angeboren ist, ist der Gebrauch von Rufen flexibler und durch Erfahrungen modifizierbar. Die Wahrnehmung von Primatenlauten, und das daraus hervorgehende Antwortverhalten, ist äußerst flexibel und hängt, im Unterschied zur Lautproduktion, von verschiedenen ontogenetischen und kognitiven Faktoren ab. Dementsprechend ist zu erwarten, dass die drei Aspekte der Kommunikation verschiedenen evolutionären Beschränkungen und selektiven Drücken unterliegen.

Das Hauptziel meiner Doktorarbeit war es, die vokale Kommunikation von Primaten unter evolutionären Gesichtspunkten zu untersuchen. Dabei studierte ich das Lautrepertoire von frei lebenden Guineapavianen (*Papio papio*) und untersuchte, wie ihre Beziehungsqualität zu den Besonderheiten ihres vokalen Verhaltens beigetragen hat. Um des Weiteren den Einfluss des sozialen Systems auf das Lautverhalten von Guineapavianen zu klären, habe ich die Struktur und den Gebrauch ihrer Laute sowie ihr Antwortverhalten untersucht und mit entsprechenden Ergebnissen von Studien an nahe verwandten Paviantaxa verglichen. Guineapaviane weichen in ihrem sozialem System stark von den bereits gut untersuchten Savannenpavianen (d.h. Bärenpaviane (*P. ursinus*), Grüne Paviane (*P. anubis*) und Gelbe Paviane (*P. cynocephalus*)) ab, wodurch sie sich hervorragend eignen, um den sozialen Einfluss auf die Merkmale ihrer vokalen Kommunikation zu studieren. Während Savannenpaviane in stabilen Mehr-Männchen-Mehr-Weibchen Gruppen leben, in denen Männchen stark kompetitive Beziehungen ausbilden, leben Guineapaviane in komplexen viel-schichtigen Gesellschaften mit weitaus friedfertigeren und eher toleranten sozialen Beziehungen zwischen den Männchen.

Zuallererst habe ich Transmissions-Experimente durchgeführt, um die Reliabilität und Validität von akustischen Parametern zu bestimmen, bevor ich sie für weitere akustische Analysen verwandt habe. Indem ich unterschiedliche Pavianrufe unter

verschiedenen Bedingungen (d.h. in verschiedenen Höhen, Distanzen und Habitat Typen) abgespielt und wieder aufgenommen habe, konnte ich untersuchen, welche Parameter besonders anfällig für Degradation sind. Akustische Parameter, wie Start- oder End-Parameter, waren gänzlich unzuverlässig, d.h. sie variierten beträchtlich, selbst dann, wenn sie unter den gleichen Aufnahmebedingungen wieder aufgenommen wurden. Beinahe alle gemessenen Parameter waren stark anfällig für Distanzdegradation, was im Wesentlichen amplitudenbasierten Dämpfungseffekten zugeschrieben werden kann. Tonale Parameter hingegen waren von den verschiedenen Aufnahmebedingungen nur gering betroffen und erwiesen sich als äußerst valide, selbst wenn die Rufe von großer Distanz aufgenommen wurden. Basierend auf diesen Experimenten habe ich die Aufnahmebedingungen von Guineapavianlauten im Feld angepasst. Weiterhin konnte ich so meine Wahl der akustischen Parameter für die darauffolgenden Analysen des Lautrepertoires begründen.

Im zweiten Teil meines Projektes habe ich das vokale Repertoire von Guineapavianen empirisch untersucht und ihre Laut-Struktur sowie den Gebrauch ihrer Laute analysiert. Ich fand wichtige Unterschiede und Gemeinsamkeiten im vokalen Verhalten von Guineapavianen im Vergleich zu anderen Pavianarten. Während die Struktur ihres vokalen Repertoires mit den Lautstrukturen anderer Paviane übereistimmte, d.h. dieselben Lauttypen traten auf, wich der Gebrauch ihrer Laute stark von anderen Pavianen ab und stimmte mit dem wenig kompetitiven und affiliativen sozialen Stil von Guineapavianen überein. Im Gegensatz zu männlichen Bärenpavianen, wiesen männliche Guineapaviane einen geringen Lautgebrauch während aggressiver Interaktionen auf, wobei sie in affiliativen Situationen sowie während Begrüßungen weitaus häufiger Laute verwendeten. Meine Ergebnisse lassen darauf schließen, dass der Gebrauch von Lauten (mit einer relativ stark angeborenen Lautstruktur) an die Notwendigkeiten des sozialen Systems angepasst ist und dass Konkurrenz sowie Kooperation das Signalverhalten beeinflussen und somit soziale Interaktionen regulieren.

Abschließend habe ich Vorspiel-Experimente durchgeführt, um zu untersuchen, wie das Antwortverhalten von männlichen Guineapavianen von den Eigenschaften ihrer sozialen Beziehungen beeinflusst wird. Speziell habe ich Laute von Männchen aus

verschiedenen sozialen Einheiten (d.h. aus ihrer eigenen Einheit, benachbarten Einheiten sowie aus fremden Einheiten) vorgespielt und geprüft, wie die Versuchstiere zwischen ihren Artgenossen unterscheiden. Entsprechend ihres toleranten sozialen Stils, haben die Versuchstiere Männchen außerhalb ihrer eigenen sozialen Einheit ignoriert, unabhängig davon, ob ein Ruf von einem Nachbar vorgespielt wurde oder von einem komplett fremden Individuum. Solch ein Antwortverhalten steht im starken Kontrast zu vielen anderen in Gruppen lebenden Primatenarten. Auf der anderen Seite haben Männchen stark auf die Laute von Männchen aus ihrer eigenen sozialen Einheit reagiert, mit welchen sie soziale Beziehungen ausbilden. Meine Ergebnisse lassen darauf schließen, dass die Qualität und Beschaffenheit sozialer Interaktionen wichtig für das Antwortverhalten von Primaten ist und dass die Verteilung sozialer Aufmerksamkeit abgestimmt ist auf die Besonderheiten der jeweiligen sozialen Organisation.

Zusammenfassend kann man sagen, dass die Evolution der Primatenkommunikation stark vom sozialen System der jeweiligen Art gesteuert wird, wobei die drei verschiedenen Aspekte (d.h. Signalstruktur, Signalgebrauch sowie das Antwortverhalten auf Signale) ungleich betroffen sind. Während phylogenetische Beschränkungen eine wichtige Rolle bei der Limitierung der strukturellen Variation in der Primatenvokalisation spielen, können der Gebrauch von Lauten und die Art und Weise wie Affen auf Laute reagieren flexibel an die Bedürfnisse der jeweiligen sozialen Struktur und sozialen Organisation angepasst sein. Um den weitgehenden Einfluss der entscheidenden Faktoren (d.h. Phylogenie, soziales System) auf die Evolution der tierischen Kommunikation zu verstehen, ist es somit wichtig die Unterschiede und Gemeinsamkeiten in der Signal-Produktion sowie dem Antwortverhalten des Empfängers aufzuklären.

GENERAL INTRODUCTION

1.1. Evolution of animal communication

Animal communication can be characterized as any signalling interaction, "which alters the behaviour of others, which evolved because of that effect, and which is effective because the receiver's response has also evolved" (Smith and Harper 2003). Hence, when studying the evolution of animal communication it is important to consider both, the signaller (i.e. signal structure and usage) and the receiver (i.e. signal response). One of the central questions from an evolutionary-ecological perspective is to ask how communicative signals arise under varying conditions and how they function. Importantly, to constitute an evolutionary stable strategy (ESS) signals need to be "honest" and have to reliably indicate the condition, needs and/or motivations of the signaller, otherwise the receiver would stop attending to such signals, and signalling interactions would disappear (Smith and Harper 2003, Searcy and Nowicki 2005, Fischer 2012). To understand the evolution of such stable systems is one of the major goals of animal communication research.

1.1.1. Interests of signaller and receiver

For the "signaller it is always advantageous to manipulate the behaviour of others to its own benefit, while the receiver is trying to 'mind read' the signaller and estimate how his own interests equals to the interest of the signaller" (Krebs and Dawkins 1984, Fischer 2012). To what extent the interests of both parties overlap strongly predicts how the stability of signal interactions can be maintained (Smith and Harper 2003, Fischer 2012).

During conflicts, evolutionary game theory suggest that individuals should display before fighting and attempt to resolve conflicts at the lowest possible cost (Smith 1976, Bradbury and Vehrencamp 2011). However, the interests of the signaller and receiver under competitive conditions are typically opposed, and the benefits of 'bluffing' or exaggerating are apparent (Smith and Harper 2003, Bradbury and Vehrencamp 2011).

Despite the benefits of such 'deceptive' signalling, most displays are reliable indicators of an individual's competitive ability. To maintain reliability during conflicts, there needs to be some type of cost or constraint on signallers that makes cheating a less optimal strategy than revealing the truth (Smith and Harper 2003). The costs that constrain the signallers` behaviour can take various forms and may be physiological, social or ecological [see Bradbury and Vehrencamp 2011 for examples]. How contest signals are employed during agonistic interactions seems to be closely linked to the competitive abilities of the interactants (Enquist and Leimar 1990, Bradbury and Vehrencamp 2011). Game theoretical models predict that competitors who differ widely in their competitive skills should resolve conflicts relatively quickly via signals, while competition among individuals of more similar competitive abilities is less likely be resolved by signals alone (Enquist and Leimar 1990, Bradbury and Vehrencamp 2011). Accordingly, in many terrestrial vertebrates males produce loud repetitive calls that function as displays, with the temporal and/or structural features of these signals being largely constrained by body size or condition (Smith and Harper 2003, Bradbury and Vehrencamp 2011).

However, not all honest signals need be costly to be effective (Krebs & Dawkins 1984, Smith 1991, 1994). During cooperation, neither party benefits from deceiving the other, and nothing is gained by lying. Therefore, low- cost signals ('cheap talk') can arise (Smith 1991, 1994, Searcy and Nowicky 2003, Bradbury and Vehrencamp 2011). Maynard Smith (1991) explored the dynamics of 'cheap' signals when the interests between participants overlap and demonstrated that if interactants have some stake in each other's survival because they are kin or share a common interest in the outcome of an interaction, then cost-free signals may evolve (the conclusion emerges from analysis of the Philip Sidey Game, see Smith (1991) for the detailed payoff structure for this game). Game theory models further demonstrated that honest, low-cost signals can be evolutionary stable even when there might be a certain conflict of interest between participants once partners interact more often. Cheap signals under such conditions are effective, because individuals interact repeatedly, remember their interactions, and can modify their responses on the basis of past experience (Silk 2000).

In sum, signals can evolve under various conditions, and evolution takes different dynamics in relation to distribution of interests between signaller and receiver.

However, until now, only few empirical studies have investigated how signal design is linked to the specific characteristics of the species' social behaviour. For example, once competition among males is reduced, there might be less pressure to settle conflicts via display signals and in this situation individuals my benefit by employing alternative, less costly, signal strategies, to resolve their disputes (Preuschoft and Van Schaik 2000, Bradbury and Vehrencamp 2011). One of the major aims of my thesis is to examine how the characteristics of animals' social relationships, i.e. competition or cooperation, might have contributed to their vocal signalling system, using a baboon species as a model. In particular, I will describe the vocal signals produced by adult Guinea baboons and investigate how differences in their signalling as well as response behaviour, compared to other baboons, may be attributed to differences in their social style.

1.2. Primate communication

In the following I will elucidate the vocal communication system in primates and highlight the most important mechanisms underlying the production and perception of primate vocal signals. I will focus on the **structure** and **usage** of vocal signals, since both aspects exhibit some important differences in their physiological constraints and developmental flexibility. Afterwards, I will turn to the call receiver and will briefly illustrate what mechanisms determine **the response** to vocal signals in primates. I will further indicate some constraints and selective pressures acting on the different aspects of primate vocal communication.

1.2.1. Signal structure

Mechanism

By now, the developmental and physiological mechanisms underlying sound production in primates are well understood and, in marked contrast to the flexible phonation for example found in human language, are highly constrained. Each species has a relatively small repertoire of calls, with acoustic features largely fixed at birth and showing little modification during development (see Hammerschmidt and Fischer 2008 for a review). Although age-related acoustic changes exist in several primate calls, they can be commonly attributed to maturational factors, such as growth (e.g. Ey et al. 2007) or practice (e.g. Hammerschmidt et al. 2000). Neither rearing nor auditory experiences appear to influence changes in the call structure during development (e.g. Hammerschidt et al. 2000, Ey et al. 2007, Seyfarth and Cheney 2010).

Thanks to studies based on human speech (e.g. Liebermann and Blumstein 1988), the mechanisms of sound production for terrestrial mammals, including nonhuman primates, are well known (Fitch 1997, Reby and McComb 2003, Taylor and Reby 2010). To briefly summarize, most vocal signals are produced by an outward flowing air stream, generated by the lungs (Fitch 1997, Reetz 1999, Taylor and Reby 2010). The lung capacity allowing variation in the duration of the air flow and the speed of the airflow determines the amplitude of the produced sound. The signal then passes the laryngeal system, which includes the larynx and vocal folds. The tension and the size of the vocal folds (i.e. the source) determine the characteristics of the fundamental frequency. The tenser the vocal folds, the higher their oscillation rate, and hence the higher the fundamental frequency, and vice versa: the longer and thicker the vocal folds, the slower they oscillate and the lower the fundamental frequency (see Bradbury and Vehrencamp 2011 for a review). Oscillations at the fundamental frequency are accompanied by oscillations at multiple integers of the fundamental frequency (i.e. the harmonics). The source signal then passes to the supralaryngeal system, made up of the oral and nasal cavity and becomes modified depending on the length, shape and boundary conditions of this system (i.e. the sound filter). The vocal tract acts as a filter allowing only a narrow range of frequencies to pass, with the filter characteristics strongly related to size (Fitch 1997, Riede and Fitch 1999, Taylor and Reby 2010). An increase in the length of the vocal tract will lead to a decrease in the average spacing between successive formants, i.e. the formant dispersion (Lieberman and Blumstein 1988, Fitch 1997). Movement of tongue, lips, velum and/or epiglottis (articulators) can also alter the sound. Finally, the sound radiates from the mouth, or less often from the nose (see Fitch and Hauser 1995 for a detailed description).

The neural foundations of primate vocal production were mainly laid by Jürgens and colleagues in the 1970s. Due to their comparative research conducted on squirrel monkeys, the most important neural circuitries controlling for vocal production in primates have been revealed. Mainly responsible for the readiness to vocalize, the periaquaeductal grey (PAG) is an important relay station, which is getting inputs from the anterior cingulate cortex (‘cingulate-PAG-pathway’) from several limbic brain areas (limbic-PAG-pathway’) as well as from the sensory system. The PAG than innervates the phonatory motor neurons, via the formatio reticularis, and triggers an innate vocal pattern in response to internal as well as external stimuli (Jürgens 2009). Another subsystem runs from the motor cortex directly into the reticular formation and from there to the phonatory motoneurons (Jürgens 2009). This system includes two feedback loops and seems to be responsible for generating the final motor commands (Jürgens 2009). Direct connection between the motor cortex and the phonatory motoneurons is largely absent in most non-human animals, which is believed to constrain the ability for vocal learning in most animals (Hammerschmidt and Fischer 2008, but see Arriaga et al. 2013 for a possible exception in mice).

Certain acoustic variations of primate calls also occur later in life and are more flexible. Call duration and amplitude for example appear to be subject to minor modifications and can be adjusted appropriately to the ambient noise level (i.e. “Lombard” effect [Brumm 2004, Egnor and Hauser 2006]). Such effects, however, can easily be mediated via feedback loops in the lower brain stem, without any inclusion of higher cortical areas (Jürgens 2009).

Phylogeny

Since the acoustic features of calls are strongly innate, vocalizations are expected to show a strong phylogenetic signal (Hauser 1993, Bradbury and Vehrencamp 2011). Studies conducted on closely related species revealed high inter-specific concordance in several acoustic features and phylogenetic analyses have shown that genetic distances correlate strongly with the degree of vocal variability between species. For example, recent studies conducted on leaf monkeys (Meyer et al. 2012) and crested gibbons (Thin et al. 2011) showed highly similar acoustic features within the genus and inter-specific acoustic variability was highly constrained by phylogenetic relatedness. Furthermore, within taxa variation in call structure between populations could be largely explained by geographic distances. Most likely, limited gene flow caused by geographical barriers account for these differences (Thin et al. 2011, Meyer et al. 2012). Similar results have also been found in other taxa (e.g. Wich et al. 2008).

Environment

The environment is thought to constitute a strong selective pressure on primates' vocal communication, and acoustic structures are commonly described as being adapted to counteract degradation during sound propagation ("acoustic adaption hypothesis", Marler 1967, Waser and Brown 1984, 1986). Indeed, experiments of sound propagation clearly demonstrated the effect of the habitat on relevant acoustic features (reviewed in Wiley and Richards 1978). Each environment has its own acoustic characteristics for sound transmission (e.g. Aylor 1972, Date and Lemon 1993). In closed habitats like forests with a high vegetation density, surfaces for reverberation and absorption are more important and acoustic conditions are more constant than in open habitats (Waser and Brown 1986). Open habitats, with less dense vegetation and more turbulent air, provide more variable conditions for sound propagation (Morton 1975). Other important factors are calling height as well as the call structure (see Chapter 2 for more details).

Several theoretical predictions have been made to explain observed differences in in the vocal variability of species living in different environments. Marler (1967) hypothesized that arboreal animals, which inhabit relatively dense habitats, should exhibit a more discrete and stereotyped vocal repertoire, while in contrast, in terrestrial species ranging in open habitats more graded repertoires might be possible. Discrete repertoires contain signals with no intermediates between call types (Marler 1967); hence, they can operate without accompanying visual or other contextual cues. A graded signal system on the other hand is characterized by continuous variation between and/or within signal types. Several studies fits with Marler's hypothesis and vocal structures of primates living in closed forest habitats seem to be characterized by less inter-call type variability, compared to call structures of primates living in open habitats (between species: Marler 1973, Waser 1982; between populations: Mitani et al.

1999). Furthermore, vocal repertoires of arboreal species seem to contain a larger number of call types (Marler 1973, Schott 1973, Schrader and Todt 1993). Repertoires of terrestrial primates on the other hand, are rather characterized by a limited number of call types with a higher intra- as well as inter-call type variability (e.g. Aich et al. 1990, Fischer and Hammerschmidt 2002).

However, for several species the predictions proposed above are not met and a recent review conducted by Ey and colleagues (2009) revealed mixed results. Especially for animals ranging through varying habitat types (e.g. deciduous forests, grassland savannah and open rocks, see above), which are characterized by different habitat acoustics, their environment appears does not appear to constitute such strong selective pressure (e.g. Koda et al. 2008, Ey and Fischer 2009).

Function

As mentioned in Paragraph 1.1.2., the structure of vocal signals is related to their function. In societies with intense male competition, contest or display signals regularly occur during agonistic interactions (e.g. Chaffin et al. 1995, Kitchen et al. 2003), while in species with less intense competitive relationships, such status signals, appear to be uncommon (e.g. Boinski and Mitchell 1997, Preuschoft and Van Schaik 2000). Hereby, animals more often apply a variety of assessment or appeasement signals to resolve social conflicts (DeWaal 1988, Tierry et al. 1989, Hohmann 1991). Furthermore, in primate societies with extensive affiliative relationships, animals exhibit several vocal signals to facilitate friendly interactions (e.g. Soltis et al. 2002, Gustison et al. 2012).

In addition, it has been proposed that the complexity of primate social systems should act as a selective pressure on the vocal design, irrespective of the characteristics of the social relationships (e.g. McComb and Semple 2005). In accordance with the social complexity hypothesis, animals living in large and complex groups, with numerous social relationships, should exhibit a more complex vocal repertoire with a higher number of call types (e.g. McComb and Semple 2005, Pollard and Blumstein 2012, Freeberg et al. 2012). Until now, the clear interplay between social system and vocal production is largely unknown and comparative data are definitely needed to resolve this issue.

1.2.2. Signal usage

Mechanism

Primates use acoustically different vocalizations in different behavioural contexts. Some calls, for example, are only uttered when specific predators are spotted (e.g. Cheney and Seyfarth 1980, Zuberbühler 2000b, Wheeler 2009), others are mainly given when approaching an infant (e.g. Rendall 1999, Fischer and Hammerschmidt 2002) or when callers are at the risk of losing contact with preferred associates (e.g. Cheney and Seyfarth 1996, Rendall et al. 2000, Ramos-Fernandez 2005). However, in contrast to the call structure, much less is known about the developmental and physiological mechanisms underlying call usage.

Several studies suggest that although call usage is also largely innate and strongly constrained by the affective state of the caller (e.g. aversiveness [Jürgens 1979, Schrader and Todt 1993], arousal [Rendall et al. 2003]), learning and experience during ontogeny play a role in the usage of calls. Cheney and Seyfarth (1997b) for example reported some degree of flexibility in the development of the vervet monkeys' alarm calling system. Adult vervets give acoustically different alarm calls to leopards, eagles, and snakes, and each call type elicits a different adaptive response. Individuals on the ground run into trees when they hear a leopard alarm, look up in the air when they hear an eagle alarm, and peer into the grass around them when they hear a snake alarm (Seyfarth et al. 1980). Adult vervets are highly selective, giving alarm calls only to a narrow range of predators (mammalian carnivores, eagle and snakes). Infant and juveniles, however, make many more "mistakes", albeit not completely random, by giving leopard calls also to warthogs, or eagle calls to pigeons that pose no danger to them (Seyfarth and Cheney 1986). Hence, although young vervets appear to be predisposed to divide other species into different classes (i.e. terrestrial versus aerial), they need time and experience to learn the appropriate context for the utterances of their predator specific vocalizations (Cheney and Seyfarth 1997b). The mixture of relatively innate mechanisms and experience on the vocal usage is not unique to vervet alarm calls and has also been documented in the development of vervet grunts (Seyfarth and Cheney 1986), intergroup wrrs (Hauser 1989), rhesus macaque coos and gruffs [*Macaca mulatta*, Owren et al. 1993] and the alarm calls of sifakas (*Propithecus verrauxi*, [Fichtel and van

Schaik 2006]). Furthermore, several studies have shown that infants differ from adults in their calling rate, i.e. infants vocalize more frequently. While some of this vocal activity might be related to the weaning process (e.g. Todt et al. 1995), it might also provide vocal practise (Elowson et al. 1998). Infant pygmy marmosets (*Cebuella pygmaea,* [Snowdon and Elowson 2001]) for example go through an intense vocal phase, termed as ‘babbling period’, in which they produce long bouts of calls that resemble in most features the calls of the species repertoire.

As with mechanisms underlying the ontogenetic changes in vocalisations, the neural mechanisms involved in call usage are also poorly understood. As already mentioned, the PAG functions as an important relay station between the vocalization-controlling pathways and the motor neurons responsible for the vocal output (Jürgens 2009). Besides inputs from the limbic and sensory system, the PAG receives additional connections from the anterior cingulate cortex which allows certain voluntary control over the initiation and possible the duration of vocalization (Jürgens 2009). Lesioning studies in macaques have shown that monkeys trained to master a vocal operant conditioning task (i.e. to increase vocalization rate to a conditioned stimulus with food as a reward), are no longer able to do this task after a bilateral destruction of the anterior cingulate cortex (Sutton et al. 1974).

Phylogeny

How the usage of vocal signals is influenced by phylogenetic constraints is not well known, but the developmental and neural mechanism mentioned above predicts a much smaller phylogenetic impact. Indeed, the limited studies conducted among closely related taxa appear to show certain-interspecific differences in the use of vocal signals in different contexts. For example, rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques produce coo and gruff calls, but individuals in the two species use them in different ways. When Japanese macaques vocalize during play, they give a coo. Conversely, while rhesus macaques can produce coos, they give gruffs when they play (Owren et al. 1993). Similar results have been found in facial signals among closely related macaque taxa. Although signals do not vary strongly in number and/or structure they do sometimes differ in the context of usage (Thierry 2000).

Environment

Environmental features, such as vegetation density, affects sound transmission and primates use different strategies to improve signal transmission (see above). In correspondence to the flexibility in the rate of calling, previous research has shown that short-term fluctuations in visibility may directly affect calling rates. When the visibility was poor and the risk of losing contact with social partners increased, primates calling more frequently than in open habitats (Rendall et al. 2000, Ey et al. 2009). Some primates may even adjust the timing of their calls to utter them mostly in predictable time intervals with low background noise level (Egnor and Hauser 2006, Schneider et al. 2008). However, in general, it is difficult to isolate the ecological influence on the call usage, since other factors, such as the context of calling or the proximity between caller and recipients, also influence calling rates and might override the effect of the environmental related usage variability (e.g. Koda et al. 2008).

Function

Flexible vocal usage has been demonstrated in several primate species, with much work focusing on the role of the social “audience” in explaining variation in call utterances. Vervet monkeys for example, will not utter alarm calls in the absence of conspecifics (Cheney and Seyfarth 1992). They even modify their calling rate based on the presence of kin (Cheney and Seyfarth 1992). Thomas langurs (*Presbythis thomasi*) pay more attention to the vocal reaction of their group members and adjust their calling rate to the calling behaviour of adult females (Wich and deVries 2006).

Studies on call usage indicate that sex-specific social roles may have an impact of the utterances of vocal signals and context specific calling rate (e.g. Gros-Louis et al. 2008, Bouchet et al. 2010, 2012). In female-bonded societies, females utter much more affiliative- and contact calls to facilitate social interactions, compared to males (e.g. Bouchet et al. 2010).

1.2.3. Signal response

Mechanism

In primates and many other mammals, selection appears to have favoured a much higher plasticity on processing and reacting to vocal signals than on producing them (Cheney and Seyfarth 2003). Although the response behaviour of primates, to at least some vocal signals, is to a certain extent mediated by innate nervous system-responses (for example the instinctive escape and avoidance responses to alarm calls (Herzog and Hopf 1984, Seyfarth and Cheney 1986]), listener’s reaction toward calls are much more flexible and depend strongly on cognitive and developmental mechanisms (e.g. see Cheney and Seyfarth 1997b, 2007 and Fischer 2012 for reviews). To get invaluable insights into the developmental and cognitive underpinnings of primate vocal responses, playback experiments present a powerful type of field experiment. By using playback experiments, variation in the development of call discriminations can be investigated, as well as how primates integrate additional cues when responding to vocal signals.

Playback studies indicate that the discrimination of primate vocal signals, as measured by the subject’s response, undergoes pronounced changes during development (e.g. Cheney and Seyfarth 1997b, Fischer et al. 2000). Barbary macaque infants, for example, begin to respond significantly more strongly to their mother's contact calls than to other females' calls from an age of about two and a half months. In the first few weeks of life, however, they hardly ever orient to any sounds in their environment, suggesting that both maturation and learning determine the onset of an appropriate call response (Fischer 2004). Studies conducted on chacma baboons indicate that infant baboons gradually develop their ability to discriminate among graded variants of certain call types (Fischer et al. 2000). Chacma baboon loud barks exhibit important acoustic differences in association to the context they were uttered in. These barks grade from harmonically rich contact calls, used when the signaller is at risk of losing contact with associates (Cheney and Seyfarth 1996), into noisier and harsh alarm barks, uttered when encountering predators (Fischer et al. 2001a). At the age of 4 months, infant baboons did not distinguished between the different bark types and responded equally strongly to both calls, while at about 6 months they started to discriminate between the contact and alarm barks and responded much more strongly to the latter (Fischer et al. 2000). Similar gradual development to predator-specific alarm calls has been documented in the responses of Goeldi's monkeys (*Callimico goeldi,* [Masataka 1983]), bonnet macaques (*M. radiata*, [Ramakrishnan and Coss 2000]) and sifakas (*Propithecus diadema*, [Fichtel and van Schaik, 2006]). The view that experience, and not simply maturation, mediates the development of vocal discrimination and subsequently the specific responses behaviour, is further supported by observations that several primate species respond to the alarm calls of birds, ungulates, and other primate species (Zuberbühler 2000a, Fichtel 2004). Hence, primates need to learn to discriminate between biologically relevant differences in acoustic structure and throughout their whole life, primates are able to form new associations between particular sounds and certain ecological or social events, as long as there is a predictable link between the vocal signal and an external object or event (Cheney and Seyfarth 2010).

In addition to responding to variation in the acoustic structure of a call, primates may also take contextual cues into account before responding to a signal (see Wheeler and Fischer 2012 for a review). Important cues, such as the relationship status between subject and caller (e.g. Engh et al. 2006, Cheney et al. 2010), may result in the signaller attributing different "meanings" to a signal or signalling event (used here as "natural meaning", described firstly by Paul Grice 1957) and accordingly, may cause different responses. For example, baboon males respond differently to female screams depending on the contextual cues available, such as whether the calling female is a "friend", has a dependent infant and whether the aggressor is likely an infanticidal male (Palombit et al. 1997). While males largely ignore the screams of non-associated females, they strongly respond to the same calls of their female friends once they are under physical attacks of other males (see introduction in Chapter 4 for more examples).

Function

As mentioned above primates distinguish minor acoustic differences in their calls, such as individual variations, and may respond differentially to vocal events due to additional contextual cues. Hence, playback studies can be used to get important insight into the social cognition of a species, such as social knowledge, i.e. the recognition of individuals and their classification according to different social attributes (Cheney and Seyfarth 2007; Fischer 2012). Social knowledge has been investigated at different levels, including individual recognition, categorization according to social attributes, and group membership recognition.

Playback studies revealed that how primates differentiate among their conspecifics' calls appears to be driven by the characteristics of the species` social relationships. In several playback experiments it has been shown that males, which exhibit highly hierarchical intra-sexual relationships, classify other individuals with regard to their dominance rank (e.g. Bergman et al. 2003, Kitchen et al. 2005). Contrary to this, in societies within which relationships are characterized by rather relaxed and affiliative interactions, subjects take different social attributes, e.g. bond strength, into account when responding to a signal (e.g. Soltis et al. 2002, Bergman 2010). In addition, primates living in stable groups often distinguish between members of their own group and individuals belonging to other groups. Importantly, the way how subjects respond to non-group members may not only depend on the competitive regime between groups, but also on the status of the individuals. Males typically consider other males as competitors (Wich 2002, Herbinger et al. 2009), while cycling females may be attracted to neighbouring or stranger males (Cheney and Seyfarth 1987, Palombit 1994; Agoramoorthy and Hsu 2000). Under specific conditions individuals may even distinguish among different neighbouring groups (see Introduction in Chapter 4 for a detailed description of the "dear-enemy" and "nasty neighbour" effect). In general, however, we know little about how the competitive regime contributes to the response behaviour of primates, and the interplay between the characteristics of individual relationships and the primates' social knowledge is until now largely unexplored.

1.3. Baboons as a model

Baboons are well suited as model system to study the different factors that may play a role in the evolution of primate vocal behaviour. Baboons comprise six closely related taxa distributed all over sub-Saharan Africa (Swedell 2011, Zinner et al. 2012). The four southern taxa (chacma baboon (*Papio ursinus*), yellow baboon (*P. cynocephalus*), olive baboon (*P. anubis*), Kinda baboon (*P. kindae*)) were traditionally referred to as ´savannah baboons´, since they exhibit similar social systems, (Swedell 2011, Zinner et al. 2012). They all live in discrete multi-male, multi-female groups with hierarchical male-male relationships and bonded females making up the stable social core of the group (Swedell 2011, albeit much less is known about the rather recently described Kinda baboons). Guinea baboons in contrast, live in a complex, multi-level social organization (Galat Luong et al. 2006, Patzelt et al. 2011, Maciej et al, 2013). Contrary to the harem-centred multi-level societies of hamadryas baboons (*P. hamadryas,* Kummer 1968), they exhibit multi-male, multi-female gangs, comprising 50-70 individuals. Although neighbouring gangs share almost identical home ranges, they meet only sporadically during the day; however they aggregate regularly at sleeping sites, and can form sleeping communities of more than 350 individuals (Galat-Luong et al. 2006, Patzelt et al. 2011). The size and composition of gangs varies considerably and while some gangs may only comprise 20-35 individuals, others consist of approximately 50-60 gang members (A Patzelt, PM, JF, unpublished data).

The social structure of Guinea baboons differs substantially from other baboons, especially with regard to the competitive regime. Although competitive interactions occur among males, they stand in stark contrast to the highly aggressive and agonistic male-male interactions commonly reported for savannah as well as hamadryas baboons (Kummer 1986, Henzi and Barett 2007, Swedell 2011). Furthermore, male Guinea baboons maintain strong affiliative bonds with other males, and engage in mutual grooming as well as ritualized greetings with each other (Whitham and Maestripieri 2003, Galat-Luong et al. 2006; Patzelt et al. 2011, Maciej et al. 2013). Because of the scarcity of agonistic interactions among Guinea baboon males within a gang, until now it was not possible to establish any dominance hierarchy among males. Female social relationships are rather weak in Guinea baboons, in contrast to the complex affiliative and agonistic relationship characteristics reported for savannah baboon females (Silk et al. 2009, Swedell 2011). Although the dispersal pattern of Guinea baboons still remains unclear, early population genetic analyses suggest female rather than male dispersal (A Goffe, G Fickenscher, D Zinner, J Fischer, unpublished data). The mating system still needs to be clarified, but the reproductive strategies of male Guinea baboons appear to be clearly different from the highly hierarchical mating system of savannah baboons (Swedell 2011) and the male-centred harem system reported for hamadryas baboons (Kummer 1968).

Although much information is available about the flexibility of baboon social systems in relation to their phylogenetic and socio-ecological history (e.g. Henzi and Barett 2007), much less is known about the impact of such variation on their vocal communication. Most studies considering baboon vocal communication have been conducted on savannah baboons, but virtually nothing is known about the vocal behaviour of wild Guinea baboons (but see [Byrne 1981]). Most of our current knowledge about baboon vocal communication comes from studies conducted on chacma baboons. In this taxon, various call types have been described (e.g. grunts [Owren et al. 1997], loud calls [Fischer et al. 2001b, 2002]) and the call type usage and calling rates have been assessed (e.g. Palombit et al. 1999, Rendall et al. 1999, Fischer et al. 2001b, Meise et al. 2011). Furthermore, the flexible response behaviour to different subjects, such as affiliative partners (Cheney and Seyfarth 1995, Crockford et al. 2007), aggressive opponents (Kitchen et al. 2005, Engh et al. 2006) or neighbouring group members (Kitchen et al. 2005) has been investigated, making chacma baboons an ideal candidate for an inter-specific comparison. For other baboons only few empirical studies of certain call types, such as grunts (e.g. Ey et al. 2009) or copulation calls (e.g. Semple 2002), plus several anecdotal repertoire descriptions exist (e.g. Hall and de Vore 1965, Kummer 1968, Waser 1982).

1.4. Aims and approaches of the thesis

My thesis has two major aims; firstly, the empirical description of the Guinea baboon vocal repertoire, illuminating both aspects of their vocal communication (structure and usage); secondly, an examination of the Guinea baboons’ social knowledge, using their response behaviour to assess how they discriminate among conspecifics. By comparing my results to studies conducted on other baboons, I will elucidate important inter-specific differences and try to assess how the Guinea baboons’ social system might have contributed to the specifics of their vocal pattern as well as their social knowledge.

According to the largely innate nature of primate calls, vocalizations should exhibit a strong phylogenetic signal and only marginally differ among closely related taxa. In accordance with the sound production mechanism, inter-specific acoustic variability might be attributed to morphological differences (e.g. body size, see ‘source-filter’ theory in Paragraph 1.2.1.). In contrast, emission rates and contexts of calling is much more flexible in primates and partly under voluntary control (see Paragraph 1.2.2.); hence, call usage is supposed to be less limited by phylogenetic constrains. Accordingly, inter-specific variation in relation to the social system or the environment might occur. The response behaviour of primates is highly flexible and underlies important developmental and cognitive mechanisms. As highlighted in Paragraph 1.2.3., primates classify other individuals in accordance to different social attributes, such as group (or unit) membership. How they respond to animals from other groups appears to be driven by the competitive regime, as well as the individual status. Hence, the characteristics of the species` social relationships should be reflected in the way how primates differentiate among their conspecifics (i.e. group vs. non-group member).

In Chapter 2 I report the results of transmission experiments to assess which acoustic parameters are particularly susceptible to degradation under different recording conditions. Specifically, I examined the influence of habitat type, transmission height and recording distance on the variation of several acoustic features of baboon calls. The results of this study are highly relevant for comparative studies, since varying recording conditions can affect the acoustic features of vocalizations and thus the outcome of the analyses. I used the outcomes of these experiments to control for recording conditions in the field as well as to justify the selection of certain parameter for the acoustic analyses of the Guinea baboons’ vocal repertoire. The results are published in *PLoS ONE* (Maciej et al. 2011).

In Chapter 3, I quantitatively describe the overall vocal repertoire of adult Guinea baboons and investigate the call morphology as well as the call usage. To examine the structure of the Guinea baboon repertoire, cluster analysis was employed together with an audio-visual classification scheme. I investigated call usage based on focal follows and assessed the context specific emission rates of the different call types. In accordance to the constrained sound production mechanism, Guinea baboons' vocalizations should exhibit a strong phylogenetic signal and only marginally differ from calls of other baboons. Inter-specific acoustic variability might be attributed to morphological differences between Guinea and other baboons. Call usage on the other side, may differ from other taxa. Following the hypothesis that the vocal communication of a species is driven by the specifics of their social interactions (i.e. call function, see Paragraph 1.1.2.), due to their largely tolerant and affiliative social structure, Guinea baboons should exhibit a pronounced rate of affiliative calls while they should only show a diminished occurrence of contest or display signals. The manuscript is presently under review in *Frontiers in Zoology*.

Chapter 4 reports the results of experiments in which I investigate how male Guinea baboons differentiate between subjects from their own social unit, a neighbouring social unit, and stranger males by using playback experiments. Male grunts from different categories ("own gang", "neighbouring gang" and "stranger gang") were broadcasted to 12 focal males and their response behaviour was analysed. Due the highly tolerant and less-competitive social style of Guinea baboons, males should not consider males from other gangs as intruders or direct competitors (a common characteristic among male chacma baboons), and thus largely ignore them. They should rather focus their social attention on the members of their own gang; since they are strongly associated and engage in frequent social interactions with those (see Chapter 4 for detail predictions). The results are published in *Behavioural Ecology and Sociobiology* (Maciej et al. 2013).

In Chapter 5, I summarize my results and try to illustrate how my project contributes to our current knowledge about the evolution of primate vocal communication and social cognition. Finally, I shortly discuss the most important methodological and analytical results of my project and will mention some implications for further bioacoustics research.

CHAPTER 2

Transmission characteristics of primate vocalizations: implications for acoustic analyses

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Abstract

Acoustic analyses have become a staple method in field studies of animal vocal communication, with nearly all investigations using computer-based approaches to extract specific features from sounds. Various algorithms can be used to extract acoustic variables that may then be related to variables such as individual identity, context or reproductive state. Habitat structure and recording conditions, however, have strong effects on the acoustic structure of sound signals. The purpose of this study was to identify which acoustic parameters reliably describe features of propagated sounds. We conducted broadcast experiments and examined the influence of habitat type, transmission height, and re-recording distance on the validity (deviation from the original sound) and reliability (variation within identical recording conditions) of acoustic features of different primate call types. Validity and reliability varied independently of each other in relation to habitat, transmission height, and re-recording distance, and depended strongly on the call type. The smallest deviations from the original sounds were obtained by a visually-controlled calculation of the fundamental frequency. Start- and end parameters of a sound were most susceptible to degradation in the environment. Because the recording conditions can have appreciable effects on acoustic parameters, it is advisable to validate the extraction method of acoustic variables from recordings over longer distances before using them in acoustic analyses.

Introduction

With the advent of affordable recording equipment and computer-based analytical tools, acoustic analyses have become an important part of ethological research. Formal training in bioacoustics is frequently lacking from standard curricula, and despite the existence of some first rate textbooks on the subject, such as Bradbury and Vehrencamp's Principles of Animal Communication (Bradbury and Vehrencamp 1998), most novices are faced with sketchy information regarding methodological pitfalls and considerations. Particularly when it comes to the analysis of vocalizations recorded in the field, a number of problems may arise when measurements are taken from spectrograms or amplitude waveforms. Specially, recording distance, calling height and habitat structure may have a strong effect on different acoustic variables.

Many of the earlier bioacoustic studies, as well as the majority of current studies of bird song (Nelson and Marler 1994, Kipper et al. 2006, Ripmeester et al. 2010) were based on the visual classification of sound spectrograms. Studies on insects and anuran acoustic communication, in contrast, frequently relied on call amplitude and temporal patterns (Gerhardt 1975, Fonseca and Revez 2002, Gerhardt and Huber 2002). Studies of more complex sounds, such as bird calls (Naguib et al. 2001, Owens and Freeberg 2007), carnivore vocalizations (Pfefferle at al. 2007, Manser 2001, Townsend et al. 2010) and primate calls (Hammerschmidt and Fischer 1998a, Fischer et al. 2002, Rendall et al. 2004, Neumann et al. 2010) applied various algorithms to extract different features from the frequency-time matrix (spectrum) determined by the means of the Fourier transform (for description see Bradbury and Vehrencamp 1998).

In particular, in studies of mammalian vocalizations a detailed description of energy distribution can be useful to describe differences related to sender variables such as individual identity, context or affective state. Some commercially available or public domain sound analysis programs (e.g. Avisoft SASLab [R. Specht, Berlin], RAVEN [Cornell Lab of Ornithology], PRAAT [Institute of Phonetic Science, http://www.praat.org] or Signal [Engeneering Design, Belmont, MA]) may offer the calculation of acoustic variables describing various acoustic features, while other studies make use of custom software programs to determine different sets of acoustic features (McCowan 1995, Schrader and Hammerschmidt 1997, McCowan et al. 1999). Depending on the type of the program and the vocalizations under study, such software programs may determine the location and modulation of the fundamental frequency, the statistical distribution of the amplitude in the frequency spectrum, the peak frequency, and so on. In recent years, several studies applied LPC analyses (linear predictive coding [Markel and Gray 1976]) to extract formants from animal vocalizations (Owren and Linker 1995, Fitch 1997, Fischer et al. 2001b, Reby and McComb 2003, Pfefferle and Fischer 2006). Such analyses yield measurements such as the location and width of the formants in the frequency spectrum.

The purpose of this study was to assess which acoustic parameters are particularly susceptible to degradation during sound propagation. It is well known that propagation distance has frequency dependent effects on sound transmission (Marten and Marler 1977, Marten et al. 1977, Waser and Brown 1986, Ey and Fischer 2009). In addition, numerous studies have demonstrated that different habitats vary in terms of reflections, scattering of sound, and background noise, which all lead to additional differences in signal attenuation and reverberation (Bradbury and Vehrencamp 1998, Waser and Brown 1986, Brown et al. 1995, Naguib 1997, Nemeth et al. 2001, Nelson 2003, Nemeth et al. 2006, Sabatini and Ruiz-Miranda 2008).

In this study we examined the influence of habitat type, transmission height and re-recording distance on the variation of several acoustic features when rerecorded under different conditions. As examples, we broadcasted and rerecorded a set of calls that we recorded from baboons (*Papio* spp.). We then assessed the effect of the different recording conditions on the reliability and validity of the parameter determination, using the custom software program LMA 2010 as an exemplary tool for the calculation of acoustic features. Based on these findings, we discuss the aspects which should be taken into account when field recordings are analyzed.

Methods

Ethics statement

The paper is based on playback experiments conducted in Germany in which calls were used that had been recorded as part of a series of studies in African National Parks. For each study, permission was granted by the respective local authorities to the head researcher(s) of the field projects. Recordings from baboons in the Moremi Wildlife reserve were made by permission from the Office of the President and the Department of Wildlife and National Parks of the Republic of Botswana to Robert M. Seyfarth and Dorothy L. Cheney (JF was a postdoctoral fellow of theirs and made the recordings between 1997-1999). Recordings in Tsaobis Leopard Park were made by Kristine Meise under research permission from the Ministry of Lands and Resettlement (2006-2007) and the Ministry of Environment and Tourism to Guy Cowlishaw.

Recording experiments

We conducted transmission experiments in the Nature Park ‘Kerslingeroeder Feld’ in the Goettinger Forest, Germany. The ‘Kerslingeroeder Feld’ is a 200 ha neglected grassland with high structured forest edges and old beech woodland. The grassland is characterized by open hay meadows and pastures. The beech woodland consists of deciduous forest with little undergrowth including mainly beech (*Fagus sylvatica*), oak (*Quercus robur*) and alder (*Acer* spp.).

The audio recordings were recorded from Chacma baboons (*Papio cynocephalus*) living in the Moremi Wildlife Reserve, Botswana (Fischer et al. 2001b, Fischer et al. 2002) and in the Tsaobis Leopard Park, Namibia (Meise et al. 2011). To assess the variation in relation to differences in call structure, we chose six call types that represent the spectrum of baboon vocal repertoire: ‘harsh barks’, ‘screams’, ‘wahoos’, ‘grunts’, ‘clear calls’ and ‘clear barks’. ‘Harsh barks’ are given by adult baboons in response to large predators (Fischer et al. 2001a, Fischer et al. 2001b). ‘Screams’ are very loud, harsh calls that are given by any individual mostly during aggressive interactions (Hall and DeVore 1965). The two-syllable bark variants or ‘wahoos’ are mainly used by adult male baboons as display calls of male competitive ability or as alarm vocalizations (Fischer et al. 2002, Kitchen et al. 2003). The soft modulated ‘grunts’ are the most common short-distance baboon vocalizations (Cheney et al. 1997), are harmonically rich, and occur in a variety of social and non-social contexts (Rendall 1999, Meise et al. 2011). The juvenile ‘clear calls’ and the adult ‘clear barks’ are harmonically rich loud calls given when at risk of losing contact with the group or when separated from particular individuals (Cheney et al. 1996, Rendall et al. 2000, Ey et al. 2007). Figure 2.1 presents spectrograms of the different call types.

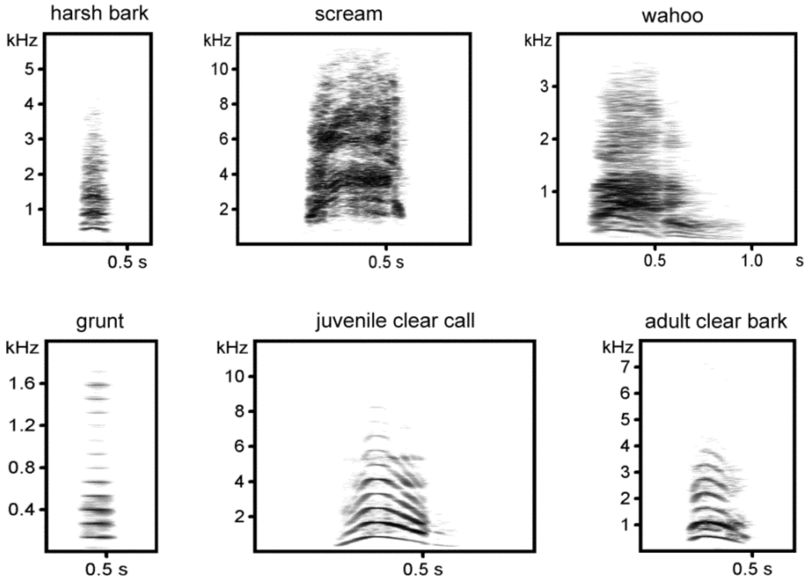


Figure 2.1. Broadcasted call types. The sampling frequency was adjusted for each all type.

To take the inter-individual variability into account, we used calls from five different individuals for each call type. The recording distances varied between call types: harsh barks were recorded from a distance of 8-12 m; screams at 3-5 m, wahoos at 8-12 m, grunts at 2-3 m, juvenile clear calls 3-5 m, and clear barks at 8-10 m. Note that information on recording distance was only available for bouts, but not for individual calls. Because the recording distance was constant within the denoted range for each call type (see above), the variable 'original recording distance' was not entered into the analysis. For the same reason, it is not possible to differentiate between the variation explained by the structure of the call and the one explained by variation in original recording distance. As a first pass at this question, we did an additional calculation with calls recorded below 5 m only (screams, grunts, and juvenile clear calls). In this analysis, the recording distance was below the re-recording distance, thus minimizing potential effects of signal degradation between the calling animal and the microphone.

As recording equipment, we used SonyWMTCD-100 DAT recorder or Marantz PMD660 solid-state recorder with Sennheiser directional microphone with a K6 power module and ME66 recording head and a MZW66 pro windscreen.

For the transmission experiments we varied the following factors: 1) habitat: open field or deciduous forest; 2) transmission height, i.e. loudspeaker and microphone were set at the same height of 0.5 m or 2 m above the ground; 3) distance between sound source and microphone: 6.25 m, 12.5 m, 25 m and 50 m. Distances and heights were measured using a measuring tape (length 50 m). In both habitats, we broadcasted and rerecorded the sounds ten times from both heights and each distance. To test to which extent the results of the experiment can be validly generalized to differing habitat conditions; we additionally broadcasted the same sounds once at five different locations (four locations together with one repetition from the locality of the first experiment) in both habitats and varied the other conditions as in the former experiment. In total we broadcasted and analyzed 6720 calls.

Calls were played back using an active speaker (David Active, VISONIK, Berlin) connected to a Marantz PMD-660 recorder. We rerecorded sounds using a Marantz PMD-661 SD-card recorder (48 kHz sampling frequency, 16 bit) and a Sennheiser directional microphone (K6 power module and ME66 recording head with ME66 Rycote windscreen). The active speaker and microphone were fixed on tripods. We measured the sound pressure level (dB) of the broadcasted calls by using a VOLTCRAFT 322 sound level meter (settings: ‘C’ weighting, response time: 125 ms). Table 2.1 shows the dB values of each call broadcasted in a sound proof chamber from 1.5 m distance.

Table 2.1. Sound pressure level (dB) of broadcasted calls measured at 1.5 m distance from the loudspeaker in a sound proof chamber.

Individual	harsh bark	scream	wahoo	grunt	clear call	clear bark
1	84.2	93.7	90.1	70.9	95.4	96.9
2	90.0	91.1	92.4	76.6	93.6	96.1
3	83.3	86.5	94.9	79.1	88.0	94.1
4	90.2	83.3	94.9	71.4	88.7	97.3
5	84.2	93.4	93.2	67.9	95.1	91.4

Temperature, humidity and wind speed were measured at each distance. In the deciduous forest the density was measured by using a wooden frame (0.5 m x 0.5 m) divided into 100 open wire mesh squares. Measurement consists of a count of the number of squares which are visually obstructed by the vegetation (see Freitas et al. 2002 for a detailed description). In the open habitat we measured the grass height by using the direct measurement method (Steward et al. 2001). The temperature in both habitats ranged between 19 and 24 °C and the humidity varied less than 20 %. The density in the forest habitat varied between 30 and 40 obstructed squares and the grass height in the open habitat ranged from 20 to 30 cm. Sounds were only broadcasted when the wind speed was below 3 km/h (anemometer: Siltknecht, Gossau Switzerland). A detailed description of the ecological data is given in Table S1 in the supplementary material.

Acoustic analyses

To describe the amplitude attenuation over distance and different broadcasting conditions, we calculated the maximal amplitude of the amplitude envelope for each call, using the Program Signal 5.0 (Engineering Design, Belmont, MA).

All broadcasted sounds were recorded with the same equipment settings and recording level was not changed during the experiments. Since we controlled for ambient noise we could automatise the extraction of the sound files, from the records, using the label function of AVISOFT SASLAB Pro (R. Specht, Berlin). To standardize the cutting process we defined a label threshold of 5 % and a fixed margin time of 0.6 s (which means that every waveform event exceeding 5 % of the ambient noise level was labeled and cut with a margin time of 0.6 s at both sides of the call). To obtain an appropriate range for the estimation of the acoustic features of the rerecorded calls we reduced the sampling frequency for each call type: harsh bark = 16 kHz, scream = 24 kHz, wahoo = 16 kHz, grunt = 4 kHz, clear call = 16 kHz and clear bark = 12 kHz. We submitted the resulting frequency time spectra to a custom software program that extracts different sets of parameters from acoustic signals (LMA 2010). To reduce the background noise we set the cut-off frequency at 100 Hz (the frequency range of all calls was above 100 Hz). The start and end thresholds were set at 20 %, which means that all time segments with a value lower than 20 % of the maximal amplitude at the beginning and end of the call were not considered.

Below, we briefly describe the underlying principle for the different groups of measurements. First, we measured the statistical distribution of the frequency amplitudes in the spectrogram (DFA). For each time segment, the overall amplitude was determined. Subsequently, we calculated the frequency at which the distribution of the amplitude reaches the first quartile of the total distribution, respectively (DFA1). Second, we calculated parameters describing the first dominant frequency band (DFB1). The dominant frequency bands are characterized by amplitudes that exceed a given threshold in a consecutive number of frequency bins. The numbers of the dominant frequency bands count from the lowest frequency up; the first DFB is not necessarily the DFB with the highest amplitude. Third, we specified the location of the peak frequency: the frequency with the highest amplitude in a certain time segment (PF). These parameters were extracted by using the general automatic extraction method of LMA.

For the tonal calls we calculated the fundamental frequency (F0), which is the lowest frequency band in harmonic calls. The F0 was calculated by using the tonal macro of LMA which is based on an autocorrelation function. Via this function, only tonal elements of a call are used to calculate the parameter whereas noisy elements are ignored. For the calculation we applied a manual as well as an automated method and compared both results. In both cases the tonality of a time segment was estimated by a cross-correlation algorithm. In the manual macro the possible F0 range is set by visual adjustment of a harmonic curser. The F0 itself was estimated by an algorithm searching the highest frequency amplitude within the range of the lowest cursor. In the automatic macro instead, the F0 is calculated automatically, with an algorithm estimating the least common divisor of the peaks of cross-correlation function. Table 2.2 provides a detailed description of the acoustic parameters.

Table 2.2. Description of the acoustic parameters used in the analyses.

Parameter	Description
Duration (ms)[1]	duration of the call
DFA 1 mean (Hz)[1]	frequency at which the distribution of frequency amplitudes reaches the first quartile, mean across time segments
DFB1 start (Hz)[2]	first dominant frequency band, at the beginning of the call
DFB1 end (Hz)[2]	first dominant frequency band, at the end of the call
DFB1 mean (Hz)[1]	mean first dominant frequency band across all time segments
PF max (Hz)[1]	frequency of the maximum frequency of the peak frequency across time segments
PF mean (Hz)[1]	mean of the frequencies with the highest amplitude across all time segments
F0 mean (Hz) [3]	mean fundamental frequency across all time segments

[1] Parameter used for reliability and validity calculation; [2] Parameter only used for reliability calculation; [3] Parameter only used for tonal calls and tonal call parameter calculation

Statistical analyses

In principle, there are two ways to explore the quality of the measurements: one is to examine the deviance from the original value (validity), the second is to assess whether a certain call yields the same readings under identical conditions (reliability). To assess the reliability we calculated the coefficient of variation (CV) for each call (n = 10 repetitions per call) under each condition and calculated the mean CV across all calls. To examine the validity, we calculated the differences in percentage between the calls rerecorded in the sound proof chamber (= Reference call) and the rerecorded calls at the respective distances and conditions. To compare the influence of the different factors we applied a linear mixed model analysis (SPSS 18.0) with call type, call variant, locality, habitat, re-recording distance and height as fixed factors.

To calculate the accuracy of the fundamental frequency we only analyzed tonal calls and applied again a linear mixed model to examine the influence of the different broadcasting conditions. To compare the accuracy of different extraction methods (manual vs. automatic) we visually compared the resulting parameters.

Results

Amplitude attenuation

Over longer distances signals showed stronger attenuation for both habitat types and transmission heights. At every distance (except at 0.5 m height and 6.25 m distance) the attenuation was stronger for the forest condition compared to the open field condition. Figure 2.2 shows the mean values for each call type. Under both habitat conditions, the signal attenuation was much stronger at low compared to the higher transmission height. For all call types at low transmission height the maximal amplitude decreased strongly already at a distance of 12.5 m. For calls broadcast in the dense habitat at low broadcasting height, amplitudes of the calls were reliably recordable (calculable) only until 25 m. Grunts were reliably recordable only until 6.25 m at low broadcasting height in both habitats. In general, signal attenuation was strongest at dense field conditions and low transmission height, and lowest in open field conditions and high transmission height.

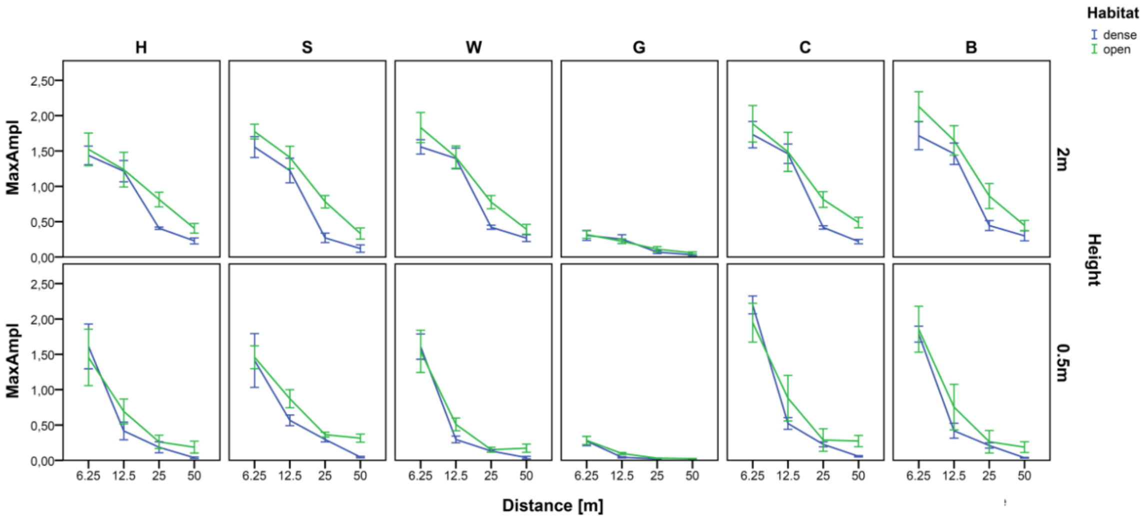


Figure 2.2. Amplitude attenuation in relation to habitat type, distances and calling height. The call types are shown in the different panels: H= harsh bark, S= scream, W= wahoo, G= grunt, C= clear call, B= clear bark. The maximal amplitude of the amplitude envelope (MaxAmpl) is calculated in mV. Mean values and standard errors are indicated.

Call structure

Reliability

Table 2.3 shows the mean CV values for each call type and parameter. The acoustic parameters describing the course of the first dominant frequency band (DFB1 start and DFB1 end) resulted in a large variability (> 10 %) for each call type and hence a poor reliability. The other acoustic parameters yielded a mean variability of less than 5 % (except Pf max = 5.27 %). The fundamental frequency (F0) in tonal calls and the DFA parameter (DFA 1mean) yielded the largest accuracy and showed variation of less than 3 %. Grunts showed the largest variability compared to the other call types. It is the only call type that showed a variation of more than 20 % for two general parameters (DFB 1 start and DFB 1end).

Table 2.3. Reliability in relation to call type and acoustic parameters measured as coefficient of variation (CV).

Call	Duration (ms)	DFA 1mean (Hz)	DFB 1start (Hz)	DFB 1end (Hz)	DFB 1mean (Hz)	Pf max (Hz)	Pf mean (Hz)	F0 (Hz)
harsh bark	1.44 %	1.34 %	10.07 %	15.00 %	4.38 %	3.48 %	3.16 %	-
scream	1.83 %	1.58 %	15.54 %	17.14 %	4.20 %	3.32 %	2.03 %	-
wahoo	4.30 %	1.67 %	12.30 %	17.19 %	4.39 %	4.99 %	3.44 %	-
grunt	9.20 %	4.45 %	27.46 %	24.97 %	6.47 %	12.36 %	8.34 %	2.20 %
clear call	1.36 %	1.34 %	14.58 %	14.31 %	3.08 %	2.37 %	1.66 %	4.30 %
clear bark	3.00 %	1.52 %	11.77 %	18.09 %	2.93 %	5.11 %	3.32 %	1.67 %
Mean	**3.52 %**	**1.99 %**	**15.29 %**	**17.78 %**	**4.24 %**	**5.27 %**	**3.66 %**	**2.73 %**

The CV-values represent mean values across the different conditions for each call, broadcasted and rerecorded ten times at each condition

Validity

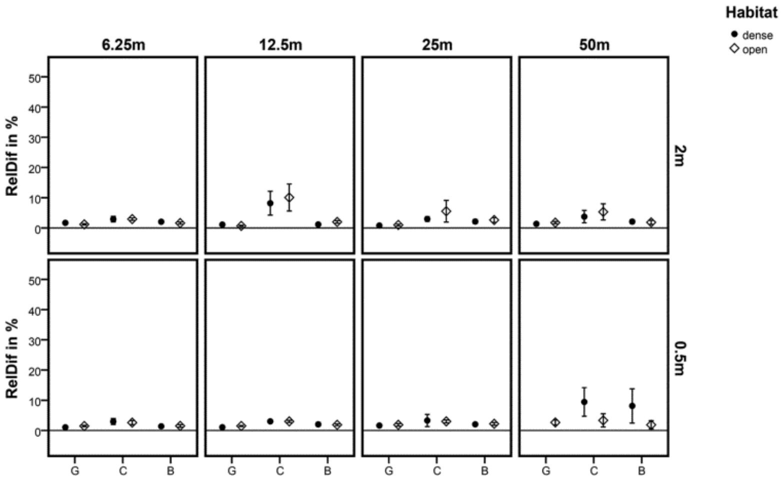
The F0 parameter revealed a high accuracy in the automatic tonal extraction method; there were no significant differences in the measurements between the reference calls and the rerecorded calls under different conditions (Table 2.4). The two methods (automatic vs. manual) for extracting the F0 yielded similar results. Both methods revealed a high accuracy, with some advantage for the manual determination for specific calls and under specific circumstances (see Figure 2.3).

Table 2.4. Validity of the fundamental frequency in tonal calls in relation to distance, height and habitat.

Tonal calls	Call variant	Locality	Distance	Height	Habitat
grunt	2.1	1.8	1.7	1.2	1.5
clear call	5.4*	2.0	2.5	0.8	0.5
clear bark	3.4*	1.3	2.5	0.6	0.8

The table shows F values of the linear mixed model analysis. Values for one repetition of every call at each locality under each condition are calculated. Grunts at 50 m distance were excluded from the analysis. * $p < 0.05$.

A) F0 automatic



B) F0 manual

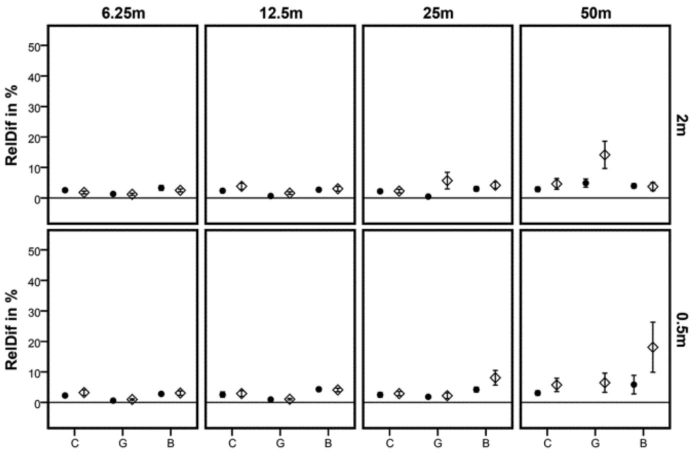


Figure 2. 3. Variability of the fundamental frequency (F0) by using two different calculation methods. The x-axis shows the different call types, G: grunt, C: clear call and B: clear bark. The y-axis shows the relative differences of the acoustic parameters for each condition. Panel rows represent different heights, while panel columns represent different distances. (A) The variability under different conditions calculated via the automatic macro. (B) The variability calculated manually. The plots indicate mean values from ten repetitions at one locality; error bars indicate the confidence interval of 95 %. The horizontal lines denote a variation of 0 %.

General call parameter calculation revealed highly significant F values for each call parameter under almost every condition, except for different locations (Table 2.5). Hence, the calculation differences were strongly influenced by the varying broadcasting conditions. The factor 'height' yielded the largest variation for almost every acoustic parameter followed by re-recording distance, call type, habitat and call variant. Different localities in contrast mainly resulted in non-significant differences. Duration was the acoustic parameter with the highest accuracy between the various conditions. Except for long distances, it showed relatively high accuracy for every condition (Figure 2.4A). By contrast, the distribution of frequency amplitudes (DFA1 mean) only revealed small calculation accuracy. In particular, DFA1 mean was strongly influenced by transmission height (Figure 2.4B). Transmission height also had a large effect on peak frequency (PF max, PF mean) and in this case caused strong parameter degradation as well (Figure 2.4C and 2.4D). Because of the lack of reliability we did not analyze the parameters DFB1 start and DFB1 end.

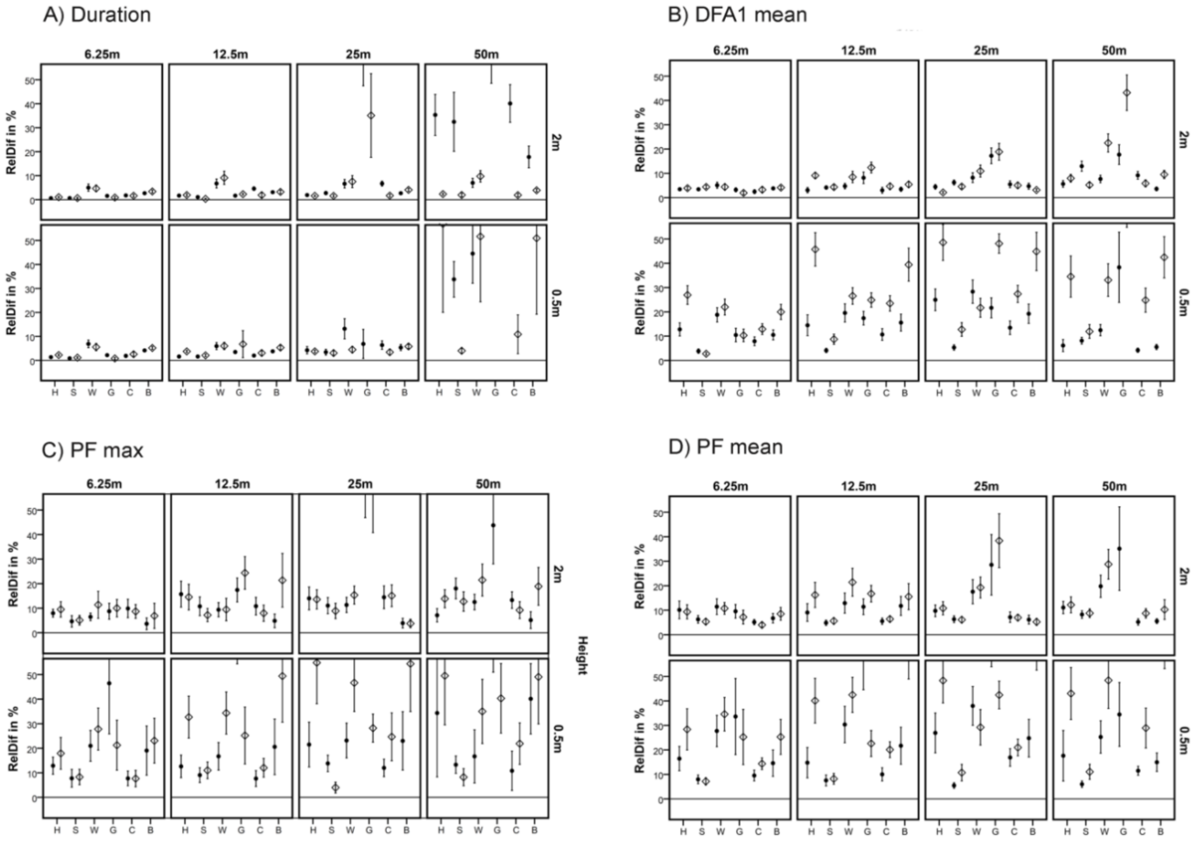


Figure 2.4. Validity of four different parameters in relation to habitat type, transmission height, distances and call type. Four different acoustic parameters are shown in the graphs; (A**)** Duration, **(**B**)** DFA1 mean, (C**)** PF max, (D) PF mean. The x-axis shows the different call types, H: harsh bark, S: scream, W: wahoo, G: Grunt, C: clear call and B: clear bark. The y-axis shows the relative differences of the acoustic parameters for each condition. Panel rows represent different heights, while panel columns represent different distances. The plots indicate mean values across five different localities; error bars indicate the confidence interval of 95 %. The horizontal lines denote a variation of 0 %. Black dots indicate dense habitats, white squares open habitats.

Similar to the reliability calculation, grunts showed the largest differences in the measurements between original calls and rerecorded calls. The spectrogram in Figure 2.5A shows a grunt example rerecorded in the sound proof chamber and in a dense habitat at 6.25 m distance and 0.5 m height. Screams instead only yielded small differences throughout all different conditions for most of the general acoustic parameters (see Figure 2.5B for a spectrogram of a scream recorded in a soundproof chamber and at 50 m distance in a dense habitat at 0.5 m height).

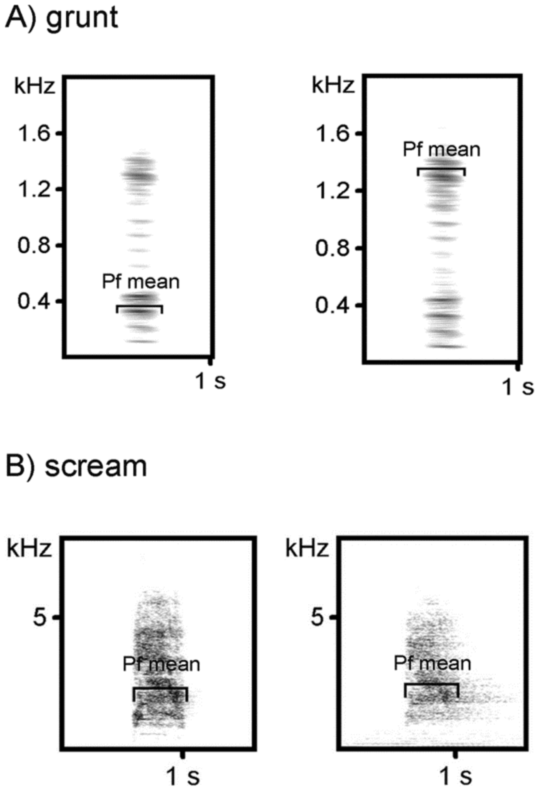


Figure 2.5. Comparison of peak frequency (PF mean) from two different call types. The Peak frequency (PF mean) of a tonal grunt (A) and a scream (B) recorded in the soundproofed chamber compared to the same grunt recorded in a dense habitat at 0.5 m height and 6.25 m distance and the same scream recorded in a dense habitat at 0.5 m height and 50 m distance. PF mean is indicated.

Table 2.5 shows the F values of the applied linear mixed model analysis for all the different call parameters under the different conditions. The F-values for each call type are shown separately in the supplementary material, Table S2 A-F. As mentioned before we were not able to include the distance of the original recordings as a continuous covariate. Therefore, we did a separate calculation for the three call types (screams, grunts, and juvenile clear calls) originally recorded at distances below 5 m (Table 2.6). We found a clear increase in F-values for the factor ‘call type’, and decrease in F values of all other factors. Overall, however, the effects of the different factors were generally following a similar pattern (Table 2.6).

Table 2.5. Validity of characteristic sound parameters in relation to distance, height and habitat.

Parameter	Call type	Call variant	Locality	Distance	Height	Habitat
Duration	31.9*	1.3	6.3*	116.84*	26.8*	1.6
DFA1 mean	46.9*	11.81*	3.5	47.3*	504.3*	188.8*
DFB1 mean	14.4*	31.8*	0.7	99.2*	99.5*	0.7
Pf max	48.1*	9.7*	1.9	22.0*	66.8*	7.5
Pf mean	50.2*	11.9*	2.2	15.1*	170.0*	33.3*

The table shows F values of the applied linear mixed model analysis. Values for one repetition of every call at each locality under each condition are calculated. * $p < 0.05$.

Table 2.6. Validity of characteristic sound parameters in relation to distance, height and habitat. Call types (screams, grunts, and juvenile clear calls) with an original recording distance below five meter are shown.

Parameter	Call type	Call variant	Locality	Distance	Height	Habitat
Duration	48.5*	1.8	3.9*	57.2*	3.1	0.6
DFA1 mean	139.5*	1.8	0.7	67.2*	120.1*	70.4*
DFB1 mean	21.6*	30.5*	0.8	28.7*	29*	0.7
Pf max	104.3*	11.3*	0.6	14.9*	4.2*	1.3
Pf mean	109.6*	2.9*	0.3	13.4*	31.4*	0.9

The table shows F values of the applied linear mixed model analysis. Values for one repetition of every call at each locality under each condition are calculated. * $p < 0.05$.

Discussion

As expected, we found significant effects of recording conditions on acoustic features. Along with re-recording distance, recording height had a large impact on the validity of acoustic parameter estimation. Calls broadcasted at low heights (e.g. 0.5 m) showed high structural degradation within short distances. Call structure was a further important explanatory factor for the variation in parameter estimation. As long as some harmonics remained, tonal calls showed a high validity in the estimation of parameters describing fundamental frequency (F0). Because we only have one broad estimate of the distance between animal and microphone for each call type, we were unable to assess the influence of the original recording distance on sound degradation within call type. In principle, the analysis of calls that are already notably degraded may lead to over-estimations (cumulative effects) or under-estimations (the sensitive components are already missing in the original recordings) of the effect of propagation. The comparison between call types originally recorded below 5 m and call types originally recorded at about 10 m showed a similar result as the analysis incorporating all call types, however. The most striking difference was that more variation was explained by the factor ‘call type’. This is due not only to the reduced number of call types, but also the fact that the degradation of sounds on parameter estimation has a significant higher influence on noisy than on tonal calls. In this analysis only two tonal and one noisy call type remained. The consideration of these three call types which were originally recorded at a shorter distance enhanced the contrast between tonal and noisy calls in comparison to the first analysis with six call types. In addition, the explained variance of the factor ‘re-recording distance’ and ‘height’ was reduced. Unfortunately, we cannot directly differentiate between the variation explained by the difference in call structure and that explained by the difference in original recording distance. To empirically address the issue of the combined effects of recording distance and re-recording distance, one would need to conduct a study where the distance between animal and microphone is systematically varied. In the present study, we aimed at reducing the variation within call types by selecting calls with a very good quality only.

One of the critical acoustic parameters is DFA (distribution of frequency amplitudes). These parameters describe the statistical distribution of energy in the whole frequency spectrum. Therefore, it is not surprising that the stronger attenuation of low frequencies at lower broadcasting levels makes it difficult to estimate the correct distribution of frequency energy of the original call. Our results are generally in agreement with other researchers’ descriptions of amplitude and frequency dependent attenuation in relation to broadcast conditions and distances (Marten et al. 1977, Wiley and Richards 1978, Brown and Waser 1988, Bradbury and Vehrencamp 1998, Nemeth et al. 2001, Pedgham 2004). The high impact on the attenuation of call amplitude and structural degradation at low heights corresponds to the ‘floor effect’ described by Nelson (2003). This effect influences in particular frequencies below 1 kHz. As a consequence the estimation of acoustic parameters is susceptible when calls are transmitted close to the ground.

Parameters describing the peak frequency (PF) are also strongly influenced by broadcasting conditions. Here call structure is an important factor. Calls with dominant single PF peaks (e.g. ‘scream’) are less influenced by broadcasting conditions than call types with several similar amplitude peaks (e.g. ‘grunt’). In such cases small changes in the amplitude of the PF can lead to incorrect identification of a different amplitude peak as the PF (see Figure 2.5). A further aspect is the frequency range of the highest amplitude. Grunts with a PFs around 300 Hz showed the strongest degradation at the transmission height of 0.5 m. Because baboons give their grunts mostly from the ground, subtle structural variation cannot be transmitted reliably over larger distances. Not surprisingly, these calls are mainly used for short distance communication. Ey and colleagues (Ey et al. 2009) showed that olive baboons produce grunts with longer call duration in dense habitats, possibly to counterbalance the worse propagation conditions. At higher transmission heights, both DFA and PF parameters revealed a much higher validity even if they were transmitted in the forest habitats. To a lesser degree, this effect was also found in other call types, including harmonically rich loud calls such as ‘clear barks’ and ‘clear calls’. In relation to mean and maximum values, start and end parameters revealed the lowest validity. One reason is that in most call types, start and end parts have a lower amplitude than the rest of the call. Therefore, degradation and absorption has a higher influence on these parts than on the rest of the vocalisation. In addition, the end of calls is most strongly influenced by reverberation over distance (Slabbekoorn et al. 2002).

Tonal calls were less susceptible to sound degradation as long as some harmonics remained in the frequency spectra. Although there are different ways to calculate the F0, many algorithms focus on the estimation of the autocorrelation function of the frequency spectra (Morton 1975, Schrader and Hammerschmidt 1997). The autocorrelation function is able to recalculate the F0 of degraded spectra as long as some harmonic peaks remain. In cases in which the degraded spectra have too little harmonic information or the original tonal call has too few harmonics to make a reliable calculation, a visual control of the F0 proposed by the algorithm can lead to a higher reliability of F0 calculation (see Figure 2.3). Other sound analysis programs, like Avisoft SASLab, PRAAT or SIGNAL offer the possibility to determine the range of F0. This is an alternative possibility to increase the reliability of F0 estimation. Temporal parameters, like call duration, depend mainly on the attenuation of sound amplitude. In contrast to open habitats, dense forest vegetations can cause considerable reverberation and absorption of a signal (Morton 1975, Waser and Brown 1986, Schrader and Hammerschmidt 1997, Slabbekoorn et al. 2002).

In sum, our results suggest that the estimation of acoustic parameters recorded from larger distances, especially transmitted by callers on the ground, lead to erratic measurements. Hence, it is advisable to assess the reliability and validity of certain parameters before they are used in further statistical analyses. The estimation of F0 seems to be the only acoustic parameter which can be reliably calculated as long as a strong signal conveys sufficient harmonics. For a higher caller position a higher microphone height might be favorable. However, this can only slightly reduce the described effects and not compensate for them. Although it is not always possible in studies of free-ranging animals to assess the exact distance at which the calls are recorded, it seems to be advisable to include as much information as possible on recording distance, to allow for a judgment of the reliability of the acoustic measurements taken.

Whilst this study shows that baboon vocalizations suffer some distortion when recorded at low transmission height and far distances, further research is required to understand the relevance of this finding to species living in different habitats and having other vocal types, with different physiological sound production mechanisms. It is also necessary to take into account that the information encoded in a given call structure needs only to be transmitted over the distance at which the animal typically communicates. Degradation that occurs at distances greater than an individual’s natural communication range would thus be functionally irrelevant. Unfortunately, very little is known about how call distortion affects the perception of calls in nonhuman primates. From birds we know that they are able to extract the distance of the signaller from the degree of signal degradation (Naguib and Wiley 2001). A playback study in African elephants showed very nicely the differences between signal detection and derived information. Although the elephants were able to recognize contact calls of family members under optimal condition up to 2.5 km, they usually achieved reliable recognition at distances below 1–1.5 km (McComb et al. 2003). The reason could be that the crucial components of social identity are distorted at a distance above 1 km due to background noise or attenuation effects. . Such playback studies that test the influence of sound degradation on conspecifics' responses are also required in nonhuman primates, before we can fully assess the reliability and validity of acoustic field recordings.

Acknowledgements

We thank our colleagues Brandon Wheeler, Barbara Tiddi, Tabitha Price, and Tanja Haus for their scientific input during long lasting debates and for helping us with the experimental settings. We also wish to thank David Reby for his useful comments on the manuscript. Thanks also go to our essential technician in the lab Ludwig Ehrenreich, who always tokes great care of the technical equipment

Appendix

Table S1. Ecological data measured at each locality.

	Locality	Density	Temperature (°C)	Humidity (%)	Wind speed (km/h)
Dense	1	35.5	20.9	65.4	0.0
	2	30.3	20.9	63.5	0.3
	3	40.2	21.3	66.5	0.0
	4	31.3	20.0	72.8	0.0
	5	38.5	19.4	78.9	0.0
		Grass height (cm)			
Open	1	29.3	19.4	83.3	2.1
	2	23.5	19.1	71.8	2.9
	3	22.0	20.8	65.1	0.5
	4	20.3	23.3	66.5	0.3
	5	22.5	24.2	65.9	0.0

Table S2. Validity of each call type in relation to distance, height and habitat.

A)	**harsh bark**	Call variant	Locality	Distance	Height	Habitat
	Duration	1.6	1.9	41.1*	21.6*	13.8*
	DFA1 mean	12.9*	1.1	8.5*	196.2*	62.9*
	DFB1 mean	30.9*	0.9	60.1*	111.2*	2.7
	Pf max	10.6*	1.9	4.2*	25.6*	14.2*
	Pf mean	51.7*	1.5	1.8	62.6*	32.4*

B)	**scream**	Call variant	Locality	Distance	Height	Habitat
	Duration	3.3	1.1	42.9*	1.0	28.1*
	DFA1 mean	7.2*	0.3	20.5*	5.6	1.6
	DFB1 mean	114.7*	0.2	15.3*	67.8*	0.1
	Pf max	4.1*	0.3	4.5	0.2	8.0*
	Pf mean	18.2*	0.2	1.5	7.1*	5.1

C)	**wahoo**	Call variant	Locality	Distance	Height	Habitat
	Duration	3.2	1.7	15.6*	15.2*	0.1
	DFA1 mean	43.5*	3.9	8.3*	172.4*	24.3*
	DFB1 mean	13.6*	1.2	68.2*	6.2*	8.6*
	Pf max	8.6*	1.1	2.5	38.3*	9.8*
	Pf mean	81.9*	2.5	5.1*	85.1*	6.1*

D)	**grunt**	Call variant	Locality	Distance	Height	Habitat
	Duration	2.2	3.4*	37.5*	2.9	6.9*
	DFA1 mean	1.4	0.3	74.6*	65.5*	34.7*
	DFB1 mean	9.7*	2.6	20.0*	13.7*	13.1*
	Pf max	13.0*	1.0	13.5*	5.8	2.2
	Pf mean	5.4*	0.6	13.7*	15.2*	0.7

E)	**clear call**	Call variant	Locality	Distance	Height	Habitat
	Duration	0.7	3.8*	61.9*	11.3*	63.2*
	DFA1 mean	15.1*	0.8	8.8*	140.2*	51.5*
	DFB1 mean	24.6*	1.1	36.3*	309.3*	27.4*
	Pf max	9.6*	0.9	5.1*	2.2	1.1
	Pf mean	14.0*	1.5	3.0	81.7*	15.7*

F)	**clear bark**	Call variant	Locality	Distance	Height	Habitat
	Duration	1.0	1.9	37.5*	30.1*	16.9*
	DFA1 mean	15.8*	2.2	7.7*	182.8*	69.2*
	DFB1 mean	37.8*	1.5	90.1*	171.4*	1.1
	Pf max	37.5*	2.0	4.9*	73.9*	13.7*
	Pf mean	29.7*	1.9	7.5*	116.6*	46.2*

The table shows F values of the applied linear mixed model analysis. Values for one repetition of every call at each locality under each condition are calculated. * $p < 0.05$.

CHAPTER 3

Vocal communication in a complex multi-level society: constrained acoustic structure and flexible call usage in Guinea baboons

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Abstract

To understand the evolution of acoustic communication in animals, it is important to distinguish between the structure and the usage of vocal signals, since both aspects underlie different constraints. While in terrestrial mammals the structure of calls is largely innate and influenced by the animal’s morphology, the usage of calls appear to be much more flexible. Hence, factors such as phylogeny, habitat or social system, should act differentially on those aspects. In the present study, we investigated the vocal repertoire of free living Guinea baboons (*Papio papio*) and examined the structure and usage of the animals’ vocal signals. Guinea baboons live in a complex multi-level social organization and exhibit a largely tolerant and affiliative social style, contrary to most other baboon taxa. To classify the vocal repertoire of male and female Guinea baboons, cluster analyses were used and focal observations were conducted to assess call rates. In general, the vocal repertoire of Guinea baboons largely corresponded to the vocal repertoire other baboon taxa, indicating a strong phylogenetic signal. The usage of calls, however, differed considerably from other baboon taxa and corresponded with the specific characteristics of the Guinea baboons’ social behaviour. While Guinea baboons showed a diminished usage of contest and display vocalizations (a common pattern observed in chacma baboons), they very frequently used vocal signals during affiliative and greeting interactions. Our study shows that the call structure of primates is largely unaffected by the species’ social system, while the usage of calls be flexibly adjusted to the requirements of the social style of the species. Instead of the complexity of a society, our results indicate that competition and cooperation strongly affect animal signalling behaviour to regulate social interactions.

Introduction

The signal design of animal calls and the resulting morphology of their vocal repertoire is assumed to be shaped by several factors, including phylogenetic history (Hauser 1993, Bradbury and Vehrencamp 2011), habitat characteristics (Marten and Marler 1977, Marten et al. 1977, Ey and Fischer 2009), receiver psychology (Seyfarth and Cheney 2003, Fischer 2011, Rowe 2013), as well as the social system of the species (McComb and Semple 2005, Gustison et al. 2012, Freeberg et al. 2012, Krams et al. 2012). To understand how these factors affect vocal production it is important to distinguish between the acoustic structure of calls on the one hand and the usage of vocalizations, i.e. the rate and contexts in which calls are produced, on the other, as both may be subjected to different selective pressures and constraints (Hammerschmidt and Fischer 2008, Seyfarth and Cheney 2010).

By now, the sound production mechanisms in terrestrial mammals are well understood. In the majority of terrestrial mammal species, the acoustic structure of calls is largely innate (but sees [Stoeger et al. 2012]) and their vocal development does not require auditory experience (Owren et al. 1993, Cheney and Seyfarth 1997b, Hammerschmidt and Fischer 2008, Hammerschmidt et al. 2012a). Age-related acoustic changes are commonly attributed to maturational factors, such as growth (Ey et al. 2007), practice (Hammerschmidt et al. 2000) or changes in the physiology, such as variation in hormone levels (Hammerschmidt et al. 2001)(but see [Stoeger 2012] for limited exceptions). The anatomy of the vocal apparatus strongly affects the acoustic features of a signal. While the fundamental frequency (i.e. the source) is mainly determined by the tension and size of the vocal folds, the formant dispersion, is shaped by the resonance characteristics of the vocal tract (i.e. the filter, see (Taylor and Reby 2010) for a detailed description of the 'source-filter'-model). The neural basis of sound production in humans and nonhuman primates involves different subsystems. The readiness to vocalize is mainly controlled by the midbrain periaqueductal grey (PAG). The PAG is an important relay station for descending pathways from the limbic system ('limbic-PAG-pathway') and the anterior cingulate cortex ('cingulate-PAG-pathway'), and innervates the phonatory motoneurons via the reticular formation

(Jürgens 2009). Another subsystem runs from the motor cortex directly into the reticular formation and from there to the phonatory motoneurons (Jürgens 2009). This system includes two feedback loops and seems to be responsible for generating the final motor commands (Jürgens 2009). Because direct connections between the motor cortex and the phonatory motoneurons are absent in terrestrial mammals (but see (Arriaga et al. 2012)), this is believed to prevent voluntary control over vocalizations, an important prerequisite for vocal imitation and learning (Jürgens 2009).

Because call production is largely innate, the structure of vocalizations is expected to show a strong phylogenetic signal. Several studies conducted among closely related species revealed a high inter-specific concordance in numerous acoustic features (Cleveland and Snowdon 1982, Gautier 1988, Hohmann 1991) and phylogenetic analyses have shown that the degree of inter-specific vocal variability is bound by genetic relatedness (Ross 2007, Wich et al. 2008, Thinh et al. 2011, Meyer et al. 2012). Furthermore, the environment is attributed to impose certain selective pressures on the inter-specific vocal variability. While discrete repertoires with a high number of call types have commonly been described in arboreal animal species living under poor visibility (Marler 1973, Schott 1973, Schrader and Todt 1993), graded repertoires frequently occur in terrestrial species occupying more open habitats (Aich et al. 1990, Fischer and Hammerschmidt 2002).

In addition, the function of calls is believed to affect signal design. In societies with high male competition, contest- or display-signals regularly occur during agonistic interactions (De Waal and Luttrell 1985, Chaffin et al. 1995, Kitchen et al. 2003), while in species with less intense competitive relationships, such status signals appear to be less common (Preuschoft and Schaik 2000, Thierry 2000); hereby animals often use a variety of assessment or appeasement signals to resolve social conflicts (De Waal 1988, Thierry et al. 1989, Boinski and Mitchell 1997). Furthermore, in primate societies with extensive affiliative relationships animals exhibit several vocal signals to facilitate friendly interactions (Soltis et al. 2002, Gustison et al. 2012). To date, the interplay between social and vocal systems is still poorly understood. In addition, it has been proposed that more complex social systems generally lead to higher vocal complexity (Blumstein and Armitage 1997, McComb and Semple 2005, Pollard and Blumstein

2012), irrespective of the competitive regime and the environmental characteristics. To resolve these issues, comparative data are direly needed.

In contrast, the usage of vocal signals is considered to be more flexible and partly under voluntary control (Jürgens 2003, Hammerschmidt and Fischer 2008). Although vocal utterances are predominantly emotionally triggered (mainly via the 'limbic-PAG-pathway'), inputs from the anterior cingulate cortex into the PAG (i.e. 'cingulate-PAG-pathway') allow certain voluntary modifications on the initiation (Sutton et al. 1974, Jürgens 2009) and perhaps duration (Larson et al. 1973, Jürgens 2009) of calls. Accordingly, several observations have shown that animals are able to adjust their call usage flexibly in response to immediate changes in their social (Karakashian et al. 1988, Townsend et al. 2012) or ecological environment (Koda et al. 2008, Ey et al. 2009). Note that effects of background noise on call duration and amplitude ('Lombard effect', e.g. [Brumm 2004]) is mediated via feedback loops in the lower brain stem, without any cortical control.

In the present study, we investigate the characteristics of the vocal repertoire of adult Guinea baboons (*Papio papio*), focusing on both vocal production and call usage, in order to elucidate how their social system affects both of these aspects of their vocal communication. Guinea baboons live in a complex, multi-level social organization (Galat-Luong et al. 2006, Patzelt et al. 2011), which differs considerably from the stable multi-male, multi-female groups of savannah baboons (i.e., chacma baboons, *P. ursinus*; olive baboons, *P. anubis*, and yellow baboons, *P. cynocephalus*) [Swedell 2011]) as well as the male-centred harem structures reported for hamadryas baboons (*P. hamadryas*) (Kummer 1968). Guinea baboon males maintain extensive affiliative and greeting relationships with various social partners (Whitham and Maestripieri 2003, Galat-Luong et al. 2006, Maciej et al. 2012), unlike Chacma baboons whose relationships are characterized by fierce competition (Swedell 2011). Furthermore, personal observations suggest that female social relationships are relatively weak in Guinea baboons, in contrast to the strong bonds observed in savannah baboon females (Silk et al. 2006, 2009). To date, little was known about Guinea baboon vocal behaviour in the wild (but see (Byrne 1981) for an exception and (Maestripieri et al. 2005) for one bioacoustical study in captivity).

Regarding the structure of the vocal repertoire, the assumption that vocal communication in nonhuman primates (and other terrestrial mammals) is highly constrained generates the prediction that the structure of the Guinea baboon vocal repertoire should differ only marginally from that of other baboon taxa, and that possible differences can be largely attributed to differences in morphology. In contrast, if social complexity indeed favours a higher vocal complexity (McComb and Semple 2005), Guinea baboons should exhibit a larger vocal repertoire size than other baboon taxa. Regarding call usage, and following the hypothesis that the vocal communication of a species is driven by the specifics of their social interactions (i.e. call function), we predict a pronounced rate of affiliative calls, due to their largely tolerant and affiliative social structure, while we expect a diminished occurrence of contest and display vocalizations, irrespective of the possible changes in repertoire structure.

We used two-step cluster analyses to quantitatively classify the Guinea baboon vocal repertoire. To estimate call rates we collected 190 h of focal observations from 18 subjects. In addition, we analysed the structure and occurrence of their “grunt” vocalizations in detail. In other baboon taxa, grunts have been shown to function to coordinate and mediate various interactions among group members (e.g. affiliation [Palombit and Cheney 1999], reconciliation [Cheney and Seyfarth 1997a] and threat [Engh et al. 2006]). In light of the strong bonds between males, we expect that grunts play an important role in the regulation of their relationships.

Methods

Study site

Research took place at the field station of the German Primate Center (DPZ), the Centre de Recherche de Primatologie (CRP), located in the Simenti region of the Niokolo Koba National Park (13°01´34 ´´N, 13°17´41´´W). The park lies across the borders between Senegal-Oriental and La Casamance close to the Guinean border in southeast Senegal and covers an area of more than 910.000 ha. The climate is of a Sudanian type with a dry season from November until June and a rainy season from July until October. The rainfall during the study period added up to 124 mm during the dry season and to 885 mm during the rainy season. The mean minimal temperature was 24.0 and 25.4 °C and the maximum mean temperature 36.9 and 32.3 °C in the dry season and in the rainy season, respectively (Simenti weather station, measured for 2010). The whole area has superficial formations of laterite and sediments and is watered by several ponds and large waterways, such as the Gambia and Niokolo Rivers. The vegetation varies from a southern Sudanian type to a Guinean savannah type and comprises gallery forests (close to the river banks), seasonally flooded grassland and dry deciduous forest. There are about 80 mammal species, 330 bird species, 36 reptiles and 20 species of amphibians recorded in the park and, despite a dramatic decrease in large mammal population sizes during the last decades, potential predators such as lions (*Panthera leo*), leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) still exist in this region (Ndao and Henschel 2011).

Subjects

Guinea baboons live in multi-male, multi-female units termed “gangs” (average adult sex ratio = 1:2.9 [Patzelt et al. 2011]), which comprise 50-70 individuals (Galat-Luong et al. 2006, Patzelt et al. 2011, Maciej et al. 2012). Although neighbouring gangs share an almost identical home range, they meet only sporadically during the day but aggregate regularly at sleeping sites. Several gangs together thus form large communities of more than 350 individuals (Dunbar and Nathan 1972, Galat-Luong et al. 2006, Patzelt et al. 2011). Since 2010 two gangs are fully- and two gangs semi-habituated to human observer (Mare gang = M, Simenti gang = S, River gang = R, N = Nose gang, i.e. around 200 individuals). The size and composition of the four study gangs varied considerably and comprised approximately 50-55 individuals in gang M, 55-60 individuals in gang S, 25-35 individuals in Gang R and 20-30 individuals in gang N. To track the whereabouts of the focal gangs, two males in each gang were fitted with radio collars. Furthermore, 12 individuals from three different gangs (gang M, gang S and gang R) were fitted with GPS collars, taking GPS fixes every two hours during the day and every three hours during the night. Based on the GPS fixes we assessed the home range of the study community to be ~ 36 km^2 (ArcGIS 2010, ESRI Inc., Redlands, US).

Ethical statement

The study was approved by the Diréction des Parcs Nationaux and the Ministère de l'Environnement et de la Protéction de la Nature de la République du Sénégal (Permit numbers: 0383/24/03/2009; 0373/10/3/2012). All capturing and handling procedures were carried out in accordance with the recommendations of the animal welfare deputy of the German primate centre (DPZ) and the conservation authorities of the Diréction des Parcs Nationaux du Senegal. They complied with the current law of Germany and Senegal and were either conducted or accompanied by veterinaries of the Diréction des Parcs Nationaux du Senegal. All measurements were performed under anaesthesia and all efforts were made to prevent suffering during and after the procedure (see below for the detailed methods). Guinea baboons do not depict a protected species and are listed as near threatened by the IUCN (IUCN ver 3.1, 2008).

Vocal repertoire

We collected data over 12 months distributed over two dry seasons (January-July 2010 and February-July 2011). Data collection began on the early morning hours, at 07:00 and proceeded until 12:00, as well as on the late afternoon from 17:00 until 19:00 UTC. We recorded vocalisation during *ad libitum* and focal animal sampling. For each audio-recorded vocalization we noted time/date, call type (see results), the identity of the caller, the behavioural context, if possible the call receiver, individuals in caller proximity as well as the height of the caller (when sitting in a tree) and the recording distance. We defined six broad behavioural contexts, two non-social and four social ones, based on the callers' behaviour (non-social contexts: 'Forage/Travel', 'Alarm'; social contexts: 'Agonistic', 'Greeting', 'Affiliation' (includes friendly approach and grooming each other) and 'Infant handling'). The potential call receiver was identified by the orientating behaviour of the caller during calling (looking, approaching toward- and/or interacting with the individual). Calls were recorded using a digital solid-state recorder (Marantz PMD 661, Marantz, Kanagawa, Japan) and a Sennheiser directional microphone (K6 power module and a ME66 recording head with a Rycote softie windscreen; Sennheiser Electronic KG, Barleben, Germany) with a sampling frequency of 44.100 Hz, 16-bit resolution and the double-mono setting.

Acoustic analyses (repertoire)

We recorded a total of 4420 calls. Since calls can be strongly distorted over longer distances, we only analyses calls recorded between 3-10 m. We used the software Avisoft-SAS Lab Pro 5.2 (R. Specht, Berlin, Germany) to select high quality calls. Calls which could not be clearly assigned to an individual or which were disturbed by background noise were excluded from the analyses. In total 1215 calls were used for the acoustic analyses. We audio-visually pre-classifed the various call structures in screams, barks, wahoos, roar grunts and grunts (see results). To obtain a balanced distribution of the different call types we randomly selected 8-12 calls from each pre-classified call structure from 18 males and 12 females. Due to the large frequency range of the different call structures we adjusted the sampling frequencies accordingly: grunts and roar grunts to 5.000 Hz and barks, wahoos, screams to 20.000 Hz, resulting in a frequency range of 2.500 Hz and 10.000 Hz. After cutting the selected calls we saved the binary spectrogram (fast Fourier transform-length: 1024-points, Hanning window, overlap 96.4 %) and exported them in the acoustic analysis software LMA 2012 (Schrader and Hammerschidt 1997). To determine the fundamental frequency (F0) in low pitched grunt-calls we further lowered the sampling frequency to 1200 Hz and exported the binary spectrogram into LMA 2012 (fast Fourier transform-length 1024 points, Hanning window, overlap 98.9 %). For all acoustic analysis we chose a set of nine acoustic parameters that broadly describe the temporal- and spectral characteristics of the vocalizations as well as the call tonality and the spectral modulation of the calls (see Table 3.1). The call morphology of the different call types could be sufficiently described with this set of acoustic parameters and a higher number of parameters did not have any advantage for the cluster analyses, as highly correlating acoustic parameters rendered the identification of appropriate cluster centers difficult. LMA was used to extract the acoustic parameters. We calculated the duration of the call (Duration), the statistical distribution of the frequency amplitudes (DFA 2 mean), the modulation of the first dominant frequency band (DFB1 mean), the overall frequency range (Range mean), the trend of the peak frequency (Pftr mean), the call consistency (Cs mean). Furthermore, tonal parameter such as the call noisiness (Noise), the harmonic to noise ratio (Hnr 1st) and the fundamental frequency (F0) were calculated. The F0 was assessed by using the manual tonality macro of LMA which is based on an autocorrelation function. This function only considers tonal elements of a call to calculate the fundamental frequency whereas noisy elements are ignored. The possible F0 range was set by visual adjustment of a harmonic curser. The F0 itself was estimated by an algorithm searching the highest frequency amplitude within the range of the lowest cursor. Figure 3.1 illustrates six acoustic parameters used for the analyses. The cut off frequency was set at 50 Hz to reduce background noise. The start and end thresholds were set at 15 % and 10 % for the calculation, which means that all time segments with a value lower than 15 % of the maximal amplitude at the beginning and 10 % at the end of the call were not considered. Cut of frequency as well as start- and end threshold were kept consistent for all call types.

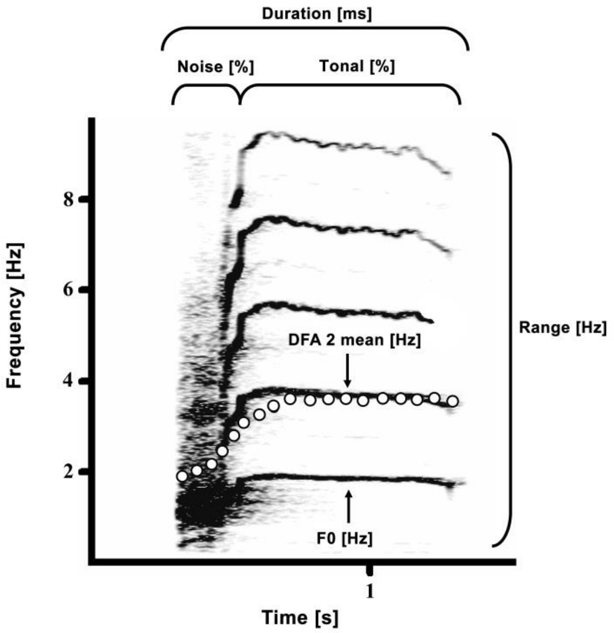

Figure 3.1. Spectrogram of a female Guinea baboon call. Five out of the nine call parameters used in the acoustic analyses are indicated in the spectrogram. White circles mark the DFA 2 (Fast Fourier transform-length 1024-points, Hann window, overlap 97.75 %, time resolution 3.2 ms).

Table 3.1. Description of the acoustic parameters used in the analysis.

Abbreviation	Formulation	Detailed description
Duration [ms]*	Duration	Call duration measured within the adjusted start- and end thresholds
DFA2 mean [Hz]*	Distribution of frequency amplitudes	Frequency at which the distribution of frequencies reaches the second quartile of the total distribution, mean values across time segments
DFB1ch mean [Hz]*	Modulation of the first dominant frequency band	Mean deviation between 1st dominant frequency band and floating average curve
Range mean [Hz]*	Frequency range	Mean difference between the highest and the lowest frequency
PFtr mean [Hz]*	Trend of the peak frequency	Mean deviation between the peak frequency (PF) and the liner trend
Cs mean	Consistency of time segments	Mean correlation coefficient of all successive time segments of the call
F0 mean [Hz]+	Fundamental frequency	Mean fundamental frequency across all time segments in which a harmonic structure could be detected
Noise [%]+	Noisiness	Percentage of time segments in which no harmonic structure could be detected
Hnr1 +	Harmonic to noise ratio	Harmonic to noise ratio in the first third of the overall call frequency (1 = no noise)

The general macro (*) as well as the manual tonal macro (+) of LMA 2012 was applied for parameter

Call rate and call usage

To examine the call rate and the call usage we conducted 15min all occurrences focal observations on 10 adult males and eight adult females in two gangs (gangs M and S). For each vocalization we noted date/time, caller ID, call type (see results), behavioural context, habitat visibility and if applicable and possible, the call receiver. Focal samples were balanced over the day and the study period. In total we collected 190 hours of focal observation (X = 10.2 ± 0.3 h/individual, X represent mean values ± SD). For each focal animal we calculated the call rate for each call type. In case of calling bouts (sequences of the same call type) we counted every call within the bout. The context specific call usage was calculated for all call types by dividing the number of calls uttered in each context by the total number of emitted calls of the respective call type.

To analyse sex-differences we compared male and female grunts (8-10 calls/individual, $N_{male} = 10$, $N_{female} = 10$) with each other. To check for context dependent differences we only analysed male grunts, since we had a sufficient number of calls produced in the different behavioural contexts only for males (6-10 calls/context/individual, $N_{male} = 8$).

Anatomical measures

During regular trapping sessions we took body measurements. Animals were lured into individual cages (100 x 100 x 100 cm) with food. A vertically sliding door (50 x 50 cm) was closed manually by pulling a string (30-50 m) from a hide. When the other group members had left the area, we anaesthetized the subjects using 500 mg Xylacin + 4 ml Ketamin solution [10%] applied with a blowpipe. We measured the individuals with a standard commercial measuring tape and weighed them with a hanging scale. The length and width of the snout and the skull were measured with a vernier caliper. During the whole process we regularly controlled the body temperature, respiration and the corneal reflexes. The head was covered with a cloth, and the cornea was continuously wetted with medical tear supplement. For six individuals body measured were repeated two times in a row, revealing a rather moderate measurement error: X = 3.7 ± 5.1 %.

After the procedure we released the animals at the trapping site and guarded them until they fully recovered and walked off to join their group.

For statistical analysis, we applied a principal component analyses (PCA) to extract a single compound body measurement. Table 3.2 shows the body measures and their loadings on the body coefficient (BC). To investigate the influence of the body size on the call structure we analysed grunts and extracted one source- (fundamental frequency) and one filter- (formant spacing) related acoustic feature. Formants were measured by linear predictive coding (LPC) using Avisoft-SAS Lab Pro Recorder 5.2 (Hann window, 15 LPC coefficients). To determine formant spacing it is essential to analyse high quality calls with at least three clearly detectable formants (F1 – F3). Only a limited number of calls fulfilled this criterion, hence, after visual inspecting our calls merely 3-5 calls per individual were suitable to analyse (N_{male} = 18, N_{female} = 5). We derived the formant spacing ($\Delta\mathrm{F}$) from the frequencies of the first three formants by finding the best fit to the equation

$$F_i = \frac{2i-1}{2}\,\Delta F,$$

which relates individual formant frequencies to average overall format spacing in the vocal tract, approximated as a uniform tube closed at one end (the glottis) and open at the other (the mouth). A detail description of this procedure is given in (Reby and McComb 2003).

Table 3.2. Body measurements of males and females. Mean ± SD (N_{male} = 18, N_{female} = 5) and respective factor loadings on the body coefficient (BC) are shown.

Body measurement	Male	Female	Correlation with BC
Chest circumference [cm]	57.9 ± 4.4	45.9 ± 3.7	0.94
Waistline [cm]	45.7 ± 2.1	38.8 ± 1.4	0.89
Arm length [cm]	53.4 ± 2.4	47.4 ± 2.5	0.90
Leg length [cm]	47.0 ± 2.5	39.7 ± 1.9	0.92
Skull length [cm]	10.9 ± 0.6	9.4 ± 0.7	0.62
Skull width [cm]	10.9 ± 0.8	9.1 ± 0.7	0.83
Snout length [cm]	9.9 ± 0.6	6.7 ± 0.5	0.88
Snout width [cm]	4.2 ± 0.4	3.2 ± 0.3	0.88
Back length [cm]	45.2 ± 2.9	39.6 ± 5.2	0.77
Body length [cm[	56.6 ± 3.2	51.1 ± 6.9	0.81
Weight [kg]	20.5 ± 2.1	11.4 ± 1.8	0.96

Statistical analyses

To statistically describe the vocal repertoire we used a two-step cluster analyses on the selected acoustic variables, which has been already successfully applied in other bioacoustic studies (Hammerschmidt et al. 2012a, Hammerschmidt et al. 2012b). We used the log-likelihood distance measure and the Schwarzsches' Bayes cluster criterion (BIC) to calculate different clusters solutions. In addition, we qualitatively assessed the cluster solution by inspecting the silhouette values (Rousseeuw 1987). The silhouette value (Sc) represents the summarized distance of all within-cluster data points (a_i) subtracted from the summarized distance to the data points of the successive cluster (b_i) and finally divided by the sum of the larger distance:

$$\mathrm{S(c)} = \frac{\mathrm{b(i)} - \mathrm{a(i)}}{\max\{\mathrm{a(i)}, \mathrm{b(i)}\}}$$

Subsequently, the average value across all call clusters of the respective solution is calculated and gives a number between -1.0 and 1.0; cluster solutions with a Sc exceeding 0.5 are usually considered to be solid (Rousseeuw 1987). Hence, we calculated a set of different cluster solutions (2-14 clusters) and extracted the Sc for each solution. We further compared the formal categorization results to the audio-visual pre-classification of the calls and calculated the percentage of accordance between both classifications.

Afterwards, we ran a discriminant function analyses (DFA, SPSS 20) with the same acoustic parameters and the calculated call-clusters as grouping variable to evaluate the selected cluster solution and to estimate how the acoustic parameters contribute to the classification. We used a stepwise DFA and the assignment of calls was cross-validated by the leaving-one-out method of SPSS 20.

To analyse sex and context differences of grunts we carried out a linear mixed model analysis (LMM) on the same acoustic variables as used for the cluster analysis, with animal ID as random factor and sex and context as fixed factors, respectively. To identify significant differences between the contexts we applied univariate least significant differences (LSD) post-hoc tests. The influence of body size on the call structure we investigated by conducting a Pearson correlation analysis between the body component and fundamental frequency as well as formant spacing. All statistical tests were two-tailed and conducted with SPSS 20 or the statistical package R (R Development Core Team). We corrected for multiple testing by adjusting all *p*-values using Simes correction.

Results

Vocal Repertoire

Call structure

The cluster solution with the highest validity (Sc = 0.62) contained only two clusters, one with screams and one with all other calls (see Figure 3.2). The next best cluster solution was the one containing six clusters (Sc = 0.51). A higher number of clusters did not lead to a higher validity. The comparison between the audio-visual classification and the six calculated call cluster revealed an accordance of 91%, and although screams were separated into two clusters, all other call clusters largely coincided with the audio-visual classification. Therefore, we settled on the six-cluster classification schemata for further analysis and labelled the clusters by using the same onomatopoetic terms as used during studies conducted on the vocal communication of savannah baboon: screams (e.g. Rendall et al. 2009), loud calls: female barks (e.g. Fischer et al. 2001b), male wahoos (a two syllable bark ([e.g. Fischer et al. 2002]), grunts (e.g.Owren 1997) and roar grunts (e.g. Hall and de Vore 1965). All call types have been clearly distinguished by the six call cluster solution. Figure 3.3 illustrates the differences between the clusters based on the results of the discriminant function analysis. The classification procedure indicated that the clusters could be discriminated well (99.2% correct classification, cross validated).

To discriminate between male wahoos and female barks the most important parameter was the consistency of time segments (Cs mean, see Table 3.1 for a detailed description of the acoustic parameters used for the analyses) within the call, which was lower in male than in female loud calls. Furthermore, the first dominant frequency band was more strongly modulated (DFB1ch mean) in male wahoos than in female barks. The screams differed mainly in the pitch parameters; where the first cluster exhibited a higher fundamental frequency (F0), a wider frequency range (Range mean) and a higher distribution of frequency amplitudes (DFA2 mean) than the second cluster. Screams uttered by males or females were structurally similar and were not distinguished by the cluster analysis. To differentiate between roar grunts and grunts the call duration (Duration) was the most important parameter followed by frequency range. Roar grunts were much longer compared to grunts and had a narrower frequency range. In Table 3.3 the mean values of the acoustic parameters for each call-cluster are shown.

In general, for the overall call-cluster discrimination of the call repertoire, the most important acoustic parameters were the harmonic to noise ratio (Hnr1), the DFA2 mean and the Cs mean; whereas the trend of the peak frequency (PFtr mean) and the noise (Noise) of the call as well as the DFB1ch mean only moderate contributed to the classification procedure.

In contrast to other baboons, female copulation calls were only rarely uttered; hence, we could only qualitatively assess the acoustic structure of Guinea baboons' copulation calls (see Table 3.3). Furthermore, threat calls, a common vocal pattern in savannah baboons, where extremely soft, precluding any acoustic analyses.

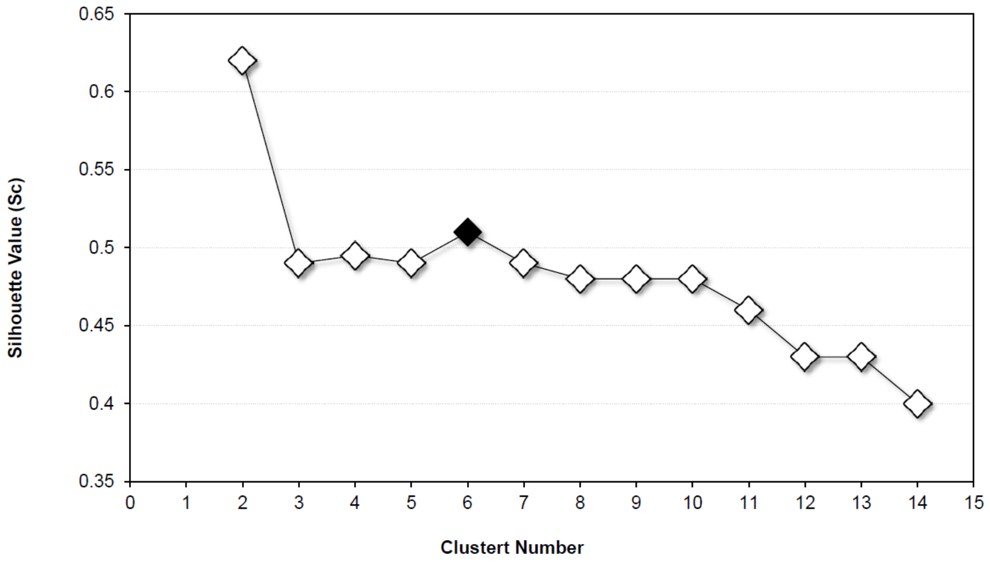

Figure 3.2. Results of a two-step cluster analysis. Respective Silhouette values (Sc) of each clustering are shown in the graph. The black dot indicates the solution chosen for the discriminant function analysis (DFA). This six call-cluster solution was the most appropriate one, since it yields a high cluster validity and corresponded to most of the audibly distinct call types.

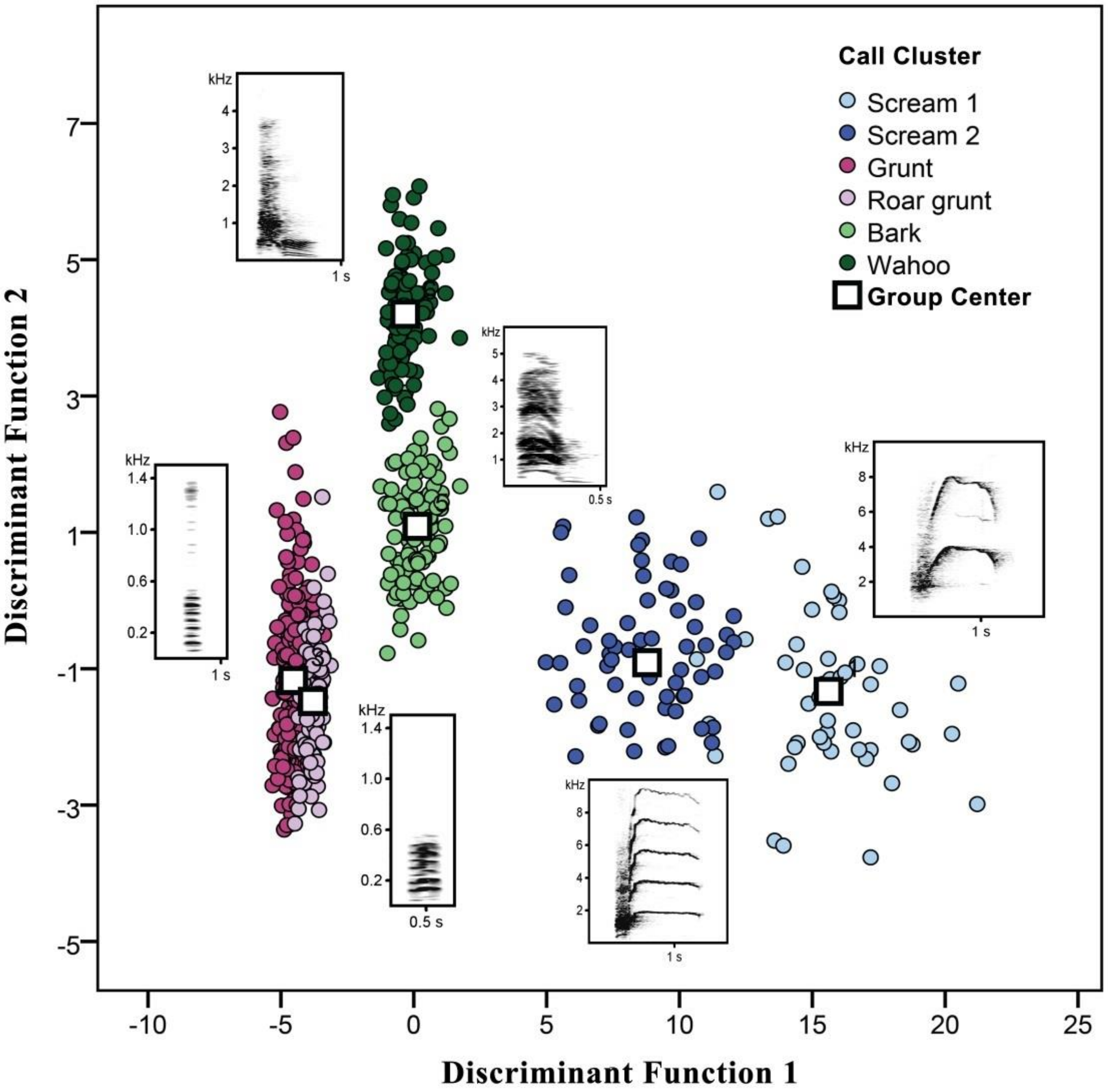

Figure 3.3. Discriminant function analyses with the six calculated call-clusters used as grouping variable. DFA2 mean and F0 mean had the highest load on the first discriminant function; Cs mean and Hnr1 loaded strongest on the second one. The five respective discriminant functions revealed a high overall classification success; i.e., 99.2 % of calls were correctly assigned (cross-validated, step-wise DFA). For each call-cluster a representative spectrogram is shown in the figure.

Table 3.3. Mean values of the acoustic parameters (X ± SD) for each call-cluster and copulation calls.

Parameter	scream 1 (*N* = 52)	scream 2 (*N* = 70)	grunt (*N* = 226)	roar Grunt (*N* = 91)	bark (*N* = 94)	wahoo (*N* = 101)	copulation calls[+] (*N* = 25)
Duration [ms]	1045 ± 359	876 ± 292	180 ± 34	455 ± 79	290 ± 58	319 ± 66	97 ± 20
DFA2 mean [Hz]	4460 ± 747	2685 ± 510	434 ± 102	341 ± 51	1087 ± 146	963 ± 142	1414 ± 625
DFB1ch mean [Hz]	127 ± 57	71 ± 44	9 ± 8	3 ± 2	49 ± 28	72 ± 22	80 ± 77
Range mean [Hz]	4468 ± 990	2444 ± 696	952 ± 316	530 ± 189	1606 ± 393	1722 ± 328	2137 ± 1150
PFtr mean [Hz]	870 ± 428	385 ± 239	72 ± 47	35 ± 27	163 ± 65	176 ± 59	236 ± 117
CS mean	0.97 ± 0.01	0.97 ± 0.01	0.97 ± 0.02	0.99 ± 0.01	0.97 ± 0.01	0.92 ± 0.01	0.97 ± 0.01
F0 [Hz]	2352 ± 577	1758 ± 267	80 ± 23	70 ± 10	588 ± 105	472 ± 81	290 ± 149
Noise [%]	63 ± 20	53 ± 18	14 ± 10	42 ± 14	24 ± 14	41 ± 12	47 ± 19
Harmonic to noise	0.16 ± 0.06	0.31 ± 0.08	0.26 ± 0.07	0.39 ± 0.07	0.46 ± 0.07	0.46 ± 0.04	0.37 ± 0.12

[+] copulation calls have not been statistically classified by the cluster analyses

Call usage

Bark

Females produced barks in three different contexts (see Table 3.4), most frequently in the Forage/Travel context (X = 74.5 ± 20.7 %). In 61.7 % of all barks uttered during Forage/Travel, visibility was middle or dense and only 5-10 animals were visible. Barks were also regularly produced during alarm situations (X = 19.5 ± 16.6 %), mostly when subjects appeared to feel threatened by the observer or by predators. Occasionally they were produced when a female was harassed by other females (X = 5.6 ± 6.0 %).

Wahoo

Similarly to female barks male wahoos were mostly produced in Forage/Travel contexts (X = 80 ± 20.1 %); 62.5 % of all wahoos produced during Forage/Travel were uttered when visibility was poor and only 5-10 animals were visible. Additionally, wahoos were uttered during alarm situations (X = 11 ± 12.6 %) and, occasionally during encounters with other gangs (X = 9 ± 11.7%). Wahoos were not produced during aggressive interactions and throughout the study period we never observed males producing wahoos while chasing or attacking other males.

Scream

Males and females produced screams mainly during agonistic interactions. While adult females occasionally started to scream during alarm situations (X = 9.8 ± 12.2 %), adult males were never observed to produce screams under such circumstances. All male screams that we heard were produced during agonistic interactions with other males. Females screamed primarily in agonistic contexts, while they were harassed or chased by other males.

Copulation call

Copulation calls consisted of low amplitude, pant-like elements, the number of which varied substantially between as well as within individuals (Figure 3.4). Copulation calls were emitted shortly after copulation, while females retreated from their copulation partner; however, they did not occur after each mating and were emitted rather infrequently. In total, we recorded only six calling events during the focal observations, and refrained from calculating the call rate.

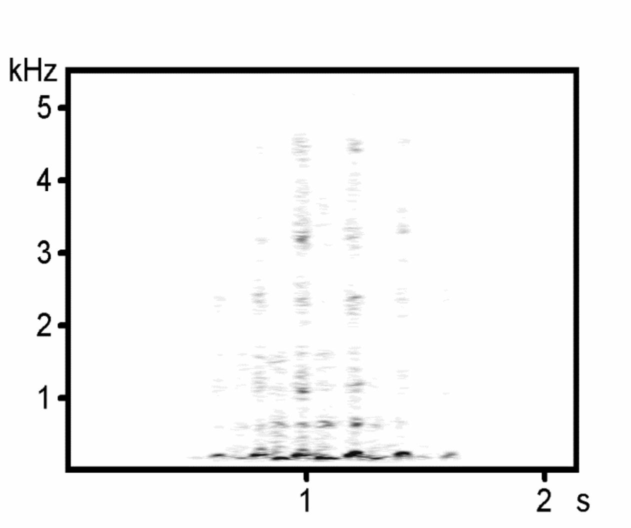

Figure 3.4. Spectrogram of a sequence of a female copulation grunt. The spectrogram was created by using Avisoft SASLabPro 5.1 (R. Specht, Berlin, Germany; fast Fourier transform resolution 1.024 points, sampling frequency: 5 kHz, time resolution: 4ms, time overlap: 96.87, Hanning window).

Roar grunt

Roar grunts often occurred during or after aggression against females (X = 84.1 ± 21.4 %). Before calling, males usually ran up a tree and showed elements of display behaviour such as yawning and branch-shaking. Roar grunts were almost always produced in calling bouts (4 – 6 calls/bout). We further observed males uttering roar grunts during Forage/Travel contexts (X = 10 ± 11.4%) when animals were widely scattered. Unlike reported for chacma baboons, roar grunts were not followed by series of long and protracted series of wahoo calls.

Grunt

Male as well as female grunts were the most common vocalizations. Grunts occurred mainly in non-agonistic, social contexts (Greeting, Infant handling and Affiliation). Only a minor proportion of grunts were produced also during non-social contexts (‘Forage/Travel’, males: X = 7.1 ± 3.4 %, females: X = 11.2 ± 9.8 %). Social grunts were almost always uttered in calling bouts with a varying number of calls per bout, contrary to non-social grunts which commonly occurred as single calls. The largest proportion of male grunts was produced when males engaged in affiliative interactions with females (X = 39.3.1 ± 5.1 %) as well as during infant handling (X = 25.2 ± 4.5 %). The remaining percentage of male grunts occurred during greeting interactions with other males (X = 28.4 ± 9.5). Females mostly grunted when interacting affiliatively with other females (X = 48.1 ± 18.9 %), as well as during infant handling (X = 20.2 ± 8.5 %) and during greeting with adult males (X = 20.5 ± 19.8 %).

Call rate

To assess the call rate we calculated the rate of each call type respectively (screams were not distinguished in the field). While the call rate of agonistic calls (i.e. scream, roar grunt) was extremely low (<0.1/h/individual), loud calls were produced slightly more often (X = 0.23 ± 0.39 calls/h/individual). Grunts were emitted at a much higher rate (X = 0.71 ± 0.19 calls/min/individual), especially during non-agonistic social interactions (see call usage above), and constitute the most common vocalization. Males grunted significantly more often than females (X_{male} = 1.18 ± 0.31 calls/min/individual, X_{female} = 0.31 ± 0.08 calls/min/individual; exact Mann-Whitney U-test, T = 36, $p < 0.001$). In Table 3.5 the call rates of the different call types are shown. Grunts were produced mostly during the early morning (7:00 - 8:00), when individuals socialised around the sleeping trees (X = 0.25 ± 0.15 calls/min/individual). Afterwards, from 8:00 - 10:00, the call rate decreased (X = 0.16 ± 0.13 calls/min/individual), shortly after subgroups start to forage or to travel, and did not change much anymore during the late morning (10:00 - 11:00, X = 0.13 ± 0.08 calls/min/individual). In the evening (17:00 - 19:00) the grunt rate was similarly low (X = 0.11 ± 0.09 calls/min/individual).

Table 3.4. Percentage of usage of the call types (X ± SD %) in the different contexts.

Context	scream	grunt	roar grunt	bark	wahoo
Forage / Travel		♂ 7.1 ± 3.4 ♀ 11.2 ± 9.8	♂ 10 ± 11.4	♀ 74.5 ± 20.7	♂ 80 ± 20.1
Alarm	♀ 9.8 ± 12.2		♂ 5.7 ± 7.3	♀ 19.5 ± 16.6	♂ 11 ± 12.6
Agonistic	♂ 100.0 ± 0 ♀ 90.2 ± 20.1		♂ 84.1 ± 21.4	♀ 5.6 ± 6.0	♂ 9 ± 11.7
Affiliation		♂ 39.3 ± 5.1 ♀ 48.1 ± 18.9			
Infant Handling		♂ 25.2 ± 4.5 ♀ 20.2 ± 8.5			
Greeting		♂ 28.4 ± 9.5 ♀ 20.5 ± 19.8			

Table 3.5. Call rate (X ± SD) of the different call types for both sexes.

Sex	scream	grunt	roar grunt	bark	wahoo
Male	0.04 ± 0.00 calls / h	1.18 ± 0.31 calls / min	0.08 ± 0.17 calls / h		0.14 ± 0.16 calls / h
Female	0.08 ± 0.01 calls / h	0.31 ± 0.08 calls / min		0.32 ± 0.61 calls / h	

Vocal variation of grunts

Relationships with caller sex

Male- and female grunts differed most in pitch characteristics of the calls such as fundamental frequency (F0, F = 112.9, p < 0.001) and distribution of the frequency amplitudes (DFA2 mean, F = 46.6, p < 0.001) which was higher in females than in males; as well as in call noisiness which was higher in males than females (e.g. Noise, F = 60.4, p < 0.001). Call modulation also differed between the sexes and was stronger in males than females, although to a lesser extent (e.g. DFB1ch mean, F = 5.2, p = 0.034; PFtr mean, F = 6.2, p = 0.023; see Table 3.6).

Table 3.6. Differences in grunt characteristics between males and females. LMM-analyses have been conducted with caller sex as fixed factor and caller ID as random factor. Adjusted *p* vales are shown (Simes correction for multiple testing).

Parameters	Female	Male	*F*	*p*
Duration [ms]	173 ± 32	186 ± 34	4.6	0.046
DFA2 mean [Hz]	502 ± 105	379 ± 55	46.6	0.000
DFB1ch mean [Hz]	10 ± 7	8 ± 7	5.2	0.034
Range [Hz]	984 ± 379	927 ± 253	0.5	0.488
PFtr mean [Hz]	85 ± 52	72 ± 40	6.2	0.023
Cs mean	0.96 ± 0.02	0.97 ± 0.01	3.8	0.067
F0 mean [Hz]	103 ± 15	61 ± 6	112.9	0.000
Noise [%]	11 ± 2.3	31 ± 19	60.4	0.000
Hnr1	0.22 ± 0.5	0.29 ± 0.05	24.1	0.000

Relationships with behavioural context

For the analysis of context-related differences, we only compared calls produced in the three social contexts, since we did not have a sufficient amount of calls uttered during the Forage/Travel context. Grunts uttered in the three contexts differed most in terms of noisiness (Noise, F = 91.5, p < 0.001), followed by the fundamental frequency (F0, F = 16.1, p < 0.001), the modulation of the first frequency band (DFB1ch mean, F = 11.5, p < 0.001), and the harmonic to noise ratio (Hnr1, F = 11.2, p < 0.001). The results of the LMM for each acoustic parameter are shown in Table 3.7. An LSD post-hoc test conducted on those four parameters revealed significant differences only between the Greeting- and Infant handling context (and between the Greeting- and Affiliation context), but no statistical difference was found between Infant handling- and Affiliation. The percentage of noise (Noise) in the calls was significantly higher in the Greeting context (X = 53 ± 38 %, p < 0.001) compared to both other contexts but was rather equally low during Infant handling (X = 10 ± 15%) and Affiliation (X = 5 ± 11 %, p = 0.808). Similar results were found for the fundamental frequency (F0) which was higher during Greeting (X = 62 ± 11, p < 0.001) compared to the Infant handling (X = 55 ± 6) and Affiliation context (X = 56 ± 7, p = 0.837). In Figure 3.5 the error bars of noise and fundamental frequency are illustrated for each context. The first frequency band was more strongly modulated (DFB1ch mean) during Greeting (X = 6 ± 3, p < 0.001), than during Infant handling (X = 2 ± 3) and Affiliation (X = 2 ± 2, p = 0.165) and harmonic to noise (Hnr1) was lowest in the Greeting context (X = 0.06 ± 0.04, p < 0.001) compared to the Infant handling- (X = 0.10 ± 0.03) and Affiliation context (X = 0.09 ± 0.03, p = 0.665).

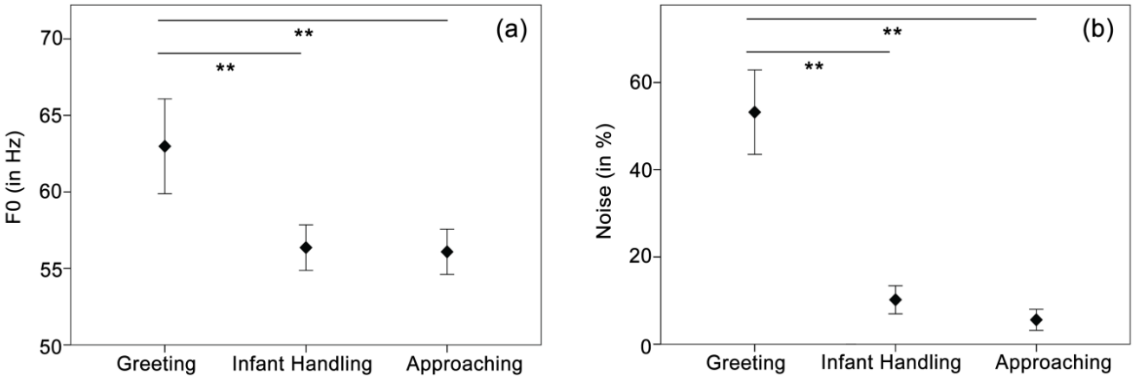

Figure 3.5. Differences of (a) fundamental frequency and (b) call noisiness between the social contexts. Statistical significant differences (LSD Post-hoc test) only occurred between Greeting- and Infant handling/Affiliation context, but no differences were found between Infant handling and Affiliation. Vertical lines represent standard deviation. ** indicates statistical significance, p < 0.01 (p values were adjusted by using Simes correction for multiple testing).

Table 3.7. Variation in male grunt characteristics in three different contexts. Mean and SD, and results of LMM analysis with context as fixed factor and caller ID as random factor, with adjusted *p* vales (Simes correction for multiple testing).

Acoustic parameters	Greeting	Infant handling	Affiliation	*F*	*p*
Duration [ms]	289 ± 76	294 ± 219	229 ± 53	4.9	0.008
DFA2 mean [Hz]	400 ± 50	410 ± 42	396 ± 35	3.2	0.042
DFB1ch mean [Hz]	6 ± 3	2 ± 3	2 ± 2	11.5	0.000
Range [Hz]	741 ± 240	820 ± 293	896 ± 318	5.4	0.005
PFtr mean [Hz]	56 ± 34	53 ± 35	47 ± 35	1.3	0.262
Cs mean	0.99 ± 0.01	0.98 ± 0.01	0.99 ± 0.01	0.61	0.941
F0 mean [Hz]	**62 ± 11**	**55 ± 6**	**56 ± 7**	**16.1**	**0.000**
Noise [%]	**53 ± 38.5**	**10 ± 15**	**5 ± 11**	**91.5**	**0.000**
Hnr1	0.06 ± 0.0	0.10 ± 0.03	0.09 ± 0.03	11.2	0.000

Bold numbers indicate the both most important parameters.

Relationships with body size

To investigate the relationship between the vocal structure of grunts and body size we conducted correlation analysis between the calculated body component (BC) and the fundamental frequency (F0) as well as formant spacing ($\Delta\mathrm{F}$). Both F0 and $\Delta\mathrm{F}$ correlated significantly with body size. Animals with a higher BC uttered grunts with a lower fundamental frequency and smaller formant spacing (see Figure 3.6). The correlation between BC and formant spacing was marginally higher (N = 23, r = 0.96, p < 0.01) than the correlation between BC and fundamental frequency (N = 23, r = 0.89, p < 0.01). When the analysis was restricted to male calls only, formant spacing still correlated strongly with BC (N = 18, r = 0.92, p < 0.01), whereas the correlation between fundamental frequency and BC slightly decreased (N = 18, r = 0.71, p < 0.01); nevertheless, both correlation coefficients still showed a strong association between the vocal characteristics and individual body size. In Figure 3.6 (a-d) the scatter plots for formant spacing and fundamental frequency are shown.

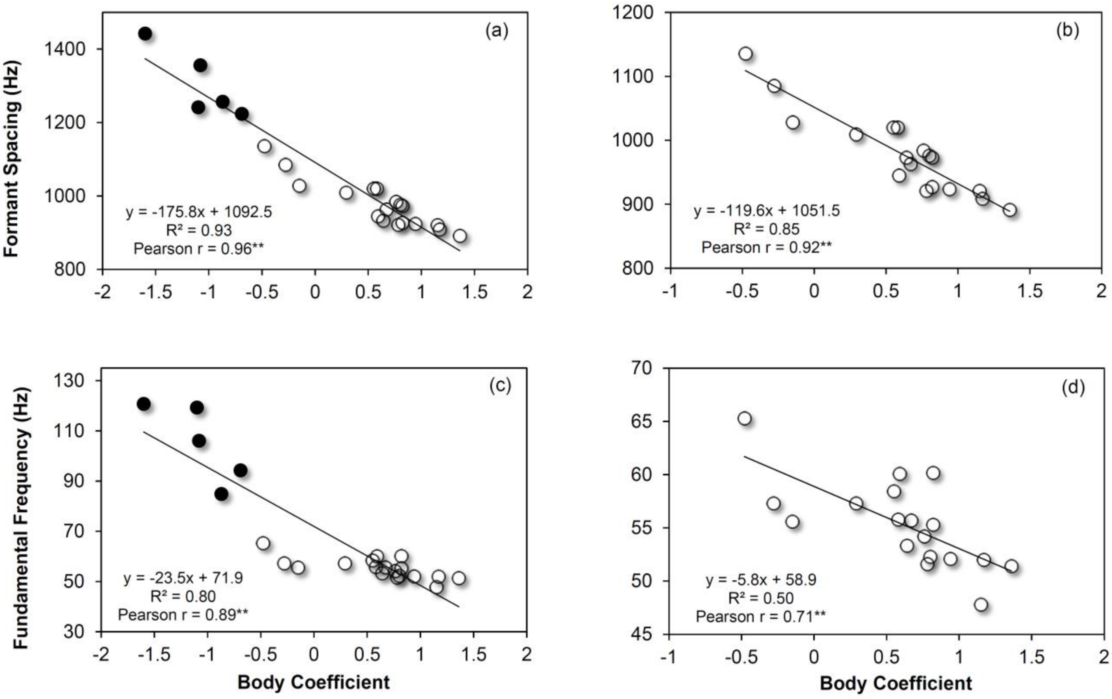

Figure 3.6. Correlations between formant spacing (a-b) as well as fundamental frequency (c-d) and the calculated body coefficient (BC). The left graphs shows the measures of all subjects (black dots indicating females, N = 5, and white dots indicating males, N = 18); the right graphs only show measures of males. BC is a compound measure of body size calculated from all body measurements by using principal component analysis. ** indicates statistical significance, p < 0.01 (p values were adjusted by using Simes correction for multiple testing).

Discussion

The call types found in Guinea baboons, namely grunts, screams, barks, wahoos, roar grunts, and copulation calls, had all been described, either audio-visually or statistically, in several other baboon taxa (e.g. Hall and DeVore 1965, Kummer 1968, Waser 1982, Owren et al. 1997, Fischer et al. 2001b, 2002, Rendall et al. 2009). This is compatible with the assumption that evolutionary constraints play an important role limiting the variation in the structure of nonhuman primate vocalizations. Some of the differences between the values obtained here and those reported for other baboon taxa are most likely related to differences in body size. For instance, grunts of male- and female-Guinea baboons had a higher fundamental frequency than in chacma baboons (Rendall et al. 2005). The descriptions of other call types in baboons, such as loud calls (Fischer et al. 2002), suggest a similar morphological pattern, although the calculation of different acoustic parameters hampers a detailed inter-specific comparison. Unlike predicted by the “vocal complexity” hypothesis, we did not find any evidence that the vocal repertoire of Guinea baboons is more complex than that of other baboon taxa with a more stable and less complex social organization.

The usage of the Guinea baboon vocal signals shows considerable differences from that of other baboon taxa. One of the most striking findings is males hardly ever emit loud calls during competitive interactions. Although agonistic interactions occur among male Guinea baboons, the competition is much less pronounced than in chacma baboons, for instance. In chacma baboons, males compete aggressively for social rank which confers priority of access to resources and, most importantly, fertile females (Alberts et al. 2003). Male loud call displays function as an important indicator of fighting ability (Kitchen et al. 2003, Fischer et al. 2004), but they are also used to coerce females (Kitchen et al. 2009). Males use loud call displays as a conflict management strategy to avoid the costs of fighting (Kitchen et al. 2003). In Guinea baboons however, competition appears to be much less intense and male-male relationships lack obvious dominance hierarchies; thus, there is less pressure to settle conflicts using signals in order to avoid costly fighting (Smith and Parker 1976). The observation that competition in male Guinea baboons is reduced is, perhaps, also reflected by the diminished usage and structure of female copulation calls. In savannah baboons, they are uttered after almost each mating and consist of a rhythmic succession of high intensity, pant like calls (Hamilton and Arrowood 1978, Semple et al. 2002), and they are believed to incite male competition for females (Pradhan et al. 2005). Furthermore, formalized threats, an important dominance behaviour of female savannah baboons (Engh et al. 2006), only occurred occasionally in Guinea baboons.

While the usage of display vocalizations is greatly reduced, males grunt much more frequently than chacma baboons. These grunts occurred mainly during greetings or affiliative interactions, reflecting a higher rate of positive interactions (Patzelt A, IN, Fickenscher G, JF, unpublished data). Particularly noteworthy is the high rate of greetings among males (Whitham and Maestripieri 2003). Greetings may be used not only to bond with other males, but also as “agonistic buffering” to reduce aggressive tendencies (Colmenares 1990, Hohmann and Fruth 2000). Males also grunt during affiliative interaction with females, and during infant handling, a pattern that can also be found in other baboon taxa (Palombit and Cheney 1999). Female Guinea baboons grunted mostly during affiliative interactions. However, their calling rates were much lower than those of males which may mirror the relatively weak bonds among females [Goffe A, JF, unpublished data], which differs from the female-bonded savannah baboon societies (Swedell 2011).

Differences in grunts structure between males and females are probably simply a reflection of the size dimorphism. Formant dispersion as well as fundamental frequency where higher in female- compared to male-grunts and strongly correlated with individual body size (Fitch 1997, Pfefferle and Fischer 2006). In addition, it may be that the sexes differ with regard to the affective state during calling (Fischer et al. 2001b, Rendall 2003). Male grunts varied in relation to behavioural context; grunts uttered during male-male greetings were much harsher and noisier compared to non-greeting grunts, which may be related to a higher degree of arousal (Rendall 2003, Stoeger et al. 2011).

Whether or not differences in habitat quality affect the morphology of vocal repertoires of different baboon taxa remains a question for empirical investigation. We do not deem this to be an important driver though, as there is more variation in environmental conditions within than between taxa (Swedell 2011). Nevertheless, previous research has shown that short-term fluctuations in visibility may directly affect calling rates. When the visibility was poor and the risk of losing contact with the social partners increased, olive baboons females called more frequently than in open habitats (Rendall et al. 2000, Ey et al. 2009).

The structure of the vocal repertoire of adult Guinea baboons largely resembles that of other baboon taxa, while their call usage differs substantially. Corresponding to their less competitive social style, male Guinea baboons do not use loud calls as displays of their fighting ability, while they frequently grunt during male-male greetings and other affiliative interactions. Thus, the use of calls (with a relatively innate structure) can be adapted to the requirements of the specific social structure and social organisation.

Importantly though, our results refute the assumption that an increased social complexity necessarily leads to higher vocal complexity. Instead, competition and cooperation more specifically affect the use of vocal signals to regulate social relationships.

Authors' contributions

PM recorded the data, conducted the analyses and wrote the paper, IN did the veterinary work in the field and collected body measurements, KH designed the study and contributed to the acoustic and statistical analyses and assisted by drafting the paper, JF designed the study and wrote the paper. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests

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CHAPTER 4

Social monitoring in a multi-level society: a playback study with male Guinea baboons

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Abstract

Keeping track of social interactions among conspecifics is a driving force for the evolution of social cognition. How social cognition, such as social knowledge, ties in with a species' social organization is however largely unexplored. We investigated the social knowledge of wild Guinea baboons (Papio papio) ranging in Senegal, a species that lives in a fluid multi-level society with overlapping habitat use. Using playback experiments, we tested how adult males differentiate between subjects from their own vs. a neighbouring or a stranger social unit ("gang"), and assessed ranging patterns with Global Positioning System (GPS) data. While territorial species usually differentiate between group and non-group members and often respond more strongly to strangers than neighbours (the "dear enemy" effect), subjects in this highly tolerant species should largely ignore other unit members and mainly attend to subjects from their own unit. Males responded strongly after playback of calls recorded from members of their own gang, while they attended only briefly to neighbour or stranger calls. Apparently, males benefit from monitoring the social manoeuvres in their own social unit, while it remains to be resolved whether they are unmotivated or unable to keep track of the identities and actions of individuals outside their own gang. The study highlights how the allocation of social attention is tuned to the specifics of a species' social organization, while a complex social organization does not necessarily translate into the need for more elaborate social knowledge.

Introduction

Social living is widespread across animal taxa, but there is considerable variation in terms of the frequency, nature and consistency of social interactions among group members. According to the social complexity hypothesis, keeping track of the social interactions within one’s group is a major driving force for brain evolution and intelligence (Dunbar and Shultz 2007, Dunbar 2011, Freeberg et al. 2012). One constitutive element of social cognition is social knowledge, that is, the recognition of individuals and their classification according to different social attributes, including their relationships with third parties (Cheney and Seyfarth 2007, Fischer 2012). Yet, little is known how social knowledge is adapted to, or influenced by, a species’ social organization. Recently, it was hypothesized that life in groups with fission-fusion dynamics may add an additional layer of social complexity, as animals do not only have to keep track of the interactions in their own group, but also process the composition of other sub-groups and negotiate the merging and splitting of units (Amici et al. 2008, Aureli et al. 2008).

To date, social knowledge has been investigated at different levels, including individual recognition, categorization according to social attributes, and group membership recognition. Regarding individual recognition there are numerous studies showing that kin recognize each other vocally (Rendall et al. 1996, Hammerschmidt and Fischer 1998b, Charrier et al. 2003, Fischer 2004, Müller and Manser 2008). There is also evidence that nonhuman primates living in stable groups are able to classify other individuals with regard to different social attributes, such as dominance rank or bond strength (Soltis et al. 2002, Bergman et al. 2003, Kitchen et al. 2005, Range 2005). In addition, animals living in stable groups have been shown to distinguish between members of their own group and those belonging to other groups (e.g. Cheney and Seyfarth 1982, Hopp et al. 2001, Wich et al. 2002, Range 2005, Meunier et al. 2012 for the vocal domain; Schell et al. 2011 for the visual domain). Importantly, in which way subjects respond to neighbours or strangers may not only depend on the competitive regime between groups, but also on the status of the individuals. Males typically consider other males as competitors, while lactating females may fear infanticidal attacks (van Schaik and Janson 2000, Ren et al. 2011). In contrast, cycling females may be attracted to neighbouring or stranger males (Cheney and Seyfarth 1987, Palombit 1994, Agoramoorthy and Hsu 2000).

In territorial species, individuals may distinguish among different neighbouring groups (Cheney and Seyfarth 1982, Hyman and Hughes 2006) and differentiate between members of stranger vs. adjacent groups. According to Fisher, territory owners may respond less strongly to neighbouring group members, because subjects are familiar with each other (the so-called “dear enemy” effect; Fisher 1954), and there is ample evidence for this phenomenon (e.g. Temeles 1994, Wich et al. 2002, Radford 2005). In contrast, when territory boundaries are at stake, the reverse “nasty neighbour” effect may set in (Temeles 1990, Müller and Manser 2007, Herbinger et al. 2009).

Not all socially living species live in clearly delineated social units with well-defined inter-group boundaries, but may exhibit a rather fluid social organization instead. Such complex multi-level social systems are characterized by low territoriality and frequently changing animal aggregations (e.g. hamadryas baboons (*Papio hamdryas*) [Kummer 1968]; gelada baboons (*Theropithecus gelada*) [Snyder-Mackler et al. 2012]; snub-nosed monkeys (*Rhinopithecus bieti*) [Ren et al. 2012]). In such cases, the responses to neighbours or strangers may be less pronounced.

In the present study we focused on Guinea baboons and tested neighbour-stranger discrimination in males. Specifically, we assessed how males differentiate between subjects from their own social unit, a neighbouring social unit, and stranger males. The broader aim is to understand the relationship between social organization and social knowledge using baboons as a model. Guinea baboons exhibit a complex multi-level social organization that differs substantially from the stable groups reported for savannah baboons (chacma, olive, and yellow baboons), the male-centred harem structure found in hamadryas baboons or the female-centred one-male units in gelada baboons (Galat-Luong et al. 2006, Patzelt et al. 2011, Swedell 2011).

Guinea baboons live in multi-male, multi-female units, comprising 50-70 individuals, which we termed “gangs”, to differentiate clearly between the multi-level social organization of this species and the stable social groups of savannah baboons. Neighbouring gangs aggregate frequently during the day and at sleeping sites, and can form large communities of more than 350 individuals (Dunbar and Nathan 1972, Galat-

Luong et al. 2006, Patzelt et al. 2011). Despite the extensive spatial overlap in the territory use by different gangs, and the frequent close proximity of individuals belonging to different gangs, socio-positive as well as socio-negative interactions are largely restricted to members of the own gang (AP, PM, IN, D Zinner, JF, unpublished data).

To investigate how adult male Guinea baboons differentiate between their own, neighbouring and stranger gang males we conducted playback experiments. We also assessed the spatial and temporal overlap between gangs using Global Positioning System (GPS) data from collared individuals. In the playback experiments, we broadcasted male grunts from different categories ("own gang", "neighbouring gang" and "stranger gang"). According to the theory outlined above, we would expect that Guinea baboon males respond strongly to stranger, but not to neighbouring males, as they do not consider these males as potential threats (the "dear enemy" effect). Alternatively, because of the high tolerance, they may not consider any members from other gangs as competitors and thus, largely ignore them. In this case, it might be that they focus their social attention on the members of their own gang and thus, respond most strongly after presentation of calls from their own gang members.

Methods

Study site

Research took place from March 2011 until July 2011 at the field station of the German Primate Center (DPZ), the Centre de Recherche de Primatologie (CRP), in the Simenti region (13°01´34´´ N, 13°17´41´´ W). The area is located in the Niokolo Koba National Park in south-eastern Senegal. The climate in this region is highly seasonal with a dry season from November until June and a rainy season from July until October. The annual rainfall ranges from 1000-1100 mm (Dupuy 1971) and occurs mainyl in the rainy season. The vegetation in this area varies from grassland savannah to deciduous forest, with gallery forest limited to the river banks. Despite a dramatic decrease in large mammal population sizes during the last decades, potential predators such as lions (*Panthera* *leo*), leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) still exist in this region (Ndao and Henschel 2011).

Subjects

The Guinea baboon community within the research area comprises approximately 350-400 individuals, separated into several gangs. 12 subjects were fitted with radio- and GPS-collars (Tellus GPS, Televilt, Sweden). Systematic observation began in 2010 and since June 2010 two gangs are fully- and one gang is semi-habituated to humans (Mare gang = M, Simenti gang = S, River gang = R, i.e. around 200 individuals), which makes detailed focal observations possible. GPS-fixes from six individuals in the three gangs were used (two collars per gang) to analyse spatiotemporal interactions between gangs. GPS-fixes during the day were taken every two hours and during the night every three hours. By using a Ultra High Frequency (UHF) download system (RCD-04, Televilt, Sweden) GPS fixes were downloaded from the collars. We analysed GPS-data for five months during the dry season (X = 1970 GPS points per individual). We calculated home ranges of the three gangs via minimum convex polygons (MCP) (ArcGIS 2010, ESRI Inc., Redlands, US, the MCP of the three neighbouring gangs are illustrated in Fig. 4.1a). The software “at” (programmed by Ch. Franzl) was used to assess the spatial distance between the three gangs by calculating, from all possible GPS points in the given period, the percentage of points the gangs spend within a radius of 500 m of each other (X = 25.52 ± 3.37 %).

To date, the dispersal pattern of Guinea baboons remains unclear, although preliminary observations suggest that females transfer between gangs (A Goffe, G Fickenscher, D Zinner, JF, unpublished data). Competition for access to females between males appears to be rare and altogether clearly different from male competition witnessed in chacma baboons (U Kalbitzer, JF, personal observations). Males maintain strong bonds with specific other males, and engage in both grooming and ritualized greetings (Whitham and Maestripieri 2003). Because of the scarcity of agonistic interactions among Guinea baboon males within a gang, it was not possible to establish a dominance hierarchy for the animals tested in this study.

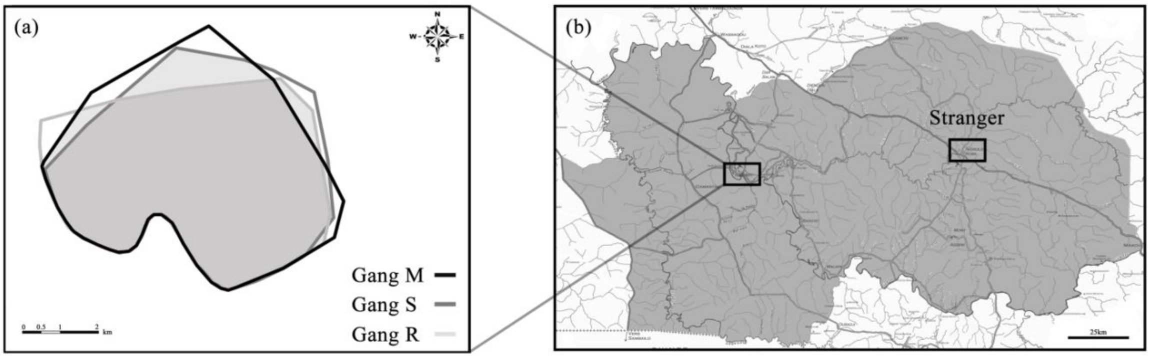

Figure 4.1. Recording sites of male grunt vocalizations. In Figure 1a the home ranges of three neighbouring gangs of the study area were calculated by using GPS-points of six collared individuals (M = Mare gang, S = Simenti gang, R = River gang). Figure 1b shows a simplified map of the Niokolo Koba National Park and the recording site of stranger males' vocalizations.

Gang aggregations of Guinea baboons are flexible and may vary from day to day (AP, PM, IN, D Zinner, JF, unpublished data). During aggregations, members of different gangs may come in close proximity to one another, so that it is difficult to delineate one gang from another (Galat-Luong et al. 2006, Patzelt et al. 2011).

Experimental design and data analysis

We simulated the presence of another male by playing back a bout of male grunts. Grunt vocalizations are the most common vocalizations in baboons and are individually distinctive (Owren et al. 1997, Rendall 2003). In other baboon species (Rendall et al. 1999, Meise et al. 2011), they are typically given as a signal of "benign intent" (Cheney and Seyfarth 1997a) when one animal approaches another to engage in socio-positive behaviour. They may also function as "contact calls" when animals are initiating a move (Fischer and Zinner 2011), or while travelling (Rendall et al. 1999, Meise et al. 2011). For all experiments we used naturally occurring sequences of eight-12 grunts which were matched for duration (≈ 4 s); Fig. 4.2 shows a spectrogram of a male grunt bout. The amplitude of the call sequences was adjusted by using a Voltcraft 322 sound level meter (Voltcraft, Germany; 'C' weighting, response time: 125 ms) and sound pressure level was kept constant (X = 70.4 ± 1.8 dB, measured at 1.5 m distance from the loudspeaker). Call sequences were recorded during focal sampling from March 2010 until June 2010 and

February 2011 until March 2011, using a Marantz solid state recorder PMD 661 and a Sennheiser ME-66 directional microphone. Only calls recorded from less than 6 m and with a high signal-to-noise-ratio were used for the experiments. Calls from stranger males were recorded from a baboon community ranging more than 60 km away from our study area, as depicted in Fig.4.1b.

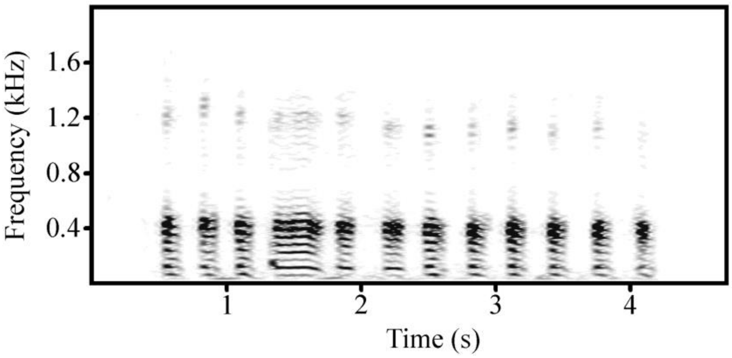

Figure 4.2. Spectrogram of a playback sequence of a male grunt bout. The spectrogram was created by using Avisoft SASLabPro 5.1 (R. Specht, Berlin, Germany; fast Fourier transform resolution 1.024 points, sampling frequency: 4 kHz, time resolution: 4ms, time overlap: 98.43, Hamming window).

Grunts were played back to eight males from gang M and four males from gang S in a balanced order. In total, we conducted 36 playback trials with the 12 males (11 were adult, one was just reaching adulthood). Calls of both neighbouring gangs of gang M and gang S were used in the neighbour condition. Each male was tested no more than once per week to minimize habituation effects. As members of the same gang were rarely far away from each other, playback trials were only conducted when the caller had been seen in the gang that day, but had been out of sight for at least 15 minutes. In all trials, the loudspeaker was hidden behind large objects (e.g. termite hills, tree-trunks), 10-15 m away from the caller. Calls were played back using an active speaker (David Active, VISONIK, Berlin) connected to a Marantz PMD-661 recorder. Although the ability to conduct the playbacks was limited by natural conditions (presence of the caller, dense vegetation), we attempted to playback calls only in situations when the subject was at the edge of the gang and did not socially interact or was in physical contact with any other individual. In two trials, however, another individual came within a distance of 10 m to the subject during the experiment, but did not interact socially with it. Altogether, each male was tested a total of three times.

We filmed all playback experiments using a Sony Handycam (DCR-HC90E). Subsequently, we digitised the videotapes and saved them in Windows Media video format. We did a frame-by-frame analysis using VirtualDub 1.9.11 (freeware, www.virtualdub.org). We examined the subjects’ reaction by scoring the orienting response in one of the four categories: 1: no reaction, 2: looking in the direction of the speaker, 3: approaching (walking toward the speaker, which may include looking towards the speaker) and 4: approaching the speaker and vocalizing while approaching. We further determined the duration of the orienting response within 30 s following the onset of the playback. In cases of several orienting responses within 30 s, we summed the duration of each orienting response (irrespective of the response category). Finally, we investigated the latency to respond (the time between the onset of the call and the onset of the orienting response). A subset of randomly selected trials was “blind” coded by a second observer, who was unaware of the experimental conditions. Cronbachs’ alpha for response duration and response latency was 0.988 ($n = 18$) and 0.975 ($n = 18$), indicating excellent inter-observer reliability. For the behavioural categories, the inter-observer reliability was similarly high (Cronbachs’ alpha = 0.984 ($n = 18$)). We used exact Friedman tests and exact Wilcoxon signed-rank tests to analyse the differences in relation to category, and exact Mann-Whitney U-test to consider possible differences between the two gangs (Mundry and Fischer 1998). All tests were two-tailed and significance level was set at 0.05. SPSS 19 was used for the analysis.

Results

Subjects oriented toward the speaker in 35 out of 36 trials. There were no significant differences in the responses between the two gangs in any of the conditions (Mann-Whitney U-test, own gang: $n_M = 8$, $n_S = 4$, $W = 22.5$, $p = 0.384$; neighbour gang: $W = 20$, $p = 0.333$; stranger gang: $W = 20$, $p = 0.333$). Subsequently, we pooled the data of both gangs and analysed the differences in relation to the call categories. The behavioural scores (no reaction, looking, approaching, approaching plus vocalizing) differed significantly between the different playback conditions (Friedman test, k = 3, n = 12 χ^2 = 14, p = 0.001). Males responded most strongly to their own gang members' calls compared to neighbouring and stranger males' calls. Post-hoc comparison revealed a significant difference between non-gang members' calls: own vs. neighbouring (Wilcoxon signed-rank test, n = 12, W = 28, p = 0.016) and own vs. stranger gangs (Wilcoxon signed-rank test, n = 12, W = 28, p = 0.016), but no difference was found in the response behaviour between neighbouring and stranger males' calls (Wilcoxon signed-rank test, n = 12, W = 0, p = 1). The results of the post-hoc tests still remained significant after Bonferroni correction (p = 0.017). In seven out of the 12 trials the male approached the loudspeaker when calls from the same gang were played back. Grunt vocalization occurred only once, in response to the calls from the same gang. Neither approaches nor vocalizations occurred in response to calls of members from other gangs.

The observed pattern of the response duration corroborates the previous findings. Differences between the two gangs were not significant for all conditions (Mann-Whitney U-test, own gang: n_M = 8, n_S = 4, W = 18, p = 0.808; neighbour gang: n_M = 8, n_S = 4, W = 23.5, p = 0.230; stranger gang: n_M = 8, n_S = 4, W = 18, p = 0.808). There was a significant difference across the three playback conditions (Friedman test, n =12, χ^2 = 10.34, p = 0.004). In response to calls from the same gang the orienting time was significantly longer (X = 14.3 ± 12.55 s) compared to the orienting time towards calls from neighbouring gangs (X = 4.02 ± 3.16 s, Wilcoxon signed-rank test, n = 12, W = 69.5, p = 0.013) and stranger gangs (X = 1.95 ± 1.59 s, Wilcoxon signed-rank test, n = 12, W = 71, p = 0.009), as shown in Fig. 4.3. We found no differences in the orienting time between neighbouring and stranger gang vocalizations (Wilcoxon signed-rank test, n = 12, W = 40, p = 0.577). The response latency did not differ across the different playback conditions (Friedman test, n = 12, χ^2 = 0.326, p = 0.906).

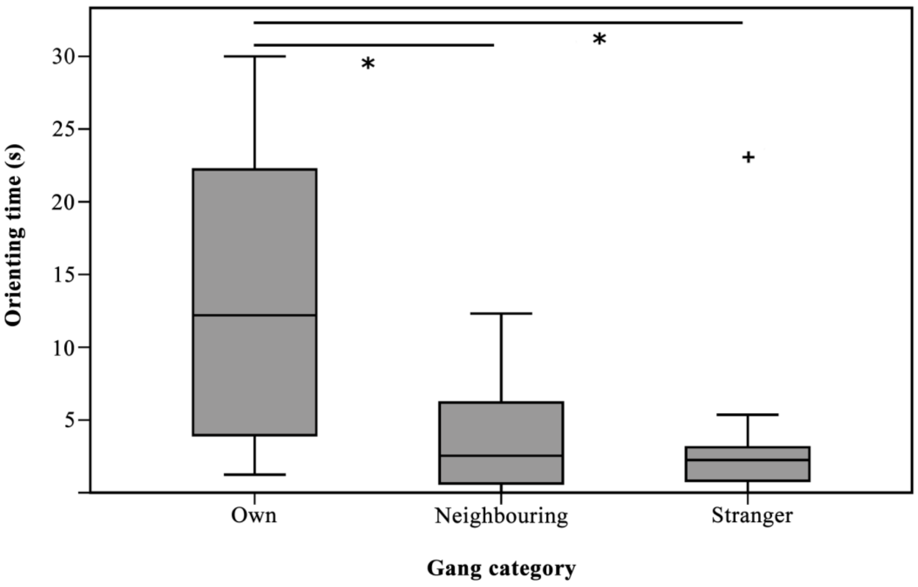

Figure 4.3. Orienting time towards the speaker. Median is shown as a black line. Box plots represent quartiles and error bars represent 95% confidence interval. * symbolize statistical significance and $^+$ represent outliers.

Discussion

In the playback experiments, male Guinea baboons showed a significantly longer orienting behaviour towards the loudspeaker after being presented with vocalizations of their own gang members than in the other two conditions; in seven out of 12 trials they even interrupted their previous activity and approached the loudspeaker. In contrast, they only looked briefly in response to calls of males that did not belong to their own gang. There was no difference in the orienting time following the playback of neighbour or stranger males' calls. These findings are in line with the view that male Guinea baboons do not consider males from other gangs as intruders or direct competitors, as they showed a remarkably unconcerned response toward members from other gangs, and focus their social attention mainly on members of their own gang.

Generally, the response pattern indicates that Guinea baboon males discriminate the vocal characteristics of their gang members and differentiate between gang and non-gang members. Within their own gang, Guinea baboons are permanently associated and frequently engage in socio-positive as well as socio-negative interactions with other gang members (AP, PM, IN, D Zinner, JF, unpublished data). Hence, the own gang members differ in their social relevance compared to neighbouring individuals with whom gang members show only spatial proximity. The distinction depending on the consistency of social interactions and the ability to differentiate between group (or unit) vs. non-group (or non-unit) members has also been found in other fluid animals societies, although the specific response pattern may differ (African elephants (*Loxodonta africana*) [McComb et al. 2000]; sooty mangabeys (*Cercocebus torquatus atys*) [Range 2005]; spider monkeys (*Ateles geoffroyi*) [Ramos-Fernandez 2005] and ravens (*Corvus corax*) [Boeckle and Bugnyard 2012]). African elephants for example, live in large multi-level societies with a high fission-fusion dynamic (McComb et al. 2000). Although neighbouring units regularly aggregate and largely overlap, strong social associations only exist between members of their own family units or bond groups. A previous study has shown that individuals distinguish between calls of their unit members and non-unit members and, while subjects engaged in a high amount of contact calling and affiliative approaches toward their unit members' calls, they largely ignore vocalizations of neighbouring non-unit individuals (McComb et al. 2000). Unit members mingle frequently around non-unit individuals and are often visually separated from each other, hence to stay in contact with their social allies, via contact calling, and to discriminate their associates' calls seems to be essential in the fluid multi-level society of African elephants.

Another playback study conducted on female sooty mangabeys showed a similar discrimination pattern, albeit with a different response pattern (Range 2005). In sooty mangabeys, different sexes employ different group membership strategies. While males may join and leave the group for months, females remain resident all year round (Range et al. 2007). Neighbouring non-group males are encountered frequently and sometimes walk through the group for several minutes; however, they only rarely interact with females and are usually viewed as infanticidal threat. Resident males in contrast, associate and interact regularly with their group members. Playback experiments have shown that females recognize the residence status of the males, irrespective of whether males are full- or part time residents, while they respond strongly only to non-resident males; i.e. they often leave their position when calls from non-resident males were played back. Thus, in different species the distinction of own group (or unit) vs. neighbouring group (or unit) members may be driven by different selective pressures.

The long orienting time and approach responses toward their own gang members' vocalizations suggest that Guinea baboon males are attentive to the social interactions of members of their own gang. Although we are unable to determine how social attributes (such as kinship) influence the response behaviour in Guinea baboons, our findings lend support to the notion that the gang constitutes the social entity within the multi-level Guinea baboon society. In other baboon taxa, such as chacma baboons, males exhibit enduring relationships with other group members, such as 'friendships' with lactating females (Nguyen et al. 2009, Huchard et al. 2010), consortships with oestrous females (Crockford et al. 2007) and dominance relationships with adult males (Kitchen et al. 2003). Previous playback studies have demonstrated that male and female subjects pay particular attention to the calls of their associates and are sensitive to the social events their bond partners and/or competitors are involved in (Bergman et al. 2006, Crockford et al. 2007, Lemasson et al. 2008). Rank differences at least, seem not to explain the response pattern in Guinea baboons, since this concept appears not to be suited to characterize Guinea baboon male relationships, and neither does the strength of the relationship predict response strength (AP, PM, IN, D Zinner, JF, unpublished data). Further observations and field experiments will be needed to clarify by which social attributes Guinea baboons differentiate among their gang members and how well individuals of different sexes and age classes track their social relationships.

In contrast to gang member and non-gang member distinction, Guinea baboon males do not differ in their response behaviour toward neighbouring and stranger males and largely ignore any non-gang member, irrespective of familiarity; that is, they neither show a "dear enemy" nor "nasty neighbour" effect. While at present we are unable to clarify whether this is due to an inability to distinguish between such a large number of voices or a lack of motivation to do so, such lack of concern about potential unfamiliar individuals lies in sharp contrast to other baboon species and many group living primates (Wich et al. 2002, Kitchen et al. 2004, Herbinger et al. 2009, Meunier et al. 2012). Theory predicts that neighbour-stranger differentiation should mostly occur when inter-group competition is high (e.g. Radford 2005, Müller and Manser 2007, Herbinger et al. 2009). Guinea baboon males do not seem to consider members from other gangs as competitors and by ignoring any non-gang members' call they justify their classification as a highly tolerant species. A playback study conducted on gelada baboon males revealed a similar lack of responses to the playback of males outside the harem holders' social unit (Bergman 2010). The author pointed out that through the absence of competitive relationships between gelada baboon harem holders, they do not need to differentiate among their unrelated neighbouring units who they regularly encounter.

Another possibility might be that Guinea baboon males are simply unable to recognize all of their neighbours' call characteristics. A Guinea baboon community can comprise more than 350 individuals and the composition of subgroups varies substantially over time (Galat-Luong et al. 2006, Patzelt et al. 2011). Savannah baboons, such as chacma or olive baboons, in contrast live in stable medium sized social groups with individual numbers ranging from 20 to 80 animals (Swedell 2011). Possibly, the recognition and discrimination of all males in the vicinity may be beyond the limits of Guinea baboon males. From our results, we are unable to decide whether a lack of ability or a lack of motivation accounts for the observed response pattern. Yet, the experiments clearly demonstrate that Guinea baboon males are able to discriminate the voice characteristics of their own gang members from those not belonging to their own social unit.

Our findings have important implications for the assumption that social complexity is a driving force in the evolution of social cognition. The costs and benefits, that is, the fitness consequences of tracking social interactions between others appears to be more important than the multi-layered structure of the society per se. It may indeed be likely that high levels of competition or direct links between stable social bonds and reproductive success (Silk et al. 2003, Silk et al. 2009) are more decisive for the evolution of a "Machiavellian" mind (Byrne and Whiten 1988) than fission-fusion dynamics. In sum, our playback experiments showed that males took interest only in the (simulated) social interactions of their own gang members, while they ignored both neighbour and stranger calls. The generally low responsiveness toward males from other gangs is probably an expression of the low level of competition between gangs. Our findings suggest that Guinea baboon males' social relationships are characterized by the quality and consistency of the social interactions, while simple spatial aggregation does not appear to be important. Taken together, our study supports the view that the animals allocate their social attention in relation to the requirements and selective pressures generated by the specific social system they live in, while a complex social organization does not necessarily translate into the need for more elaborate social knowledge.

Acknowledgments

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Ethical standards

All playback experiments, as well as capturing and handling procedures, comply with the current law of Senegal and Germany and were conducted under permits issued by the Diréction des Parcs Nationaux du Senegal.

Conflicts of interest

The authors declare that they have no conflict of interest.

GENERAL DISCUSSION

The call structures of Guinea baboons showed a strong phylogenetic signal, i.e. the same call types as in other baboons occurred. The call usage however, differed from other taxa in the rate and context of utterances and reflected the less-competitive and affiliative social relationships of Guinea baboons. The response pattern of Guinea baboons corresponded to their highly tolerant and relaxed social style. Hence, the specific characteristics of Guinea baboons' social relationships act as a strong selective pressure on their vocal communication as well as their social cognition, although the different aspects were affected differentially.

In this general discussion, I will shortly summarize the most important findings and highlight how my study has contributed to our understanding about the influence of sociality on the evolution of primate vocal communication as well as their social cognition. Afterwards, I will briefly summarize some methodological aspects from both bioacoustics studies and what implications they might have for further studies. Finally, I will give a short outlook.

5.1. Vocal communication in Guinea baboons

5.1.1. Constrained structure

The call types found in Guinea baboons namely *grunts, screams, barks, wahoos, roar grunts*, and *copulation calls*, have all been described either onomatopoetically or quantitatively in other baboon taxa (e.g. Hall and DeVore 1965, Owren et al. 1997, Fischer et al. 2001b, Fischer et al. 2002, Rendall et al. 2009, see results in Chapter 3). Hence, my results suggest a strong phylogenetic signal in the Guinea baboon vocal repertoire and indicate that phylogenetic inertia in baboons largely limit the variability of their vocal production.

Although Guinea baboons live in a tolerant and complex multi-level society with flexible grouping patterns (i.e. gang aggregations can vary from day to day [Patzelt et al. submitted]) and sometimes exceed more than 350 individuals), which largely differs from the stable multi-male, multi-female groups of savannah baboons (Swedell 2011), this had no effect on the structure of their vocalisations. Hence, albeit the species' social system is supposed to act a strong selective pressure on primate vocal communication (see Chapter 1-General Introduction), this did not affect the Guinea baboons` signal design.

The outcome of my study has implications for the social complexity hypothesis, which argues that a species' vocal variability is largely driven by their social complexity, i.e. species living in more complex social organizations should exhibit a larger number of different call types (e.g. Semple and McComb 2005, Pollard and Blumstein 2012, Freeberg et al. 2012). At least among baboons, as soon as phylogenetic relation is taken into account, as in our study, the importance of the species' social system on the morphology of their repertoire structure appears to be largely negligible. Hohmann (1991) found similar results. Although macaques as well as langurs, largely differ in their social organization within the genus [i.e. *Macaca silenus* as well as *Presbytis johnii* live in one-male groups, while *M. radiatia* as well as *P. entellus* live in much larger multi-male groups], this did not lead to any socially related intra-genus vocal variability (see Gautier 1988 for similar results among guenons).

Even though we did not look specifically at environmental effects, the habitat type did not have an effect on the structure of the Guinea baboons' vocalizations. However, since Guinea baboons range in largely similar habitats as other baboons and since there is more variation in environmental conditions within than between taxa, we did not deem this to be an important driver.

The variability of the vocal structures among baboons corresponds to the innate sound production mechanism in primates. In Guinea baboons, certain vocal features were largely determined by the callers' morphology (i.e. fundamental frequency, formant dispersion, see Chapter 3 for more details) and the differences between the values obtained in my study and those reported for other baboon taxa are also most likely related to differences in body size. For instance, grunts of male and female Guinea baboons had a higher fundamental frequency than those in chacma baboons (Rendall et al. 2005). Other features of the Guinea baboon call structures were rather influenced by the arousal state of the caller (e.g. the noisiness of grunts, see Chapter 3 for more details). How they might contribute to inter-specific differences remains a question for further comparative research. In general, the calculation of different acoustic parameters among different studies largely hampered a detailed inter-specific comparison. Yet, to unravel how differences in the sound production apparatus may contribute to the vocal variability among closely related taxa, more systematic comparisons are definitely needed.

5.1.2. Flexible usage and call function

The call usage of Guinea baboons differed substantially from other baboon taxa; hence, phylogeny only slightly constrained the utterance of the Guinea baboon call types. The inter-specific differences in the context-usage corresponds to differences between the Guinea baboons’ and other baboon taxa's social style. In accordance to the hypothesis that the vocal communication of a species is largely driven by the characteristics of their social relationships, call usage, especially during competitive interactions, differed from savannah baboons. Guinea baboons did not produce any display or contest signals, which is an important signal category in highly competitive animal societies (Bradbury and Vehrencamp 2011). Display signals evolved among many vertebrates and may serve as indicators of an individual’s competitive ability (e.g. Fischer et al. 2004, Reby et al. 2005). They constitute an important assessment strategy to resolve aggressive interactions at the lowest possible cost. In chacma baboons for example, males fight aggressively for social rank, which confers priority of access to resources, most importantly fertile females (e.g. Alberts et al. 2003). Chacma males use loud call displays to resolve aggressive disputes via signalling rather than by costly fights (Kitchen et al. 2003). Guinea baboons however, differ in their conflict behaviour and although competitive interactions occur among male Guinea baboons, they appear to be much less intense. Accordingly, there is less pressure to resolve social conflicts via signalling in male Guinea baboons than in chacma baboons, rendering costly contest signals superfluous. In contrast, in Guinea baboons, greeting interactions, accompanied by grunting, appear to serve as an important conflict management strategy among adult males (Whitham and Maestripieri 2003). Although the specific function of mutual greetings in Guinea baboons still needs to be clarified, in other animal societies mutual greetings serve as an important assessment tactic to evaluate behavioural tendencies during conflicting situations, (Preuschoft and van Schaik 2000) and to reduce aggressive tendencies (e.g. in Bonobos (*Pan paniscus*) Hohmann and Fruth 2000). Hence, once competition is less intense, animals appear to exhibit less costly behavioural strategies to resolve their conflicts. Signal usage outside the competitive regime was largely similar to that in other baboon taxa. Besides greetings, males often grunted during affiliative interaction with females, and during infant handling, a vocal pattern which has commonly been observed in other baboons (e.g. chacma baboons [Palombit et al. 1999], olive baboons [Ey et al. 2009]). Female Guinea baboons grunted almost exclusively during affiliative interactions. However, their calling rates were much lower compared to males, probably reflecting the lower rate of affiliative interactions compared to males, which differs from the female-bonded savannah baboon societies (e.g. Cheney and Seyfarth 1995, Meise et al. 2011).

How the habitat influences the usage and rate of vocal signals was not addressed by this thesis and still needs to be clarified. Previous research on other baboons has shown, however, that short-term fluctuations in visibility may directly affect calling rates. When the visibility was poor and the risk of losing contact with social partners increased, females called more frequently than in open habitats (Rendall et al. 2000, Ey et al. 2009). However, as already mentioned (see Chapter 1) it renders to be difficult to isolate the ecological influence on the call usage, since other factors, such as the contexts of calling or the proximity between caller and recipients, might override the effect of the environmental related usage variability (e.g. Ey and Fischer 2009, Koda et al. 2008).

The higher flexibility in the socially driven call usage corresponds with the developmental and neurophysiological mechanisms involved in the vocal usage of primate calls. As mentioned in the Paragraph 1.2.2., experience plays an important role in acquiring the context specific vocal usage in primates, and individuals are able to flexibly adjust their calling rates due to changes in their social environment.

5.1.3. Social knowledge and caller relevance

My playback experiments have shown that male Guinea baboons distinguished between the simulated social events of their own gang members and those of non-gang members. While subjects were highly attentive toward their associate’s calls, they largely ignored any call of non-gang members. This response pattern indicates that male Guinea baboons discriminate the vocal characteristics of their gang members and classify them due to their membership status, a characteristic of social knowledge which is widespread among social primates, although the specific response patterns differ (e.g. sooty mangabeys *Cercocebus torquatus atys* [Range 2005], spider monkeys, *Ateles geoffroyi* [Ramos-Fernandez 2005]). In contrast, Guinea baboons did not distinguish among neighbouring individuals and ignored any calling/social events from non-gang members, irrespective of whether the caller was a neighbour or a stranger. Such lack of concern about potential unfamiliar individuals stands in stark contrast to the response pattern observed in savannah baboons and many other group living primates (e.g. Wich 2002, Herbinger et al. 2009, Meunier et al. 2012, see Chapter 4 for a detailed explanation of the “dear enemy” as well as “nasty neighbour“ effect) and justifies the classification of Guinea baboons as a highly tolerant species.

Primates are well known to integrate additional contextual cues, such as group (or unit) membership or relationship quality, into their call assessment, and based on that information, decide how to respond to a vocal signal (e.g. Palombit et al. 1997, Cheney et al. 2010, see Wheeler and Fischer 2012 for a recent review). Since Guinea baboons are permanently associated, and engage frequently in social interactions with their own gang members, their own gang members may be more socially relevant than non-associated neighbouring individuals, with whom they only spatially overlap. The obvious response behaviour (i.e. long orienting time and approach, see results in Chapter 4) suggests that Guinea baboon males are highly attentive to the simulated social interactions of their own gang members. Although I was unable to determine in detail how specific social attributes, such as kinship or social bonds, influenced their response behaviour, the resident status of their gang member appears to be relevant for the subjects (see Chapter 4 for detailed discussion). This low responsiveness toward non-associates and the lack of differentiation probably reflects their low level of competition between gangs, i.e. males Guinea baboons appear not to consider males of other social units as competitors or potential threats.

5.2. Summary and conclusions

The outcome of my study elucidates how different constraints and selective pressures have acted on the Guinea baboon vocal communication. In accordance with the innate pattern of primate vocal production, phylogenetic inertia largely determined the structure of the Guinea baboons' vocal repertoire. Irrespective of possible selective pressures generated by the specifics of their social system (or their environment), the observed acoustic variability among closely related baboon taxa might rather be explained by sender-related morphological or physiological constraints.

In contrast, the call utterance of Guinea baboons differs from other taxa in the context specific usage and the calling rate, and corresponds to the less competitive characteristics of their social relationships. Male Guinea baboons do not use loud calls as displays of their fighting ability, while they frequently grunt during male-male greetings and affiliative interactions. Hence, the specifics of the Guinea baboons' social system constitute a strong selective pressure on their vocal production, whereby the social impact was mainly reflected by the flexible utterance of their vocal signals.

The receiver`s response to calls also differs from other baboons, and the social knowledge of male Guinea baboons, i.e. the discrimination of membership status, largely reflects their highly tolerant and relaxed social style. How males distinguished among non-associates corresponds to the less competitive relationships between social units, which differ strongly from other primates. On the other hand, males discriminated the vocal characteristics of their own gang members, with whom they are socially associated, and were attentive to their social manoeuvres. Hence, Guinea baboon males allocate their social attention in a manner compatible to the specific requirements of the social system they live in and the quality and consistency of the Guinea baboon's social interactions appear to be essential for the formation of their social knowledge and to the specifics of their response behaviour.

In general, albeit phylogeny imposes constraints on their vocal repertoire, the vocal communication of Guinea baboons was strongly driven by the specific requirements of their social system. The differential variability of call structure, usage and receiver`s responses largely reflects the different constraints and flexibility underlying those aspects in primate vocal communication.

5.3. Implications for further studies

Even though comparative studies are crucial to understand the evolutionary dynamics of animal communication (see above), until now no standardized methods exist neither to describe nor to analyse vocal variations in primates. For detailed comparative analyses however, uniform procedures to select acoustic features, to reduce redundant information or to classify vocal structures are crucially needed. In the next paragraph I will illustrate by which criteria's we selected acoustic parameters and analysed the vocal variations of Guinea baboons' and will shortly indicate, what implications our methodological approaches may have for further comparative studies.

5.3.1. Parameter selection

When analysing vocal structures in primates, one should try to reduce the variation caused by recording conditions and only valid sound parameters should be used to assess vocal variability among different species. As revealed via our transmission experiments, habitat type, transmission height and re-recording distance influenced the structural properties of the re-recorded chacma baboon calls (see detailed results in Chapter 2) and most acoustic features were affected by degradation, a result which has also been found during former sound transmission experiments conducted on other animal sounds (e.g. Wiley and Richards 1978, Brown and Waser 1988, Nemeth et al. 2001, Pedgham 2004). However, the influence of the respective re-recoding conditions differed and certain acoustic parameters were more affected than others. Firstly, parameters which described start- and the end parts of a call (e.g. Dfb1 start/end), appeared to be highly unreliable, even when recorded under the same conditions (see discussion Chapter 2 for possible explanations), hence to use them for acoustical analyses might not be advisable. Mean parameters on the other hand showed a much higher validity, however, they were affected by recording distance and recording height. The DFA mean for example, which describes the statistical distribution of energy, is particularly susceptible to low broadcasting levels and far distances. Since these parameters describe the statistical distribution of energy in the whole frequency spectrum, it is not surprising that the attenuation in relation to broadcasting height and distances makes it difficult to estimate the correct distribution of frequency energy of the original call. Our results are generally in agreement with other researchers' descriptions of amplitude- and frequency- dependent attenuation due to varying broadcasting conditions (e.g. Nelson 2003, see discussion in Chapter 3 for further examples). Hence, the value of amplitude- based parameters of animal sounds recorded from larger distances, especially transmitted by callers on the ground, can lead to erratic measurements. Accordingly, recording distance should be minimized, and as much information as possible on distance should be included to allow for a judgment of the reliability of such acoustic measurements. Tonal parameters on the other hand, such as fundamental frequency (F0), were much less affected by varying re-recording conditions and, as long as some harmonics remained in the frequency spectra, could be reliably calculated, also over larger distances. The fundamental frequency is commonly estimated based on the autocorrelation function of the frequency spectra (Schrader and Hammerschmidt 1997). The autocorrelation function is able to recalculate the F0 of degraded spectra as long as some harmonic peaks remain. A visual control of the F0 estimation can lead to an even higher reliability of F0 calculation.

In sum, recording distances should be minimized to compensate for strong attenuation effects. In my study of the Guinea baboons' vocal repertoire I did not analysed calls recorded from a distance of more than 10 m to reduce variation caused by recording conditions. Furthermore, acoustic analyses should focus on a limited set of robust acoustic features. Accordingly, I mainly used valid mean parameters, as well as tonal measurements to describe Guinea baboons' vocal structures. In sum, acoustic parameters should be selected appropriately and before using certain parameters for comparative analyses, it might be necessary to assess their measurement reliability and validity.

5.3.2. Parameter reduction

To classify vocal repertoires, it is important to reduce redundant information. There are different ways for parameter reduction to be carried out, and while some researchers use formal analytic procedures, such as principal component analysis (PCA) (e.g. Wich 2008, Rendall et al. 2009) others prefer a manual selection of meaningful acoustic features (e.g. Hammerschmidt et al. 2012, Bouchet et al. 2012). In my study, a PCA did not appear to be appropriate and I manually chose a set of nine acoustic parameters, which broadly described the temporal- and spectral quality of the vocalizations as well as the call tonality including spectral modulation (see methods in Chapter 3 for detailed parameter descriptions).

Although a PCA is commonly used in bioacoustic research it does not always lead to appropriate results. While using an orthogonal transformation, the PCA tries to reduce a multidimensional data set into a smaller set of variables, and loads them onto different components or factors. Assigned factor scores are then used for further statistical analysis. However, if numerous variables load on a single factor, it often becomes difficult to interpret them, and important parameters might not be detectable anymore. In my study, most variance of my data set could be explained by a single factor; hence, using factor scores for further analyses was not appropriate. Based on the vocalizations under study, different ways to reduce redundant information need to be considered and the use of formal reduction procedures might not always lead to suitable results.

5.3.3. Cluster analysis

Quantitative classification procedures (i.e. cluster analyses) use formal algorithms to detect natural patterns in the acoustic space of a species. Such approaches are largely independent of the authors’ tendencies to categorize and accordingly, allow systematic inter-specific comparisons of the species’ repertoire characteristics. Different cluster analysis exists (e.g. k-means, two-step) to categorize a given data set and the way how clusters are calculated largely differs. After trying different methods, the two-step cluster algorithm, together with a log likelihood distance measure, appeared to be the most appropriate one for the Guinea baboons` vocal variability, since the formal classification results largely coincided to the onomatopoetical impression of the Guinea baboons´ vocal structure. Irrespective which solution was considered, to describe the vocal repertoire, the data set partition based on the two-step cluster algorithm mirrored the natural pattern of the Guinea baboons' acoustic configurations (Figure 5.1.).

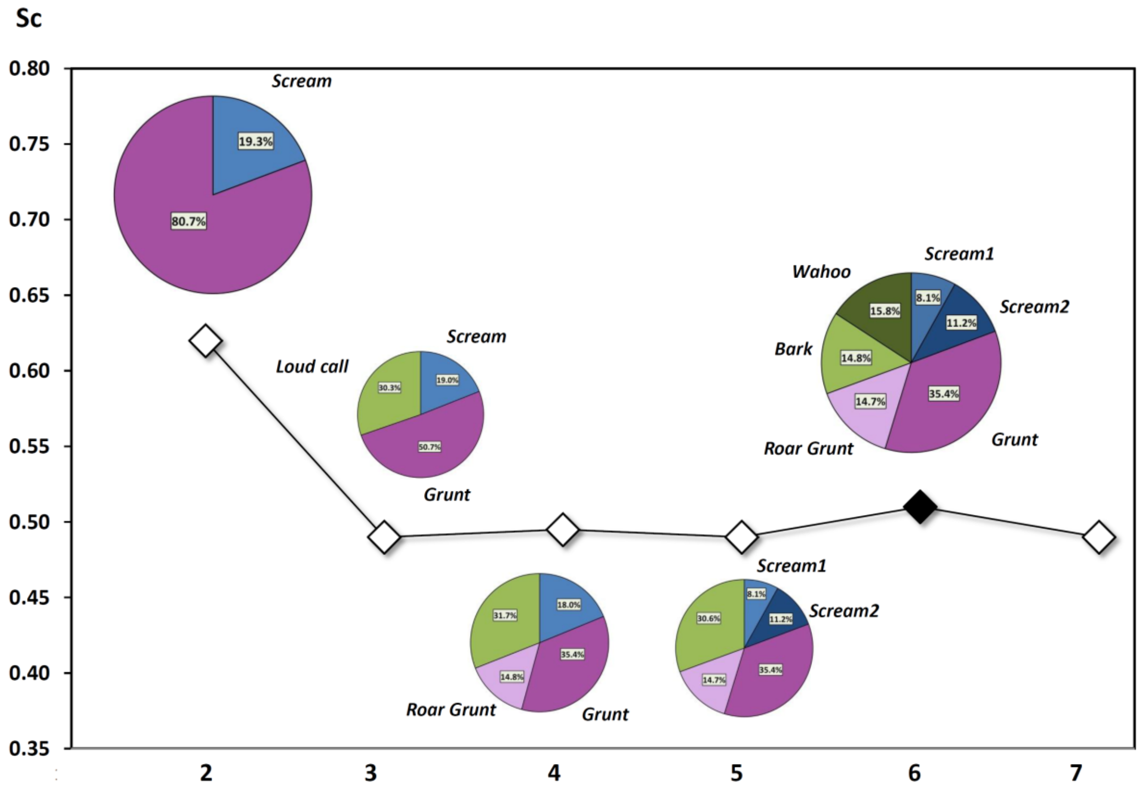

Figure 5.1. Different cluster solutions and the respective data set partitions are shown, together with the silhouette values (SC). Assigned call clusters largely corresponded to the onomatopoetic impressions of the calls. Irrespective which cluster solution was chosen, each clustering showed a meaningful partition of the given data set. The process of the clustering procedure nicely illustrates the continuous transition from on solution to another. The six cluster solution was applied because of the slightly higher statistical validity (mirrored by SC) and the best fit between most audio-visually distinct call types and the calculated call cluster. On the x-axis the different cluster solutions are shown, the y-axis shows the respective silhouette values.

Irrespective which cluster solution was considered, only a low amount of misclassifications occurred in the Guinea baboons' vocal repertoire and limited intergradation between calls types was detected. Given this, the quantitative analysis of the Guinea baboons call variants led to the identification of rather discrete and stable call types (except for screams). Bioacoustic studies conducted on single call types in other baboons however, have shown that within call types, acoustic structures are less discrete and grade continuously from one sub- type into another (e.g. female (Fischer et al. 2001b) and male loud calls (Fischer et al. 2002)). Hence, further studies are needed to investigate if there is similar within-call type variability in Guinea baboons.

Acoustic repertoires of primates are not always characterized by discrete call types and formal clusters analyses are often hampered by a large intra- as well as inter-call type variability (e.g. Hammerschmidt and Fischer 1998a). A study conducted on Barbary macaques for example, found substantial variability within and between call types (Hammerschmidt and Fischer 1998a). Although certain acoustic configurations could be observed via cluster analysis, the Barbary macaques' repertoire structure did not reveal such distinct call types as in my study. Further categorizing algorithms are needed to empirically describe such continuously distributed call types (a promising approach describing highly graded repertoires might be the use of fuzzy logic, which has already been successfully applied to describe neural network activities [e.g. Battaglia et al. 2013]).

5.4. Outlook

1. My study on the vocal communication of Guinea baboons provided insights into how their vocal repertoire relates to the characteristics of their social behaviour. The Guinea baboons´ vocal behaviour reflected their less competitive and more affiliative social style. How other signal categories outside the competitive regime, such as contact signals for example, might be associated to the specifics of their social system remains a question for further research.

2. How Guinea baboon males distinguished among members of other gangs was largely driven by the low level of competition between gangs. However, by which attributes males classify within their own social unit, and how well they keep track of the various social relationships they exhibit within a gang still needs to be clarified.

3. A detailed comparative analysis was hampered by the authors' different tendencies to analyse vocal signals. As already mentioned, until now, no standardized methods exist to extract and analyse acoustic features, or to classify vocal repertoires. Hence, standardized analytic procedures conducted on a comparable set of acoustic variables are definitely needed to unravel the inter-specific vocal variability among baboons in more detail.

REFERENCES

Agoramoorthy G, Hsu MJ (2000) Extra group copulation among wild red howler monkeys in Venezuela. Fol Primatol 71:147–151

Aich H, Moos-Heilen R, Zimmermann E (1990) Vocalizations of adult gelada baboons *(Theropithecus gelada):* Acoustic structure and behavioural context. Fol Primatol 55:109–132

Alberts SC, Watts HE, Altmann J (2003) Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. Anim Behav 65:821–840

Amici F, Aureli F, Call J (2008) Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. Curr Biol 18:1415–1419

Arriaga G, Zhou EP, Jarvis ED (2012) Of mice, birds, and men: the mouse ultrasonic song system has some features similar to humans and song-learning birds. PloS one 7:e46610

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, et al. (2008) Fission-fusion dynamics new research frameworks. Curr Anthropol 49:627–654

Aylor D (1972) Noise reduction by vegetation and ground. J Acoust Soc Am 51:197–205

Battaglia D, Karagiannis A, Gallopin T, Gutch HW, Cauli B (2013) Beyond the frontiers of neuronal types. Front Neur Circ 7:13

Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM (2003) Hierarchical classification by rank and kinship in baboons. Science 302:1234–1236

Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM, Whitten PL (2006) Interactions in male baboons: the importance of both males' testosterone. Behav Ecol Sociobiol 59:480–489

Bergman TJ (2010) Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. Proc R Soc Lond B 277:3045–3053

Blumstein DT, Armitage KB (1997) Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. Am Natural 150:179–200

Boeckle M, Bugnyar T (2012) Long-term memory for affiliates in ravens. Curr Biol 22:801–806

Boersma P (1993) Accurate short-term analysis of the fundamental frequency and the harmonics-to-noise-ratio of a sampled sound. Proc Inst Phon Sc 17: 97–110

Boinski S, Mitchell CL (1997) Chuck vocalizations of wild female squirrel monkeys (*Saimiri sciureus*) contain information on caller identity and foraging activity. Int J Primatol 18:975–993

Bouchet H, Pellier A-S, Blois-Heulin C, Lemasson A (2010) Sex differences in the vocal repertoire of adult red-capped mangabeys (*Cercocebus torquatus*): A multi-level acoustic analysis. Am J Primatol 72:360–75

Bouchet H, Blois-Heulin C, Pellier A-S, Zuberbühler K, Lemasson A (2012) Acoustic variability and individual distinctiveness in the vocal repertoire of red-capped mangabeys (*Cercocebus torquatus*). J Comp Psychol 126:45–56

Bradbury JW, Vehrencamp SL (1998) Principles of acoustic communication. Sinauer Associations, Sunderland

Bradbury JW, Vehrencamp SL (2011) Principles of acoustic communication. Sinauer Associations, Sunderland

Brown CH, Gomez R, Waser PM (1995) Old-world monkey vocalizations -adaption to the local habitat. Anim Behav 50: 945–961

Brown CH, Waser PM (1988) Environmental influences on the structure of primate vocalizations. In: Todt D, Goedeking P, Symmes D (eds.) Primate vocal communication. Springer, Berlin, pp. 51-68

Brumm H (2004) Acoustic communication in noise: regulation of call characteristics in a New World monkey. J Exp Biol 207:443–448

Byrne R, Whiten A (1988) Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans. Oxford University press, Oxford

Byrne RW (1981) Distance vocalisations of Guinea baboons (*Papio Papio*) in Senegal: an analysis of function. Behaviour 78:283–312

Chaffin CL, Friedlen K, de Waal FBM (1995) Dominance style of Japanese macaques compared with rhesus and stumptail macaques. Am J Primatol 35:103–116

Charrier I, Mathevon N, Jouventin P (2003) Vocal signature recognition of mothers by fur seal pups. Anim Behav 65:543–550

Cheney DL, Seyfarth RM (1982) Recognition of individuals within and between groups of free-ranging vervet monkeys. Am Zool 22:519–529

Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behav Ecol Sociobiol 21:375–386

Cheney DL, Seyfarth RM (1992) How monkey see the world. Insides in the mind of another species. University of Chicago press,Chicago

Cheney DL, Seyfarth RM, Silk JB (1995) The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. Anim Behav 50: 249–257

Cheney DL, Seyfarth RM, Palombit, R (1996) The function and mechanisms underlying baboon ‘contact’ barks. Anim Behav 52: 507–518

Cheney D, Seyfarth R (1997a) Reconciliatory grunts by dominant female baboons influence victims' behaviour. Anim behav 54:409–18

Cheney DL, Seyfarth RM (1997b) Some general features of vocal development in nonhuman primates. In: Snowdon CT, Hausberger M (eds.) Social influences on vocal development. Cambridge University press, Cambridge, pp. 249–273

Cheney DL, Seyfarth RM (2007) Baboon Metaphysics: The evolution of a social mind. University of Chicago press, Chicago

Cheney DL, Moscovice LR, Heesen M, Mundry R, Seyfarth RM (2010) Contingent cooperation between wild female baboons. Proc Natl Acad Sci USA 107:9562–9566

Cleveland J, Snowdon CT (1982) The complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). Z Tierpsychol 58:231–270

Colmenares F (1990) Greeting behaviour in male baboons, I: communication, reciprocity and symmetry. Behaviour 113:81–115

Crockford C, Wittig RM, Seyfarth RM, Cheney DL (2007) Baboons eavesdrop to deduce mating opportunities. Anim Behav 73:885–890

Date E, Lemon R (1993) Sound transmission: a basis for dialects in bird song? Behaviour 124:291–312

Dunbar RIM, Nathan MF (1972) Social organization of the Guinea baboon, *Papio papio*. Fol Primatol 17:321–334

Dunbar RIM, Shultz S (2007) Understanding primate brain evolution. Philos T Roy Soc B 362:649–658

Dunbar RIM (2011) Evolutionary basis of the social brain. In: Decety J, Cacioppo J (eds.) Oxford handbook of social neuroscience. Oxford University press, Oxford, pp. 28-38

Dupuy A (1971) Le Niokolo-Koba, premier grand parc national de la République du Sénégal. Grande Imprimerie Africaine, Dakar

Engh AL, Hoffmeier RR, Cheney DL, Seyfarth RM (2006) Who, me? Can baboons infer the target of vocalizations? Anim Behav 71:381–387

Egnor S, Hauser M (2006) Noise-induced vocal modulation in cotton-top tamarins (*Saguinus oedipus*). Am J Primatol 68:1183–90

Elowson AM, Snowdon CT, Lazaro-Perea C (1998) Infant "babbling" in a nonhuman primate: complex vocal sequences with repeatedcall types. Behaviour 135:643—664

Enquist M, Leimar O (1990) The evolution of fatal fighting. Anim Behav 39:1–9

Ey E, Hammerschmidt K, Seyfarth RM, Fischer J. (2007) Age- and sex– related variations in clear calls of Papio ursinus. Int J Primatol 28: 947–960

Ey E, Fischer J (2009) The "acoustic adaptation hypothesis" – A review of the evidence from birds, anurans and mammals. Bioacoustics 19: 21–48

Ey E, Rahn C, Hammerschmidt K, Fischer J (2009) Wild female olive baboons adapt their grunt vocalizations to environmental conditions. Ethology 115: 493–503

Fichtel C (2004) Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. Anim Cogn 7:45–52

Fichtel C, Schaik CP van (2006) Semantic Differences in Sifaka (*Propithecus verreauxi*) Alarm Calls: A Reflection of Genetic or Cultural Variants? Ethology 112:839–849

Fischer J, Cheney DL, Seyfarth RM (2000) Development of infant baboons' responses to graded bark variants. Proc R Soc Lond B 267:2317–2321

Fischer J, Metz M, Cheney, DL, Seyfarth RM (2001a) Baboon responses to graded bark variants. Anim Behav 61: 925–931

Fischer J, Hammerschidt K, Cheney DL, Seyfarth RM (2001b) Acoustic features of female chacma baboon barks. Ethology 107: 33–54

Fischer J, Hammerschmidt K, Cheney DL, Seyfarth RM (2002) Acoustic features of male baboon loud calls: Influence of context, age, and individuality. J Acoust Soc Am 111: 1465–1474

Fischer J, Hammerschmidt K (2002) An overview of the barbary macaque, *Macaca sylvanus*, vocal repertoire. Fol primatol 73:32–45

Fischer J (2004) Emergence of individual recognition in young macaques. Anim Behav 67:655–661

Fischer J, Kitchen DM, Seyfarth RM, Cheney DL (2004) Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. Behav Ecol Sociobiol 56:140–148

Fischer J (2011) Where is the information in animal communication? In: Menzel R, Fischer J (eds.) Animal thinking: contemporary issues in comparative cognition. MIT press, Cambridge, pp. 151–161

Fischer J, Zinner D (2011) Communicative and cognitive underpinnings of animal group movement. In: Boos M, Kolbe M, Kappeler PM, Ellwart T (eds.) Coordination in human and primate groups. Springer, Berlin, pp. 229–244

Fischer J (2012) Affengesellschaft. Suhrkamp Verlag, Berlin

Fisher J (1954) Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB (eds.) Evolution as a process. Allen and Unwin, London, pp. 71–83

Fitch W, Hauser M (1995) Vocal production in nonhuman primates: Acoustics, physiology, and functional constraints on “honest” advertisement. Am J Primatol 219:191–219

Fitch WT (1997) Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. J Acoust Soc Am 102: 1213–1222

Fonseca PJ, Revez MA (2002) Temperature dependence of cicada songs (Homoptera, Cicadoidea). J Comp Psychol 187: 971–976

Freeberg TM, Dunbar RIM, Ord TJ (2012) Social complexity as a proximate and ultimate factor in communicative complexity. Philos T Roy Soc B 367:1785–1801

Freitas SR, Cerqueira R, Vieira MV (2002) A device and standard variables to describe microhabitat structure of small mammals based on plant cover. Braz J Biol 62 (4B): 795–800

Galat-Luong A, Galat G, Hagall S (2006) The social and ecological flexibility of Guinea baboons: Implications for Guinea baboons social organization and male strategies. In: Swedell L, Leig S (eds.) Reproduction and fitness in baboons. Behavioral, ecological and life history perspectives. Springer, New York, pp. 105–121

Gautier JP (1988) Interspecific affinities among guenons as deduced from vocalizations. In: Gautier-Hion A, Bourliere F, Gautier JP, Kingdon J (eds.) A primate radiation: evolutionary biology of the African guenons. Cambridge University press, Cambridge, pp. 194–226

Gerhardt HC (1975) Sound pressure levels and radiation patterns of the vocalizations of some North American frogs and toads. J Comp Physiol 102: 1–12

Gerhardt HC, Huber F (2002) Acoustic Communication in insects and anurans. University of Chicago press, Chicago

Grice H (1957) Meaning. Philol Rev 66:377–388

Gros-Louis J, Perry SE, Fichtel C, Wikberg E, Gilkenson H, Wofsy S, Fuentes A (2008) Vocal repertoire of *Cebus capucinus*: acoustic structure, context, and usage. Int J Primatol 29:641–670

Gustison ML, Roux A le, Bergman TJ (2012) Derived vocalizations of geladas (*Theropithecus gelada*) and the evolution of vocal complexity in primates. Philos T Roy Soc B 367:1847–1859

Hall KRL, DeVore I (1965) Baboon social behavior. In: De Vore I (ed.) Primate Behavior: Field Studies of Monkeys and Apes. Holt, Rinehart and Winston, New York, pp. 53–110

Hamilton W, Arrowood P (1978) Copulatory vocalizations of chacma baboons (*Papio ursinus*), gibbons (*Hylobates hoolock*), and humans. Science 200:1405–1409

Hammerschmidt K, Fischer J (1998a) The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system. Ethology 104: 203–216

Hammerschmidt K, Fischer J (1998b) Maternal discrimination of offspring vocalizations in Barbary macaques (*Macaca sylvanus*). Primates 39:231–236

Hammerschmidt K, Newman JD, Champoux M, Suomi SJ (2000) Changes In rhesus macaque "coo" vocalizations during early development. Ethology 106:873–886

Hammerschmidt K, Jürgens U, Freudenstein T (2001) Vocal development in squirrel monkeys. Behaviour 138:1179–1204

Hammerschmidt K, Fischer J (2008) Constraints in primate vocal production. In: Griebel U, Oller K (eds.) The evolution of communicative creativity: from fixed signals to contextual flexibility. MIT press, Cambridge, pp. 93–119

Hammerschmidt K, Reisinger E, Westekemper K, Ehrenreich L, Strenzke N, et al. (2012a) Mice do not require auditory input for the normal development of their ultrasonic vocalizations. BMC Neurosci 13:40

Hammerschmidt K, Radyushkin K, Ehrenreich H, Fischer J (2012b) The structure and usage of female and male mouse ultrasonic vocalizations reveal only minor differences. PloS one 7:e41133

Hauser M (1989) Ontogenetic changes in the comprehension and production of vervet monkey (*Cercopithecus aethiops).* J Comp Psychol 103:149–158.

Hauser MD (1993) The evolution of nonhuman primate vocalizations: effects of phylogeny, body weight, and social context. Am Nat 142:528–42

Henzi SP, Barrett L (2007) Coexistence in Female-Bonded Primate Groups. Adv Stud Behav 37:43–81

Herbinger I, Papworth S, Boesch C, Zuberbühler K (2009) Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study. Anim Behav 78:1389–1396

Herzog M, Hopf S (1984) Behavioral responses to species-specific warning calls in infant squirrel monkeys reared in social isolation. Am J Primatol 7:99–106

Hohmann G, Fruth B (2000) Use and function of genital contacts among female bonobos. Anim behav 60:107–120

Hohmann G (1991) Comparative analyses of age- and sex-specific patterns of vocal behaviour in four species of Old World monkeys. Fol Primatol 56:133–156

Hopp SL, Jablonski P, Brown JL (2001) Recognition of group membership by voice in Mexican jays, *Aphelocoma ultramarina*. Anim Behav 62:297–303

Huchard E, Alvergne A, Féjan D, Knapp L, Cowlishaw G, et al. (2010) More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons. Behav Ecol Sociobiol 64:769–781

Hyman J, Hughes M (2006) Territory owners discriminate between aggressive and nonaggressive neighbours. Anim Behav 72:209–215

Jürgens U, Pratt R (1979) Role of the periaqueductal grey in vocal expression of emotion. Brain Res 167:367–378

Jürgens U (2009) The neural control of vocalization in mammals: a review. J Voice 23:1–10

Karakashian SJ, Gyger M, Marler P (1988) Audience effects on alarm calling in chickens (*Gallus gallus*). J Comp Psychol 102:129–135

Kipper S, Mundry R, Sommer C, Hultsch H, Todt D (2006) Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. Anim Behav 71: 211–217

Kitchen D, Seyfarth R, Fischer J, Cheney DL (2003) Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). Behav Ecol Sociobiol 53:374–384

Kitchen D, Seyfarth R, Cheney D (2004) Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). Behaviour 141:197–218

Kitchen DM, Cheney DL, Seyfarth RM (2005) Male chacma baboons (*Papio hamadryas ursinus*) discriminate loud call contests between rivals of different relative ranks. Anim Cogn 8:1–6

Kitchen DM, Beehner JC, Bergman TJ, Dorothy L, Crockford C, et al. (2009) The causes and consequences of male aggression directed at female chacma baboons. In Muller R, Wrangham R (eds.) Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females. Harvard University press, Cambridge pp. 128–156

Koda H, Shimooka Y, Sugiura H (2008) Effects of caller activity and habitat visibility on contact call rate of wild Japanese macaques (*Macaca fuscata*). Am J Primatol 1063:1055–1063

Krams I, Krama T, Freeberg TM, Kullberg C, Lucas JR (2012) Linking social complexity and vocal complexity: a parid perspective. Philos T Roy Soc B 367:1879–1891

Krebs J, Dawkins R (1984) Animal signals: mind-reading and manipulation. In: Krebs J, Davies N (eds.) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp. 380–402

Kummer H (1968) Social organization of hamadryas baboons: A field study. Karger, Basel

Larson CR, Sutton D, Taylor EM, Lindeman R (1973) Sound spectral properties of conditioned vocalization in monkeys. Phonetica 27:100–110

Lemasson A, Palombit R, Jubin R (2008) Friendships between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback experiments. Behav Ecol Sociobiol 62:1027–1035

Liebermann P, Blumstein S (1988) Speech physiology, speech perception, and acoustic phonetics. Cambridge University press, Cambridge.

Maciej P, Patzelt A, Ndao I, Hammerschmidt K, Fischer J (2012) Social monitoring in a multilevel society: a playback study with male Guinea baboons. Behav Ecol Sociobiol 67:61–68

Maestripieri D, Leoni M, Raza SS, Hirsch EJ, Whitham JC (2005) Female copulation calls in Guinea cbaboons: evidence for postcopulatory female choice ? Int J Primatol 26:737–758

Manser MB (2001) The acoustic structure of suricates' alarm call varies with predator type and the level of response urgency. Proc R Soc B 268: 2315–2324

Marler P (1967) Animal Communication Signals: We are beginning to understand how the structure of animal signals relates to the function they serve. Science 157:769–74

Marler P (1973) A Comparison of vocalizations of red-tailed monkeys and blue monkeys, *Cercopithecus ascanius* and *C. mitis*, in Uganda. Z Tierpsychol 33:223–247

Markel JD, Gray AH (1976) Linear prediction of speech. Springer, New York

Marten K, Marler P (1977) Sound transmission and its significance for animal vocalization I. Temperate habitats. Behav Ecol Sociobiol 2: 271–290

Marten K, Quine D, Marler P (1977) Sound transmission and its significance for animal vocalization II. Tropical Forest Habitats. Behav Ecol Sociobiol 2: 291–302

Masataka N (1983) Categorical responses to natural and synthesized alarm calls in Goeldi's monkeys (*Callimico goeldii*). Primates 24:40–51

McComb K, Moss C, Sayialel S, Baker L (2000) Unusually extensive networks of vocal recognition in African elephants. Anim Behav 59:1103–1109

McComb K, Reby D, Baker L, Moss C, Sayialel S (2003) Long-distance communication of acoustic cues to social identity in African elephants. Anim Behav 65: 317–329

McComb K, Semple S (2005) Coevolution of vocal communication and sociality in primates. Biol lett 1:381–385

McCowan B (1995) A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottle-nose dolphins (Delphinidea, *Tursiops truncatus*). Ethology 100: 177–193

McCowan B, Hanser SF, Doyle LR (1999) Quantitative tools for comparing animal communication systems: information theory applied to bottlenose dolphin whistle repertoires. Anim Behav 57: 409–419

Meise K, Keller C, Cowlishaw G, Fischer J (2011) Sources of acoustic variation: implications for production specificity and call categorization in chacma baboon (*Papio ursinus*) grunts. J Acoust Soc Am 129:1631–1641

Meunier H, Molina-Vila P, Perry S (2012) Participation in group defence: proximate factors affecting male behaviour in wild white-faced capuchins. Anim Behav 83:621–628

Meyer D, Hodges JK, Rinaldi D, Wijaya A, Roos C, et al. (2012) Acoustic structure of male loud-calls support molecular phylogeny of Sumatran and Javanese leaf monkeys (genus *Presbytis*). BMC Evol Biol 12:16

Mitani J, Hunley K, Murdoch M, Arbor A (1999) Geographic variation in the calls of wild chimpanzees : a reassessment. Am J Primatol 151:133–151

Morton ES (1975) Ecological sources of selection on avian sounds. Am Nat 109: 17–34

Mundry R, Fischer J (1998) Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: examples from Animal Behaviour. Anim Behav 56:256–259

Müller CA, Manser MB (2007) "Nasty neighbours" rather than "dear enemies" in a social carnivore. Proc R Soc Lond B 274:959–965

Müller CA, Manser MB (2008) Mutual recognition of pups and providers in the cooperatively breeding banded mongoose. Anim Behav 75:1683–1692

Naguib M (1997) Use of song amplitude for ranging in Carolina wrens, *Thryothorus ludovicianus*. Ethology 103: 723–731

Naguib M, Hammerschmidt K, Wirth J (2001) Microgeographic variation, habitat effects, and individual signature cues in calls of chiffchaffs, *Phylloscopus collybita canarensis*. Ethology 107: 341–355

Naguib M, Wiley RH (2001) Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. Anim Behav 62: 825–837

Nelson BS (2003) Reliability of sound attenuation in Florida shrub habitat and behavioral implications. J Acoust Soc Am 113: 2901–2911

Nemeth E, Winkler H, Dabelsteen T (2001) Differential degradation of antbird songs in a Neotropical rainforest: Adaptation to perch height? J Acoust Soc Am 110: 3263–3274

Nemeth E, Pederson SB, Winkler H (2006) Rainforests as concert halls for birds: Are reverberation improving sound transmission of long song elements? J Acoust Soc Am 119: 620–626

Neumann C, Assahad G, Hammerschmidt K, Perwitasari-Farajallah D, Engelhard A. (2010) Loud calls in male crested macaques, *Macaca nigra*: a signal of dominance in a tolerant species. Anim Behav 79: 187–193

Ndao I, Henschel P (2011) Rapport de l'etude sur la population des lions au parc national Niokolo Koba. Tambacounda

Nguyen N, Van Horn R, Alberts S, Altmann J (2009) "Friendships" between new mothers and adult males: adaptive benefits and determinants in wild baboons (*Papio cynocephalus*). Behav Ecol Sociobiol 63:1331–1344

Owren MJ, Dieter JA, Seyfarth RM, Cheney DL (1993) Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques cross-fostered between species show evidence of only limited modification. Dev Psychobiol 26:389–406

Owren MJ, Linker CD (1995) Some analysis methods that may be useful to acoustic primatologists. In: Zimmermann E, Newman JD, Jürgens U. (eds.) Current topics in primate vocal communication. Plenum, New York, pp. 1–27

Owren M, Seyfarth RM, Cheney DL (1997) The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cyncephalus ursinus*): Implications for production processes and functions. J Acoust Soc Am 101:2951–2963

Owens JL, Freeberg TM (2007) Variation in chick-a-dee calls of tufted titmice, *Baeolophus bicolor*, note type and individual distinctiveness. J Acoust Soc Am 119: 620–626.

Palombit R (1994) Extra-pair copulations in a monogamous ape. Anim Behav 47:721–723

Palombit R, Seyfarth R, Cheney D (1997) The adaptive value of "friendships" to female baboons: experimental and observational evidence. Anim Behav 54:599–614

Palombit R, Cheney D (1999) Male grunts as mediators of social interaction with females in wild chacma baboons (*Papio cynocephalus ursinus*). Behaviour 136:221–242

Patzelt A, Zinner D, Fickenscher G, Diedhiou S, Camara B, et al. (2011) Group composition of Guinea baboons (*Papio papio*) at a water place suggests a fluid social organization. Int J Primatol 32:652–668

Pedgham M (2004) Reverberation and frequency attenuation in forests – implications for acoustic communication in animals. J Acoust Soc Am 115: 402–410

Pfefferle D, Fischer J (2006) Sounds and size: identification of acoustic variables that reflect body size in hamadryas baboons, *Papio hamadryas*. Anim Behav 72: 43–51

Pfefferle D, West PM, Grinnell J, Packer C, Fischer J (2007) Do acoustic features of lion, *Panthera leo*, roars reflect sex and male condition? J Acoust Soc Am 121: 3947–3953

Pollard K, Blumstein DT (2012) Evolving communicative complexity: insights from rodents and beyond. Philos T Roy Soc B 367:1869–78

Pradhan GR, Engelhardt A, Schaik CP, Maestripieri D (2005) The evolution of female copulation calls in primates: a review and a new model. Behav Ecol Sociobiol 59:333–343

Preuschoft S, Schaik CP Van (2000) Dominance and communication. In: Aureli F, Waal FBM de (eds.) Natural conflict resolution. University of Chicago press, London, pp. 77–105

Radford AN (2005) Group-specific vocal signatures and neighbor-stranger discrimination in the cooperatively breeding green woodhoopoe. Anim Behav 70:1227–1234

Ramakrishnan U, Coss R (2000) Age differences in the responses to adult and juvenile alarm calls by bonnet macaques (*Macaca radiata*). Ethology 106:131–144

Range F (2005) Female sooty mangabeys (*Cercocebus torquatus atys*) respond differently to males depending on the male’s residence status-preliminary data. Am J Primatol 65:327–333

Range F, Förderer T, Meystre Y, Benetton C, Fruteau C (2007) The structure of social relationships among sooty Mangabeys in Tai. In: McGraw S, Zuberbühler K, Noë R (eds.) Monkeys of the Taï forest. Cambridge university press, Cambridge, pp. 109–130

Ramos-Fernandez G (2005) Vocal communication in a fission-fusion society: Do spider monkeys stay in touch with close associates? Int J Primatol 26:1077–1092

Reby D, McComb K (2003) Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Anim Behav 65: 519–530

Reby D (2005) Red deer stags use formants as assessment cues during intrasexual agonistic interactions. Proc R Soc Lond B 292:941–947

Reetz H (1999) Artikulatorische und akustische Phonetik. Wissenschaftlicher Verlag, Trier.

Ren B, Li D, He X, Qiu J, Li M (2011) Female resistance to invading males increases infanticide in langurs. PloS one 6:e18971

Ren B, Li D, Garber P, Li M (2012). Fission–fusion behavior in yunnan snub-nosed monkeys (*Rhinopithecus bieti*) in Yunnan, China. Int J Primatol 33:1096–1109

Rendall D, Rodman PS, Emond RE (1996) Vocal recognition of individuals and kin in free-ranging rhesus monkeys. Anim Behav 51:1007–1015

Rendall D, Seyfarth R, Cheney D, Owren M (1999) The meaning and function of grunt variants in baboons. Anim behav 57:583–592

Rendall D, Cheney DL, Seyfarth RM (2000) Proximate factors mediating "contact" calls in adult female baboons (*Papio cynocephalus ursinus*) and their infants. J Comp Psychol 114: 36–46

Rendall D (2003) Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. J Acoust Soc Am 113:3390–3402

Rendall D, Owren MJ, Weerts E, Hienz D (2004) Sex differences in the acoustic structure of vowel-like grunt vocalizations in baboons and their perceptual discrimination by baboon listeners. J Acoust Soc Am 115: 411–421

Rendall D, Kollias S, Ney C, Lloyd P (2005) Pitch (F0) and formant profiles of human vowels and vowel-like baboon grunts: the role of vocalizer body size and voice-acoustic allometry. J Acoust Soc Am 117:944–955

Rendall D, Notman H, Owren MJ (2009) Asymmetries in the individual distinctiveness and maternal recognition of infant contact calls and distress screams in baboons. J Acoust Soc Am 125:1792–1805

Riede T, Fitch T (1999) Vocal tract length and acoustics of vocalization in the domestic dog (*Canis familiaris*). J Exp Biol 202:2859–2867

Ripmeester EAP, Kok JS, van Rijssel JC, Slabbekoorn H (2010): Habitat-related birdsong divergence: a multi-level study on the influence of territory density and ambient noise in European blackbirds. Behav Ecol Sociobiol 64: 409–418

Ross M (2007) Call diversity of wild male orangutans: a phylogenetic approach. Am J Primatol 69:305–324

Rousseeuw PJ (1987) Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. J Comput Appl Math 20:53–65

Rowe C (2013) Receiver psychology: a receiver's perspective. Anim Behav 85:517–523

Sabatini V, Ruiz-Miranda CR (2008) Acoustical aspects of the propagation of long calls of wild *Leontopithecus rosalia*. Int J Primatol 29: 207–223

Schaik CP van, Janson CH (2000) Infanticide by males and its implications. Cambridge University press, Cambridge

Schell A, Rieck K, Schell K, Hammerschmidt K, Fischer J (2011) Adult but not juvenile Barbary macaques spontaneously recognize group members from pictures. Anim Cogn 14:503–509

Schneider C, Hodges K, Fischer J, Hammerschmidt K (2008) Acoustic niches of siberut primates. Int J Primatol 29:601–613

Schott D (1973) Quantitative analysis of the vocal repertoire of squirrel monkeys (*Saimiri sciureus*). Z Tierpsychol 38:225–250

Schrader L, Todt D (1993) Contact call parameters covary with social context in common marmoset, *Callithrix j. jacchus*. Anim Behav 46:1026–1028

Schrader L, Hammerschmidt K (1997) Computer-aided analysis of acoustic parameters in animal vocalizations: a multi-parametric approach. Bioacoustics 7: 274–265

Searcy W, Nowicki S (2005) The evolution of animal communication: reliability and deception in signaling systems. Princeton University press, Princeton.

Semple S, McComb K, Alberts S, Altmann J (2002) Information content of female copulation calls in yellow baboons. Am J Primatol 56:43–56

Seyfarth R, Cheney D, Marler P (1980) Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science 210:801–803

Seyfarth RM, Cheney DL (1986) Vocal development in vervet monkeys. Anim Behav 34:1640–1658

Seyfarth RM, Cheney DL (2003) Signalers and receivers in animal communication. Annu Rev Psychol 54:145–173

Seyfarth RM, Cheney DL (2010) Production, usage, and comprehension in animal vocalizations. Brain Lang 115:92–100

Silk J, Kaldor E, Boyd R (2000) Cheap talk when interests conflict. Anim behav 59:423–432

Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. Science 302:1231–1234

Silk JB, Altmann J, Alberts SC (2006) Social relationships among adult female baboons (*Papio cynocephalus*). I. Variation in the strength of social bonds. Behav Ecol Sociobiol 61:183–195

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, et al. (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc R Soc Lond B 276:3099–3104

Smith J, Parker G (1976) The logic of asymmetric contests. Anim Behav 24:159–175

Smith J (1991) Honest signalling: the Philip Sidney game. Anim Behav 42:1034–1035

Smith J (1994) Must reliable signals always be costly? Anim Behav 47:1115-1120

Smith J, Harper D (2003) Animal signals. Oxford University press, New York.

Slabbekoorn H, Ellers, J, Smith TB (2002) Birdsong and sound transmission: the benefits of reverberations. Condor 104: 564–573

Snowdon C, Elowson a. M (2001) “Babbling” in pygmy marmosets: development after infancy. Behaviour 138:1235–1248

Snyder-Mackler N, Beehner JC, Bergman TJ (2012) Defining higher levels in the multilevel societies of geladas (*Theropithecus gelada*). Int J Primatol 33:1054–1068

Soltis J, Bernhards D, Donkin H, Newman JD (2002) Squirrel monkey chuck call: vocal response to playback chucks based on acoustic structure and affiliative relationship with the caller. Am J Primatol 57:119–130

Steenbeek R (1999) Tenure related changes in wild Thomas's langurs I: Between-group interactions. Behaviour 136:595–625

Stoeger AS, Charlton BD, Kratochvil H, Fitch WT (2011) Vocal cues indicate level of arousal in infant African elephant roars. J Acoust Soc Am 130:1700–1710

Stoeger AS, Mietchen D, Oh S, Silva S de, Herbst CT, et al. (2012) An Asian elephant imitates human speech. Curr Biol 22:1–5

Steward KEJ, Bourn NAD, Thomas JA (2001) An evaluation of three quick methods commonly used to assess sward height in ecology. J Appl Ecol 38: 1148–1154

Sutton D, Larson C, Lindeman RC (1974) Neocortical and limbic lesion effects on primate phonation. Brain Res 71:61–75

Swedell L (2011) African Papionins: Diversity of social organization and ecological flexibility. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds.) Primates in perspective 2nd edn. Oxford university press, Oxford, pp. 241–277

Temeles EJ (1990) Northern harriers on feeding territories respond more aggressively to neighbours than to floaters. Behav Ecol Sociobiol 26:57–63

Temeles EJ (1994) The role of neighbours in territorial systems: when are they "dear enemies"? Anim Behav 47:339–350

Taylor M, Reby D (2010) The contribution of source-filter theory to mammal vocal communication research. J Zool 280:221–236

Thierry B, Demaria C, Preuschoft S, Desportes C (1989) Structural convergence between silent bared-teeth display and relaxed open-mouth display in the tonkean macaque (*Macaca tonkeana*). Fol Primatol 52:178–184

Thierry B (2000) Covariation of conflict management patterns across macaque species. In: Aureli F, Waal FBM de (eds.) Natural conflict resolution. University of Chicago press, London, pp. 106–128

Thinh VN, Hallam C, Roos C, Hammerschmidt K (2011) Concordance between vocal and genetic diversity in crested gibbons. BMC Evol Biol 11:36

Todt D, Hammerschmidt K, Ansorge V, Fischer J (1995) The vocal behavior of Bar- bary macaques (Macaca sylvanus): call features and their performance in infants and adults. In: Zimmermann E, Newman J, Jurgens U (eds.) Current topics in primate vocal communication. Plenum press, New York, pp. 141–160.

Townsend SW, Rasmussen M, Clutton-brock T, Manser MB (2012) Flexible alarm calling in meerkats: the role of the social environment and predation urgency. Behav Ecol 23:1360–1364

Waal FBM de, Luttrell LM (1985) The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. Am J Primatol 9:73–85

Waal FBM de (1988) The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. Behaviour 106:183–251

Waser PM (1982) The evolution of male loud calls among mangabeys and baboons. In: Brown CH, Petersen MR, Snowdown CT (eds.) Primate communication. Cambridge University press, Cambridge, pp. 117–143

Waser PM, Brown CH (1984) Is there a sound window' for primate communication? Behav Ecol Sociobiol 15: 73–76

Waser PM, Brown CH (1986) Habitat acoustics and primate communication. Am J Primatol 10: 135–154

Wheeler BC (2009) Monkeys crying wolf ? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. Proc R Soc Lond B 276:3013–3018

Wheeler BC, Fischer J (2012) Functionally referential signals: a promising paradigm whose time has passed. Evol Anthropol 21:195–205

Wich S, Assink P, Becher F (2002) Playbacks of loud calls to wild Thomas langurs (*Presbytis thomasi*): the effect of familiarity. Behaviour 139:79–87

Wich SA, Vries H de (2006) Male monkeys remember which group members have given alarm calls. Proc R Soc Lond B 273:735–40

Wich S, Schel AM, Vries H de (2008) Geographic variation in Thomas langur (*Presbytis thomasi*) loud calls. Am J Primatol 70:566–574

Wiley RH, Richards DG (1978) Physical constraints on acoustic communication in atmosphere – implications for evolution of animal vocalizations. Behav Ecol Sociobiol 3: 69–94

Whitham JC, Maestripieri D (2003) Primate rituals: the function of greetings between male Guinea baboons. Ethology 859:847–859

Zinner D, Wertheimer J, Liedigk R, Groeneveld LF, Roos C (2012) Baboon phylogeny as inferred from complete mitochondrial genomes. Am J Phys Anthropol 150:133-140

Zuberbühler K (2000a) Interspecies semantic communication in two forest primates. Proc R Soc Lond B 267:713–718

Zuberbühler K (2000b) Referential labelling in Diana monkeys. Anim Behav 59:917–927

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2002–2008	Study of Biology at the Leipzig University (Behavioural biology, Neuroscience, Psychology and Zoology)
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Experiences

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Publications

2013	Patzelt A, Maciej P, Fickenscher G, Ndao I, Kalbitzer U, Zinner D, Fischer J, **Spatial, social and genetic relationships of Guinea baboons (*Papio papio*) reveal a new dimension in primate social diversity.** Proc. Natl. Acad. Sci. USA (submitted)
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Associations

Since 2011	International Bioacoustics Council (IBAC)
Since 2009	Greenpeace (Africa)
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EIDESSTATTLICHE ERKLÄRUNG

Hiermit erkläre ich, dass ich diese Dissertation selbstständig ohne Hilfe Dritter und ohne Benutzung anderer als der angegebenen Quellen und Hilfsmittel verfasst habe. Alle den benutzten Quellen wörtlich oder sinngemäß entnommenen Stellen sind als solche einzeln kenntlich gemacht.

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Des Weiteren erkläre ich, dass ich mich nicht anderweitig einer Doktorarbeit ohne Erfolg unterzogen habe und dass diese Arbeit in gleicher oder ähnlicher Form noch keiner anderen Prüfungsbehörde vorgelegen hat.

Göttingen, den	Peter Maciej	
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