https://doi.org/10.35662/unine-thesis-3221

Université de Neuchâtel

AUDIENCE EFFECTS IN SOOTY MANGABEYS

PhD Thesis submitted to the Faculty of Science

Institute of Biology

University of Neuchâtel

For the degree of Doctor of Philosophy

By

Fredy QUINTERO

Dissertation committee:

Prof Klaus ZUBERBÜHLER, University of Neuchatel, thesis director

Prof Steven Paul MORAN, University of
Neuchatel

Prof Robert SEYFARTH, University of
Pennsylvania

Defended on the 19th of April, 2023

Université de Neuchâtel
Faculté des sciences

Rue Emile-Argand 11
CH-2000 Neuchâtel
doctorat.sciences@unine.ch

IMPRIMATUR POUR THESE DE DOCTORAT

La Faculté des sciences de l'Université de Neuchâtel autorise l'impression de la présente thèse soutenue par

Monsieur Fredy QUINTERO

Titre :

"Audience effects in sooty mangabeys"

sur le rapport des membres du jury composé comme suit :

- **Prof. Klaus Zuberbühler,** directeur de thèse, Université de Neuchâtel, Suisse
- **Prof. ass. Steven Moran,** Université de Neuchâtel, Suisse
- **Prof. Robert Seyfarth,** University of Pennsylvania, USA

Neuchâtel, le 25 novembre 2025

Le Doyen, Prof. P. Brunner

ACKNOWLEDGMENTS

This thesis is dedicated to María Laura, Benjamin, Mateus and Brownie. They are the driving force of my life. I also dedicate it to my parents, my brothers and Eko, who always supported me.

First of all, I want to thank Klaus Zuberbühler, the only crazy guy capable of trusting a colombian guy, who did not know a word in French, to re-start and re-build a research project in Ivory Coast, build a road in the middle of the jungle, go against Ivorian strikes, forest armies, Ebola and rivalries with other research projects. He's not only a great researcher and a magnificent editor, but a wonderful human being who never gave up on me during all these years.

I would also like to thank the Swiss National Science Foundation and the Swiss National Centre of Competence in Research for funding my research. This work would not be possible without the permission and the support to conduct research in Taï National Park from the Centre Suisse de Recherches Scientifiques (CSRS), the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales, the Office Ivoirien des Parcs et Réserves (OIPR) of Côte d'Ivoire and the staff of the C.R.E. research station. Thanks to the University of Neuchatel and all their staff. Never knew the name of the ladies at the cafeterias, but they always kept for me the veggie menu that I loved the most. Thanks to Natacha Schneiter for all the help in settling in Neuchatel, for getting me in touch with Mary-Jo and doing all the paperwork for me while I was abroad. Thanks to Mary-Jo for being my mom during all my years at Neuchatel. Thanks to all my fellow Neuchatel PhD students Noemi Lamon, Gladez Shorland, Brittany Fallon, Yaelle Bouquet, Stefanie Mercier, Corinne Ackerman, Melissa Berthet, Adwait Deshpande, Julie Andrieu, Alice Bouchard, and the Post-Docs Guillaume Dezecache, Pawel Fedurek, Claudia Stephan, Cristof Neumman, Thibaud Gruber, Zanna Clay, Cristoph Dahl and Emilie Genty.

I experienced an incredible adventure in Ivory Coast and there are many people that helped me there in so many ways that this text would be endless if I describe them in detail. Thanks to the most amazing field assistants from l'armée mangabey: Paterson Kalo, Benjamin Zahi, Gerard Gha and Richard Peho, your work, knowledge and support is priceless. I would also like to thank to Bertin Diero, who taught me how to drive like an expert in the middle of the jungle and the Abidjan streets. Thanks to Ferdinand Bele, Frederic Gnepa, Arsene, Ernest and Djobely for all the Ivorian meals, stories and good conversations that we had at the forest. Anderson Bitty helped me to settle in Ivory Coast both in Adbijan and Taï. Ouasuoooo to all the people from Pauleoula, Gouleako I, Gouleako II, Taï and Ponan. Special thanks to Dr. Magris and Dr. Touitou who helped me collecting valuable data and setting up the experiments that are the basis of the PhD thesis, without you I would not be able to be called Dr. Thanks to Erin, Camille, Alex, Mikael, Weiyeen, Claudia, Cristof, Vera and Fee, for all the good and not so good times we spent in the forest.

This research was also possible thanks to the valuable statistical and scientific advice from Victor Hoyos, Radu Slobodeanu, Gwendolyn Wirobski, Cristof Neumann, Claudia Stephan and Ronald Noë. Thanks to all the people that walked and suffered with me all these years through this thesis. Finally, I want to thank the sooty mangabeys for being the cutest subjects of study I could ever expected.

ABSTRACT

The ability to take others into account during communication is an important feature of human language. Although, there is evidence of the audience effects in several animal taxa, it is not known for most species if signallers consider the social consequences of communicating. In apes, there is evidence that individuals are able to adjust signal production depending on the attention state of the receiver, but it is currently unknown whether this is restricted to some contexts or generally present during communication. A related question is if the ability to take the attention of others into account is a general feature of primate cognition or present just in some species. Sooty mangabeys (*Cercocebus atys*) are forest dwelling monkeys that live in groups of around 100 individuals with a stable linear dominance hierarchy. The focus of this thesis is on how sooty mangabeys employ communication signals in the presence of different audiences, particularly how communication is used in resolving social conflict, discovering food, and dealing with predators. I was interested in whether and how sooty mangabeys showed signs of awareness of their audiences in each of these situations and how this impacted their communicative behaviour. My results suggest that audience composition always plays a role, sometimes just by the number of individuals and others because of the presence of socially important members. The evidence I presented supports a gradual view, that features and components of human language are already present deep in the evolutionary tree of primates and most have therefore evolved early. Finally, all the patterns I have described are not in line with a notion of animal calls as hardwired or reflexive responses to specific stimuli, but appear to involve considerable amounts of social cognition, allowing individuals to make assessments of both ecological and social variables in ways that meet criteria of intentional signalling.

Keywords: audience effects, primate cognition, vocal communication, Sooty mangabeys, intentionality.

TABLE OF CONTENT

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1. INTRODUCTION

THE COMPARATIVE APPROACH TO LANGUAGE EVOLUTION

Human language has no comparison with any other communication system in the animal kingdom. Even chimpanzees, our closest relatives, are not able to acquire anything that is even remotely similar to human speech or sign language, even if raised in a human home with all the cultural input of a normal human child (e.g. Gardner & Gardner, 1969; Hayes, 1951). How and why language evolved just in humans and not in other species is therefore a major question. Unfortunately, language evolution cannot be studied directly, mainly because there is no relevant fossil record. For investigating the evolutionary roots of language scientists have therefore used other methods, notably the comparative approach, which has helped to establish the differences between humans and other animals (Shettleworth, 2010).

The language faculty is often thought of as a conglomerate of capacities, each of which may have its own evolutionary history (Fitch & Zuberbühler, 2013). One such capacity and key ingredient is the ability to take others into account as independent agents with personal beliefs and intentions that may differ from one's own. Human language, in other words, builds on a more general awareness that others have minds, which then enables speakers to adjust their communication output accordingly (Tomasello, 2010). What are the evolutionary roots of audience-aware communication, one of the defining features of human language? Studies on primate cognition are the most likely source of evidence for answering questions about human language evolution, particularly how individuals use their vocalisations in their daily lives.

Cognition and communication

Like many other groups of animals, non-human primates are constantly in the search for food while, at the same time, need to adhere to predator avoidance strategies and navigate between competing and cooperating with members of their own and other groups. Vocalisations have evolved as a response to help individuals to deal with all these challenges they face daily. A transversal skill, across all these contexts, is for signallers to be able to take their receivers into account, both in terms of who they are and how they are likely to react. Such audience awareness can vary dramatically, ranging from simple presence/absence effects (Grosenick et al., 2017; Matos et al., 2003; Pollick et al., 2005; Ridley et al., 2007; Sherman, 1977; Zajonc et al., 1969) to taking into account others' apparent knowledge (Bouchard & Zuberbühler, 2022; Cartmill & Byrne, 2007, 2010; Crockford et al., 2012; Drayton & Santos, 2014; Flombaum & Santos, 2005; Genty et al., 2015; Hobaiter & Byrne, 2014; Phillips et al., 2009; Schel et al., 2013). The more complex an individual perceives its audience during communication, the closer its cognition resembles the one underlying human communication – the basic premise of this study. The goal of this research is to provide progress on the nature of audience awareness in three naturalistic contexts – avoiding predation, finding food and dealing with social competition – in a non-human primate, the sooty mangabey.

Avoiding predation

The first focus of investigation in this study is the predation context. Predation is one of the most important ecological challenges that animals face on a daily basis. In some species, predation is the biggest cause of mortality (Hill et al., 2019). Being able to deal with predation threats is absolutely essential and specific adaptation should be expected in virtually every species. Social animals have developed antipredator strategies that involve specific communication skills that allow them to coordinate specific responses to specific threats. A noteworthy example are the acoustically distinct alarm calls that some species produce for different predators (Manser et al., 2002; Ridley et al., 2007; Seyfarth et al. 1980; Sherman 1985; Zuberbühler et al., 1999a).

One of the first studies that showed evidence of the comprehension of signals by primates in alarm calls is from vervet monkeys. Vervet monkeys produce different alarm calls depending of the type of predator, which turned out to be meaningful to receivers (Seyfarth et al., 1980). In the last decades, several studies have replicated this basic finding and demonstrated that semantic abilities are widespread in primates and other groups of animals (Zuberbühler, 2003, 2007). Experiments with Diana monkeys, for example, have shown that, rather than just responding to the calls directly, these animals are able to take into account the cause of an event (Zuberbühler et al., 1999a; Zuberbühler, 2000). Further studies with Diana and Campbell's monkeys have revealed some advanced vocal behaviour in this context, such as suffixation as an active part of alarm call production, which can change the meaning of a predatory call (Ouattara et al., 2009; Coye et al., 2015). Subsequent work on Titi monkeys has suggested that primates can combine alarm calls to create probabilistic meaning (Berthet et al., 2019). For sooty mangabeys, it was shown that young individuals tend to classify unfamiliar terrestrial threats either as leopard - or snake-related (Leon et al., 2022), but that individuals can easily learn to use one of the two categories after hearing the alarm calls of a more experienced group member. Remarkably, this learning was extraordinarily efficient and long lasting, with one single exposure sufficient for long-term memories lasting more than one year. These sorts of findings have revealed some fundamental properties of the primate mind in terms of its flexibility and retention capacity.

For comparative purposes, studies on chimpanzees and other great apes are of special importance. Here, it has been reported that individuals detecting a snake model were more likely to produce warning calls if they were in the company of ignorant group members, compared to when with individuals who already knew about the snake (Crockford et al., 2012; Schel et al., 2013). It is unknown if the patterns seen in chimpanzees, i.e., taking the shared past history into account, are a general feature of primate cognition, mainly because comparable studies have not yet been made with monkeys. In one relevant study, sooty mangabeys did not adjust call production to the presence of socially important or referentially unaware partners when finding Gaboon vipers (Mielke et al., 2019), but it is possible that this negative finding was due to methodological issues. More generally it is still unclear whether monkeys and apes differ fundamentally in their cognitive abilities, so more directly comparable research is urgently needed. This is also true for audience effects in terms of how they compare in monkeys and apes.

Finding food

The second focus of investigation in this study is the foraging context. The search for food must be the main goal and central part on the daily routine of almost all animals. As such, social species have evolved strategies to coordinate feeding in an efficient manner, depending on the social and ecological configurations inherent to their environments. Regulating space with other members of their group is often a key factor in this context and many species produce specific ‘contact-calls’ for this function, including during feeding (Radford & Riley, 2008; Range & Fischer, 2004; Rogers et al., 2018; Wilkinson & Boughman, 1998). Other animals have evolved vocalizations that are specifically produced only during feeding (Gros-Louis, 2004; Slocombe & Zuberbühler, 2006; Sierro et al., 2020). Remarkably these ‘food-specific’ calls are in many cases structurally similar to general, ‘close-range, contact’ calls (Clark & Wrangham, 1993; Clay et al., 2015; Laporte & Zuberbühler, 2010; Slocombe & Zuberbühler, 2006), which suggests that food calls may have emerged within the broader category of ‘close-range’ vocalisations by an evolutionary process of acoustic modification and functional specialisation.

Besides this, calling patterns reflect this need for coordination while foraging, and even in species with no ‘food-specific’ calls show increased calling when inside food patches, indicating that is at least important to know where others are (Clay & Zuberbühler, 2009; Range & Fischer, 2004). Traditionally, studies on vocalisations while feeding have mainly focused on species with ‘food-specific’ calls (e.g., Elowson et al., 1991; Fedurek & Slocombe, 2013; Hauser & Marler, 1993), probably because these are conspicuous, making them not only easier to study, but also theoretically more interesting because of relevance for questions about reference. Here, an important construct is the notion of (functionally) referential signals, defined as those that inform others about a receiver-relevant event experienced by the caller (Clay et al., 2012). The topic has been hotly debated for decades, mainly because of its implications for questions about animal awareness and cognitive precursors to language (Fitch, 2005; Tomasello, 2010). As with alarm calls, studies of underlying social cognition of food calls have been mainly conducted with chimpanzees, the species closest in the phylogenetic tree to humans, which has increased the ape-monkey divide in knowledge about their cognition.

Some species of monkeys, such as, macaques often give specific calls in response to food (Mitani, 1986; Hauser & Marler, 1993), but remarkably there are no comparable records for baboons [Papio spp.; Silk et al. (2016)], vervet monkeys [*Chlorocebus pygerythrus*; Mercier et al. (2017)] or sooty mangabeys [*Cercocebus atys*; Range and Fischer (2004) and Neumann and Zuberbühler (2016)], despite the fact that they live in somewhat similar societies with presumably similar socio-ecological pressures and despite the obvious advantages that they have. The more general point is that little is known about the evolutionary emergence of food-associated calls in animal communication. Currently, there are two theories about the function of food associated calls: attract vs repel others, but there are no studies that have attempted to show how and why these calls evolved in some species and not in others.

Resolving conflicts

The third focus of investigation is the social context. Aggression, a behavioural function documented in taxa ranging from solitary invertebrates to socially complex mammals (Hamburg, 1971), is broadly defined as any action that inflicts, attempts to inflict or threatens to inflict harm on another animal (Berkowitz, 1993; Miczek et al., 2002). Across disciplines, aggression has been of broad scientific interest, including the social sciences' quest for explaining why humans, a highly cooperative species, are capable of extraordinary levels of violence that include war and genocide (Georgiev et al., 2013). When trying to explain aggression in animals, researchers usually agree that behaviours, including aggressive ones, are the result of context-specific evolutionary adaptations, while for humans the role of evolution is either ignored, not adequately considered or fiercely contested (Bernstein & Gordon, 1974; Holekamp & Strauss, 2016).

A primary function of aggressive behaviour is during situations of direct competition over limited resources, such as food, sexual partners or space, which can give individuals direct fitness benefits (Knott et al., 2010; Lemoine et al., 2020). Indirect fitness benefits are also frequent, such as when males behave aggressively towards neonates of females they want to mate with, which can result in infanticide and a subsequent increase in the perpetrators' future reproductive success (Hrdy, 1979; Lucas & Huchard, 2014; van Schaik & Janson. 2000). Furthermore, in social species, individuals sometimes behave aggressively in the absence of actual resource conflicts, simply to compete over positions in the group's dominance hierarchy, but this will then again translate to better access to resources, reproductive success, offspring survival, collective behaviours, migratory strategies and co-operative decision-making processes, depending on the species (Pusey et al., 2008).

However, aggression also has a secondary, less explored social function, as a form of punishment of individuals that refuse or have refused to cooperate (Clutton-Brock & Parker, 1995). The key difference to competitive aggression is that the aggressor is not directly engaged in a resource conflict but uses its aggression to enforce cooperative behaviour or tolerance and prevent the pursuing of selfish goals in the future (Bernstein & Gordon, 1974). Here, aggression works as a partner control mechanism by increasing the costs of selfish behaviour and therefore making cooperative alternatives the more economical solution.

In some species, punitive aggression can even be directed at third parties, a form of policing. Adult male chimpanzees, for example, can intervene in ongoing conflicts by other group members and so play a pacifying role (Boehm, 1994; Townsend et al., 2007).

Similarly, Tonkean macaques and other monkey species have also been seen to intervene in conflicts between others, although this is often in support of kin or friends (Petit & Thierry, 1994). In chimpanzees, victims of aggression appear to be aware of this fact, by exaggerating their victim screams in the presence of high-ranking audiences that are capable of successful intervention (Slocombe & Zuberbühler, 2007). Aggressive behaviour qualifies as punishment (Wubbs et al., 2016), if there are immediate payoff costs to the punisher, which can only be offset in the future, if the aggressed individual turns out to be more cooperative (Raihani et al., 2012). What is common about all these cases is that aggressors are not directly competing over a resource but seek to prevent selfish behaviour in others.

A more indirect way of enforcing cooperation and tolerance in others is to display aggressive motivation preventively, which is likely a viable strategy for lower-ranking individuals who, during an escalated conflict, would struggle to defend a resource. The only viable strategy for these individuals is to display their willingness to defend a resource when potential adversaries are watching them. Being aggressive in front of an audience, in other words, could have delayed benefits for the aggressor that are unrelated to the ongoing conflict but may lower chances of being aggressed by them in the future, and increase their future tolerance.

Studies of animal aggression have mostly focused on the first function, competitive aggression by individuals directly involved in competitive interactions, for instance by invoking game theory to explain the adaptive value of different conflict management strategies (e.g., hawk-dove model) (Eldakar, 2020) and the fact that intra-group aggression is a dynamic process that usually results in mild and rarely lethal consequences (Bernstein & Gordon, 1974; Dunbar & Dunbar, 1975; Fedurek et al., 2015; Range & Noë, 2002; Symons, 1974).

Audience effects in animal behaviour

Research on audience effects is well documented in the animal kingdom. A first major finding is that all kinds of animals, from insects to mammals, can be affected by the presence of others (Cheney & Seyfarth, 1990; Marler et al., 1986; Matos et al., 2003; Pollick et al., 2005; Ridley et al., 2007; Sherman, 1977; Zajonc et al., 1969). Audience effects are usually detected if the signalling behaviour of an individual is affected by the mere presence of other individuals, although sometimes there are additional effects due to specific features of the audience, such as group composition or presence of individuals with specific importance (Zuberbühler, 2008; Townsend & Zuberbühler, 2009), which is also the topic of this thesis.

From a cognitive perspective, audience effects can be very interesting because of the possibility that signals are emitted strategically, that is, based on an evaluation of the impact the signal has on the receiver (Zuberbühler, 2008). As said, audience effects are generally well documented across species, but most studies do not specifically address the question of strategic signalling, which often requires specifically designed experiments (Tomasello & Call, 1997). As a consequence, animal vocalisations are usually interpreted as manifestations of differences in arousal, not as strategically intended vocalisations, even if there is evidence of some form of audience awareness (Morton, 1977; Owren & Rendall, 1997).

Overall, natural selection is expected to favour signallers that are able to adjust signal production to maximise their own reproductive success, by taking into account characteristics of their audiences, such as composition and attention (Zuberbühler, 2008). Such audience awareness is likely to be found in species where individuals attend and learn from watching the social interactions between the members of their group. Here, compelling evidence is from primates, birds and fish that can deduce, for example, the dominance relations of other individuals by just looking at the outcome of conflicts (Bond et al., 2003; Davis, 1992; Gillian, 1981; Grosenick et al., 2007; Lazareva et al., 2004; McGonigle & Chalmers, 1977; Rapp et al., 1996; Roberts & Phelps, 1994; Steirn et al., 1995; von Fersen et al., 1991).

Audience and intentionality

For non-human primates, the evidence suggests that individuals can take into account the goals and intentions of others and adjust their own signalling behaviour accordingly (Call & Tomasello, 2007; Hare, 2011). For example, studies with captive orangutans, chimpanzees and bonobos have all shown that individuals are capable of modifying their signal output depending on the attentional state and familiarity of the recipient, with evidence for persistence and elaboration when dealing with unresponsive recipients (Cartmill & Byrne, 2007, 2010; Genty et al., 2015; Hobaiter & Byrne, 2014). A number of great ape field studies have also concluded that some vocal behaviour meets key criteria for intentionality (e.g., chimpanzees: Crockford et al., 2012, Hobaiter et al., 2014, Schel et al., 2013; bonobos: Genty & Zuberbühler, 2014). One challenging hypothesis from this research is that great apes are not only able to perceive and attribute intentions to others, but that they are also able to communicate their own and, if misunderstood or ignored, modify their signalling strategy to achieve the desired goal (Zuberbühler, 2008).

As remarked in previous sections, the main advances have come from great ape research while comparably less is known from other groups of primates and non-primate mammals. This is problematic for evolutionary theories of cognition, for example, whether audience awareness evolves along phylogenetic lines, perhaps as mere by-products of increasingly large brains or whether it can evolve by convergent evolution in response to specific socio-ecological challenges (Emery & Clayton, 2004). To address these questions, research on monkeys and non-primate species is crucial.

Here, some relevant findings come from captive rhesus macaques (*Macaca mulatta*) and tufted capuchins (*Sapajus apella*), which show that subjects can be sensitive to others' goals and intentions (e.g., Drayton & Santos, 2014; Flombaum & Santos, 2005; Hare et al., 2003; Phillips et al., 2009; Santos et al., 2006). In the wild, there is also evidence showing that some monkey species are able to produce alarm calls with the apparent purpose of influencing others' behaviours (Zuberbühler, 2018). In one study, wild Thomas langur males continued to produce alarm calls to predator model until every group member had responded with at least one alarm call, as if to ensure that others were aware of the danger (Wich & de Vries, 2006). In another study, wild Diana monkey females continued to alarm call until their own male produced the semantically matching ('correct') alarm calls, i.e., the predator spotted by the females, in response to which they stopped producing alarm calls (Stephan & Zuberbühler, 2016). Also, playback experiments with blue monkeys showed that males produced significantly more alarm calls to simulations of crowned eagle presence if other group members were closer to the presumed predator than far away (Papworth et al., 2008), further demonstrating some basic audience awareness, but not ruling out explanations based on basic changes in affective states.

Overall, the evidence suggests that apes, and some other primates, do more than just evaluate their audience in terms of biologically important categories; they also take into account psychological variables, such as attention, ability to comprehend (Call & Tomasello, 2007, Crockford et al., 2012) and capacity to help (Slocombe & Zuberbühler, 2007). However, is not clear if this is a general feature of primate cognition or limited to some species and behavioural contexts. Although research on great apes continues to provide evidence for audience effects and intentional communication (e.g., Bouchard & Zuberbühler, 2022; Gruber & Zuberbühler, 2013; Schel et al., 2013), to my knowledge, there are no comparable studies on free-ranging monkeys designed to tackle the same questions. Studying cognition in the wild is generally difficult, suggesting that no single experiment will be powerful enough to provide conclusive answers.

Overall goals

The focus of this thesis is on how sooty mangabeys employ communication signals in the presence of different audiences, particularly how communication is used in resolving social conflict, discovering food, and dealing with predators. The general approach was to first describe the basic patterns of vocal communication in mangabeys using focal animal data. In a second stage, a number of field experiments were carried out. To this end, I simulated artificially the call-eliciting event, for example, by positioning food or a predator model on the anticipated travel path of a focal animal. Aggression was not elicited experimentally, for ethical reasons. I was interested in whether and how sooty mangabeys showed signs of awareness of their audiences in each of these situations and how this impacted their communicative behaviour.

Sooty mangabeys are a suitable species for this research, for theoretical but also practical reasons. They are mainly terrestrial Old-World primates, phylogenetically related to baboons and living in groups of up to 100 individuals, with large group spread and inter-individual distances. Their big group size is important because, in primates, group size is related to relative brain size, the most likely source of cognitive differences (Dunbar, 1996). They live in dense forest habitats that limits the visibility individuals have with each other, which makes them more likely to experience more variation in audience composition. Also, this visibility restriction is likely to favour the ability to mentally represent others and their social relations. One prediction here is that natural selection will have favoured advanced communication in mangabeys, compared with other monkeys.

Regarding foraging behaviour, individuals spend much of their time foraging in small parties through the forest leaf-litter in search for insects and plant matter, such as the fallen fruits of *Anthonota spp*., *Saccoglotis gabonensis* and *Dialium spp*. (Janmaat et al., 2006; McGraw et al., 2011; Range & Noë, 2002). Occasionally, they climb into trees to pick fruits, or they sometimes consume high quality foods on the ground, such as bird or frog eggs, mushrooms and termites (Range & Noë, 2002; Rödel et al., 2002). Sooty mangabeys produce two close-range social calls, ‘twitters’ and ‘grunts’, both during foraging and in a range of other situations, including travelling (Neumann & Zuberbühler, 2016), or greeting other members of their group (Range & Fischer, 2004).

The main monkey predators in Tai Forest are crowned eagles (*Stephanoaetus coronatus*), leopards (*Panthera pardus*), chimpanzees (*Pan troglodytes*) and humans (Boesch & Boesch-Achermann, 2000; Covey & McGraw, 2014; Range & Fischer, 2004; Shultz et al., 2004), with different hunting strategies to which mangabeys have evolved specific adaptive responses. When a leopard is detected, individuals climb rapidly to the trees with some individuals mobbing the predator and other giving leopard specific alarm calls at high-rates (León et al., 2022; Zuberbühler et al., 1999b; Zuberbühler & Jenny, 2002, 2007).

To crowned eagles mangabeys react depending on the eagle's behaviour: if it flies over, the monkeys seek cover in the lower canopy and look up scanning the sky while producing eagle-specific alarm calls at high-rates. However, if the eagle is perched on a tree, they give alarm calls at lower rates, while slowly approaching it until it flies off (Range & Fischer, 2004; Shultz & Noë, 2002).

Snakes are not considered important predators, but encounters are common and for some species can be dangerous. Here, sooty mangabeys produce snake-specific alarm calls, but only when detecting Gaboon (*Bitis gabonica)* and Rhinoceros (*Bitis nasicornis*) vipers, while ignoring most other species (León et al., 2022; Penner et al., 2008; Range & Fischer, 2004). Although snakes do not usually prey on monkeys, lethal accidents can occur, which causes mangabeys to jump aside and show startle responses, followed by standing bipedally and cautiously approaching and scanning the area around the snake (León et al. 2022; Mielke et al., 2019). Finally, to chimpanzees, mangabeys adopt a cryptic behaviour and rapidly move away in silence (Zuberbühler et al., 1999b). Chimpanzees in Tai rarely target sooty mangabeys (Boesch & Boesch-Achermann, 2000), but they regularly attack red colobus monkeys, suggesting that mangabeys have witnessed many chimpanzee attacks on other monkey groups.

Due to the large group spread and inter-individual distances, sooty mangabeys only interact with a small proportion of the group at any given time, with individuals spending much of their time feeding in large food patches (Range & Noë, 2002). They have very stable matrilineal hierarchies with some indication of competition inside food patches, with high-ranking individuals clustering in the centre of the groups (Gba et al., 2019; Mielke et al., 2020). As expected, aggression rates are higher inside food patches, and usually from high-ranking to lower-ranking individuals (Range & Noë, 2002).

Research questions

Sooty mangabeys appear to be an ideal species for direct comparisons with chimpanzees because they live in the same habitat and their social structure has some similarities. To my knowledge, no previous studies have investigated the nature of audience effects in this species and much of their vocal communication system is only superficially described (Range & Noë, 2002). Recent research failed to find evidence for socially aware alarm calling in snake model experiments similar to what has already been done with chimpanzees (Mielke et al., 2019). While it is possible that this is the result of a true ape-monkey difference, the importance of the claim justifies further research.

My general approach was as follows. For the predation context, I repeated the snake model experiment as previously done with chimpanzees (Crockford et al., 2012; Schel et al., 2013). Unlike Mielke et al. (2019), I focused only on adult individuals as alarm calling behaviour is not completely developed in youngsters (Leon et al., 2022; Zuberbühler et al., 2022). I also made sure the snake models were highly authentic, crafted and painted to mimic real Gaboon and rhinoceros vipers to truly simulate with natural encounters. I analysed data from the point of view of both the snake finder and the call recipients to assess the two perspectives during a communication event. I expected individuals to call only if they were the ones to first find the snakes, to call more if there were fewer audience members in visible range and also when a socially important individual is in the vicinity.

While foraging sooty mangabeys increase grunt and twitter production (Range & Fischer, 2004). Here, I was also interested in vocal production when finding highly valuable food items. As these are rare events, they are difficult and document, particularly during the discovery phase. Here, I designed a food placing experiment where I could measure subject and audience reaction when discovering chicken eggs. Although sooty mangabeys do not have acoustically distinct food calls the question was what kind of vocalisations they produced in such instances and whether there was evidence of actively informing others. For single egg presentations I predicted that individuals would remain silent, as is not possible to share a single chicken egg, but for multiple eggs I predicted socially driven calling behaviour.

During conflicts with individuals from the same groups sooty mangabeys are more likely to attack individuals lower-ranking than them and inside food patches (Range & Noë, 2002). In this context, I recorded data on audience composition to better understand whether the presence of socially important individuals had a moderating effect. I also divided analyses along the severity of aggression as indicators of different levels of motivation. I predicted that individuals might be more likely to be mildly aggressive towards lower ranking individuals inside food patches and within the presence of high-ranking individuals, as a possible pre-emptive act to avoid being aggressed by others. Severe aggression should happen regardless of whether inside or outside a food patch and within the presence of social allies that be able to help.

REFERENCES

Berkowitz, L. (1993). *Aggression. Its causes, consequences and control*. (Mc Graw Hill).

Bernstein, I., & Gordon, T. (1974). The Function of Aggression in Primate Societies: Uncontrolled aggression may threaten human survival, but aggression may be vital to the establishment and regulation of primate societies and sociality. *American Scientist,* **62**, 304-311. https://www.jstor.org/stable/27844884

Berthet, M., Mesbahi, G., Pajot, A., Cäsar, C., Neumann, C., & Zuberbühler, K. (2019). Titi monkeys combine alarm calls to create probabilistic meaning. *Science Advances*, *5*(5), eaav3991. https://doi.org/10.1126/sciadv.aav3991

Boehm, C. (1994). Pacifying interventions at Arnhem Zoo and Gombe in *Chimpanzee Cultures* (eds. Wrangham, R., McGrew, W., de Waal, F., Heltne, P.) 211-226. Harvard University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. Oxford University Press, USA.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, *65*(3), 479-487**.**

https://doi.org/10.1006/anbe.2003.2101

Bouchard, A., & Zuberbühler, K. (2022). An intentional cohesion call in male chimpanzees of Budongo Forest. *Animal Cognition*, *25*(4), 853-866. https://doi.org/10.1007/s10071-022-01597-6

Call, J., & Tomasello, M. eds. (2007). *The Gestural Communication of Apes and Monkeys* (New York: Lawrence Erlbaum Associates).

Cartmilll, E. & Byrne, R. (2007). Orangutans modify their gestural signaling according to their audience's comprehension*. Current Biology 17*(15), 1345-1348.

Cartmilll, E. & Byrne, R. (2010). Semantics of primate gestures: intentional meanings of orangutan gestures. *Animal Cognition 13*(6),793-804.

Cheney, D., & Seyfarth, R. (1990). Attending to behavior versus attending to knowledge: examining monkey's attribution of mental states. *Animal Behaviour, 40*,742-745.

Clark, A. P., & Wrangham, R. W. (1993). Acoustic analysis of wild chimpanzee pant hoots: do Kibale Forest chimpanzees have an acoustically distinct food arrival pant hoot?. *American Journal of Primatology*, *31*(2), 99-109. https://doi.org/10.1002/ajp.1350310203

Clay, Z., & Zuberbühler, K. (2009). Food-associated calling sequences in bonobos. *Animal Behaviour*, *77*(6), 1387-1396. https://doi.org/10.1016/j.anbehav.2009.02.016

Clay, Z., Smith, C. L., and Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: what do these calls really mean? *Animal Behaviour 83*, 323–330. https://doi.org/10.1016/j.anbehav.2011.12.008

Clay, Z., Archbold, J., & Zuberbühler, K. (2015). Functional flexibility in wild bonobo vocal behaviour. *PeerJ*, *3*, e1124. https://doi.org/10.7717/peerj.1124

Clutton-Brock, T. & Parker, G. (1995). Punishment in animal societies. *Nature,* **373**, 209-216. https://doi.org/10.1038/373209a0

Covey, R., & McGraw, W. S. (2014). Monkeys in a West African bushmeat market: implications for cercopithecid conservation in eastern Liberia. *Tropical Conservation Science*, *7*(1), 115-125. https://doi.org/10.1177/1940082914007001

Coye, C., Ouattara, K., Zuberbühler, K. & Lemasson, Alban. (2015). Suffixation influences receivers' behaviour in non-human primates*. Proceedings of the Royal Society B*. 282: 20150265. http://doi.org/10.1098/rspb.2015.0265

Crockford, C., Wittig, R., Mundry, R. & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology, 22* (2), pp. 142-146. https://doi.org/10.1016/j.cub.2011.11.053

Davis, H. (1992). Transitive inference in rats (Rattus norvegicus). *Journal of Comparative Psychology*, *106*(4), 342. https://doi.org/10.1037/0735-7036.106.4.342

Drayton, L. & Santos, L. (2014). Capuchins' (*Cebus apella*) sensitivity to others' goal-directed actions in a helping context*. Animal Cognition, 17*(3), 689–700.

https://doi.org/10.1007/s10071-013-0700-5

Dunbar, R. I. M. (1996). *Grooming, gossip and the evolution of language*. Cambridge, MA: Harvard Univ. Press.

Dunbar, R., & Dunbar, P. (1975). Social dynamics of gelada baboons. *Contributions to Primatology*, *6*, 1–157. S. Karger, Basel; New York. PMID: 808371.

Eldakar, O.T. (2020). Hawk-Dove Model, The. In: Zeigler-Hill, V., Shackelford, T.K. (eds) *Encyclopedia of Personality and Individual Differences.* Springer, Cham. https://doi.org/10.1007/978-3-319-24612-3_1645

Elowson, A. M., Tannenbaum, P. L., & Snowdon, C. T. (1991). Food-associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour*, *42*(6), 931-937. https://doi.org/10.1016/S0003-3472(05)80145-9

Emery, N. & Clayton, N. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science, 306*(5703), 1903–1907. https://doi.org/10.1126/science.1098410

Fedurek, P., & Slocombe, K. E. (2013). The social function of food-associated calls in male chimpanzees. *American Journal of Primatology*, *75*(7), 726-739. https://doi.org/10.1002/ajp.22122

Fedurek, P., Slocombe, K., Hartel, J. & Zuberbühler, K. (2015). Chimpanzee lip-smacking facilitates cooperative behaviour. *Scientific Reports* **5**, 13460. https://doi.org/10.1038/srep13460

Fitch, W. T. (2005). The evolution of language: a comparative review. *Biology and philosophy*, *20*, 193-203. https://doi.org/10.1007/s10539-005-5597-1

Fitch, W. T., and Zuberbühler, K. (2013). "Primate precursors to human language: Beyond discontinuity," in *Evolution of Emotional Communication: From Sounds in Nonhuman Mammals to Speech and Music in Man*, eds. *E. Altenmüller, S. Schmidt, and E. Zimmermann (Oxford: Oxford University Press)* 26–48. https://doi.org/10.1093/acprof:oso/9780199583560.003.0002

Flombaum, J. & Santos, L. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology, 15*(5), 447–452. https://doi.org/10.1016/j.cub.2004.12.076

Gardner, R.A. & Gardner, B.T. (1969). Teaching sign language to a chimpanzee. *Science, 165*, 664-72. https://doi.org/10.1126/science.165.3894.664

Gba, B. C., Bene, J. C. K., Bi, Z. B. G., Mielke, A., & Kone, I. (2019). Within-group spatial position and activity budget of wild sooty mangabeys (Cercocebus atys) in Taï National Park, Côte d'Ivoire. *International Journal of Biological and Chemical Sciences*, *13*(7), 2991-3008. https://doi.org/10.4314/ijbcs.v13i7.2

Genty, E. & Zuberbühler, K. (2014). Spatial reference in a bonobo gesture. *Current Biology 24*(14),1601-1605. https://doi.org/10.1016/j.cub.2014.05.065

Genty, E., Neumann, C. & Zuberbühler, K. (2015). Bonobos modify communication signals according to recipient familiarity. *Scientific Reports 5*, 16442. https://doi.org/10.1038/srep16442

Georgiev, A. V., Klimczuk, A. C., Traficonte, D. M., & Maestripieri, D. (2013). When violence pays: a cost-benefit analysis of aggressive behavior in animals and humans. *Evolutionary Psychology*, *11*(3), 678-699. https://doi.org/10.1177/147470491301100313

Gillan, D. J. (1981). Reasoning in the chimpanzee: II. Transitive inference. *Journal of Experimental Psychology: Animal Behavior Processes*, *7*(2), 150-164. https://doi.org/10.1037/0097-7403.7.2.150

Gros-Louis, J. (2004). The function of food-associated calls in white-faced capuchin monkeys, Cebus capucinus, from the perspective of the signaller. *Animal Behaviour*, *67*(3), 431-440. https://doi.org/10.1016/j.anbehav.2003.04.009

Grosenick, L., Clement, T., and Fernald, R. (2007). Fish can infer social rank by observation alone. *Nature 445*, 429–432. https://doi.org/10.1038/nature05511

Gruber, T., & Zuberbühler, K. (2013). Vocal recruitment for joint travel in wild chimpanzees. *Plos One, 8*(9). https://doi.org/10.1371/journal.pone.0076073

Hamburg, D. (1971). Aggressive behavior of chimpanzees and baboons in natural habitats*. Journal of Psychiatric Research,* **8**(3-4), 385–398. https://doi.org/10.1016/0022-3956(71)90032-X

Hauser, M. D. & Marler, P. (1993). Food-associated calls in rhesus macaques (*Macaca mulatta*). 1. Socioecological factors. *Behavioral Ecology*, 4, 194e205 https://doi.org/10.1093/beheco/4.3.194

Hare, B. (2011). From hominoid to hominid mind: What changed and why? *Annual Review of Anthropology, 40*(1), 293–309. https://doi.org/10.1146/annurev-anthro-081309-145726

Hare, B., Addessi, E., Call, J., Tomasello, M. & Visalberghi, E. (2003). Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour, 65*(1), 131–142. https://doi.org/10.1006/anbe.2002.2017

Hayes, C. (1951). *The Ape in Our House*. Harper: New York.

Hill, J. E., DeVault, T. L., & Belant, J. L. (2019). Cause-specific mortality of the world's terrestrial vertebrates*. Global Ecology and Biogeography, 2019,* 1-10. https://doi.org/10.1111/geb.12881

Hobaiter, C. & Byrne, R. (2014). The meanings of chimpanzee gestures. *Current Biology 24*(14),1596-1600. https://doi.org/10.1016/j.cub.2014.05.066

Hobaiter, C., Leavens, D., & Byrne, R. (2014). Deictic gesturing in wild chimpanzees (Pan troglodytes)? Some possible cases*. Journal of Comparative Psychology, 128*(1), 82–87. https://doi.org/10.1037/a0033757

Holekamp, K., & Strauss, E. (2016). Aggression and dominance: An interdisciplinary overview. *Current Opinion in Behavioral Sciences,* **12**, 44–51. https://doi.org/10.1016/j.cobeha.2016.08.005

Hrdy, S. (1979). Infanticide among animals: a review, classifcation, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology,* **1**, 13–40. https://doi.org/10.1016/0162-3095(79)90004-9

Janmaat, K. R. L., Byrne, R. W. & Zuberbühler, K. (2006). Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour.* **72**, 797-807. https://doi.org/10.1016/j.anbehav.2005.12.009

Knott, C., Emery Thompson, M., Stumpf, R. & McIntyre, M. (2010). Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *Proceedings of the Royal Society B.* **277**:105–13 https://doi.org/10.1098/rspb.2009.1552

Laporte, M. N., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour*, *80*(3), 467-473. https://doi.org/10.1016/j.anbehav.2010.06.005

Lazareva, O. F., Smirnova, A. A., Bagozkaja, M. S., Zorina, Z. A., Rayevsky, V. V., & Wasserman, E. A. (2004). Transitive responding in hooded crows requires linearly ordered stimuli. *Journal of the Experimental Analysis of Behavior*, *82*(1), 1-19. https://doi.org/10.1901/jeab.2004.82-1

Lemoine, S., Boesch, C., Preis, A., Samuni, L., Crockford, C. & Wittig, R. (2020). Group dominance increases territory size and reduces neighbour pressure in wild chimpanzees. *Royal Society Open Science.* **7**:200577. http://doi.org/10.1098/rsos.200577

León, J., Thiriau, C., Bodin, C., Crockford, C. & Zuberbühler, K. (2022). Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys. *iScience 25,* 104853. https://doi.org/10.1016/j.isci.2022.104853

Lukas, D. & Huchard, E. (2014). The evolution of infanticide by males in mammalian societies. *Science* **346**, 841–844. https://doi.org/10.1126/science.1257226

Manser, M. B., Seyfarth, R. M., & Cheney, D. L. (2002). Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*, *6*(2), 55-57.
https://doi.org/10.1016/S1364-6613(00)01840-4

Marler, P., Dufty, A., & Pickert, R. (1986). Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver?. *Animal Behaviour*, *34*, 194-198. https://doi.org/10.1016/0003-3472(86)90023-0

Matos, R. J., Peake, T. M. & McGregor, P. K. (2003). Timing of presentation of an audience: aggressive priming and audience effects in male displays of Siamese fighting fish (*Betta splendens*). *Behavioural Processes*, 63, 53–61.
https://doi.org/10.1016/S0376-6357(03)00029-9

McGonigle, B. & Chalmers, M. (1977). Are monkeys logical? *Nature 267*, 694–696.
https://doi.org/10.1038/267694a0

McGraw, W. S., Vick, A. E., & Daegling, D. J. (2011). Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (Cercocebus atys) in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, *144*(1), 140-153.
https://doi.org/10.1002/ajpa.21402

Mercier, S., Neumann, C., van de Waal, E., Chollet, E., Meric de Bellefon, J. & Zuberbühler, K. (2017). Vervet monkeys greet adult males during high-risk situations. Animal Behaviour. 132, 229–245. https://doi.org/10.1016/j.anbehav.2017.07.021

Miczek, K., Fish, E., De Bold, J. & De Almeida, R. (2002). Social and neural determinants of aggressive behavior: pharmacotherapeutic targets at serotonin, dopamine and gamma-aminobutyric acid systems. *Psychopharmacology* **163**, 434–458. https://doi.org/10.1007/s00213-002-1139-6

Mielke, A., Crockford, C., & Wittig, R. (2019). Snake alarm calls as a public good in sooty mangabeys. *Animal Behaviour. 158*, 201–209. https://doi.org/10.1016/j.anbehav.2019.10.001

Mielke, A., Crockford, C., & Wittig, R. M. (2020). Predictability and variability of association patterns in sooty mangabeys. *Behavioral ecology and sociobiology*, *74*, 1-13. https://doi.org/10.1007/s00265-020-2829-y

Mitani, M. (1986). Voiceprint identification and its application to sociological studies of wild Japanese monkeys (Macaca fuscata yakui). *Primates 27*, 397–412. https://doi.org/10.1007/BF02381886

Morton, E. (1977). On the occurrence and significance of motivation structural rules in some bird and mammal sounds. *The American Naturalist 111(981),* 855-869. https://doi.org/10.1086/283219

Neumann, C. & Zuberbühler, K. 2016. Vocal correlates of individual sooty mangabey travel speed and direction. *PeerJ 4*:e2298. https://doi.org/10.7717/peerj.2298

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's monkeys concatenate vocalizations into context-specific call sequences. *Proceedings of the National Academy of Sciences of the United States of America, 106*(51), 22026-22031. https://doi.org/10.1073/pnas.0908118106

Owren, M. J., & Rendall, D. (1997). An affect-conditioning model of nonhuman primate vocal signaling. In D. H. Owings, M. D. Beecher, & N. S. Thompson (Eds.), *Perspectives in Ethology*. New York: Plenum Press.

Papworth, S., Bose, A.-S., Barker, J., Schel, A. M., & Zuberbühler, K. (2008). Male blue monkeys alarm call in response to danger experienced by others. *Biology Letters, 4*(5), 472–475. https://doi.org/10.1098/rsbl.2008.0299

Penner, J., Fruteau, C., Range, F., & Rodel, M. (2008). Finding a needle in a haystack: new methods of locating and working with rhinoceros vipers (Bitis rhinoceros). *Herpetological Review, 39*(3), 310.

Petit, O. & Thierry, B. (1994). Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Animal Behaviour* **48**, 1427-1436. https://doi.org/10.1006/anbe.1994.1378

Phillips, W., Barnes, J., Mahajan, N., Yamaguchi, M. & Santos, L. (2009). Unwilling' versus 'unable': Capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science, 12*(6), 938–945.

https://doi.org/10.1111/J.1467-7687.2009.00840.X

Pollick, A., Gouzoules, H. & de Waal F. (2005). Audience effects on food calls in captive brown capuchin monkeys, *Cebus apella. Animal Behaviour, 70,* 1273-1281. https://doi.org/10.1016/j.anbehav.2005.03.007

Pusey, A., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E. & Goodall, J. (2008). Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania, *International Journal of Primatology,* **29** (4), 949–973. https://doi.org/10.1007/s10764-008-9281-6

Radford, A. N., & Ridley, A. R. (2008). Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Animal behaviour*, *75*(2), 519-527. https://doi.org/10.1016/j.anbehav.2007.05.016

Raihani, N., Thornton, A. & Bshary, R. (2012). Punishment and cooperation in nature. *Trends in Ecology and Evolution,* **27**, 288–295. https://doi.org/10.1016/j.tree.2011.12.004

Range, F. & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï national park. *American Journal of Primatology 56*(3), 137-153. https://doi.org/10.1002/ajp.1070

Range, F., & Fischer, J. (2004). Vocal repertoire of sooty mangabeys (Cercocebus torquatus atys) in the Taï National Park. *Ethology*, *110*(4), 301-321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Rapp, P. R., Kansky, M. T., & Eichenbaum, H. (1996). Learning and memory for hierarchical relationships in the monkey: effects of aging. *Behavioral neuroscience*, *110*(5), 887–897. https://doi.org/10.1037/0735-7044.110.5.887

Ridley, A. R., Child, M. F., & Bell, M. B. (2007). Interspecific audience effects on the alarm-calling behaviour of a kleptoparasitic bird. *Biology Letters*, *3*(6), 589-591. https://doi.org/10.1098/rsbl.2007.0325

Roberts, W. A., & Phelps, M. T. (1994). Transitive inference in rats: A test of the spatial coding hypothesis. *Psychological Science*, *5*(6), 368-374. https://doi.org/10.1111/j.1467-9280.1994.tb00287.x

Rödel, M., Range, F., Seppänen, J., Noë, R. (2002). Caviar in the rain forest: monkeys as frog-spawn predators in Taï National Park, Ivory Coast. *Journal of Tropical Ecology 18*(2), 289–294. https://doi.org/10.1017/S0266467402002195

Rogers, L.J., Stewart, L., Kaplan, G. (2018). Food Calls in Common Marmosets, *Callithrix jacchus*, and Evidence That One Is Functionally Referential. *Animals 8*, 99. https://doi.org/10.3390/ani8070099

Santos, L., Nissen, A. & Ferrugia, J. (2006). Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear*. Animal Behaviour, 71*(5), 1175–1181. https://doi.org/10.1016/j.anbehav.2005.10.007

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee alarm call production meets key criteria for intentionality. *PLoS One, 8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070-1094. https://doi.org/10.1016/S0003-3472(80)80097-2

Sherman, P. W. (1977). Nepotism and the evolution of alarm calls: alarm calls of Belding's ground squirrels warn relatives, and thus are expressions of nepotism. *Science, 197*, 1246–1253. https://doi.org/10.1126/science.197.4310.1246

Sherman, P. W. (1985). Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation?. *Behavioral Ecology and Sociobiology*, *17*, 313-323. https://doi.org/10.1007/BF00293209

Shettleworth, S (2010). *Cognition, evolution and behavior* (2 ed). Oxford: Oxford University Press.

Shultz, S., & Noë, R. (2002). The consequences of crowned eagle central-place foraging on predation risk in monkeys. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1502), 1797-1802. https://doi.org/10.1098/rspb.2002.2098

Shultz, S., Noë, R., McGraw, W. S., & Dunbar, R. I. M. (2004). A community–level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1540), 725-732. https://doi.org/10.1098/rspb.2003.2626

Sierro, J., Loretto, M. C., Szipl, G., Massen, J. J., & Bugnyar, T. (2020). Food calling in wild ravens (Corvus corax) revisited: Who is addressed? *Ethology*, *126*(2), 257-266. https://doi.org/10.1111/eth.12991

Silk, J. B., Seyfarth, R. M., and Cheney, D. L. (2016). Strategic use of affiliative vocalizations by wild female baboons. *PLoS One* 11:e0163978. https://doi.org/10.1371/journal.pone.0163978

Slocombe, K. E., & Zuberbühler, K. (2006). Food-associated calls in chimpanzees: responses to food types or food preferences?. *Animal behaviour*, *72*(5), 989-999. https://doi.org/10.1016/j.anbehav.2006.01.030

Slocombe, K. E., & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228-17233. https://doi.org/10.1073/pnas.0706741104

Stephan, C. & Zuberbühler, K. (2016). Persistent females and compliant males coordinate alarm calling in diana monkeys*. Current Biology, 26*(21), 2907-2912. https://doi.org/10.1016/j.cub.2016.08.033

Steirn, J. N., Weaver, J. E., & Zentall, T. R. (1995). Transitive inference in pigeons: Simplified procedures and a test of value transfer theory. *Animal Learning & Behavior*, *23*(1), 76-82. https://doi.org/10.3758/BF03198018

Symons, D. (1974). Aggressive play and communication in rhesus monkeys (Macaca mulatta). *American Zoologist*, *14*(1), 317-322. https://doi.org/10.1093/icb/14.1.317

Tomasello, M (2010). *Why we cooperate*. Boston: Boston Review Books.

Tomasello, M & Call, J (1997). *Primate cognition.* Oxford: Oxford University Press.

Townsend, S. & Zuberbühler, K. (2009). Audience effects in chimpanzee copulation calls. *Communicative & Integrative Biology 2(3),* 283-284. https://doi.org/10.4161/cib.2.3.6796

Townsend S., Slocombe K., Emery Thompson M. & Zuberbühler K. (2007) Female-led infanticide in wild chimpanzees. *Current Biology, 17*, R355-6. https://doi.org/10.1016/j.cub.2007.03.020

Van Schaik, C. P., & Janson, C. H. (Eds.). (2000). *Infanticide by males and its implications*. Cambridge University Press.

Von Fersen, L., Wynne, C. D., Delius, J. D., & Staddon, J. E. (1991). Transitive inference formation in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *17*(3), 334. https://doi.org/10.1037/0097-7403.17.3.334

Wich, S. & de Vries, H. (2006). Male monkeys remember which group members have given alarm calls. *Proceedings of the Royal Society B-Biological Sciences, 273*(1587), 735-740. https://doi.org/10.1098/rspb.2005.3320

Wilkinson, G. S., & Boughman, J. W. (1998). Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour*, *55*(2), 337-350. https://doi.org/10.1006/anbe.1997.0557

Wubbs, M., Bshary, R. & Lehmann, L. (2016). Coevolution between positive reciprocity, punishment, and partner switching in repeated interactions. *Proceedings of the Royal Society B.* **283**: 20160488. https://doi.org/10.1098/rspb.2016.0488

Zajonc, R.B., Heingartner, A. & Herman, E.M. (1969) Social enhancement and impairment of performance in the cockroach, *Journal of Personality and Social Psychology, 13*, 83-92

Zuberbühler, K. (2000). Causal cognition in a nonhuman primate. *Cognition, 76*, 195-207. https://doi.org/10.1016/s0010-0277(00)00079-2

Zuberbühler, K. (2003). Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language. In P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, T. J. Roper (Eds.) & M. Naguib (Collaborator), *Advances in the study of behavior,* Vol. 33, pp. 265–307). Elsevier Academic Press
https://doi.org/10.1016/S0065-3454(03)33006-2

Zuberbühler, K. (2007). Semantic information in primate alarm calls. In S. McGraw, K. Zuberbühler & R. Noë (Eds.), *Monkeys of the Taï Forest: An African monkey community.* Cambridge: Cambridge Univ. Press.

Zuberbühler, K (2008). Audience effects. *Current biology, 18,*189-190.
https://doi.org/10.1016/j.cub.2007.12.041

Zuberbühler, K. (2018). Intentional communication in primates*. Travaux neuchâtelois de linguistique, 68*, 69-75.
http://www.unine.ch/files/live/sites/tranel/files/Tranel/68/69-75_Zuberbuehler.pdf

Zuberbühler, K., & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, *43*(6), 873-886. https://doi.org/10.1006/jhev.2002.0605

Zuberbühler, K., & Jenny, D. (2007). Interaction between leopard and monkeys. In S. McGraw, K. Zuberbühler & R. Noë (Eds.), *Monkeys of the Taï Forest: An African monkey community.* Cambridge: Cambridge Univ. Press.

Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. (1999a). Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology, 113*, 33-42. https://doi.org/10.1037/0735-7036.113.1.33

Zuberbühler, K., Jenny, D., & Bshary, R. (1999b). The predator deterrence function of primate alarm calls. *Ethology*, *105*(6), 477-490. https://doi.org/10.1046/j.1439-0310.1999.00396.x

Zuberbühler, K., Leon, J., Deshpande, A., & Quintero, F. (2022). Socially scripted vocal learning in primates. *Current Opinion in Behavioral Sciences, 46*, 101153. https://doi.org/10.1016/j.cobeha.2022.101153

CHAPTER 2. AN AUDIENCE EFFECT IN SOOTY MANGABEY ALARM CALLING

Results presented in this chapter have been published in:

Quintero, F., Touitou, S., Magris, M. and Zuberbühler, K. (2022). An audience effect in sooty mangabey alarm calling. *Frontiers in Psychology 13*:816744.

https://doi.org/10.3389/fpsyg.2022.816744

The dataset, and the scripts used in this study have been published in:

https://doi.org/10.6084/m9.figshare.30251995

ABSTRACT

How does intentional communication evolve? Comparative studies can shed light on the evolutionary history of this relevant feature of human language and its distribution before modern humans. The current animal literature on intentional signalling consists mostly of ape gestural studies with evidence of subjects persisting and elaborating with sometimes arbitrary signals towards a desired outcome. Although vocalisations can also have such imperative qualities, they are typically produced in a functionally fixed manner, as if evolved for a specific purpose. Yet, intentionality can sometimes transpire even in functionally fixed calls, for example, if production is adapted to audience composition. In this study, we carried out field experiments to test whether free-ranging sooty mangabeys adjusted snake alarm call production to their audiences. We found a positive relation between alarm call production and naïve individuals arriving, suggesting that callers attempted to influence their behaviours relative to the snake. Subjects called more with smaller audiences, if they had not heard other calls before, and if socially important individuals were in the area. We concluded that sooty mangabeys alarm call production can be explained as an active attempt to refer to an external event, rather than a mere readout of an internal state.

INTRODUCTION

Studies on animal intentionality are important for a number of reasons, such as for understanding the evolutionary origins of human language and the forces that drive the evolution of communication more generally (Krupenye & Call, 2019; Zuberbühler & Gomez, 2018). Intentionality has been investigated by focusing on specific behavioural markers, such as attention-getters, checking for other's attentional states with gaze alternation, signal elaboration, as well as flexible or persistent use and response waiting (Bates, 1979; Leavens, 2004; Tomasello et al., 1994; Townsend et al., 2017). Much relevant work has been carried out with great apes, a group of animals that is of special interest for evolutionary questions, due to their phylogenetic closeness to humans. Here, several lines of evidence suggest that individuals can take into account the goals and intentions of others and adjust their own signalling behaviour accordingly (Call & Tomasello, 2008; Hare, 2011). For example, studies with captive orangutans, chimpanzees and bonobos have all shown that individuals are capable of modifying their signal output depending on the attentional state and familiarity of the recipient, with evidence for persistence and elaboration when dealing with unresponsive recipients (Cartmill & Byrne 2007, 2010; Genty, Neumann & Zuberbühler, 2015; Hobaiter & Byrne, 2014). A number of great ape field studies have also concluded some vocal behaviour also meet criteria for intentionality (e.g., chimpanzees: Crockford et al., 2012, Hobaiter, Leavens & Byrne, 2014, Schel et al., 2013a,b; bonobos: Genty & Zuberbühler, 2014). The consensus view from this research is that great apes are not only able to perceive and attribute intentions to others, but that they are also able to communicate their own and, if misunderstood or ignored, modify their signalling strategy to achieve the desired goal.

Comparably much less is known from other animals, including other groups of primates. This is problematic because there is a distinct possibility that the underlying cognitive capacities needed for intentionality do not evolve like morphological traits along phylogenetic lines. They might just be mere processing features of large brains or evolve in response to specific social or ecological selection pressures by convergent evolution (Emery & Clayton, 2004). To test whether cognitive mechanisms are part of a species' phylogenetic history (MacLean et al., 2012), research on monkeys and non-primate species is crucial. Relevant findings come from studies on captive rhesus macaques (*Macaca mulatta*) and tufted capuchins (*Sapajus apella*) which show that subjects can be sensitive to others' goals and intentions (e.g., Drayton & Santos, 2014; Flombaum & Santos, 2005; Hare *et al*., 2003; Phillips *et al*., 2009; Santos *et al*. 2006). In the wild, there is also evidence showing that some monkey species are able to produce alarm calls with the apparent purpose of influencing others' behaviours (Zuberbühler, 2018). In one study, wild Thomas langur males continued to produce alarm calls to predator model until every group member had responded with at least one alarm call, as if to ensure that others were aware of the danger (Wich & de Vries, 2006). In another study, wild Diana monkey females continued to alarm call until their own male produced the semantically matching ('correct') alarm calls, i.e., the predator spotted by the females, in response to which they stopped producing alarm calls (Stephan & Zuberbühler, 2016). Also, playback experiments with blue monkeys showed that males produced significantly more alarm calls to simulations of crowned eagle presence if other group members were closer to the presumed predator than far away (Papworth *et al*., 2008), further demonstrating some basic audience awareness, but not ruling out explanations based on basic changes in affective states.

Traditionally, studies on animal intentionality have used Dennett's stages of intentionality as a theoretical framework (Dennett, 1983). Here, a key change is between the second to higher orders of intentionality, which require the ability to attribute mental states during communication. Although Dennett's framework is appealing, one problem with it is that young children struggle with tasks that require mental state attribution (Liddle & Nettle, 2006; Wimmer & Perner, 1983), that even adults do not always attribute mental states automatically during interactions (Apperly et al., 2006; Keysar, Lin,& Barr, 2003) and sometimes even actively avoid them (McClung, Jentzsch, & Reicher, 2013).

One possibility is that human adults, and certainly pre- and non-linguistic subjects, do not primarily assess others' behaviours as governed in terms of underlying mental states (beliefs, desires, intentions), but in terms of rehearsed behavioural or social scripts that allow subjects to make judgements and predictions in how social interactions normally unfold (Taylor et al. submitted; Worden, 1996). But even though such cognitively simpler script-based accounts appear to better explain the empirical data, including much of the theory of mind literature, they still rely on intentionality as a basic force of social behaviour. For communication signals, Townsend et al. (2017) have proposed three distinct criteria that signal production needs to meet before intentionality can be ascribed to it. Although research on great apes continues to provide evidence for intentional communication (e.g., Bouchard & Zuberbühler, 2022; Gruber & Zuberbühler, 2013; Schel et al. 2013b), to our knowledge there are no comparable studies on free-ranging monkeys designed to tackle the same question.

One way to assess intentional states in animals and other non-linguistic subjects is to present them with private information that is also relevant for others, such as encountering danger. If the subject is able and willing to take another's intentions (receiver's presumed knowledge about the danger) into account, it should take active steps to inform its partner, especially if it is still ignorant and likely to endanger itself. One successful paradigm has been to present snake models to lone individuals, without others witnessing the event (Crockford *et al.* 2012). In chimpanzees, this has led to the conclusion that they are capable of taking into account others' mental states, due to the fact that they were more likely to call if newly arriving individuals were not aware of the danger (Crockford *et al.* 2012) and if they were socially important to the caller (Schel *et al.* 2013b). However, when the same experiment was replicated with sooty mangabeys in Taï Forest (Ivory Coast), callers did not adjust call production to the presence of socially important or referentially unaware partners (Mielke *et al.*, 2019). The reasons have remained unclear, but one possibility is that this represents a cognitive divide between monkeys and apes (Tomasello, 2010), or a mere age effect (mostly juveniles were tested in the monkey study). Appropriate alarm calling requires experience and it is certainly possible that juveniles were unable to process social situations in the same way as adults would (Cheney & Seyfarth, 2007).

Also, field experiments with predator models are prone to authenticity problems (see Zuberbühler & Wittig, 2011) raising the possibility that subjects processed the models differently compared to real snakes. Nevertheless, sooty mangabeys are an ideal species for direct comparisons between monkeys and chimpanzees since they live in the same forest habitat, form similarly sized multi-male, multi-female groups (up to 100), have similar foraging and locomotor habits, although, unlike chimpanzees, they do not have male philopatry and only restricted fission-fusion (Aureli *et al.* 2008; Range & Noë, 2002).

The goal of this study was to reassess the proposed monkey-ape cognitive divide by focusing only on adult individuals and to revisit the question of primate intentionality more generally. Encounters with dangerous Gaboon and Rhinoceros vipers (*Bitis gabonica*; *Bitis nasicornis*) are common in sooty mangabeys, observed around 3-4 times per week and sometimes several times per day (Range & Fischer, 2004; FQ, unpublished data). This is due to the fact that individuals spend much of their time foraging through the leaf-litter in search for insects and fallen fruits of *Anthonota spp*., *Saccoglotis gabonensis* or *Dialium spp*. (Janmaat *et al*., 2006; McGraw, *et al*., 2011; Range & Noë, 2002). Sooty mangabeys react very strongly to these two snake species, by giving acoustically distinct snake alarm calls, which can cause others to jump into the lower canopy in order to localise and subsequently approach the snake. Interestingly, adult mangabeys ignore most other species of snakes, including highly poisonous forest cobras (*Naja melanoleuca*) or green mambas (*Dendroaspis viridis*), suggesting that the Gaboon and Rhinoceros vipers had led to lethal accidents and subsequent learning, despite the fact that neither snake is likely a major predator, at least for adult individuals.

To address the previous points, we carried a field experiment in which we presented seven different viper replica models to adult sooty mangabeys (Appendix 1), under different social conditions with the following predictions. First, regarding audience size, we predicted that audience size should not influence alarm call production per se, since alarm calling is always effective, regardless of the number of listeners. However, the duration of alarm calling should be related to audience size; more specifically, the time it takes for others to arrive at the site. Regarding audience composition, we predicted that adult and experienced callers should be interested in informing mainly snake-ignorant and socially relevant group members.

METHODS

Study Site and Subjects

The study was conducted in Taï National Park in South-western Ivory Coast (5°50’N, 7°21’ W). The park is the largest remaining major block of primary forest in West Africa and covers approximately 454,000 ha of continuous forest. The forest is classified as ‘tropical moist’ with a mean annual temperature of 24°C, a mean annual rainfall of 1,875 mm and a distinct dry season in December–January (Taï Monkey Project data 2012-2015; Whitmore, 1990). The study area of about 7 km^2 was situated near the western border of the park, approximately 20 km southeast of the township Taï. The study group’s home range contained a 2-km^2 core area where groups of several monkey species had been studied since 1991, as part of a long-term research project (McGraw & Zuberbühler, 2007). The sooty mangabey study group has been under constant observation since 1997 and is well habituated to human observers (Neumann & Zuberbühler, 2016; Range & Noë, 2002). Data collection was during group follows from dawn to dusk (7:00 to 17:00 local time) over a period of 24 months in three blocks of time: January to May 2013, August 2013 to July 2014 and January to September 2015. During the study period the group size was around 80 individuals, including 25-30 adult females (>5 years old), 4 adult males (>5 years old), 3-8 juvenile females (1-4 years old), 10-18 juvenile males (1-4 years old) and 16-20 unidentified infants (<1 year old).

Experimental design

When encountering gaboon or rhinoceros vipers, sooty mangabeys respond by giving acoustically distinct ‘snake’ alarms (fig 2.1), which attract other group members. Typically, only one adult individual gives alarm calls, suggesting a sort of sentinel function, but the first individual to discover the snake is not always the first caller. Sometimes, up to three additional individuals also produce alarm calls, but these are usually infants or juveniles (FQ unpublished data).

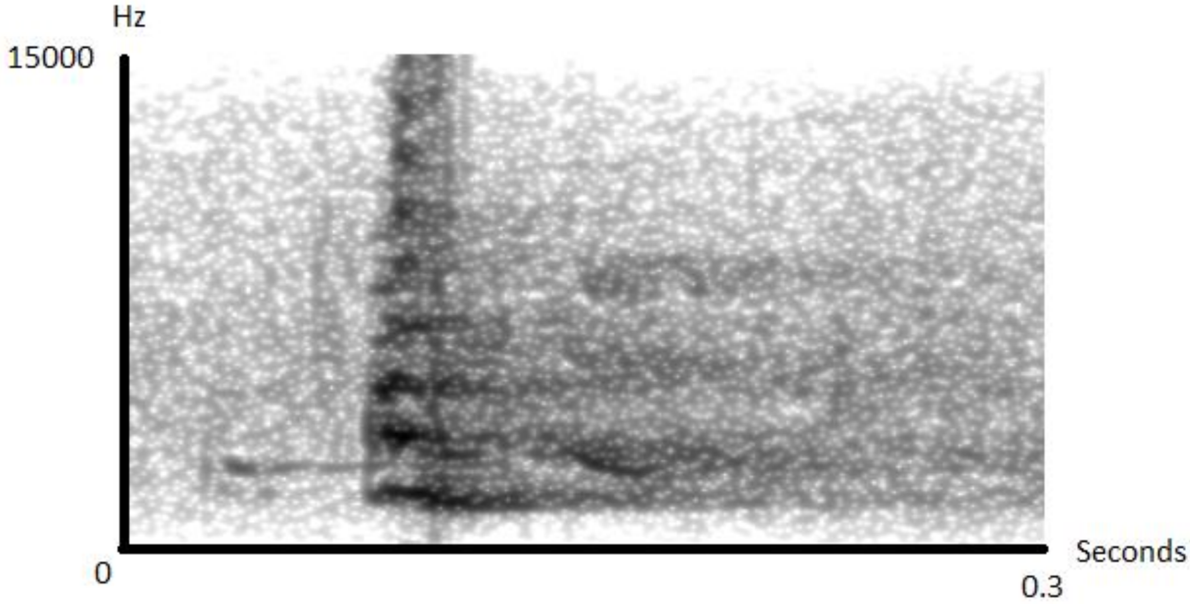

Figure 2.1. Spectrogram of a snake alarm call given by a female sooty mangabey. When encountering snakes, individuals produce sequences of up to a dozen of such. (Spectrogram made in Praat).

In the experiments, we selectively exposed N=14 adult group members to 7 different snake models, authentic replicas of *Bitis gabonica* and *Bitis nasicornis* in various natural positions (Appendix 1). Adult subjects were chosen randomly and exposed to the model. Experiments were performed no more than twice per month, with a total of N= 22 trials.

For each trial, the audience composition was determined as was the subject's reaction when discovering the snake. For each encounter, we determined if the discovering individual had already heard a snake alarm given by another group member (to the model).

We then created two data sets. In a first dataset, each snake encounter by an adult individual was entered as one data point, provided (1) no snake alarm call had been produced before the encounter and (2) no individual other than the subject was within 10m (average maximum visibility) of the model. Alarm calls given within the first 5min of the subject's first call were considered part of the same encounter ('ignorance model', see below; most experiments lasted less than 5 min). In a second data set ('encounter model', see below), we entered every individual snake encounter as an independent data point regardless of other factors.

Natural encounters

During the study period, we recorded N=20 natural snake encounters with mostly Gaboon and Rhinoceros vipers. During the wet season, natural encounters with vipers can happen every single day, but even during drier periods, 1-2 encounters per week are common. Typical encounters happen when an individual finds a viper resting motionless on the ground. Usually, the first individual then responds with a brief startle response followed by an acoustically distinct alarm call (fig. 2.1). This usually causes other individuals to approach to locate and observe the snake. We never observed anything that could qualify as mobbing behaviour, i.e., acoustically or visually conspicuous behaviour to drive away the snake or rally other group members. Instead, upon detection, most individuals simply approach and observe the snake in a calm way. In only one encounter the snake was moving, which led some individuals, mostly juveniles, to follow the snake within the lower canopy less than 4m off the ground with occasional alarm calls. During natural encounters it was nearly impossible to determine the exact moment of snake detection, although it almost always led to large gatherings of monkeys surrounding the snake, so we decided to simulate snake encounters using life size replica.

Experimental Protocol

After selecting a subject, we waited until there was no other individual around 10m. We then positioned the model so that the subject was the first to discover it. We did this by trying to predict the travel path of the subject and positioning the snake on the forest floor on the anticipated path. Occasionally another individual found the snake first, in which case we made it the subject. During each trial, a first experimenter positioned the snake ahead of the subject's anticipated travel path and determined the audience composition, by identifying all present and newly arriving group members within the visible range. The second experimenter filmed the subject as it approached the snake, recorded all calls and orally described the event. The two experimenters were accompanied by a field assistant who could assist with the different steps. Individual identification of group members present was essential, which was achieved by having a team of observers. We used a Panasonic Video-Camera SDR-26 to film each trial and Marantz PMD 661 solid state recorder with a Sennheiser MKH 418 microphone to record all calls. From the 22 trials, 6 trials in 2014 were conducted by MM; the rest by FQ. All the data from the videos were coded by FQ. Data extraction from the videos only concerned uncontroversial variables, such as time of arrival, number of calls and number of individuals, but no behavioural or proximity data, which would require interobserver reliability tests. For transparency, we have uploaded all video clips of the different snake encounter trials for inspection: https://figshare.com/s/82b6989a71e75a57e523

Statistical Analyses

During each trial we scored the number of 'snake alarms' produced by the subject (numeric: 'ncalls'), as the response variable in our models. As predictor variables we included (a) the subject's sex (binary: 'sex'), (b) the time interval between the subject's first alarm call and the arrival of the first audience member at the snake location (numeric: 'time1starrival'), (c) the number of individuals within 10m when the subject detected the snake (numeric: 'neighbours'), (d) whether the subject discovered the snake first (binary: 'ffinder'), (e) the presence of socially important individuals (binary: 'friend'; defined by a DSI score >1; Silk, Cheney & Seyfarth, 2013). For calculating the DSI we used the following behaviours as variables: 'approach', 'inspection', 'presenting groom', 'contact', 'groom', 'handle baby' and 'hug' (Appendix 2); (f) the social status of the subject (numeric: 'rank'; determined by its Elo-rating score; Neumann et al., 2011), (g) the number of individuals that arrived at snake location the first alarm call (numeric: 'nbarrivals'), (h) time the subject stayed within 10m of the snake after producing the first call (numeric: 'findertime'), (i) the number of calls heard before arriving at the snake location (numeric: 'ocbefore'). We did not use a predictor for call secession in response to detection as sooty mangabeys do not typically stop calling when others arrive. Nonetheless, if there would be a pattern in others arriving and call cessation this would be reflected in the 'time1starrival' variable. We then created two models to assess the factors driving snake alarm calling in sooty mangabeys.

The ‘encounter’ model

We used generalized linear mixed models (GLMM) with a Poisson error structure to test variation in call production for every individual that encountered the snake, regardless of the previous alarm call history. To this effect, every individual that approached the snake was entered as a data point, regardless of whether any other individual had produced a snake alarm call before or after, with the same factors entered as mentioned above, except for the ones only relevant for the caller (‘findertime’, ‘nbarrivals’ and ‘time1starrival’). With this model, we addressed whether audience size (N neighbours) affected call production, provided there were previous snake alarms (neighbours * ocbefore). Second, we addressed whether audience composition (socially important individual present) affected call production, provided there were previous snake alarm calls (friend * ocbefore). Third, we addressed whether high-status individuals were more likely to vocalize than low-status individuals, provided they detected the snake (rank * ffinder). Finally, we addressed whether the audience composition (socially important individual present) affected call production, provided they detected the snake (snake * ffinder). For all models we included random intercepts for the focal subject ID.

We then built an ‘informed null model’, which comprised all fixed terms except those that included the main predictors. The random structure was identical to the full model. We then compared these models with a likelihood ratio test (Dobson, 2002). If the comparison of full and null model revealed significance, we explored the full model with regards to our predictors of interest (i.e., those that were in the full but not in the null model).

The ‘ignorance’ model

We used linear mixed models (LMM) to determine the factors that affected the number of alarm calls produced from the caller’s perspective. Every individual that found the snake and had not heard an alarm call before was entered as an independent data point. All the factors above mentioned were included except for the number of calls heard before arriving at the location (‘ocbefore’). We included random intercepts for focal subject ID. We then conducted a model selection procedure from the global model to determine the factors that best predicted call production. Models were ordered by the value of the Akaike information criterion, with the lowest on top. The validity of the best model was then checked with a Shapiro-Wilk test.

We used R version 4.0.3 (R Core Team, 2020) for the analyses above mentioned, with the glmer and lmer functions, ‘lme4’ package (Bates, Mächler, Bolker & Walker, 2019) for the GLMMs and LMMs. We also used the dredge function, ‘MuMIn’ package (Barton, 2018) for the model selection.

Ethical note

The methods used in this study are in line with the Animal Behaviour Society Guidelines for the Use of Animals in Research. We used non-invasive methods for the observation of the subjects in their natural habitat. The animals were identified by physical features like scars, body size and shape, and they were all habituated to human observers. The experiments simulated a natural event and did not interfere with the animals’ normal daily routine. Research permission and ethical clearance were granted by the Ministère de la Recherche Scientifique et Technique de Côte d'Ivoire.

RESULTS

Experimental encounters

We carried out N=22 trials during which we presented seven snake models to N=27 individuals unaware of the snake (adult females: N=24; adult males: N=1; juvenile males: N=2). Subjects alarm called in 21 of 27 encounters (77.8%). We found that, every time a subject alarm called, other group members responded by approaching and looking for the snake, generally silently. In addition, juveniles often grabbed and smelled leaves near the snake in order to smell them, suggesting that there is an olfactory component relevant to snake encounters. Silent encounters without alarm calls were also considered in both models.

The 'encounter' model

In the encounter model, we investigated which variables best explained the number of calls produced when individuals found the snake. We registered N=150 snake encounters when considering all the individuals that approached the snake regardless of awareness. We found that the number of snake alarm calls (a) decreased with increasing numbers of individuals already present (beta ± SE = -0.8541± 0.5, p = 0.02410; fig. 2.2, table 2.1), (b) decreased with increasing caller social status (beta ± SE = 0.451 ± 0.21, p = 0.037; table 2.1), (c) increased if the callers were female (beta ± SE = 1.69 ± 0.58, p = 0.0035; fig. 2.3.

table 2.1), and (d) decreased with a lower number of calls before (beta ± SE = -9.997 ± 4.96, p = 0.044; fig. 2.4, table 2.1). Two interactions were linked to significant increases in call production: discoverer * low ranking (beta ± SE = -0.6720 ± 0.23, p = 0.00451; fig. 2.5, table 2.1), no prior alarm calls * socially important individual in the audience (beta ± SE = 9.41 ± 5, p = 0.059; table 2.1). The full model was significantly different from the null model (χ^2 = 158.36 df = 3, p = 0.000).

Table 2.1. Results of the GLMM for the number of alarm calls when individuals find a snake regardless of whether there has been a previous alarm call.

Variables	**Estimate**	**SE**	**Z**	**Pr(>|z|)**
(Intercept)	-2.791	0.716	-3.895	0.000
Rank	-0.166	0.258	-0.644	**0.037**
Sex	0.667	0.719	0.928	**0.003**
Friend	0.492	0.230	2.134	0.248
First finder	2.520	0.326	7.723	0.285
Neighbours	-0.535	0.139	-3.831	**0.024**
Call heard before	-0.239	0.076	-3.154	**0.044**
Call after	-0.348	0.215	-1.612	0.106
Ffinder:Rank	-0.672	0.236	-2.840	**0.004**
Ffinder:Friend	2.001	1.141	1.754	0.079
Friend:Call heard before	9.413	5.002	1.882	**0.059**
Neighbours:C. heard before	-1.493	0.981	-1.522	0.128

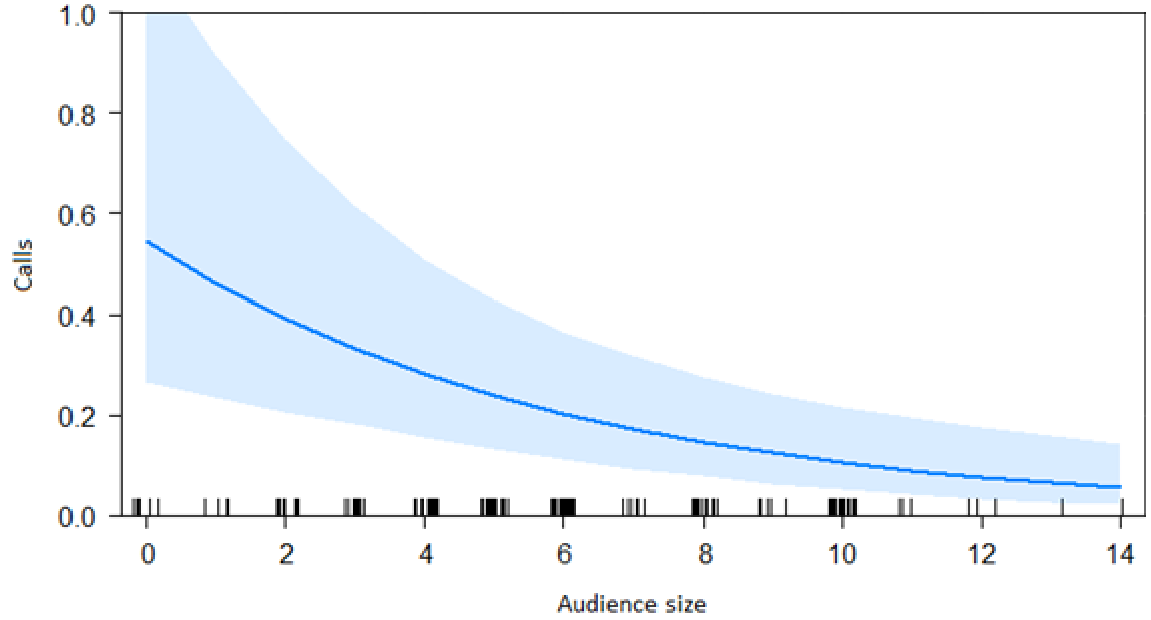

Figure 2.2. Effect of audience size on the number of calls when finding the snake. (Audience size=Number of individuals around 10m of the subject. Calls: Proportion of alarm calls given by the subject).

Figure 2.3. Effect of caller's sex on the number of calls when finding the snake. (Y-axis in log scale. Sample size 132 adult females, 8 adult males, 10 juvenile males)

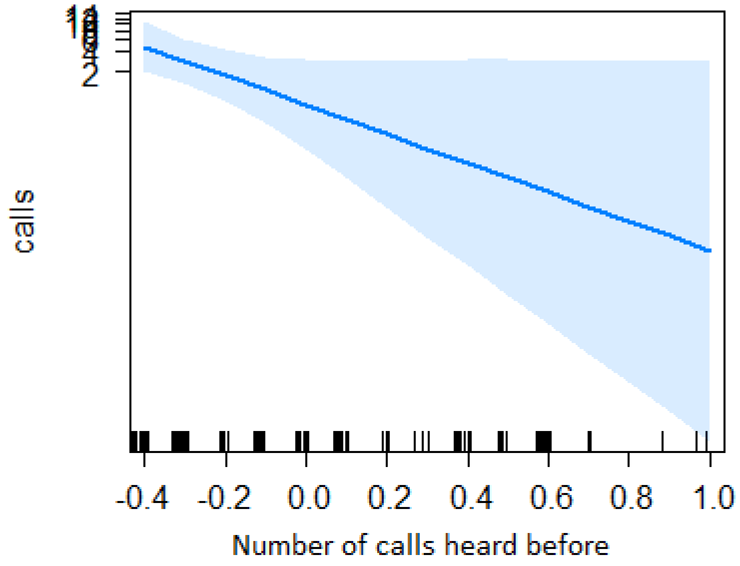

Figure 2.4. Effect of the number of calls heard before on the number of calls when finding the snake. (Y-axis in log scale)

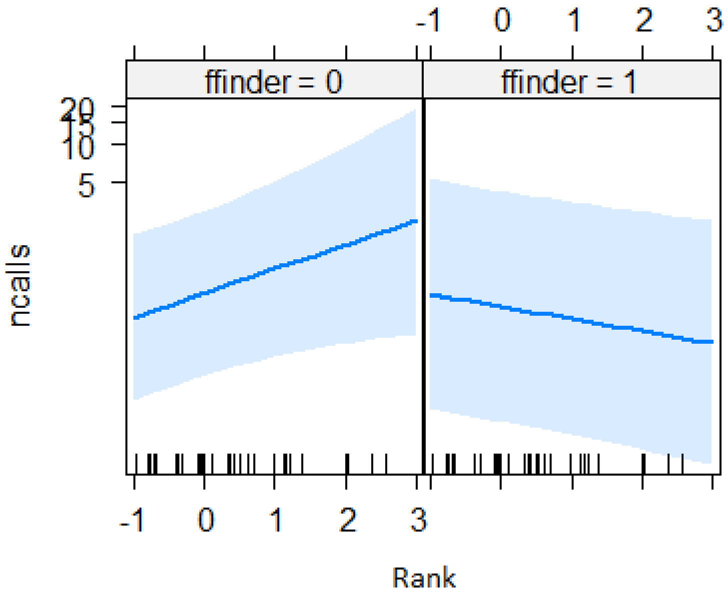

Figure 2.5. Effect of caller's rank when being the first to find the snake. (Y-axis in log scale, Rank data has also been transformed so it could be better visualized)

The 'ignorance' model

The best model for ignorant individuals detecting the snake (AIC=65.7; table 2) showed that the number of snake alarm calls (a) decreased with increasing numbers of individuals already present (beta ± SE = -0.735± 0.17, p = 0.00062; fig. 2.6, table 2.3), (b) increased with the number of socially important individuals already present (beta ± SE = 0.611 ± 0.23, p = 0.023; fig 2.7, table 2.3) and (c) predicted how many individuals would arrive to see the snake (beta ± SE = 0.285± 0.05, p = 0.0001; fig. 2.8; table 2.3). A Shapiro-Wilk test indicated that the data were normally distributed (W = 0.98387, p-value = 0.9374).

Table 2.2. Model selection table for the LMM for the number of alarm calls of ignorant individuals encountering the snake.

Intrc	Friend	Sex	Neighbours	Nbarrivals	T1starrival	Df	logLik	AICc	Delta	Pr(>|z|)
101	+		-0.7358	0.285		6	-24.7	65.7	0.00	0.268
201		+		0.290	0.1558	6	-25.2	66.6	0.87	0.174
105		+	-0.4145	0.246		6	-25.2	66.7	0.90	0.171
109	+	+	-0.6806	0.281		7	-23.4	66.8	1.00	0.162
97			-0.4591	0.2451		5	-27.2	67.3	1.56	0.123
73		+		0.228		5	-27.4	67.7	1.94	0.102

Table 2.3. Results of the best LMM for the number of alarm calls of ignorant individuals encountering the snake.

Variables	Estimate	SE	df	t value	Pr(>|z|)
(Intercept)	1.549	0.340	20.6	4.55	0.0001
Friend	0.611	0.239	13.47	2.55	0.0234
Neighbours	-0.735	0.173	16.2	-4.23	0.0006
Number of Arrivals	0.285	0.056	14.3	5.01	0.0001

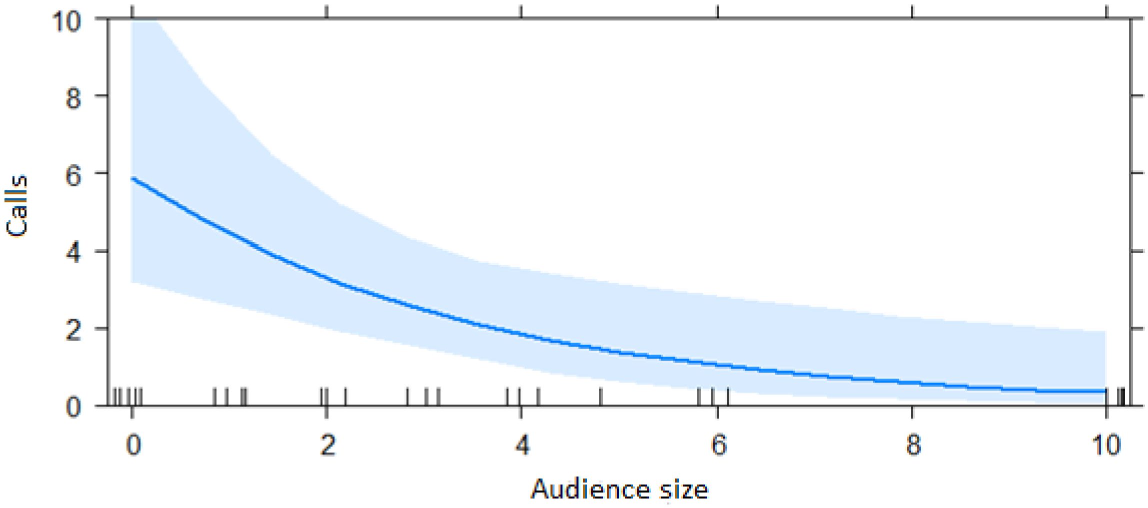

Figure 2.6. Effect of audience size on the number of alarm calls by ignorant individuals encountering the snake. (Audience size=Number of individuals within 10m of the subject. Calls: Number of alarm calls given by the subject).

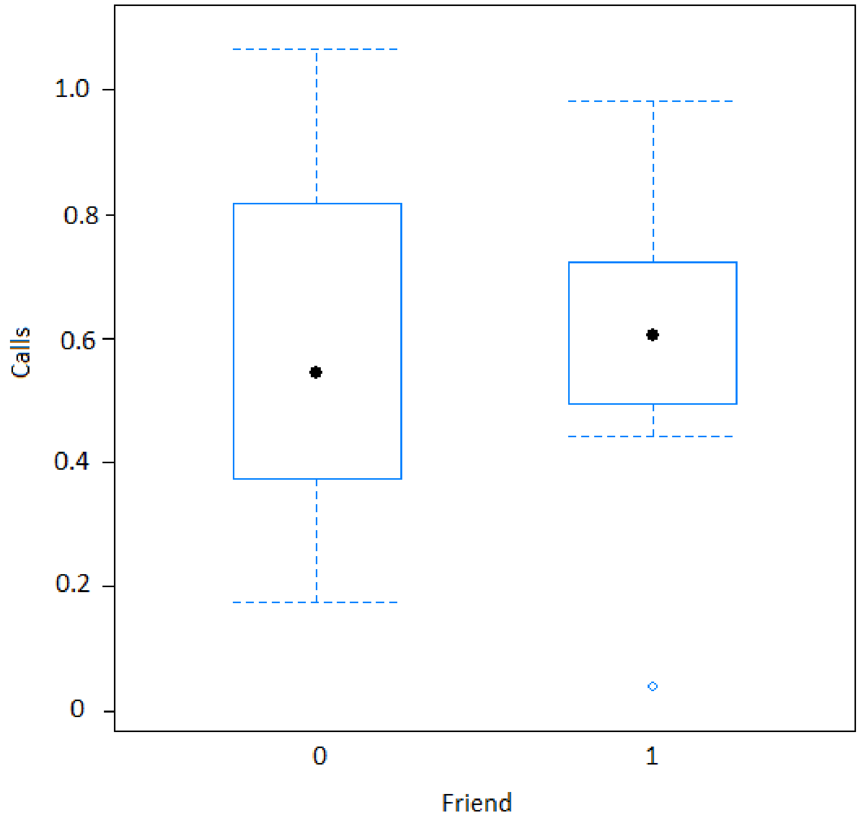

Figure 2.7. Effect of audience composition on the numbers of calls when an ignorant individual finds the snake. (Friend= Socially important individual present around 10m of the subject. Calls: Proportion of alarm calls given by the subject).

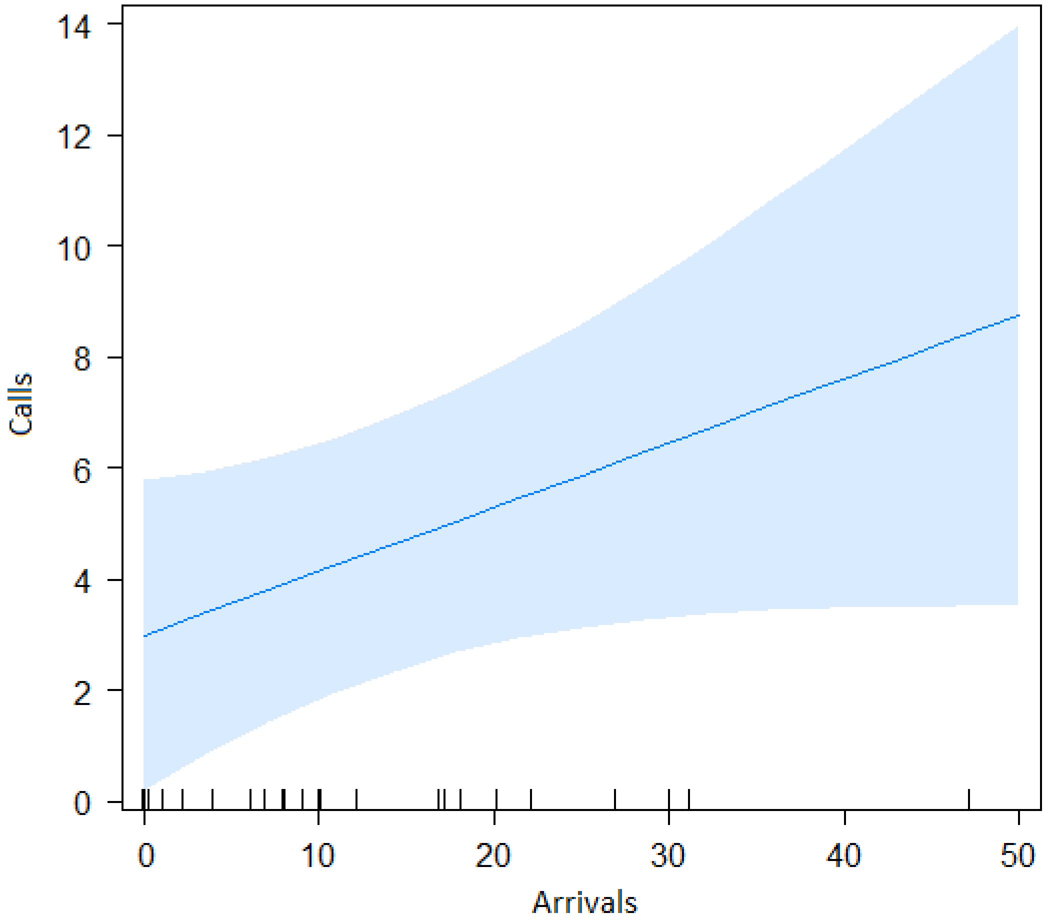

Figure 2.8. Consequence of alarm calling. Effect of the number of calls given on the number of individuals that arrive at the snake position.

DISCUSSION

We carried out field experiments with free-ranging monkeys in Tai National Park, Ivory Coast, to address the question of whether callers were capable of warning each other of the presence of dangerous snakes. Using live-sized realistic replicas of two highly dangerous vipers we managed to elicit responses from sooty mangabeys that largely matched natural observations. Individuals that first discovered the model typically alarm called and stayed with the snake until other group members arrived. In order to address questions of whether these calls qualified as intentional signals, we specifically looked at how audience-related variables impacted on call production. To this effect we tested two separate models, one considering data from any individual that discovered the snake and another one considering only encounters by individuals that were ignorant about the snake at the moment of detection.

Both models revealed that audience was an important factor influencing the number of calls when encountering snakes. Generally, subjects increased their calling efforts with decreasing audience sizes (fig 2.2, fig 2.6). For ignorant callers (callers unaware of the snake presence that find it before others), higher number of calls were related with the presence of socially important individuals (fig 2.7), and this also led to a higher number of arrivals (fig 2.8). We also found that having heard an alarm call before led to significantly fewer alarm calls than if no call was given before. These findings would be consistent with the interpretation that, similar to chimpanzees, sooty mangabeys would have some concerns for others in these potentially dangerous situations and alarm called specifically if the benefits for others were high (if most of group members were still absent and if friends were exposed to danger). But in sooty mangabeys this could also be explained by affective or physiological changes related to variation in group size and audience composition.

Sooty mangabey snake alarm calls can be heard over distances of at least 100m, suggesting that most group members will be informed if an individual calls to a snake. It is therefore somewhat surprising that audience size had an effect on alarm calling at all. As explained earlier, we never observed mobbing behaviour in sooty mangabeys, neither in natural nor during experimental snake encounters. Gaboon vipers are highly static snakes, unlikely to move in response to agitated monkey display behaviour, suggesting that mobbing would be ineffective as an anti-predator strategy. One possibility is that callers were not just interested in informing others about the snake, but that calling also served to reveal its location. Clearly, recipients will benefit mostly if they know the exact location of the danger, which is only possible following personal inspection. This is supported by the fact that the number of arrivals increased with a higher number of alarm calls. Further research is needed regarding the behaviour of the caller right after finding the snake.

We found no evidence that the timing of others' arrivals influenced the subject's calling behaviour (table 2.2), suggesting that it is not paramount for callers to make sure that all group members have seen the snake (in contrast to, for example, results from Thomas langurs; Wich & de Vries, 2006). During experiments and real encounters, we observed that only a fraction of the group approached the snake, whereas many other group members appear to ignore the event. In contrast to species living in small groups, such as Thomas langurs, it may simply not be feasible for callers to continue calling until the entire group has witnessed the snake, especially as this is unlikely to happen anyway. As mentioned, Gaboon and Rhinoceros vipers are not primary predators, despite being highly dangerous, suggesting that knowing their location is the main requirement to remain safe. Knowing which general area to avoid is therefore enough, while visually locating the snake is only needed if the subject wants to use that area, for example for foraging.

Our work partly replicates a previous study on sooty mangabeys (Mielke et al., 2019) by showing that subjects were less likely to call if they heard a call before and if they were with large audiences. This reinforces the idea that it is important for callers to ensure that as many individuals as possible know the snake location. Also, snake alarm calls are usually produced by individuals near the snake, suggesting that these individuals subsequently act as visual beacons to mark the snake's location.

However, in our study we also found both caller and audience effects: (1) the four adult males never called to snakes, (2) lower ranking individuals were more likely to call, and (3) alarm calling was more important when socially important individuals were in the audience. In mangabey groups, adult males are socially peripheral, whereas adult females form the social core of the group. Perhaps, unsurprisingly they were thus also more likely to give alarm calls to snakes (fig. 2.3), perhaps to provide social learning opportunities to their more vulnerable offspring (Seyfarth & Cheney, 2010). The fact that the presence of 'friends' was also associated with higher alarm calling rates (table 2.3; fig. 2.7), suggests that grooming could be traded with warning for Gaboon or Rhinoceros vipers.

Previous work with wild Thomas langurs has shown that callers continue until every single individual has encountered the predator, while female Diana monkeys will not stop calling to a leopard until their males have produced the same calls (Wich and de Vries, 2006; Stephan & Zuberbühler, 2016), suggesting that alarm calling is tied to underlying intentions to inform others. In our study, we did not find such pattern but calling was most common in individuals who found the snake, provided no call had been produced before (table 2.1) and with key individuals in the audience, to our knowledge a first such demonstration in free-ranging monkeys. The first criteria for intentionality is goal directed behaviour that can be measured as persistence. Nonetheless, there are significant trends where sooty mangabeys call more when there are less individuals and the more they call, the more that other individuals are recruited.

Regarding the three criteria for intentional communication, put forward by Townsend et al. (2017), we can state the following: (1) Regarding 'goal directedness', alarm calling was about detecting the snake and, presumably, ensuring that others were made aware of its location. Although we did not observe any obvious signs of persistence (i.e., callers monitoring exactly whether or when others have located the snake) we found that mangabeys called more when fewer individuals were present and that the more they called the more individuals arrived. (2) Regarding 'recipient-directedness' our data resemble findings in chimpanzees who produce food calls and snake alarms preferentially in the presence of socially important individuals, i.e., friends and high-ranking group members (Schel et al. 2013a&b), a pattern we also found (table 2.3; fig 2.7). In contrast to chimpanzees, however, we never observed an individual re-starting alarm calling with the arrival of a new individual. Whether or not these patterns could be explained with more basic changes in physiological states or arousal, rather than an intentional stance, would have to be further investigated. (3) The third criteria for intentionality states that receivers must regularly respond in a way that is in line with the signaller's presumed intentions. Although we did not address this requirement directly, there was not a single occasion when sooty mangabeys called and no individuals arrived to locate the snake, suggesting that receivers responded in line with the caller's expectations.

In conclusion, sooty mangabey snake alarm calling is driven by several factors related to the caller and affects other group members who approach the caller to then try to locate the danger. The patterns are not in line with a more traditional notion of animal calls as hardwired reflexive responses to specific stimuli, but appear to involve assessments of both ecological and social variables in ways that meet criteria of intentional signalling.

REFERENCES

Apperly, I. A., Riggs, K. J., Simpson, A., Samson, D. & Chiavarino, C. (2006). Is belief reasoning automatic? *Psychological Science 17*, 841–844.
https://doi.org/10.1111/j.1467-9280.2006.01791.x

Aureli, F, Schaffner C., Boesch, C., Bearder, S., Call, J., Chapman, C., Connor, R., Fiore, A., Dunbar, R., Henzi, S. & Holekamp, K. (2008). Fission-fusion dynamics: new research frameworks. *Current Anthropology, 49*(4):627–54.
https://doi.org/10.1086/586708

Barton, K. (2018). MuMIn: Multi-Model Inference. R package version 1.42.1. https://CRAN.R-project.org/package=MuMIn.

Bates, E. (1979). Intentions, conventions, and symbols. In: *The emergence of symbols: Cognition and communication in infancy* (pp. 33–68). Academic Press
https://doi.org/10.1016/B978-0-12-081540-1.50008-9

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software 67*(1), 1-48. https://doi.org/10.18637/jss.v067.i01

Bouchard, A., & Zuberbühler, K. (2022). An intentional cohesion call in male chimpanzees of Budongo Forest. *Animal Cognition*, *25*(4), 853–866. https://doi.org/10.1007/s10071-022-01597-6

Call, J. & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences, 12*(5), 187–192. https://doi.org/10.1016/j.tics.2008.02.010

Cartmilll, E. & Byrne, R. (2007). Orangutans modify their gestural signaling according to their audience's comprehension*. Current Biology 17*(15), 1345-1348. https://doi.org/10.1016/j.cub.2007.06.069

Cartmilll, E. & Byrne, R. (2010). Semantics of primate gestures: intentional meanings of orangutan gestures. *Animal Cognition 13*(6),793-804. https://doi.org/10.1007/s10071-010-0328-7

Cheney, D. & Seyfarth, R. (2007). *Baboon metaphysics: The evolution of a social mind* (pp. 220-223). The University of Chicago Press, Chicago.

Crockford, C., Wittig, R., Mundry, R. & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology, 22* (2), pp. 142-146. https://doi.org/10.1016/j.cub.2011.11.053

Dennett, D. (1983). Intentional systems in cognitive ethology ‘‘The Panglossian paradigm’’ defended*. Behavioral and Brain Sciences 6*(3), 343–390. https://doi.org/10.1017/S0140525X00016393

Dobson, A. J. (2002). *An introduction to generalized linear models*. Boca Raton: Chapman & Hall/CRC.

Drayton, L. & Santos, L. (2014). Capuchins' (*Cebus apella*) sensitivity to others' goal-directed actions in a helping context. *Animal Cognition, 17*(3), 689–700.
https://doi.org/10.1007/s10071-013-0700-5

Emery, N. & Clayton, N. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science, 306*(5703), 1903–1907.
https://doi.org/10.1126/science.1098410

Flombaum, J. & Santos, L. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology, 15*(5), 447–452.
https://doi.org/10.1016/j.cub.2004.12.076

Genty, E. & Zuberbühler, K. (2014). Spatial reference in a bonobo gesture. *Current Biology 24*(14),1601-1605. https://doi.org/10.1016/j.cub.2014.05.065

Genty, E., Neumann, C. & Zuberbühler, K. (2015). Bonobos modify communication signals according to recipient familiarity. *Scientific Reports 5*, 16442.
https://doi.org/10.1038/srep16442

Gruber, T., & Zuberbühler, K. (2013). Vocal recruitment for joint travel in wild chimpanzees. *Plos One, 8*(9).
https://doi.org/10.1371/journal.pone.0076073

Hare, B. (2011). From hominoid to hominid mind: What changed and why? *Annual Review of Anthropology, 40*(1), 293–309. https://doi.org/10.1146/annurev-anthro-081309-145726

Hare, B., Addessi, E., Call, J., Tomasello, M. & Visalberghi, E. (2003). Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour, 65*(1), 131–142. https://doi.org/10.1006/anbe.2002.2017

Hobaiter, C. & Byrne, R. (2014). The meanings of chimpanzee gestures. *Current Biology 24*(14),1596-1600. https://doi.org/10.1016/j.cub.2014.05.066

Hobaiter, C., Leavens, D., & Byrne, R. (2014). Deictic gesturing in wild chimpanzees (Pan troglodytes)? Some possible cases*. Journal of Comparative Psychology, 128*(1), 82–87. https://doi.org/10.1037/a0033757

Janmaat, K., Byrne, R. & Zuberbühler, K. (2006). Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour 72*(4), 797-807. https://doi.org/10.1016/j.anbehav.2005.12.009

Keysar, B., Lin, S. & Barr, D. J. (2003). Limits on theory of mind use in adults. *Cognition 89*, 25–41. https://doi.org/10.1016/S0010-0277(03)00064-7

Krupenye, C. & Call, J. (2019). Theory of mind in animals: current and future directions. *Wiley Interdisciplinary Reviews: Cognitive Science 10*, e1503. https://doi.org/10.1002/wcs.1503

Leavens, D. (2004). Manual deixis in apes and humans. *Interaction Studies, 5*(3), 387–408. https://doi.org/10.1075/is.5.3.05lea

Liddle, B. & Nettle, D. (2006). Higher-order theory of mind and social competence in school-age children. *Journal of Cultural and Evolutionary Psychology 4*(3-4), 231–244. https://doi.org/10.1556/jcep.4.2006.3-4.3

MacLean, E., Matthews, L., Hare, B., Nunn, C., Anderson, R., Aureli, F., Brannon, E., Call, J., Drea, C., Emery, N., Haun, D., Herrmann, E., Jacobs, L., Platt, M., Rosati, A., Sandel, A., Schroepfer, K., Seed, A., Tan, J., van Schaik, C. & Wobber, V. (2012). How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition, 15*(2), 223–238. https://doi.org/10.1007/s10071-011-0448-8

McClung, J., Jentzsch, I. & Reicher, S. (2013). Group membership affects spontaneous mental representation: failure to represent the out-group in a joint action task. *PLoS ONE 8*(11): e79178. https://doi.org/10.1371/journal.pone.0079178

McGraw, W. S. & Zuberbühler, K., (2007). The monkeys of the Taï forest: an introduction. In: McGraw, W. S., Zuberbühler, K. & Noë, R. (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 1–48). Cambridge University Press, Cambridge, UK.

McGraw, W. S., Vick, E. & Daegling, J. (2011). Sex and age differences in the diet and ingestive behaviors of sooty mangabeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology 144*(1), 140–153. https://doi.org/10.1002/ajpa.21402

Mielke, A., Crockford, C. & Wittig, R. (2019). Snake alarm calls as a public good in sooty mangabeys. *Animal Behaviour 158*, 201-209. https://doi.org/10.1016/j.anbehav.2019.10.001

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A. & Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour 82*(4), 911-921. https://doi.org/10.1016/j.anbehav.2011.07.016

Neumann, C. & Zuberbühler, K. (2016). Vocal correlates of individual sooty mangabey travel speed and direction. *PeerJ 4*:e2298 https://doi.org/10.7717/peerj.2298

Papworth, S., Bose, A.-S., Barker, J., Schel, A. M., & Zuberbühler, K. (2008). Male blue monkeys alarm call in response to danger experienced by others. *Biology Letters, 4*(5), 472–475. https://doi.org/10.1098/rsbl.2008.0299

Phillips, W., Barnes, J., Mahajan, N., Yamaguchi, M. & Santos, L. (2009). Unwilling' versus 'unable': Capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science, 12*(6), 938–945. https://doi.org/10.1111/J.1467-7687.2009.00840.X

R Core Team. (2020). *R: A language and environment for statistical computing (version 4.0.3)*. R Foundation for Statistical Computing, Vienna, Austria. http://www.Rproject.org/.

Range, F. & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï national park. *American Journal of Primatology 56*(3), 137-153. https://doi.org/10.1002/ajp.1070

Range, F. & Fischer, J. 2004. The vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï National Park. *Ethology 110*(4), 301-321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Santos, L., Nissen, A. & Ferrugia, J. (2006). Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear*. Animal Behaviour, 71*(5), 1175–1181. https://doi.org/10.1016/j.anbehav.2005.10.007

Schel, A., Machanda, Z., Townsend, S., Zuberbühler, K. & Slocombe, K. (2013a). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour 86*(5), 955-965. https://doi.org/10.1016/j.anbehav.2013.08.013

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013b). Chimpanzee alarm call production meets key criteria for intentionality. *PLoS One, 8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674.

Seyfarth, R. & Cheney, D. (2010). Production, usage, and comprehension in animal vocalizations. *Brain and Language, 115* (1), pp. 92-100. https://doi.org/10.1016/j.bandl.2009.10.003

Silk, J. B., Cheney, D. L. & Seyfarth, R. M. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology 22*(5), 213-225. https://doi.org/10.1002/evan.21367

Stephan, C. & Zuberbühler, K. (2016). Persistent Females and Compliant Males Coordinate Alarm Calling in Diana Monkeys*. Current Biology, 26*(21), 2907-2912. https://doi.org/10.1016/j.cub.2016.08.033

Taylor, D., Alexander, C., Gönül, G., Clément, F., Zuberbühler, K., & Glock, H. J. (2023). Reading minds or reading scripts? De-intellectualising theory of mind. *Biological reviews of the Cambridge Philosophical Society*, *98*(6), 2028–2048. https://doi.org/10.1111/brv.12994

Tomasello, M., Call, J., Nagell, K., Olguin, R. & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates, 35*(2), 137–154. https://doi.org/10.1007/BF02382050

Tomasello, M (2010). *Why we cooperate*. Boston: Boston Review Books.

Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., Braga Goncalves, I., Burkart, J. M., Flower, T., Gaunet, F., Glock, H. J., Gruber, T., Jansen, D. A. W. A. M., Liebal, K., Linke, A., Miklosi, A., Moore, R., van Schaik, C. P., Stoll, S., Vail, A., Waller, B. M., Wild, M., Zuberbühler, K., & Manser, M. B. (2017). Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals. *Biological Reviews, 92*(3), 1427-1433. https://doi.org/10.1111/brv.12289

Whitmore, T.C. 1990. *An Introduction to Tropical Rain Forests*. Clarendon Press, Oxford.

Wich, S. & de Vries, H. (2006). Male monkeys remember which group members have given alarm calls. *Proceedings of the Royal Society B-Biological Sciences, 273*(1587), 735-740. https://doi.org/10.1098/rspb.2005.3320

Wimmer, H. & Perner, J. (1983). Beliefs about beliefs: representation and constraining function of wrong beliefs in young children’s understanding of deception. *Cognition 13*, 103–128. https://doi.org/10.1016/0010-0277(83)90004-5

Worden, R. (1996). Primate social intelligence. *Cognitive Science 20*(4):579–616. https://doi.org/10.1016/S0364-0213(99)80015-9

Zuberbühler, K. (2018). Intentional communication in primates. *Travaux neuchâtelois de linguistique, 68*, 69-75.
http://www.unine.ch/files/live/sites/tranel/files/Tranel/68/69-75_Zuberbuehler.pdf

Zuberbühler, K., & Wittig, R. M. (2011). Field experiments with nonhuman primates: a tutorial. In: J. M. Setchell & D. J. Curtis (Eds.), *Field and Laboratory Methods in Primatology: A Practical Guide* (pp. 207-224). Cambridge University Press.

Zuberbühler, K. & Gomez, J. (2018). Primate intentional communication. In: Callan, H. (Ed.), *International encyclopedia of anthropology*. Wiley, London, UK.
https://doi.org/10.1002/9781118924396

CHAPTER 3. THE EVOLUTION OF FOOD CALLS - VOCAL BEHAVIOUR OF SOOTY MANGABEYS IN THE PRESENCE OF FOOD

Results presented in this chapter have been published in:

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022). The Evolution of Food Calls: Vocal Behaviour of Sooty Mangabeys in the Presence of Food. *Frontiers in Psychology*, 3663. https://doi.org/10.3389/fpsyg.2022.897318

The dataset, and the scripts used in this study have been published in:

https://doi.org/10.6084/m9.figshare.30251977

ABSTRACT

The two main theories of food-associated calls in animals propose functions either in cooperative recruitment or competitive spacing. However, not all social animals produce food calls and it is largely unclear under what circumstances this call type evolves. Sooty mangabeys (*Cercocebus atys*) do not have food calls, but they frequently produce grunts during foraging, their most common vocalisation. We found that grunt rates were significantly higher when subjects were foraging in the group's periphery and with small audiences, in line with the cooperative recruitment hypothesis. In a subsequent field experiment we presented highly desired food items and found that discovering individuals called, unless harassed by competitors, but that the calls never attracted others, confirming that the grunts do not convey any information referential to food. Our data thus suggest that the evolution of cooperative food calling is a two-step process, starting with increased motivation to vocalise in the feeding context, followed by the evolution of acoustic variants derived from context-general contact calls. This evolutionary transition may only occur in species that feed on clumped, high-quality resources where social feeding is competitive, a condition not met in sooty mangabeys.

INTRODUCTION

Food-associated calls have been reported in many socially living avian and mammalian species (Clay, Smith & Blumstein, 2012), produced when individuals find food or during feeding (Clay et al., 2012; Elowson, Tannenbaum & Snowdon, 1991; Slocombe & Zuberbühler, 2006; Valone, 1996). The behaviour is interesting because it raises basic questions about signal evolution and call meaning, as well as the evolution of cooperative behaviour more generally. For example, one theoretically relevant line of enquiry has focused on whether food calls qualify as 'functionally referential' signals, that is, whether they inform others about a receiver-relevant event experienced by the caller (e.g. Di Bitetti, 2003; Evans & Evans, 1999; Fedurek & Slocombe, 2013; Gros-Louis, 2004; Hauser & Marler, 1993a, b; Kalan, Mundry & Boesch, 2015; Kitzmann & Caine, 2009; Schel, Machanda, Townsend, Zuberbühler & Slocombe, 2013; Slocombe & Zuberbühler, 2006), a debate also relevant for questions about animal social awareness and cognitive precursors to language (Fitch, 2005; Tomasello, 2008).

Despite much cross-disciplinary interest, however, comparatively little is known about the evolutionary emergence of food-associated calls in animal communication. Importantly, not all social species produce food-associated calls but, in species where the behaviour has been reported, two main functions have been proposed. A first one states that calls advertise a food resource to other group members, a seemingly altruistic act and a form of food sharing. This is largely because food-associated calls tend to attract others while there appears to be no direct benefit to the caller (Clay et al., 2012; Fedurek & Slocombe, 2013). This hypothesis requires either evidence for enhanced inclusive fitness (Hauser & Marler, 1993 a, 1993b; Judd & Sherman, 1996), for instance via reduced predation risk or vigilance costs (Clay et al., 2012; birds: Sridhar, Beauchamp & Shanker, 2009; red-bellied tamarins: Caine, Addington & Windfelder, 1995; greater spear-nosed bats: Wilkinson& Boughman, 1998). Other direct benefits may be in terms of increased foraging success. For example, by attracting conspecifics some species of flocking birds increase the chance of tracking insect swarms (Brown, Brown & Shaffer, 1991), while ravens and bats attract others to cooperatively defend a food resource against competitors (Heinrich & Marzluff, 1991; Wilkinson & Boughman, 1998). Further benefits concern a lowered risk of conflict by increasing predictability (Fedurek & Slocombe, 2013) and this may even lead to reproductive advantages for a caller (Dahlin, Balda & Slobodchikoff, 2005; Evans & Marler, 1994; Marler, Dufty & Pickert, 1986; Pizzari, 2003; Van Krunkelsven, Dupain, Van Elsacker & Verheyen, 1996). As always, several functions may be acting jointly. In chimpanzees, for example, it has been argued that the production of food-associated calls raises a caller's social status and also secures cohesion with the rest of the travelling party (Slocombe & Zuberbühler, 2006). Other studies have shown that advertising food is not necessarily altruistic, for example, if the benefits that arise from advertising food are a by-product of others' selfish behaviours (Connor, 1995). In bottlenose dolphins, for example, there is evidence that role-specialised foraging behaviour is a cooperative by-product mutualism, where participants obtain benefits as a result of the actions of others (Gazda et al., 2005; Gazda, 2016).

The second main hypothesis argues that food-associated calls function in the opposite way, that is, to repel group members from the food source by signalling ownership and an intention to defend it (Boinski & Campbell, 1996; Caine et al., 1995; Gros-Louis, 2004). White-faced capuchins (*Cebus capucinus*), for example, produce 'huhs' when approaching a food patch, or when already feeding and a higher-ranking individual approaches them.

Subjects are less likely to receive aggression from higher-ranking individuals when calling than when remaining silent (Gros-Louis, 2004). A repelling function has also been proposed for the 'coo' calls of rhesus macaques (*Macaca mulatta*; Hauser & Marler, 1993b) and 'who' calls in ravens (*Corvus corax*) (Bugnyar, Kijne & Kotrschal, 2001). However, it has also been shown that, depending on their age and sex, ravens can use food-associated calls to advertise feeding opportunities (Sierro et al., 2019). In another study, pied babblers remained distanced from speakers playing close-calls and increased their calling rate while feeding in larger groups, indicating that spacing was crucial for foraging efficiency (Radford & Ridley, 2008). Food-associated calls, under these hypotheses, function to signal ownership, motivation to defend and keep other group members at distance, and not to inform them about food, although this naturally occurs as an unintended by-product.

Although both hypotheses predict opposite underlying motivations, they conceptualise food-associated calls as specifically evolved signals to help individuals optimising the cost/benefit ratio when dealing with food. Despite the obvious advantage of possessing such a signal, it is unclear why some species evolved them and others did not. For example, as mentioned earlier, macaques often give 'coo' calls in response to food (Hauser & Marler 1993a, Mitani, 1986), but there are no comparable records for baboons (*Papio spp*; Silk, Seyfarth & Cheney 2016), vervet monkeys (*Chlorocebus pygerythrus*; Mercier et al., 2017) or sooty mangabeys (*Cercocebus atys*; Neumann & Zuberbühler, 2016; Range & Fischer, 2004), despite the fact that they live in somewhat similar societies with presumably similar socio-ecological pressures. For example, sooty mangabeys are terrestrial and live in the same forest habitat as chimpanzees and have a similar social structure as rhesus macaques or white-faced capuchins (multi-male, multi-female groups with some fission-fusion dynamics), species that all produce food-associated calls.

We are not aware of any comprehensive theory that explains why food-associated calls have evolved in some species but not others. An important finding is that, in some species, the acoustic structure of food-associated calls is often similar to the acoustic structures of calls given during close social interactions that do not involve food, usually termed contact or greeting calls. For example, in chimpanzees, the acoustic structure of food-elicited 'rough-grunts' (Slocombe & Zuberbühler, 2006) is very similar to the acoustic structure of 'pant-grunts', which are given by lower ranking individuals when a social interaction with a higher ranking one is likely to occur (i.e., 'greeting calls', Laporte & Zuberbühler, 2010). Another relevant finding in bonobos is that food-elicited 'peeps' are also given in non-feeding contexts, such as during grooming, traveling, foraging, or when encountering others, with no obvious acoustic differences (Clay, Archbold & Zuberbühler, 2015). Therefore, it is likely that acoustically distinct food-associated calls have evolved from more general close-range and individually distinct social calls that draw attention to the caller, while the underlying social functions are similar. Food calls, in other words, may have emerged within the broader category of 'close-range' vocalizations by an evolutionary process of acoustic modification and functional specialisation.

In this study, we explore the vocal behaviour during foraging in sooty mangabeys, a forest-dwelling, terrestrial primate that lives in groups of up to 100 individuals, with large group spread. Individuals are often visually isolated from most other group members and spend much time foraging through the forest leaf-litter in search for insects and plant matter, such as the fallen fruits of *Anthonotha spp*., *Saccoglotis gabonensis* and *Dialium spp*.

(Janmaat, Byrne & Zuberbühler, 2006; McGraw, Vick & Daegling, 2011; Range & Noë, 2002). Occasionally, they climb into trees to pick fruits or they consume high-quality but rare foods on the ground, such as eggs, termites, or mushrooms (Range & Noë, 2002; Rödel, Range, Seppänen, Noë, 2002). Individuals produce two close-range social calls during foraging, 'twitters' and 'grunts', but also in a range of other situations, including travelling (Neumann & Zuberbühler, 2016) or greeting other group members (Range & Fischer, 2004), but acoustically distinct food-associated calls have not been documented in this species despite years of observation (Neumann & Zuberbühler, 2016; Range & Fischer, 2004).

Nonetheless, it has been observed that, on rare occasions, when sooty mangabeys find highly-valued foods, they can produce calls that appear to instantly attract others to the location (Janmaat et al., 2006, FQ personal observation). The call is very different from the grunts and strongly resembles vocalisations uttered during fights, a situation that generally attracts bystanders, suggesting that callers anticipate physical aggression when in possession of high-valued foods. Importantly, individuals do not usually call when finding mushrooms, termites, or other high-quality foods, suggesting that the default response is to remain silent.

Our first question concerned the factors that determine grunt production, the most common vocalisation in this species, during the main foraging activity, forest-floor browsing. Our basic theory was that the grunts are the evolutionary raw material from which food calls would evolve. To test this, we predicted that, although mangabeys do not possess food calls, grunt rates should be higher inside food patches than elsewhere, even when not engaged in directed social interactions. We also predicted that, if calling was driven by food competition, call rates should be positively related with the number of potential competitors nearby. Alternatively, if calling was driven by cooperative recruitment rather than competitive spacing, call rates should be negatively related to audience size.

Our second question concerned the factors governing vocal behaviour when finding rare but highly valuable foods, a situation when food calling would be particularly advantageous. Since natural encounters with high quality foods were very infrequent, we carried out a field experiment, during which we let subjects individually encounter eggs in the presence of different audiences. Again, we predicted that if calling was driven by competition, subjects should refrain from calling if no competitors were nearby and the opposite if calling was the product of a cooperative motivation.

METHODS

Study Site and Subjects

The study was conducted in Taï National Park in South-western Ivory Coast (5°50'N, 7°21'W), the largest remaining major block of primary forest in West Africa with approximately 454,000 ha of continuous cover. With a mean annual temperature of 24°C, a mean annual rainfall of 1,875 mm (average of 2012–2015; data: Taï Monkey Project) and a distinct dry season in December–January, the park is classified as a 'tropical moist' forest (Whitmore, 1990). The study area of about 7 km^2 was situated near the western border of the park, approximately 20 km southeast of the township Taï. The study group's home range contained a 2-km^2 core area where several monkey species had been studied since 1991 as part of a long-term research project (McGraw & Zuberbühler, 2007). The study group has been under constant observation since 1997 and is well habituated to human observers (Quintero et al., 2022; Range & Noë, 2002). Data collection was mainly during focal animal follows from dawn to dusk over a period of 24 months during different periods: January to May 2013, August 2013 to July 2014 and January to September 2015. See Table 2 for details on experimental trials. During the study period the group size was around 80 individuals.

Observational data

Sooty mangabeys produce grunts and twitters during social interactions. The calls are structurally different, but not much is known about their specific functions. Although both calls appear to be given in the same circumstances, we decided to restrict the analyses to grunts only (observational data), mainly because twitters were far less common, the topic of future research. If a grunt was produced during a direct social interaction, that is, when one individual approached another to less than 1m (see Bernstein, 1971; Range & Noë, 2002), we excluded that event from further analyses, assuming that, in these situations, the calls had a contextually-defined specific social function, such as an invitation for an affiliative interaction (Appendix 2). Hence, our dataset consisted of socially undirected calls only, i.e., when the caller was more than 1m away from its nearest neighbour. We then scored the subject's (a) activity (foraging: y/n), (b) location (inside a food patch: y/n) and (c) audience size (number of neighbours within 10m, the average range of maximum visibility). We predicted that if food calls had a cooperative function, call rates should be high during foraging, inside food patches and with small audiences.

Data collection was in the form of focal animal and instantaneous sampling (Altmann, 1974) on N=33 adult individuals (5 males and 28 females). Focal samples were 1 hour long and individuals were not sampled twice during the same day. A total of 371 hours of focal sampling were carried out on all individuals. During focal animal sampling, data collection included details of each social interaction and calling event that involved the focal animal. Data from social interactions were used for establishing the dominance hierarchy and social bonds between the individuals. The complete list of behaviours used and a full description for these calculations are described in detail in Quintero *et al*. (2022). Every 15min we collected an instantaneous sample, which also included information on the general activity of the focal individual. We analysed a total of N= 1,058 samples collected in time blocks of 15min. Call discrimination was based on the classification by Range & Fischer (2004). Grunts are short (102-188ms), low-pitched vocalizations, the most common call type given by sooty mangabeys (Range & Fischer, 2004). When a grunt was produced, we recorded the same variables as the ones recorded every 15min to be able to compare calling vs no calling.

Experimental data

To test whether sooty mangabeys showed elevated call rates when encountering high quality foods, we experimentally provided high-quality food items (chicken eggs) to a number of subjects in controlled ways (showing the eggs when alone or with neighbours). In each trial, we determined the identities of individuals around the focal animal and documented the subject's reaction when finding the food. We used chicken eggs due to their similarity with guinea fowl eggs (*Agelastes meleagrides*), which can be found naturally in the forest. The eggs were boiled to avoid transmission of parasites and placed in the projected travel path of a subject, such that it was impossible to form an association between the eggs and the human observers.

Statistical Analyses

For the observational data, we used generalized linear mixed models with binomial error structure to investigate the variation in call production. We divided each focal sampling session into time-blocks of 15min. Within each time block we scored whether the focal animal produced at least one grunt (binary, hereafter: call) as the response variable. As mentioned, we only took calls produced in non-directed situations into account. Calls given during grooming, greeting or any other close physical interaction were considered to be part of targeted social interaction. As predictor variables, we included the sex of the focal animal (binary, hereafter: sex), whether or not it was inside a food patch (binary, hereafter: patch type; Range & Noë, 2002), the number of individuals within 10m (numeric, hereafter: neighbours), the general activity of the focal animal (Binary: foraging or not; hereafter: activity), the presence or absence of socially important individual ('friends'; defined by a DSI score >1; binary, hereafter: friend; Silk, Cheney & Seyfarth, 2013). For calculating the DSI we used the following behaviours as variables: 'approach', 'inspection', 'presenting groom', 'contact', 'groom', 'handle baby' and 'hug'. High values of DSI (above 1) indicated for example, regular grooming partners, while low values of DSI (below 1) indicated dyads that rarely groomed, amongst other behaviours. The social status of the focal individual was assessed by its Elo-rating score (numeric, hereafter: Ranking; Neumann *et al.*, 2011). Elo-rating scores varied from 1,542 for the highest ranking individual (Norm, the dominant male) to 568 (Tatiana, the lowest ranking female). Finally, the position within the group was scored as central or peripheral (binary, hereafter: position; Range & Noë, 2002). Observer ID was also included on the models as a fixed factor to control for possible observer differences in data collection (N=2 observers. Binary, hereafter: observer).

In a first model, we addressed the possibility that the number of neighbours affected calling when inside but not outside a food patch (patch * neighbours interaction). We also found it plausible that individuals with high social status were more likely to vocalize than individuals with low social status, but again only inside a food patch (ranking * patch interaction). Third, we addressed the possibility that any status effect on calling might be modulated by the number of neighbours (ranking * neighbours interaction), fourth, we addressed the possibility that the number of neighbours only affected calling when foraging (activity * neighbours interaction), five, we addressed the possibility that the number of neighbours affected calling when in the centre of the group or in the periphery (position * neighbours) and six, we addressed the possibility that the position in the group affected calling when inside, but not outside a food patch (position * patch).

We included random intercepts for focal subject ID and date of observation and added uncorrelated random slopes. Specifically, for focal ID, we included random slopes for all fixed terms in the model that varied within individuals and that represented our main variables of interest (patch, number of neighbours, activity). We did not include random slopes for Elo-rating because we used only Elo-ratings at the end of the study period, i.e., ratings did not change within individuals.

We then built an "informed null model", which comprised all fixed terms except those that included the three main predictors. The random structure was identical to the full model and we then compared these models with a likelihood ratio test (Dobson, 2002). If the comparison of full and null model revealed a significant difference, we explored the full model with regards to the predictors of interest (i.e., those in the full but not the null model).

Once we assessed the significance of the full model, we tested the interactions. We used R version 3.3.3 (R Core Team, 2017) for the analyses above mentioned, with the glmer function, 'lme4' package (Bates, Mächler, Bolker & Walker, 2015) for the GLMMs.

For the experiments, we used generalized linear mixed models with binomial error structure to investigate whether the subjects did or did not call when finding the eggs. For every trial we scored whether the focal animal produced a grunt or a twitter (binary, hereafter: call) as the response variable. As predictor variables, we included the number of individuals within 10m (numeric, hereafter: neighbours), the time in seconds that it took for another individual to approach the focal animal (numeric, hereafter: time 1st arrival) and whether or not the focal individual was chased after finding the egg (binary, hereafter: chased). We also included random intercepts for focal subject ID. We used conditional inference trees (Hothorn, Hornik & Zeileis, 2006) to select the most significant variables.

Ethical note

The experiments replicated natural events (guinea fowl eggs resemble chicken eggs) and we did not interfere with the animals' normal daily routines, in line with the Animal Behaviour Society Guidelines for the Use of Animals in Research. Research permission and ethical clearance were granted by the Ministère de la Recherche Scientifique et Technique de Côte d'Ivoire.

RESULTS

Foraging behaviour (observational data)

We analysed a total of N= 1,063 samples (time blocks of 15min) collected from 33 individuals during 71 days of observation to determine the main factors influencing call production near food patches. The full model was significantly different from the null model (χ^2=33.87, df=11, p=0.0003). We thus proceeded to explore it with regards to whether individuals were inside or outside a food patch, activity and number of neighbours. We removed two of the four interactions as they were non-significant. These changes resulted in the final model (table 3.1), which indicated that sooty mangabeys were more likely to produce grunts in a 15min sampling period if they were foraging (beta±SE=0.61±0.231, p=0.008; fig. 3.2), if they had fewer neighbours (beta±SE=-0.17±0.07, p=0.026; Fig. 3.1), if they were in the periphery of the group (beta±SE=0.69±0.2, p=0.001) and, finally, if there were with fewer neighbours while being in the periphery of the group (beta±SE=0.292±0.116, p=0.012).

Table 3.1. Results of the final model for the observational data

Variables	**Estimate**	**SE**	**Z**	**Pr(>|z|)**
(Intercept)	-3.541	0.667	-5.309	0.000
Sex	0.375	0.607	0.617	0.536
Observer	0.500	0.330	1.515	0.129
Forage	0.608	0.231	2.630	**0.008**
Friend	0.116	0.267	0.437	0.662
Neighbours	-0.174	0.078	-2.214	**0.026**
Inside Food Patch	0.394	0.310	1.269	0.204
Ranking	0.092	0.187	0.493	0.622
Position	0.695	0.207	3.348	**0.001**
Neigh * Position	0.292	0.116	2.503	**0.012**

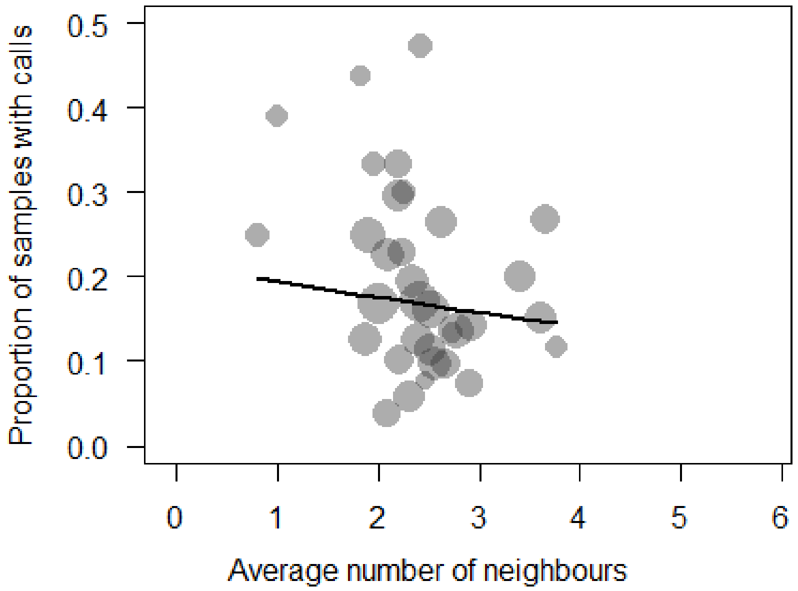

Figure 3.1. Probability of call production by a focal animal expressed as a function of the number of neighbours within 10m. (Circle sizes are proportional to the number of samples per individual).

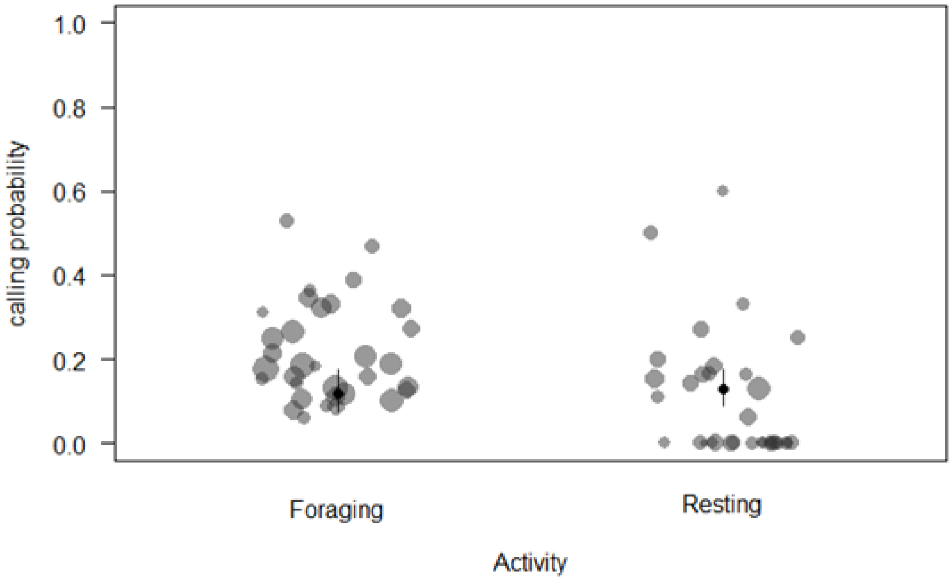

Figure 3.2. Probability of call production by a focal animal during two main daily activities (circle sizes proportional to the number of samples per individual).

Encountering rare foods (experimental data)

We conducted N= 23 experimental trials during which we presented a single chicken egg to 11 focal individuals. Subjects called on 9 occasions when others approached (less than 5m) to them and only on 3 occasions when they were alone. Subjects produced calls in 12 of 23 trials (52.2%). In N=5 further trials, we offered a large number of eggs (>5), thus creating a situation where high-valuable food could not be monopolised. No subject ever vocalised in these situations (0.0%). Importantly, calls produced after finding food did not lead to approaches by others. In all but one occasion, when the subjects were chased after finding food, the finders responded by climbing about 10m into a tree to escape and eat the eggs alone. As expected with only one egg, there was no evidence for food sharing or tolerance. Other individuals sometimes stayed close to eat pieces of eggshell dropped by the finder, or to lick leaves covered with egg leftovers.

We recorded all social interactions and found that call production was best explained by whether or not the subject experienced physical aggression (i.e., being chased). Using a conditional inference tree we found that calling was only determined by whether or not the subject was chased after finding the food. Specifically, after removing the variable 'time 1st arrival', the resulting model (table 3.2) indicated that calling only occurred in cases where the focal animal that found the food was not chased (beta±SE= -4.41±1.823, p=0.015; fig. 3.3). Audience size was not significant (beta±SE= -1.37±0.82, p=0.096).

Table 3.2. Results of the final model for the food experiments

Variables	Estimate	SE	Z	Pr(>|z|)
(Intercept)	4.016	1.933	2.078	0.037
Chased	-4.4174	1.823	-2.422	**0.015**
Neighbours	-1.3793	0.8287	-1.664	0.096

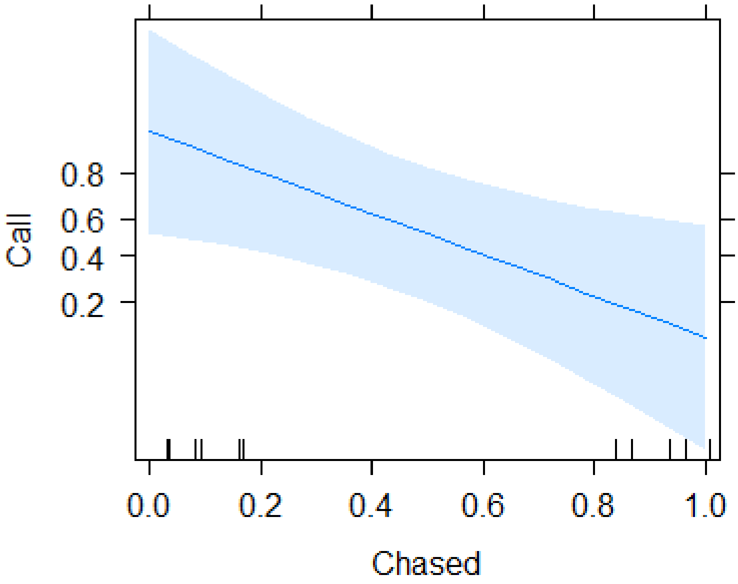

Figure 3.3. Probability of call production by the subject as a function of whether it was chased or not.

DISCUSSION

We were interested in how a social primate that does not possess an acoustically distinct food call uses its vocal behaviour when encountering food, particularly in relation to the two main theories of animal food calls, which make opposite predictions regarding the role of the audience. The cooperative recruitment hypothesis predicts that subjects discovering high-valued foods should call more if alone compared to when surrounded by many of individuals. The competitive hypothesis predicts the opposite, i.e., subjects should call more if in the presence of competitors that are likely to compete over access.

From the observational data, the variables that accounted for most of the variation in calling rates were the number of neighbours, the caller's own activity and whether the caller was inside a food patch (Table 3.1). We also found an interaction between the position in the group and the number of neighbours, with subjects more likely to call in the periphery and with small audiences. These findings are in line with the cooperative recruitment hypothesis and do not suggest that calls were uttered as a means to compete over food access. Sooty mangabeys usually forage by browsing through the forest leaf litter of the forest floor, which creates little competition between individuals and only occasionally climbing into trees to harvest fruits or flowers. In the experiments, involving a high-valued food source, we found the same pattern insofar as subjects also vocalised regularly when discovering the food, provided that they were not chased by others (table 3.2, fig. 3.3).

Our data suggest that sooty mangabeys, a species with no food calls, uses its close-range social calls in ways similar to how a cooperatively food-calling species uses its acoustically distinct food calls. If correct, this suggests that 'grunts', the most common call type of sooty mangabeys, represent an ancestral condition in primate vocal evolution, in which food calls and social calls have not diverged acoustically over evolutionary time; something that did happened in chimpanzees, bonobos, and various capuchin monkey vocal evolution. Instead, mangabeys produce the same call type in feeding and non-feeding contexts, although call production patterns are in line with the prediction of the cooperative hypotheses of food calling. In the experiments, we did not find evidence that calls attracted others to the food although, as always with negative evidence, we remain cautious with drawing firm conclusions.

In species with acoustically distinct food calls, the general finding is that these calls are more likely produced to high-valuable foods, such as ripe fruit (chimpanzees: Fedurek & Slocombe, 2013; White-face capuchins: Boinski & Campbell, 1996), which are usually consumed in distinct feeding bouts, something that sooty mangabeys rarely do. Another finding in species with food-associated calls is that call production is governed by the presence of others, usually at the onset or during a feeding bout. As stated, sooty mangabeys do not have distinct feeding bouts, but spend most of the day browsing the forest floor to feed on low-quality foods (Janmaat et al., 2006; McGraw et al., 2011). Here, we found increased call rates when foraging (as opposed to moving or resting; fig 3.2, table 3.1). We take this finding as supporting the general view that the evolution of food calls may have taken place as an acoustic diversification of more general contact calls, provided it was especially beneficial for a caller to do so when foraging.

As mentioned, amongst the two main functional theories of food calling our data are more in line with the cooperative recruitment theory than the competitive spacing theory. Subjects in the observational dataset were more likely to call with smaller audiences (fig. 3.1, table 3.1), in line with a function to attract a manageable number of co-feeders in species that do produce acoustically distinct calls. In the experiments, they called more when they were not chased, regardless of the number of neighbours, again suggesting that calls are not used to competitively secure access. Nonetheless, we would not expect individuals to produce food calls (to attract or to repel others) when feeding on ordinary foods, such as *Anthonotha spp.*, *Saccoglotis gabonensis* or *Dialium spp.*, but when finding valuable foods. In line with this, we found that call rates were higher when foraging, with smaller audiences and when in the periphery, suggesting that grunts in this species function as a context-unspecific contact call. Unfortunately, naturalistic data on encounters with valuable foods, such as mushrooms or termites, were scarce which prevented a systematic analysis. In the experiments, we found that individuals called significantly more when they were not chased regardless of the number of neighbours and, surprisingly these calls never attracted other individuals. This finding is even more striking when taking into account that the eggs were monopolisable in most of the experiments, yet individuals never produced any call when the number of eggs was more than two.

We found no interactions between some of the main variables, particularly between audience size and being inside a food patch, suggesting that calling patterns were similar inside and outside food patches but augmented by the presence of food. A likely reason for this generalised function of sooty mangabey grunts is that they might function to seek contact (Range & Fischer, 2004), a pattern that also emerged during the experiments. Here, subjects called either directly in response to finding the food or delayed when approached by another individual, provided there was no physical aggression, suggesting callers attempted to establish social contact but, since this did not trigger immediate approaches, listeners were probably not able to make inferences about the event. This is different, for example, in chimpanzees where pant grunts (contact calls) are acoustically similar from rough grunts (food calls) (Slocombe & Zuberbühler, 2006; Laporte & Zuberbühler, 2010).

Evolutionary transitions to food calls

Why do sooty mangabeys produce calls to food in ways that would make them suitable as referential signals, but have not evolved the necessary context-specific acoustic features? Our theory is that a species' dietary habits and niche specialisation are the main evolutionary driver of acoustically distinct food calls. Mangabeys forage by ingesting large amounts of low-quality foods, mainly collected on the forest floor, while monopolisable high-value foods are rarely consumed, in contrast to chimpanzees and other primates that specialised on high-quality fruits. Most likely, signalling the discovery of low-quality foods is of no adaptive significance, while individuals are almost always surrounded by other group members, hereby removing two main sources of call evolution. Announcing ownership is equally futile, as the food is abundant and found in large patches that cannot be monopolized (McGraw et al. 2011; Range & Noë, 2002), again in contrast to fruit trees where feeding space and availability is limited. Some social structures, such as matrilineally-based hierarchies with stable dominance relations, may further remove the potential for conflicts, as it is the case in mangabeys but not chimpanzees.

In conclusion, although sooty mangabeys call when finding high-value foods, they do so not because they want to inform others or to claim ownership, but because of a general motivation for social cohesion, allowing listeners to know the caller's whereabouts (Schamberg, Wittig & Crockford, 2018) and reduce the risk of group fission, which is always high when individuals stop to feed, a situation also created by our experiments. Nevertheless, calling patterns were identical to species that cooperatively denote food sources, suggesting that sooty mangabeys possess calling patterns that are suitable for the evolution of food-specific vocalisations.

REFERENCES

Altmann J. (1974). Observational study of behaviour: sampling methods. *Behaviour 49*(3), 227–267. https://doi.org/10.1163/156853974X00534

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software 67*(1), 1-48. http://dx.doi.org/10.18637/jss.v067.i01

Bernstein, I.S. (1971). The influence of introductory techniques on the formation of captive mangabey groups. *Primates 12*(1), 33–44. https://doi.org/10.1007/BF01730380

Brown, C. R., Brown, M. B. & Shaffer, M. L. (1991). Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour 42*(4), 551-564. https://doi.org/10.1016/S0003-3472(05)80239-8

Boinski, S. & Campbell, A. F. (1996). The huh vocalization of white-faced capuchins: a spacing call disguised as a food call? *Ethology 102*(6), 826-840. https://doi.org/10.1111/j.1439-0310.1996.tb01204.x

Bugnyar, T., Kijne, M. & Kotrschal, K. (2001). Food calling in ravens: are yells referential signals? *Animal Behaviour 61*(5), 949-958. https://doi.org/10.1006/anbe.2000.1668

Caine, N. G., Addington, R. L. & Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour 50*(1), 53-60. https://doi.org/10.1006/anbe.1995.0220

Clay, Z., Smith, C.L. & Blumstein, D.T. (2012). Food-associated vocalizations in mammals and birds: what do these calls really mean? *Animal Behaviour 83*(2), 323–330. https://doi.org/10.1016/j.anbehav.2011.12.008

Clay, Z., Archbold, J. & Zuberbühler, K. (2015). Functional flexibility in wild bonobo vocal behaviour. *Peer J3*:e1124. https://doi.org/10.7717/peerj.1124

Connor, R. (1995). The benefits of mutualism: a conceptual framework. *Biological Reviews 70*:427-57. https://doi.org/10.1111/j.1469-185X.1995.tb01196.x

Dahlin, C. R., Balda, R. P. & Slobodchikoff, C. (2005). Food, audience and sex effects on pinyon jay (*Gymnorhinus cyanocephalus*) communication. *Behavioural Processes 68*(1), 25-39. http://dx.doi.org/10.1016/j.beproc.2004.09.003

Di Bitetti, M. S. (2003). Food associated calls of tufted capuchin monkeys (*Cebus apella*) are functionally referential signals. *Behaviour 140*(5), 565-592. http://dx.doi.org/10.1163/156853903322149441

Dobson, A. J. (2002). *An introduction to generalized linear models*. Boca Raton: Chapman & Hall/CRC.

Elowson, A.M., Tannenbaum, P.L. & Snowdon, C.T. (1991). Food associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour 42*(6), 931–936. https://doi.org/10.1016/S0003-3472(05)80145-9

Evans, C. S. & Marler, P. (1994). Food calling and audience effects in male chickens, *Gallus gallus*: their relationships to food availability, courtship and social facilitation. *Animal Behaviour 47*(5), 1159-1170. https://doi.org/10.1006/anbe.1994.1154

Evans, C. S., & Evans, L. (1999). Chicken food calls are functionally referential. *Animal Behaviour 58*(2), 307-319. https://doi.org/10.1006/anbe.1999.1143

Fedurek, P. & Slocombe, K. (2013). The social function of food-associated calls in male chimpanzees. *American Journal of Primatology 75*(7), 726–739. https://doi.org/10.1002/ajp.22122

Fitch, W. T. 2005. The evolution of language: a comparative review. *Biology and Philosophy 20*:193-230. https://doi.org/10.1007/s10539-005-5597-1

Gazda, S., Connor R., Edgar R. & Cox, F. (2005). A division of labor with role specialization in group–hunting bottlenose dolphins (Tursiops truncatus) off Cedar Key, Florida. *Proceedings of the Royal Society B: Biological Sciences* 272:135-40 https://doi.org/10.1098%2Frspb.2004.2937

Gazda, S. (2016). Driver- barrier feeding behavior in bottlenose dolphins (Tursiops truncatus): New insights from a longitudinal study. *Marine Mammal Science 32*:1152-60 https://doi.org/10.1111/mms.12314

Gros-Louis, J. (2004). The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. *Animal Behaviour 67*(3), 431-440. https://doi.org/10.1016/j.anbehav.2003.04.009

Hauser, M. D. & Marler, P. (1993a). Food-associated calls in rhesus macaques (*Macaca mulatta*). 1. Socioecological factors. *Behavioral Ecology 4*(3), 194-205. https://doi.org/10.1093/beheco/4.3.194

Hauser, M. D. & Marler, P. (1993b). Food-associated calls in rhesus macaques (*Macaca mulatta*). 2. Costs and benefits of call production and suppression. *Behavioral Ecology 4*(3), 206-212. https://doi.org/10.1093/beheco/4.3.206

Heinrich, B. & Marzluff, J. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology, 28*(1), 13-21. https://doi.org/10.1007/BF00172134

Hothorn, T., Hornik, K. & Zeileis, A. (2006). Unbiased Recursive Partitioning: A Conditional Inference Framework. *Journal of Computational and Graphical Statistics, 15*(3), 651–674. https://doi.org/10.1198/106186006X133933.

Janmaat, K. R. L., Byrne, R. W. & Zuberbühler, K. (2006). Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour 72*(4), 797-807. https://doi.org/10.1016/j.anbehav.2005.12.009

Judd, T. & Sherman, P. (1996). Naked mole-rats recruit colony mates to food sources. *Animal Behaviour, 52*(5), 957-969. https://doi.org/10.1006/anbe.1996.0244

Kalan, A. K., Mundry, R., Boesch, C. (2015). Wild chimpanzees modify food call structure with respect to tree size for a particular fruit species. *Animal Behaviour 101*:1-9. https://doi.org/10.1016/j.anbehav.2014.12.011

Kitzmann, C. & Caine, N. (2009). Marmoset (*Callithrix geoffroyi*) food-associated calls are functionally referential. *Ethology 115*(5), 439-448. https://doi.org/10.1111/j.1439-0310.2009.01622.x

Laporte, M.N. & Zuberbühler K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour 80*(3), 467–473. https://doi.org/10.1016/j.anbehav.2010.06.005

Marler, P., Dufty, A. & Pickert, R. (1986). Vocal communication in the domestic chicken: I. Does a sender communicate information about the quality of a food referent to a receiver? *Animal Behaviour 34*(1), 188-193. https://doi.org/10.1016/0003-3472(86)90022-9

McGraw, W. S. & Zuberbühler, K., (2007). The monkeys of the Taï forest: an introduction. In: McGraw, W. S., Zuberbühler, K. & Noë, R. (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 1–48). Cambridge University Press, Cambridge, UK.

McGraw W. S., Vick A. E. & Daegling D. J. (2011). Sex and age differences in the diet and ingestive behaviors of sooty mangabeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology 144*(1), 140–153. https://doi.org/10.1002/ajpa.21402

Mercier, S., Neumann, C., van de Waal, E., Chollet, E., Meric de Bellefon, J., Zuberbühler, K. (2017). Vervet monkeys greet adult males during high-risk situations. *Animal Behaviour 132*:229–245. https://doi.org/10.1016/j.anbehav.2017.07.021

Mitani M. (1986). Voiceprint identification and its application to sociological studies of wild Japanese monkeys (*Macaca fuscata yakui*). *Primates* 27(4), 397-412. https://doi.org/10.1007/BF02381886

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A. & Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour 82*(4), 911-921. http://dx.doi.org/10.1016/j.anbehav.2011.07.016

Neumann, C. & Zuberbühler, K. (2016). Vocal correlates of individual sooty mangabey travel speed and direction. *PeerJ 4*:e2298 https://doi.org/10.7717/peerj.2298

Pizzari, T. (2003). Food, vigilance, and sperm: the role of male direct benefits in the evolution of female preference in a polygamous bird. *Behavioral Ecology 14*(5), 593-601. https://doi.org/10.1093/beheco/arg048

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022). An audience effect in sooty mangabey alarm calling. *Frontiers of Psychology 13*:816744 https://doi.org/10.3389%2Ffpsyg.2022.816744

R Core Team. (2017). *R: A language and environment for statistical computing (version 3.3.3)*. R Foundation for Statistical Computing, Vienna, Austria. http://www.Rproject.org/.

Radford, A. & Ridley, A. (2008). Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Animal Behaviour 75*(2), 519-527. https://doi.org/10.1016/j.anbehav.2007.05.016

Range, F. & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï national park. *American Journal of Primatology 56*(3), 137-153. https://doi.org/10.1002/ajp.1070

Range, F. & Fischer, J. 2004. The vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï National Park. *Ethology 110*(4), 301-321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Rödel, M., Range, F., Seppänen, J., Noë, R. (2002). Caviar in the rain forest: monkeys as frog-spawn predators in Taï National Park, Ivory Coast. *Journal of Tropical Ecology 18*(2), 289–294. https://doi.org/10.1017/S0266467402002195

Schamberg, I., Wittig, R., Crockford, C. (2018). Call type signals caller goal: a new take on ultimate and proximate influences in vocal production. *Biological Reviews 93*(4), 2071-2082. https://doi.org/10.1111/brv.12437.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour 86*(5), 955-965. https://doi.org/10.1016/j.anbehav.2013.08.013

Sierro, J., Loretto, M., Szipl, G., Massen, J., & Bugnyar, T. (2019). Food calling in wild ravens (Corvus corax) revisited: Who is addressed? *Ethology 2019*;00:1–10. https://doi.org/10.1111/eth.12991

Silk, J. B., Cheney, D. L. & Seyfarth, R. M. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology 22*(5), 213-225. https://doi.org/10.1002/evan.21367

Silk, J. B., Seyfarth, R. M., & Cheney, D. L. (2016). Strategic use of affiliative vocalizations by wild female baboons. *PLoS ONE 11(10):* e0163978. https://doi.org/10.1371/journal.pone.0163978

Slocombe K.E. & Zuberbühler K. (2006). Food-associated calls in chimpanzees: responses to food types or food preferences? *Animal Behaviour 72*(5), 989–999. https://doi.org/10.1016/j.anbehav.2006.01.030

Sridhar, H., Beauchamp, G. & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour, 78*(2), 337-347. https://doi.org/10.1016/j.anbehav.2009.05.008

Tomasello, M. 2008. *Origins of human communication*. Cambridge, MA: MIT Press.

Valone, T. J. (1996). Food-associated calls as public information about patch quality. *Oikos* 77(12), 153-157. https://doi.org/10.1007/s00265-010-1006-0

Van Krunkelsven, E., Dupain, J., Van Elsacker, L. & Verheyen, R. F. (1996). Food calling by captive bonobos (*Pan paniscus*). *International Journal of Primatology 17*(2), 207-217. https://doi.org/10.1007/BF02735448

Whitmore, T.C. 1990. *An Introduction to Tropical Rain Forests*. Clarendon Press, Oxford.

Wilkinson, G. & Boughman, J. (1998). Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour 55*(2), 337-350. https://doi.org/10.1006/anbe.1997.0557

CHAPTER 4. AUDIENCE EFFECTS IN SOOTY MANGABEY AGONISTIC BEHAVIOUR

Results presented in this chapter have been accepted
for publication in Frontiers in Psychology:

Quintero, F., Touitou, S., Magris, M. & Zuberbühler, K. 2025. Audience Effects in Sooty Mangabey Agonistic Behaviour, *Frontiers in Psychology 16.*

https://doi.org/10.3389/fpsyg.2025.1551210

The dataset, and the scripts used in this study have been published in:

https://doi.org/10.6084/m9.figshare.20380347

ABSTRACT

The term 'Audience Effects', refers to behavioural changes triggered by the mere presence of others and has been extensively studied in animals to explore their capacity for social awareness and intentionality. Research shows that a wide range of species—from insects to primates—alter behaviours depending on their audience, with primates, especially great apes, demonstrating the most complex audience-aware behaviours, such as adjusting communication based on the recipient's attention or understanding. These findings suggest that some animals can infer intentions, remember social dynamics, and strategically act depending on who is watching. However, there is still limited data from non-ape primates and other mammals, raising questions about whether such cognitive traits evolved through shared ancestry or convergent evolution. Aggressive behaviours also reveal audience effects, with individuals, especially lower-ranking ones, using strategic aggression in front of influential bystanders to influence future interactions. While audience effects are well-documented in aggressive contexts across species, evidence for higher-level cognition remains limited outside of great apes and very few primates, underscoring the need for broader, species-diverse studies to fully understand the evolution of social cognition. We investigated how free-ranging sooty mangabeys, a terrestrial forest-dwelling primate living in large groups, used aggression depending on the composition of the audience. We found that individuals were significantly more aggressive to opponents if they were observed by large audiences that contained higher ranking individuals. These displays of aggression were often accompanied by vocalisations, further suggesting that aggressors were interested in attracting the audience's attention. We discuss these patterns of audience-dependent aggressive behaviour and propose that sooty mangabeys adjust their social behaviour depending on the composition of the bystanding audience, reacting in the most appropriate way depending on the situation, which provides additional support to the growing body of research showing that the underlying mechanisms necessary for the evolution of complex social cognition are more widespread in the animal kingdom than was previously thought.

Key words: Cercocebus atys, rank, audience effects, aggression, social cognition, communication, social awareness

INTRODUCTION

The term 'Audience Effect' comes from human psychology studies from more than 100 years ago (Triplett, 1898) and it is defined as the change on a subject's behaviour by the mere presence of someone else (the audience) (Coppinger et al., 2017). They have been the subject of many comparative studies on animals due to the possibility of intentionality; animals might change their behaviours strategically depending on who's in the audience (Zuberbühler, 2008). There are many reasons why this is important, but to put it simple, how aware are animals of other animals is one of the biggest differences between them and humans, the consensus is that great apes can perceive and attribute intentions to others. They can also communicate their own intentions and, if misunderstood or ignored, modify their signalling strategy to achieve their goal. (Call & Tomasello, 2008; Krupenye et al., 2016; Townrow & Krupenye, 2025). Thus, understanding how the audience is driving the occurrence of certain behaviours in animals will shed light on the underlying mechanisms that led to the development of the human-mind like behaviours.

Research on audience effects is well documented in the animal kingdom. A first major finding is that all kinds of animals, from insects to mammals, can be affected by the presence of others (Cheney & Seyfarth, 1990; Marler et al., 1986; Matos et al., 2003; Pollick et al., 2005; Ridley et al., 2007; Sherman, 1977; Zajonc et al., 1969). Most studies on audience effects in animals have been focused on how certain audiences affect an individual's calling rate and composition (Slocombe & Zuberbühler, 2007). This focus on signalling behaviours may be due to the fact that they are easy to measure, and can be replicated and manipulated to simulate the presence of certain audiences, both in captivity and in the wild.

Overall, natural selection is expected to favour animals that are able to adjust their behaviours to maximise their own reproductive success, by taking into account characteristics of their audiences, such as composition and attention (Zuberbühler, 2008). Such audience awareness is likely to be found in species where individuals attend and learn from watching the social interactions between the members of their group. Here, compelling evidence is from primates, birds and fish that can deduce, for example, the dominance relations of other individuals by just looking at the outcome of conflicts (Bond et al., 2003; Davis, 1992; Gillan, 1981; Grosenick et al., 2007; Lazareva et al., 2004; McGonigle & Chalmers, 1977; Rapp et al., 1996; Roberts & Phelps, 1994; Steirn et al., 1995; Von Fersen et al., 1991).

For non-human primates, the evidence suggests that individuals can take into account the goals and intentions of others and adjust their own behaviours accordingly (Call & Tomasello, 2007; Hare, 2011). For example, studies with captive orangutans, chimpanzees and bonobos have all shown that individuals are capable of modifying their signal output depending on the attentional state and familiarity of the recipient, with evidence for persistence and elaboration when dealing with unresponsive recipients (Cartmill & Byrne, 2007, 2010; Genty et al., 2015; Hobaiter & Byrne, 2014). A number of great ape field studies have also concluded that some vocal behaviour meets key criteria for intentionality (e.g., chimpanzees: Crockford et al., 2012; Hobaiter et al., 2014; Schel et al., 2013; bonobos: Genty & Zuberbühler, 2014. One challenging hypothesis from this research is that great apes are not only able to perceive and attribute intentions to others, but that they are also able to communicate their own and, if misunderstood or ignored, modify their signalling strategy to achieve the desired goal (Zuberbühler, 2008).

As remarked above, the main advances have come from great ape research while comparably less is known from other groups of primates and non-primate mammals. This is problematic for evolutionary theories of cognition, for example, whether audience awareness evolves along phylogenetic lines, perhaps as mere by-products of increasingly large brains or whether it can evolve by convergent evolution in response to specific socio-ecological challenges (Emery & Clayton, 2004). To address these questions, research on monkeys and non-primate species is crucial.

Here, some relevant findings come from captive rhesus macaques (Macaca mulatta) and tufted capuchins (Sapajus apella), which show that subjects can be sensitive to others' goals and intentions e.g., Drayton & Santos, 2014; Flombaum & Santos, 2005; Hare et al., 2003; Phillips et al., 2009; Santos et al., 2006). In the wild, there is also evidence showing that some monkey species are able to produce alarm calls with the apparent purpose of influencing others' behaviours (Zuberbühler, 2018). In one study, wild Thomas langur males continued to produce alarm calls to predator model until every group member had responded with at least one alarm call, as if to ensure that others were aware of the danger (Wich & de Vries, 2006).

In another study, wild Diana monkey females continued to alarm call until their own male produced the semantically matching ('correct') alarm calls, i.e., the predator spotted by the females, in response to which they stopped producing alarm calls (Stephan & Zuberbühler, 2016). Also, playback experiments with blue monkeys showed that males produced significantly more alarm calls to simulations of crowned eagle presence if other group members were closer to the presumed predator than far away (Papworth et al., 2008), further demonstrating some basic audience awareness, but not ruling out explanations based on basic changes in affective states.

Overall, the evidence suggests that apes, and some other primates, do more than just evaluate their audience in terms of biologically important categories; they also take into account psychological variables, such as attention, ability to comprehend (Call & Tomasello, 2007; Crockford et al., 2012) and capacity to help (Slocombe & Zuberbühler, 2007). However, it is not clear if this is a general feature of primate cognition or limited to some species and behavioural contexts. Although research on great apes continues to provide evidence for audience effects and intentional communication (e.g., Bouchard & Zuberbühler, 2022; Gruber & Zuberbühler, 2013; Schel et al., 2013), to our knowledge, there are no comparable studies on free-ranging monkeys designed to tackle the same questions. Studying cognition in the wild is generally difficult, suggesting that no single experiment will be powerful enough to provide conclusive answers.

One group of behaviours that would require certain audience awareness and cognitive resources that may not be available to every species, because of the time dimension, social complexity and the corresponding long-term memory load, are the aggressive behaviours (F. P. Santos et al., 2021). This is relevant for species in which bystanders intervene in ongoing conflicts, either in support of the victim or, more commonly, the aggressor (Petit & Thierry, 1994; Schino, 2007). Being aggressive and whether to intervene becomes part of an equation based on past events, current dispositions and future consequences for which keeping track of third-party relationships (i.e., who will support whom) is key.

There are interesting species differences in terms of what kind of support individuals can expect from their audiences. In vervet monkeys, for example, bystanders largely prefer to support aggressors (Mercier et al., 2019), whereas in chimpanzees, victims can get help from bystanders, which has led to the finding that victims sometimes use vocalisations strategically (Slocombe & Zuberbühler, 2007). But even if bystanders do not interfere, they will usually take note of the nature and outcome of an ongoing conflict. This is especially important for lower-ranking individuals, who may decide to engage in aggression if this is observed and remembered by uninvolved bystanders. For example, being aggressive in front of high-ranking observers may inform them of one's fighting ability or readiness to escalate (Arnott & Elwood, 2009; Martín & López, 2007; Yasuda & Koga, 2016) and, as a consequence, result in future tolerance from them. To summarise, being aggressive in front of uninvolved higher-ranking bystanders is one solution for how low-ranking individuals can avoid harassment from higher-ranking individuals, but this requires a minimum degree of audience awareness.

There is substantial literature on audience effects in aggressive situations, but mostly from non-primate species and without much evidence for complex decision-making. For instance, cichlid fish experience changes in androgen levels after watching fights (Oliveira et al., 2001), male red-bellied woodpeckers reduce displays to other males and increase social vocalisations when females arrive (Miles & Fuxjager, 2019) or male fiddler crabs are more aggressive to intruders if they have witnessed aggression before (Darden et al., 2019). The focus of our study was different insofar as we were interested in whether animals increased their aggressive behaviour when watched by others, not before and after the arrival of certain 'audience' individuals, nor before and after the occurrence of a determined event, but in average in the presence of specific bystanders. In order to keep it simple for this study, we defined audience effects as the change in the behaviour of the 'approacher' (the individual that has the intention of interacting with another) towards the 'approached' (the individual who is target of the approacher's behaviour), by the presence of at least another individual that is not part of the interaction.

To this end, we aimed to test whether sooty mangabeys, a highly social and generally tolerant forest monkey (Range et al., 2007), were capable of modifying their aggressive tendencies when locked into competitive interactions with other group members, depending on the audience composition. In forest habitats with limited visibility, audience compositions change all the time, suggesting that forest primates, on which social structure, personal space and group composition are of paramount importance, need to keep track of who is able to observe them and what their likely response will be (Seyfarth & Cheney, 2015). Additionally, this type of habitat with dense vegetation and limited visibility, is believed to be one of the evolutionary forces that helped develop higher cognitive capacities in animal species such as great apes, as it required them to remember the spatiotemporal characteristics of feeding spots, while also impeding the sight of predators and other groups or individuals within the same species (Ban & Normand, 2019; Fichtel et al., 2025; Janmaat et al., 2021).

We predicted that if subjects took the presence of uninvolved bystanders into account, then their aggressive behaviour should be different in the presence of socially important individuals in the audience. Among other categories, we classify as socially important individuals in regards of socially close individuals (kin-related or not) and higher-ranking individuals. For example, they should be especially prone to aggressive behaviour in the presence of high-ranking observers, assuming that this is likely to secure future tolerance from them. On the other hand, they could be more aggressive towards others in the presence of friends (socially close) that might help them to reinforce their higher-ranking over others lower ranking than them. A key factor here is 'calling', because it could function to attract the attention of others, simply to gain reputation or to get potential supporters thus serving as a measure of intention. The more an individual would call during an aggression, the more likely is this aggression to be severe (chase or physically attack others), vs mild (growling and staring at others). Similarly, the effect of the audience could be different in all the previous contexts depending on the severity of the aggression.

METHODS

Study Site and Subjects

The study was conducted in Taï National Park in south-western Ivory Coast (5°50'N, 7°21'W). The park is the largest protected block of primary forest in West Africa and covers approximately 454,000 ha of continuous forest. The forest is classified as 'tropical moist' (Whitmore, 1990), with a mean annual temperature of 24°C, a mean annual rainfall of 1,875mm (average of 2012–2015; Taï Monkey Project long-term data) and a distinct dry season in December–January. The study area of about 7 km2 was situated near the western border of the park, approximately 20 km southeast of the township Taï.

Sooty mangabeys are mainly terrestrial and live in groups of up to 100 individuals, with large group spread and inter-individual distances. One consequence of this social system is that individuals only interact with a small proportion of the group at any given time.

Although mangabey groups do not fission, individuals spend much of their time foraging in small parties going through the forest leaf-litter in search of food, such as insects or fallen Anthonota, Saccoglotis and Dialium fruits(Janmaat et al., 2006; McGraw et al., 2011; Range & Noë, 2002). Conflicts can occur in and outside of food patches, during which individuals can produce grunts, twitters, growls and screams (Quintero et al., 2022a; Range & Fischer, 2004). Prior studies on sooty mangabey aggression were mainly conducted in captivity, involving the introduction of new group members and formation of new groups (Bernstein, 1971; Bernstein & Gordon, 1974), situations that are unsuitable to test evolutionary questions about the function of aggression.

Observational data

The study group's home range contained a 2 km2 core area where groups of several monkey species had been studied since 1991 as part of a long-term research project (McGraw & Zuberbühler, 2007). The study group has been under constant observation since 1997 and is well habituated to human observers (Quintero et al., 2022a, 2022b; Range & Noë, 2002). Data collection was by following individuals from dawn to dusk over a period of 20 months (N=92 observation days) from August 2013 to July 2014 and January to September 2015. During the study period the group size was around 80 individuals. Data collection was in the form of focal animal and instantaneous sampling (Altmann, 1974) on N=33 adult individuals (N=5 males; N=28 females). We only worked with adults to avoid confounds due to ontogeny. Subjects were identified by physical features, such as scars, body size and general appearance. Focal samples lasted 60 min and individuals were not sampled twice during the same day. A total of N=371 hours of focal sampling was carried out on all N=33 individuals (11.24 h ± 4.05 h/individual; mean

± SD; Appendix 3). The observation times for the different individuals excluded out-of-sight, low-visibility or bad weather conditions. We curtailed the data further to only include interactions that occurred in full visibility between unambiguously identifiable individuals.

We defined a social interaction as an instance during which a focal animal approached, or was approached, by another individual to <1 m distance (see Bernstein, 1971; Quintero et al., 2022a; Range & Noë, 2002). When this was the case, we assumed that any call produced was socially directed. Call type discrimination followed the classification scheme by Range & Fischer (2004). We categorised a social interaction as 'agonistic' if it contained at least one aggressive behaviour, e.g., slapping, chasing, biting, staring or lunging (see Quintero et al., 2022a). In addition, we collected information on the general activity of the focal individual every 15 min. For each social interaction, we also determined the audience composition every 15 min ('neighbours'), i.e., the identity (ID) of every individual visible within a radius of about 10 m of the focal animal. These general activity factors were collected at the moment 15 minutes have passed (instant sampling) and not as the audience composition during that time frame.

Statistical Analyses

We were interested in what explained a focal animal's agonistic behaviour, in particular how it was linked to audience composition. Most agonistic interactions in sooty mangabeys are mild but occasionally interactants escalate and a conflict becomes severe. In two separate models, we therefore distinguished between (1) overall aggression ('**agonistic**') with all aggressive encounters during focal follows as data points and (2) severe aggression only ('**severe**') with the corresponding subset of data. Severe aggression is defined as every aggressive encounter where the aggressor is actively chasing the victim with or without physical contact.

If an encounter led to aggression, we considered it for the subsequent analyses and treated the approaching individual as the 'aggressor' and the approached individual as the 'victim'. As predictor variables we used (a) whether the aggressor produced a call during the approach (binary, '**aggressor call**'), (b) whether the approached individual produced a call (binary, '**victim call**'), (c) the social status of the aggressor (Elo-rating score; numeric, '**ranking**', Appendix 3; see Neumann et al., 2011), (d) the size of the audience (numeric, '**neighbours**'), (e) the presence of higher-ranking individuals in the audience (binary, '**HR**'; defined by a neighbour's Elo-rating score above the subject's own score (Neumann et al., 2011), (f) the presence of bond partners in the audience (binary '**friend**', defined by a dyadic composite sociality index (DSI) score >1 and ranging from 0-15, which we calculated using the socio-positive behaviours 'approach', 'inspection', 'presenting groom', 'contact', 'groom', 'handle infant' and 'hug'(Appendix 4; see Silk et al., 2013), (g) whether aggression was mild (stare, growl) or severe (chase, contact) (binary, '**severe**'), (h) whether the aggressor and the victim had visual contact for more than 20 s before the interaction (binary, '**sight**'). Finally, we included observer ID as a fixed factor to control for possible observer differences in data collection (N=2; binary, '**observer**'). We included the IDs of the focal and the encountered animal, as well as the date, as random factors.

Model 1: Overall Aggression

We used generalised linear mixed models (GLMM) with a binomial error structure to test variation in the occurrence of aggressive interactions with the response variable 'agonistic'. To avoid singularity fit issues, we reran the models within a Bayesian framework using Wishart priors. After confirming that the results were similar, we reported the results from the Bayesian GLMMs. We used R v4.0.3 (R Core Team, 2020) with the 'lme4' (Bates et al., 2015) and 'blme' (Chung et al., 2013) packages for all GLMMs. Also, for all the models we ran diagnostics with the 'DHARMa' package (Hartig, 2022) using the simulateResiduals() function, the variance inflation using the vif() function from the 'car' package (Fox & Weisberg, 2018), the normal distribution of the residuals using the qqnorm() function from the 'ggplot2' package (Wickham, 2016), the normality of the random effects using the qqmath() function from the 'lattice' package (Sarkar, 2008), the singularity in the random effects structure with the isSingular() function from the package 'lme4', the influence of the random effects levels on the fixed effects with the influence() function from the 'influence.ME' package (Nieuwenhuis et al., 2012). The first model was set up to determine under what circumstances agonistic interactions were likely to occur (compared to friendly or neutral interactions). In this model, we did not distinguish between severe and mild aggression, so the variable 'severe' was not considered. We included interactions between the aggressor and the victim calling with the two audience factors 'friend' and 'HR', as well as with 'sight', except the control variables (observer ID and random factors) and the two excluded aggression-related variables. We ran the model with all interactions and then deleted one-by-one all non-significant ones, starting with the least significant interaction until arriving at a final model with only significant interactions. We included random intercepts for focal subject ID (IDF), encountered subject ID (IDE) and date. We did not include random slopes for Elo-rating because we used only Elo-ratings at the end of the study period, i.e., the ranks did not change. We then built an ‘informed null model’, which only comprised the fixed term ‘observer’. The random structure was identical to the full model. We then compared these models with a likelihood ratio test (Dobson & Barnett, 2018). If the comparison between full and null models revealed a significant difference, we explored the full model with regards to the predictors of interest, i.e., those in the full but not in the null model.

Model 2: Severe Aggression

In order to understand the role of the audience in cases of aggression, we used generalised linear mixed models (GLMM) with a binomial error structure. We used all interactions that qualified as agonistic, with the response variable ‘severe’ (binary; mild=0, severe=1). We used all the same functions described for the previous model. We also ran the model with the same interactions described above and then deleted one-by-one the non-significant ones until we were left with the final model. We tested the significance of this model with a likelihood ratio test between the full and a null model, as mentioned above.

Ethical note

We adhered to non-invasive data collection by following and observing individuals habituated to human observers in their natural habitat. Research permission and ethical clearance was granted by the Ministère de la Recherche Scientifique et Technique de Côte d’Ivoire. The methods are in line with the Animal Behaviour Society Guidelines for the Use of Animals in Research.

RESULTS

Overall Aggression

We followed N=33 individuals with an average of 674.4 minutes (11.24h) (Appendix 3) per focal animal over N=88 observation days. Individuals had about 4.6 directly observed social interactions per hour (N=1,722 encounters; N=371 observation hours), with about 1.6 agonistic encounters per hour (N=595). As mentioned, we only considered encounters where we could see the interaction clearly and unambiguously identify the individuals, which led to a reduced dataset of N=29 focal individuals during N=52 days of observations (N=47 days with at least one agonistic interaction). During the 52 observation days, we scored N=887 social interactions, with N=359 (40.5%) scored as agonistic, with either severe (N=179) or mild (N=180) aggression. During the N=359 agonistic interactions, subjects produced N=141 vocalisations (N=100 growls, N=20 screams, N=19 grunts, N=1 twitter, N=1 copulation call).

The full model with all the interactions was significantly different from the informed null model ($\chi^2=211.67$; df= 13, $p < 0.001$). We step-by-step removed the non-significant interactions which resulted in the final model with no interactions (Table 4.1). The final model was significantly different from the informed null model ($\chi^2 = 203.1$; df = 7, $p < 0.001$). We found that subjects were more likely to be aggressive during social encounters if they were (a) higher-ranking than the partner (Table 4.1, fig. 4.1a), (b) in visual contact with the partner before the encounter (Table 4.1, fig. 4.1b), (c) producing a call (Table 4.1, fig. 4.1c), (d) encountering a victim that called (Table 4.1, fig. 4.1d), (e) with a large audience (Table 4.1, fig. 4.1e) and, crucially, (f) with a higher-ranking individual in the audience (Table 4.1, fig. 4.1f). Finally, the presence of social allies had no significant influence on the overall aggression (Table 4.1).

Table 4.1. Model results for overall probability of aggression

Variables	**Estimate**	**SE**	**Z**	**Pr(>|z|)**
Observer ID	0,01563	0,34908	0,045	0,96428
Ranking	1,08951	0,14059	7,749	**9,24E-15**
Neighbours	0,32866	0,10244	3,208	**0,00133**
Aggressor call	1,90724	0,2823	6,756	**1,42E-11**
Friend	0,01626	0,26605	0,061	0,95125
Sight	1,01407	0,24155	4,198	**2,69E-05**
Victim call	1,08131	0,35336	3,06	**0,00221**
HR	0,70744	0,23148	3,056	**0,00224**

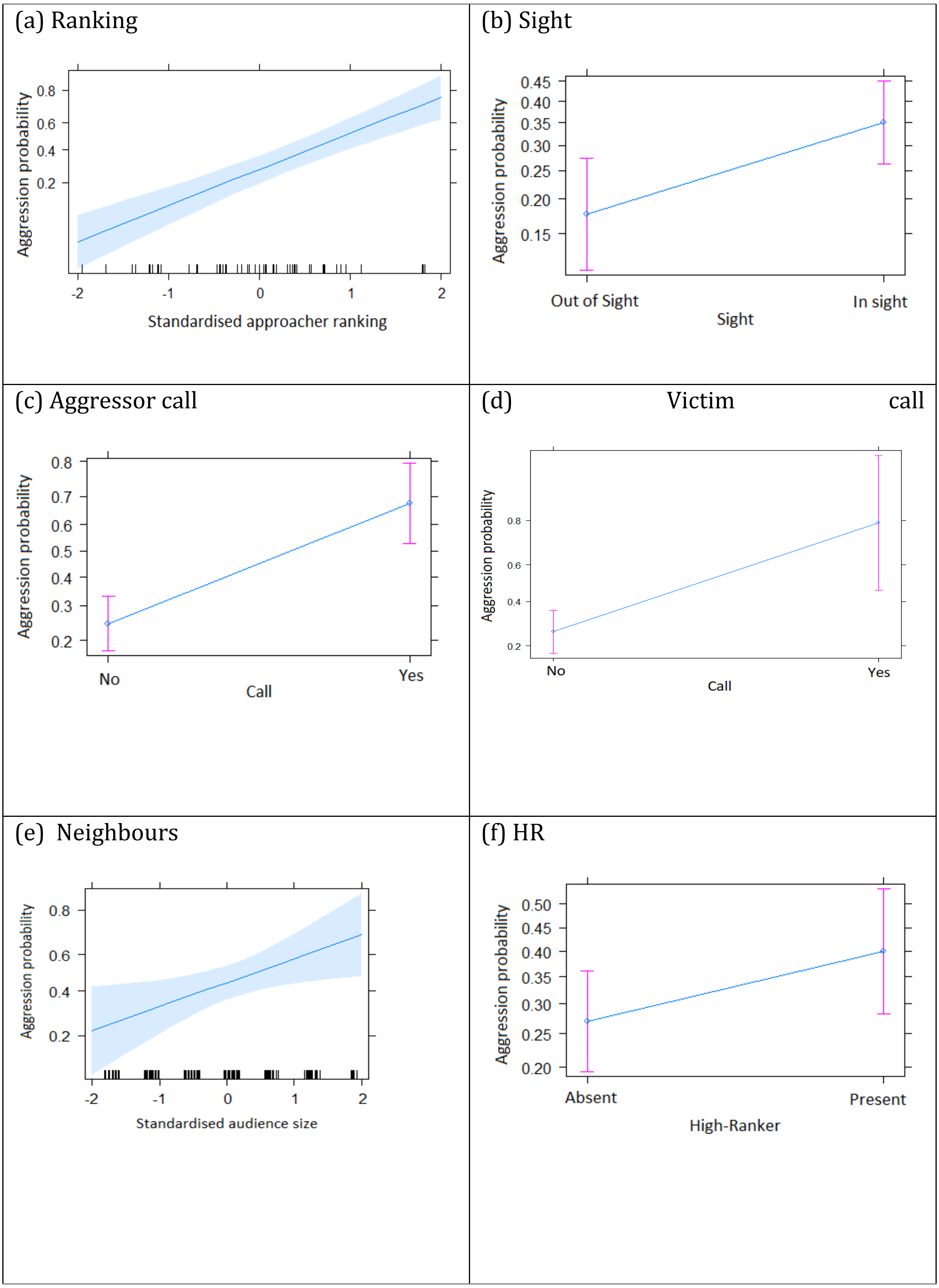

Figure 4.1. Overall probability of aggression as a function of different predictors (main effects only, a-f: means +/- SE).

Severe Aggression

N=179 of N=359 agonistic interactions that occurred between N=29 individuals over N=47 days qualified as severe. The full model was significantly different from the informed null model ($\chi^2 = 35.46$; df = 13, $p < 0.001$). As before, we step-by-step removed the non-significant interactions, which resulted in a final model with one interaction: aggressor calling * HR. The final model was significantly different from the informed null model ($\chi^2 = 25.116$; df = 8, $p < 0.001$). We found aggression was more likely to be severe when (a) the victim was calling (Table 4.2, fig. 4.2a) and if the aggressor was calling and there was a higher-ranker in the audience (Table 4.2, Fig. 4.2b).

Table 4.2. Model results for the probability of severe aggression only

Variables	**Estimate**	**SE**	**Z**	**Pr(>|z|)**
Observer ID	0,38695	0,32626	1,186	0,2356
Ranking	0,16106	0,15529	1,037	0,2997
Neighbours	0,22914	0,13185	1,738	0,0822
Friend	-0,03089	0,32483	-0,095	0,9242
Sight	-0,10834	0,34357	-0,315	0,7525
Victim call	0,82611	0,37278	2,216	**0,0267**
HR	-0,05255	0,34956	-0,15	0,8805
Aggressor call	0,43193	0,3403	1,269	0,2043
HR:Aggressor calling	1,22992	0,60663	2,027	**0,0426**

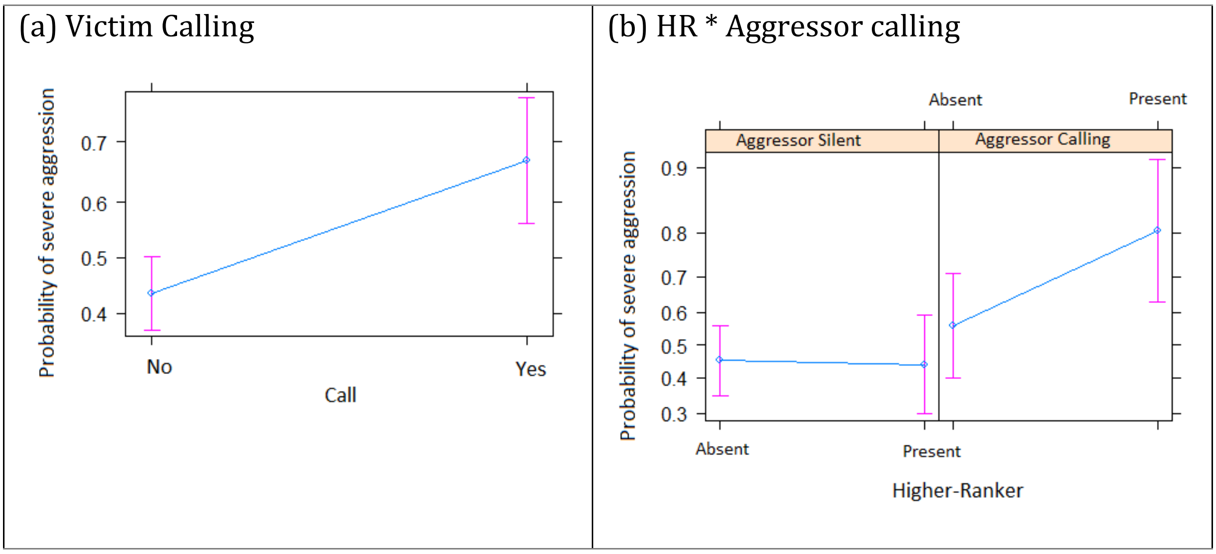

Figure 4.2. Probability of severe aggression as a function of different predictors (means +/- SE)

DISCUSSION

We were interested in sooty mangabey aggressive behaviour to address a less explored problem in animal behaviour, the degree to which aggressive interactions are determined by an observing audience. Aggression, whether if it is in a competition over resources (food or mating partners) or as a partner control mechanism, is typically examined as a dyadic process not taking into account the role of the audience on triggering these behaviours, especially in mild aggression. Additionally, these behaviours largely reserved to more dominant individuals in a group, the question is how middle and lower-ranking individuals achieve their goals. We hypothesised that one way of doing so was to display aggressive behaviour in ways that uninvolved bystanders take note of the interaction.

To this end, we investigated the dynamics of aggressive behaviour in sooty mangabeys in the presence of different audiences. As expected, and in line with the main function of aggression, we found that higher-ranking individuals were more aggressive than lower-ranking ones (probably to maintain social hierarchy), towards individuals in-sight within the last 15 seconds (individuals that are constantly on the radar, which would evidence certain intentionality rather than a simple emotional reaction), with a higher number of neighbours and that severe aggression was accompanied by vocal behaviour suggests an element of planning and audience awareness (Bernstein, 1971; Janmaat et al., 2006; Mielke et al., 2017; Quintero et al., 2022a; Range et al., 2007; Range & Noë, 2002), as predicted by sociobiological theory (Clutton-Brock, 2016; Emlen & Oring, 1977). Crucially, we found effects that appeared to go beyond the predictions of dyadic resource conflicts and suggested that aggressors had an interest in being observed. We found that the presence of higher-ranking individuals in the audience was linked to agonistic interactions more generally (fig 4.1f). The presence of a friend in the audience did not matter during overall or severe aggression and there was no interaction of this factor with any of the other investigated variables, suggesting that mangabeys attempt to 'attract the attention' of others by their ranking and not by their social bondness (Tables 4.1 and 4.2). In conclusion, the patterns of aggression in sooty mangabeys found in this study complied with predictions of a basic function in resource competition but also with some form of social advertisement.

Audience effects appear to play a general role in primate decision-making. In a previous study (Quintero et al., 2022a), we found that the audience impacted on alarm calling, which was enhanced if socially important individuals were nearby, although this may be a group-specific or seasonal pattern (see Mielke et al., 2017). Audience effects are also very common in chimpanzees, such as when encountering snakes (Schel et al., 2013; Crockford et al., 2012), when discovering food (Slocombe et al., 2010) and during aggression (Slocombe & Zuberbühler, 2007). Relevant for the current study is that chimpanzees that are victims of aggression tend to exaggerate the nature of the attack, provided they are observed by high-ranking audiences (Slocombe et al., 2009), presumably to persuade nearby group members to intervene on behalf of them. This is similar to what we found, insofar as severe aggression was correlated with the aggressors calling when higher-rankers were in the audience (table 4.2, fig. 4.2b), which suggests an attempt to attract higher-rankers attention to the event, although the reasoning behind it remains unclear. Future studies will need to include what happens after these aggressive encounters, especially between the aggressor and the higher-rankers in the audience.

We also found that the sudden arrival of out-of-sight individuals did not increase the likelihood of aggression. Instead, individuals were more likely to be aggressive to those already in sight and higher-ranking group members watching, implying some sort of planning rather than impulsive reactions. This goes in line with the more strategic pattern seen in chimpanzees who actively try to draw attention from their audiences by modifying the acoustic structure of their calls (Slocombe & Zuberbühler, 2007).

Unfortunately, we were unable to study whether being aggressive in the presence of high-ranking bystanders leads to future tolerance from them, which is an argument that has also been made with regard for redirected aggression (Ito et al., 2018). Therefore, we cannot rule out the possibility that the presence of high-ranking individuals makes others more anxious and more likely to act aggressively.

Importantly, we did not find that the presence of friends in the audience had a measurable impact during aggressions (tables 4.1 and 4.2), which is similar to what has been reported before in the same species. Range & Noë (2002) found that coalitions in sooty mangabeys were rare (<4%) and mainly between high-ranking females against lower-ranking opponents, suggesting that victims cannot hope for support. Most coalitions only occurred once, providing further evidence against the idea that social bonds function to secure future support, as has been argued repeatedly for chimpanzees (Koyama et al., 2006; Watts, 2002) or vervet monkeys (Borgeaud & Bshary, 2015; Seyfarth & Cheney, 1984).

Our study suggests that mangabeys attempt to attract the attention of higher-rankers during 'severe' conflicts, but how does the audience play a role during aggressive behaviour? As we did not measure immediate interactions between the higher-ranker and the approacher, we can only speculate. The cooperation literature has coined the notion of indirect (negative) reciprocity as another form of partner control to foster cooperation and future tolerance in others. If social interactions take place in front of others, then uninvolved bystanders will possibly remember the outcome for their future decision-making (Parrish et al., 2013). Having observed one individual being overly aggressive during food competition will likely result in this animal obtaining a reputation as being socially difficult, combative or even dangerous, which may increase the observer's future tolerance towards this animal (Számadó et al., 2021). However, in sooty mangabeys' society, higher-rankers in the audience would not need to be impressed by a 'socially difficult' individual attacking another so they can tolerate it later on during a competition over resources, because they are already in the 'higher-rank'. In this case, it is possible that as it has been argued with redirected aggression (Watts et al., 2000), individuals are being aggressive towards others to divert the attention of a possible high-ranker aggressor, but before that 'possible' aggression towards them.

Humans evidently take into account the interaction history, the identity and social role of bystanders, which raises questions about the origins of such abilities in primate cognition (Zuberbühler, 2008). Recently, it has been argued that in order to handle such multidimensional problems primates follow more basic social scripts, which allow them to make accurate predictions about other group members' future behaviours in most cases (Taylor et al., 2023). Yet, our data cannot distinguish between the main reputation hypotheses currently available. Nevertheless, the audience effects we observed may be due to some form of reputation building, and perhaps may even qualify as negative indirect reciprocity. Here, a key prediction from future research would be that, once an individual has performed an aggressive act in front of a higher-ranking bystander, it will gain future tolerance from the same individual, compared to cases when no aggressive acts were performed. Future analyses would therefore have to focus on the long-term effects of aggressive interactions, especially those that cannot be explained in terms of dyadic conflicts over access to resources.

To conclude, we have provided further evidence for a general primate propensity to adjust social behaviour depending on the composition of the bystanding audience and react in the most appropriate way depending on the situation, which goes in line with recent works in this species (Quintero et al., 2022a). Primates arguably follow social scripts, which allows them to make predictions about the consequences of their own current behaviour on future events (Taylor et al 2023). The patterns described here are not in line with a notion of animal calls as hardwired or reflexive responses to specific stimuli, but appear to involve considerable amounts of social cognition, allowing individuals to make assessments of both ecological and social variables in ways that would meet criteria for intentionality.

AUTHOR CONTRIBUTIONS

FQ and KZ: study design; ST, MM and FQ: data collection; FQ: statistical analysis; FQ and KZ: interpretation and drafting the article; KZ: provision of necessary tools and resources. All authors read and approved the final manuscript.

COMPETING INTERESTS

The authors declare no competing interests.

DATA AVAILABILITY

The raw data used for the analyses in this study are available through the following link: https://doi.org/10.6084/m9.figshare.20380347

ACKNOWLEDGMENTS

The research has been funded by the Swiss National Science Foundation (310030_143359), the Swiss National Centre of Competence in Research 'Evolving Language' (#51NF40 180888). We thank the Centre Suisse de Recherches Scientifiques (CSRS), the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales and the Office Ivoirien des Parcs et Réserves (OIPR) of Côte d'Ivoire for support and permission to conduct research in the Taï National Park. We thank the staff of the C.R.E. research station in Taï for logistical support. Paterson Kalo, Richard Peho, Benjamin Zehi and Gerard Gha assisted data collection. We thank Anderson Bitty for logistic support, Radu Slobodeanu and Gwendolyn Wirobski for statistical advice and Ronald Noë, Steve Moran and Robert Seyfarth for their valuable comments.

REFERENCES

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3–4), 227–266. https://doi.org/10.1163/156853974X00534

Arnott, G., & Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal Behaviour*, *77*(5), 991–1004. https://doi.org/10.1016/j.anbehav.2009.02.010

Ban, S. D., & Normand, E. (2019). Spatial cognitive abilities in foraging chimpanzees. In C. Boesch & R. Wittig (Eds.), *The Chimpanzees of the Taï Forest: 40 Years of Research* (pp. 440–450). Cambridge University Press. https://doi.org/DOI: 10.1017/9781108674218.028

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bernstein, I. S. (1971). The influence of introductory techniques on the formation of captive mangabey groups. *Primates*, *12*(1), 33–44. https://doi.org/10.1007/BF01730380

Bernstein, I. S., & Gordon, T. P. (1974). The Function of Aggression in Primate Societies: Uncontrolled aggression may threaten human survival, but aggression may be vital to the establishment and regulation of primate societies and sociality. *American Scientist*, *62*(3), 304–311. http://www.jstor.org/stable/27844884

Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, *65*(3), 479–487. https://doi.org/https://doi.org/10.1006/anbe.2003.2101

Borgeaud, C., & Bshary, R. (2015). Wild Vervet Monkeys Trade Tolerance and Specific Coalitionary Support for Grooming in Experimentally Induced Conflicts. *Current Biology*, *25*(22), 3011–3016. https://doi.org/10.1016/j.cub.2015.10.016

Bouchard, A., & Zuberbühler, K. (2022). An intentional cohesion call in male chimpanzees of Budongo Forest. *Animal Cognition*, *25*(4), 853–866.

Call, J., & Tomasello, M. (2007). *The gestural communication of apes and monkeys*. Psychology press.

Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. In *Trends in Cognitive Sciences* (Vol. 12, Issue 5, pp. 187–192). https://doi.org/10.1016/j.tics.2008.02.010

Cartmill, E. A., & Byrne, R. W. (2007). Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology*, *17*(15), 1345–1348.

Cartmill, E. A., & Byrne, R. W. (2010). Semantics of primate gestures: intentional meanings of orangutan gestures. *Animal Cognition*, *13*(6), 793–804.

Cheney, D., & Seyfarth, R. (1990). Attending to behaviour versus attending to knowledge: Examining monkeys' attribution of mental states. *Animal Behaviour*, *40*(4), 742–753.

Chung, Y., Rabe-Hesketh, S., Dorie, V., Gelman, A., & Liu, J. (2013). A Nondegenerate Penalized Likelihood Estimator for Variance Parameters in Multilevel Models. *Psychometrika*, *78*(4), 685–709. https://doi.org/DOI: 10.1007/s11336-013-9328-2

Clutton-Brock, T. (2016). *Mammal Societies*. Wiley. https://books.google.com.co/books?id=EugxrgEACAAJ

Coppinger, B., Cannistraci, R. A., Karaman, F., Kyle, S. C., Hobson, E. A., Freeberg, T. M., & Hay, J. F. (2017). Studying audience effects in animals: what we can learn from human language research. In *Animal Behaviour* (Vol. 124, pp. 161–165). Academic Press. https://doi.org/10.1016/j.anbehav.2016.12.020

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology*, *22*(2), 142–146.

Darden, S. K., May, M. K., Boyland, N. K., & Dabelsteen, T. (2019). Territorial defense in a network: audiences only matter to male fiddler crabs primed for confrontation. *Behavioral Ecology*, *30*(2), 336–340. https://doi.org/10.1093/beheco/ary169

Davis, H. (1992). Transitive inference in rats (Rattus norvegicus). *Journal of Comparative Psychology*, *106*(4), 342.

Dobson, A. J., & Barnett, A. G. (2018). *An introduction to generalized linear models*. CRC press.

Drayton, L. A., & Santos, L. R. (2014). Capuchins' (Cebus apella) sensitivity to others' goal-directed actions in a helping context. *Animal Cognition*, *17*(3), 689–700. https://doi.org/10.1007/s10071-013-0700-5

Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, *306*(5703), 1903–1907.

Emlen, S. T., & Oring, L. W. (1977). Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science*, *197*(4300), 215–223. http://www.jstor.org/stable/1744497

Fichtel, C., Henke-von der Malsburg, J., & Kappeler, P. M. (2025). Cognitive performance is linked to fitness in a wild primate. *Science Advances*, *9*(28), eadf9365. https://doi.org/10.1126/sciadv.adf9365

Flombaum, J. I., & Santos, L. R. (2005). Rhesus Monkeys Attribute Perceptions to Others. *Current Biology*, *15*(5), 447–452. https://doi.org/10.1016/j.cub.2004.12.076

Fox, J., & Weisberg, S. (2018). *An R Companion to Applied Regression*. SAGE Publications. https://books.google.com.co/books?id=SfNrDwAAQBAJ

Genty, E., Neumann, C., & Zuberbühler, K. (2015). Bonobos modify communication signals according to recipient familiarity. *Scientific Reports*, *5*(1), 16442.

Genty, E., & Zuberbühler, K. (2014). Spatial reference in a bonobo gesture. *Current Biology*, *24*(14), 1601–1605.

Gillan, D. J. (1981). Reasoning in the chimpanzee: II. Transitive inference. *Journal of Experimental Psychology: Animal Behavior Processes*, *7*(2), 150.

Grosenick, L., Clement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation alone. *Nature*, *445*(7126), 429–432. https://doi.org/10.1038/nature05511

Gruber, T., & Zuberbühler, K. (2013). Vocal Recruitment for Joint Travel in Wild Chimpanzees. *PLOS ONE*, *8*(9), e76073-. https://doi.org/10.1371/journal.pone.0076073

Hare, B. (2011). From hominoid to hominid mind: What changed and why? *Annual Review of Anthropology*, *40*(1), 293–309.

Hare, B., Addessi, E., Call, J., Tomasello, M., & Visalberghi, E. (2003). Do capuchin monkeys, Cebus apella, know what conspecifics do and do not see? *Animal Behaviour*, *65*(1), 131–142. https://doi.org/https://doi.org/10.1006/anbe.2002.2017

Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. *CRAN: Contributed Packages*. https://doi.org/10.32614/cran.package.dharma

Hobaiter, C., & Byrne, R. W. (2014). The meanings of chimpanzee gestures. *Current Biology*, *24*(14), 1596–1600.

Hobaiter, C., Leavens, D. A., & Byrne, R. W. (2014). Deictic gesturing in wild chimpanzees (Pan troglodytes)? Some possible cases. *Journal of Comparative Psychology*, *128*(1), 82.

Ito, M. H., Yamaguchi, M., & Kutsukake, N. (2018). Redirected aggression as a conflict management tactic in the social cichlid fish *Julidochromis regani*. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1871), 20172681. https://doi.org/10.1098/rspb.2017.2681

Janmaat, K. R. L., Byrne, R. W., & Zuberbühler, K. (2006). Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour*, *72*(4), 797–807. https://doi.org/10.1016/j.anbehav.2005.12.009

Janmaat, K. R. L., de Guinea, M., Collet, J., Byrne, R. W., Robira, B., van Loon, E., Jang, H., Biro, D., Ramos-Fernández, G., Ross, C., Presotto, A., Allritz, M., Alavi, S., & Van Belle, S. (2021). Using natural travel paths to infer and compare primate cognition in the wild. *IScience*, *24*(4), 102343. https://doi.org/https://doi.org/10.1016/j.isci.2021.102343

Koyama, N. F., Caws, C., & Aureli, F. (2006). Interchange of Grooming and Agonistic Support in Chimpanzees. *International Journal of Primatology*, *27*(5), 1293–1309. https://doi.org/10.1007/s10764-006-9074-8

Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science*, *354*(6308), 110–114.

Lazareva, O. F., Smirnova, A. A., Bagozkaja, M. S., Zorina, Z. A., Rayevsky, V. V, & Wasserman, E. A. (2004). Transitive responding in hooded crows requires linearly ordered stimuli. *Journal of the Experimental Analysis of Behavior*, *82*(1), 1–19.

Marler, P., Dufty, A., & Pickert, R. (1986). Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Animal Behaviour*, *34*, 194–198.

Martín, J., & López, P. (2007). Scent may signal fighting ability in male Iberian rock lizards. *Biology Letters*, *3*(2), 125–127. https://doi.org/10.1098/rsbl.2006.0589

Matos, R. J., Peake, T. M., & McGregor, P. K. (2003). Timing of presentation of an audience: aggressive priming and audience effects in male displays of Siamese fighting fish (Betta splendens). *Behavioural Processes*, *63*(1), 53–61.

McGonigle, B. O., & Chalmers, M. (1977). Are monkeys logical? *Nature*, *267*(5613), 694–696.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (2011). Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai forest, Ivory coast. *American Journal of Physical Anthropology*, *144*(1), 140–153. https://doi.org/10.1002/ajpa.21402

McGraw, W. S., & Zuberbühler, K. (2007). The monkeys of the Taï forest: an introduction. In W. S. McGraw, R. Noë, & K. Zuberbühler (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 1–48). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.002

Mercier, S., Déaux, E. C., van de Waal, E., Bono, A. E. J., & Zuberbühler, K. (2019). Correlates of social role and conflict severity in wild vervet monkey agonistic screams. *PLOS ONE*, *14*(5), e0214640-. https://doi.org/10.1371/journal.pone.0214640

Mielke, A., Samuni, L., Preis, A., Gogarten, J. F., Crockford, C., & Wittig, R. M. (2017). Bystanders intervene to impede grooming in Western chimpanzees and sooty mangabeys. *Royal Society Open Science*, *4*(11), 171296. https://doi.org/10.1098/rsos.171296

Miles, M. C., & Fuxjager, M. J. (2019). Social context modulates how the winner effect restructures territorial behaviour in free-living woodpeckers. *Animal Behaviour*, *150*, 209–218. https://doi.org/10.1016/j.anbehav.2019.02.011

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., & Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, *82*(4), 911–921. https://doi.org/10.1016/j.anbehav.2011.07.016

Nieuwenhuis, R., Grotenhuis, M. te, & Pelzer, B. (2012). *Influence. ME: Tools for detecting influential data in mixed effects models*.

Oliveira, R. F., Lopes, M., Carneiro, L. A., & Canário, A. V. M. (2001). Watching fights raises fish hormone levels. *Nature*, *409*(6819), 475. https://doi.org/10.1038/35054128

Papworth, S., Böse, A.-S., Barker, J., Schel, A. M., & Zuberbühler, K. (2008). Male blue monkeys alarm call in response to danger experienced by others. *Biology Letters*, *4*(5), 472–475.

Parrish, A. E., Perdue, B. M., Evans, T. A., & Beran, M. J. (2013). Chimpanzees (Pan troglodytes) transfer tokens repeatedly with a partner to accumulate rewards in a self-control task. *Animal Cognition*, *16*(4), 627–636. https://doi.org/10.1007/s10071-013-0599-x

Petit, O., & Thierry, B. (1994). Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Animal Behaviour*, *48*(6), 1427–1436. https://doi.org/10.1006/anbe.1994.1378

Phillips, W., Barnes, J. L., Mahajan, N., Yamaguchi, M., & Santos, L. R. (2009). ‘Unwilling’versus “unable”: capuchin monkeys’(Cebus apella) understanding of human intentional action. *Developmental Science*, *12*(6), 938–945.

Pollick, A. S., Gouzoules, H., & de Waal, F. B. M. (2005). Audience effects on food calls in captive brown capuchin monkeys, Cebus apella. *Animal Behaviour*, *70*(6), 1273–1281.

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022a). An Audience Effect in Sooty Mangabey Alarm Calling. *Frontiers in Psychology*, *13*. https://doi.org/10.3389/fpsyg.2022.816744

Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022b). The Evolution of Food Calls: Vocal Behaviour of Sooty Mangabeys in the Presence of Food. *Frontiers in Psychology*, *13*. https://doi.org/10.3389/fpsyg.2022.897318

Range, F., & Fischer, J. (2004). Vocal Repertoire of Sooty Mangabeys (*Cercocebus torquatus atys*) in the Taï National Park. *Ethology*, *110*(4), 301–321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Range, F., Förderer, T., Storrer-Meystre, Y., Benetton, C., & Fruteau, C. (2007). The structure of social relationships among sooty mangabeys in Taï. In W. S. McGraw, R. Noë, & K. Zuberbühler (Eds.), *Monkeys of the Taï Forest: An African Primate Community* (pp. 109–130). Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511542121.005

Range, F., & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. *American Journal of Primatology*, *56*(3), 137–153. https://doi.org/10.1002/ajp.1070

Rapp, P. R., Kansky, M. T., & Eichenbaum, H. (1996). Learning and memory for hierarchical relationships in the monkey: effects of aging. *Behavioral Neuroscience*, *110*(5), 887.

Ridley, A. R., Child, M. F., & Bell, M. B. V. (2007). Interspecific audience effects on the alarm-calling behaviour of a kleptoparasitic bird. *Biology Letters*, *3*(6), 589–591.

Roberts, W. A., & Phelps, M. T. (1994). Transitive inference in rats: A test of the spatial coding hypothesis. *Psychological Science*, *5*(6), 368–374.

Santos, F. P., Pacheco, J. M., & Santos, F. C. (2021). The complexity of human cooperation under indirect reciprocity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1838). https://doi.org/10.1098/rstb.2020.0291

Santos, L. R., Nissen, A. G., & Ferrugia, J. A. (2006). Rhesus monkeys, Macaca mulatta, know what others can and cannot hear. *Animal Behaviour*, *71*(5), 1175–1181. https://doi.org/https://doi.org/10.1016/j.anbehav.2005.10.007

Sarkar, D. (2008). *Lattice: multivariate data visualization with R*. Springer.

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee alarm call production meets key criteria for intentionality. *PloS One*, *8*(10), e76674.

Schino, G. (2007). Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, *18*(1), 115–120. https://doi.org/10.1093/beheco/arl045

Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, *308*(5959), 541–543. https://doi.org/10.1038/308541a0

Seyfarth, R. M., & Cheney, D. L. (2015). How sociality shapes the brain, behaviour and cognition. *Animal Behaviour*, *103*, 187–190. https://doi.org/10.1016/j.anbehav.2015.01.026

Sherman, P. W. (1977). Nepotism and the Evolution of Alarm Calls: Alarm calls of Belding's ground squirrels warn relatives, and thus are expressions of nepotism. *Science*, *197*(4310), 1246–1253.

Silk, J., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 213–225. https://doi.org/10.1002/evan.21367

Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., & Zuberbühler, K. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology*, *64*(12), 1959–1966.

Slocombe, K. E., Townsend, S. W., & Zuberbühler, K. (2009). Wild chimpanzees (Pan troglodytes schweinfurthii) distinguish between different scream types: evidence from a playback study. *Animal Cognition*, *12*(3), 441–449.

Slocombe, K. E., & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228–17233. https://doi.org/10.1073/pnas.0706741104

Steirn, J. N., Weaver, J. E., & Zentall, T. R. (1995). Transitive inference in pigeons: Simplified procedures and a test of value transfer theory. *Animal Learning & Behavior*, *23*(1), 76–82.

Stephan, C., & Zuberbühler, K. (2016). Persistent females and compliant males coordinate alarm calling in Diana monkeys. *Current Biology*, *26*(21), 2907–2912.

Számadó, S., Balliet, D., Giardini, F., Power, E. A., & Takács, K. (2021). The language of cooperation: reputation and honest signalling. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1838). https://doi.org/10.1098/rstb.2020.0286

Taylor, D., Gönül, G., Alexander, C., Züberbühler, K., Clément, F., & Glock, H.-J. (2023). Reading minds or reading scripts? De-intellectualising theory of mind. *Biological Reviews*, *98*(6), 2028–2048. https://doi.org/https://doi.org/10.1111/brv.12994

Team, R. C. (2020). R Core Team R: a language and environment for statistical computing. *Foundation for Statistical Computing*.

Townrow, L. A., & Krupenye, C. (2025). Bonobos point more for ignorant than knowledgeable social partners. *Proceedings of the National Academy of Sciences*, *122*(6), e2412450122. https://doi.org/10.1073/pnas.2412450122

Triplett, N. (1898). The Dynamogenic Factors in Pacemaking and Competition. *The American Journal of Psychology*, *9*(4), 507–533. https://doi.org/10.2307/1412188

Von Fersen, L., Wynne, C. D., Delius, J. D., & Staddon, J. E. (1991). Transitive inference formation in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *17*(3), 334.

Watts, D. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, *139*(2), 343–370. https://doi.org/10.1163/156853902760102708

Watts, D., Colmenares, F., & Arnold, K. (2000). Redirection, Consolation, and Male Policing: How Targets of aggression Interact with Bystanders. In F. Aureli & F. de Waal (Eds.), *Natural Conflict Resolution* (pp. 281–301). University of Chicago Press.

Whitmore, T. C. (1990). *An introduction to tropical rain forests.* Clarendon Press.

Wich, S. A., & de Vries, H. (2006). Male monkeys remember which group members have given alarm calls. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1587), 735–740.

Wickham, H. (2016). Data analysis. In *ggplot2: elegant graphics for data analysis* (pp. 189–201). Springer.

Yasuda, C. I., & Koga, T. (2016). Importance of weapon size in all stages of male–male contests in the hermit crab Pagurus minutus. *Behavioral Ecology and Sociobiology*, *70*(12), 2175–2183. https://doi.org/10.1007/s00265-016-2221-0

Zajonc, R. B., Heingartner, A., & Herman, E. M. (1969). Social enhancement and impairment of performance in the cockroach. *Journal of Personality and Social Psychology*, *13*(2), 83.

Zuberbühler, K. (2008). Audience effects. *Current Biology*, *18*(5), R189–R190. https://doi.org/10.1016/j.cub.2007.12.041

Zuberbühler, K. (2018). Intentional communication in primates. *Travaux Neuchâtelois de Linguistique*, *68*, 69–75.

CHAPTER 5. DISCUSSION

Summary

The overall goal of this thesis was to investigate the cognitive abilities of a non-ape primate. Research on the psychological processes available to monkeys is important for several theoretical reasons, such as the question of evolutionary precursors of human language and the question of cognitive evolution more generally as well as how acoustically distinct signals evolve. To address these questions, I was interested in how a social primate, sooty mangabeys, used its vocal behaviour when dealing with everyday real-life problems, such as avoiding predators, finding food and resolving conflicts with others.

My research has contributed to current theories in several ways. First, I found evidence that sooty mangabeys have more complex vocal behaviour than described so far. For example, although I could confirm the absence of acoustically distinct food calls, I also found that, monkeys produced general-purpose contact calls in the presence of food and that their usage was the same as normally found for species that produce acoustically distinct food calls. Second, in the predation context when finding snakes, I found evidence that monkeys produced more alarm calls if socially close individuals were in the audience and some of the factors driving call production were in line with intentional signalling criteria. Lastly, my results indicated that aggression was strongly affected by the composition of the audience. In particular, mild aggression was more common when high-ranking individuals were present and severe aggression, in contrast, was more significant when socially close individuals were absent.

Evolution of communication – Signal form and function

One of the main questions of my thesis was about the emergence of advanced behaviour patterns and the factors that can cause complex behaviour traits to evolve and why this happens in some species and not in others. For example, current theories about food calls state that there are at least three reasons for why food calls can emerge, and that they depend on the social structure and environmental factors affecting each species (Clay et al. 2012).

First, in stable social groups with repeated inter-individual contact, individuals are highly interdependent to the effect that cooperative helping can be selected for even amongst unrelated individuals (Bshary & Bergmüller, 2008). If food calls are mainly produced to help others, then this behaviour might be additionally enhanced if it raises a caller's social status and likelihood of future reciprocation by recipients.

Second, in large stable foraging groups food calls might be given with a purely selfish motivation if they function to announce resource ownership and if this reduces the risks of misunderstandings and likelihood of future costly agonistic interactions. Here, lower-ranking and less competitive individuals should be particularly prone to vocalising during foraging near higher ranking individuals.

Lastly, smaller-bodied species suffer from higher predation pressure and generally benefit more from the presence of others, as predicted by the selfish herd effect (Hamilton, 1971; Piccolo et al., 2022). If food calls attract others to a food resource, they may function to increase group size in situations when individuals are particularly exposed to predation and need higher protection.

A first goal of my thesis was to test what function was most likely responsible for mangabey vocal behaviour in the presence of food. A second goal concerned the problem of what can trigger a structural evolution of calls produced in the food context, i.e., the origins of acoustically distinct food calls. As mentioned in previous studies there is no indication that mangabeys produce acoustically distinct food calls, which led to the question of why some species evolve and other species do not evolve acoustically distinct food calls. For instance, macaques often give 'coo' calls in response to food (Hauser & Marler, 1993), but there are no analogous calls in sooty mangabeys, vervet monkeys or baboons, species with many behavioural similarities and similar ecology.

To address this question, I first studied sooty mangabeys' non-social vocal production while feeding. As they are a species that has large stable foraging groups, they should produce food calls to announce resource ownership for the reasons mentioned before. Indeed, I did find that individuals increased calling while foraging, but also when in the periphery of the group and with fewer neighbours, which was not in line with a resource notifying function. Also, I found that being inside a food patch did not influence their calling behaviour, although this usually concerned ordinary, non-high quality stable foods. I therefore predicted that more targeted calling should become apparent when individuals found high quality foods.

I thus designed and carried out a food placing experiment where I provided subjects with highly desirable foods - boiled chicken eggs. This experiment simulated a real situation, i.e., finding highly prized guinea fowl eggs, a situation that occurs naturally but is very difficult to witness and is even more difficult to analyse in terms of reactions during the initial encounters.

Here, I found that, regardless of the number of neighbours, subjects always produced calls when finding these eggs as long as they were not chased by others but, in line with the absence of food call hypothesis, these calls never attracted others. Sooty mangabeys are clearly able to call when finding food, but they do so without specifically evolved vocalisations and with no apparent awareness of potential impact on their audiences.

I explored the reasons for this blatant lack of an otherwise common primate vocal behaviour and conclude that, at least in the case of sooty mangabeys, food availability may have played a big role in preventing the evolution of food calls. The argument is that, as the species lives in an evergreen forest and has specialised on relatively low-quality food that are nearly always available, there has been a corresponding lack of evolutionary pressure to evolve specific food calls. Additionally, the species' stable matrilinear social hierarchy unequivocally specifies priorities of access to food, which reduces the risk of misunderstandings and need to announce food ownership. These two factors are different in chimpanzees, who regularly feed on high quality foods and who social relationships are not determined by matrilinear membership. There are probably numerous other factors involved as well in the evolution of food calls, so clearly more targeted research is needed in the future involving other species as well.

Evolution of communication – Audience awareness

Another main goal of this thesis was to provide data on the evolutionary emergency of audience aware communication. Previous studies have shown that great apes, and some other primates, do more than just evaluate their audience in terms of biological categories, but also take into account psychological variables, such as attention, ability to comprehend (Call & Tomasello, 2007; Crockford et al., 2012) and capacity to help (Slocombe & Zuberbühler, 2007). Nonetheless, the overall picture is still patchy and many times only some basic audience awareness has been demonstrated without ruling out simpler explanations based on affective states.

In the wild, some of the best evidence of audience awareness communication and intentional signalling comes from snake model experiments where it was shown that chimpanzees are capable of taking into account others' mental states, due to the fact that they were more likely to call if newly arriving individuals were not aware of the danger (Crockford et al., 2012) and if they were socially important to the caller (Schel et al., 2013). However, when the same experiment was replicated with sooty mangabeys in Taï Forest, callers did not adjust call production to the presence of socially important or referentially unaware partners (Mielke et al., 2019). The reasons have remained unclear, but one theoretically very important possibility is that this represents a cognitive divide between monkeys and apes (Tomasello, 2010). Given the importance of the implications, it is crucial to rule out lower-level explanations, such as mere age effects, since mostly juveniles were tested in the Mielke et al., 2019 study. Appropriate alarm calling develops gradually and requires key experience youngsters (Deshpande et al., 2022; Leon et al., 2022; Zuberbühler et al., 2022) and it is certainly possible that juveniles were unable to process social situations in the same way as adults would (Cheney & Seyfarth, 2007).

I conducted the same snake model experiments, but I focused on adult individuals to rule out possible age effects. Sooty mangabeys produced significantly more alarm calls when socially close individuals were present in the audience, with fewer individuals around and individuals arrived more with an increasing number of calls. Patterns of alarm call production were consistent with key criteria for intentionality, suggesting that Mielke et al.'s 2019 cognitive divide conclusion was premature.

Intentionality cannot be measured directly but has to be inferred from behavioural indicators (Graham et al., 2020). The following criteria are usually cited as evidence for intentionality (Townsend et al., 2017). A first one is about "goal directedness", centred around the notion of motor processes organised as actions towards physical targets (Kenward et al., 2009), which in non-human primates can be measured as persistence (Leavens et al., 2005). Although I did not observe any obvious signs of persistence (i.e., callers monitoring exactly whether or when others have located the snake, staring at individuals that are ignorant of the snake and repeating or enhancing signalling in case of misunderstanding), I found that mangabeys called more when fewer individuals were present and a relationship between call rates and individuals arriving (fig 2.2, 2.6, 2.8).

A second criterion is "recipient directedness", the notion that - to be intentional - behaviour must be under volitional control and recipient-directed (Leavens et al., 2004, Moore, 2016). My data are in line with this criterion, as alarm calling was about detecting the snake and, in all likelihood, ensuring that others were made aware of its location.

These results also resemble findings in chimpanzees, which produce food calls and snake alarms preferentially in the presence of socially important individuals, i.e., friends and high-ranking group members (Schel et al., 2013), a pattern also present in my data. In contrast to chimpanzees, however, I never observed an individual re-starting alarm calling with the arrival of a new individual.

The third criterion for intentionality states that receivers must regularly respond in a way that is in line with the signaller's presumed intentions. I did not address this requirement directly, but there was not a single occasion when sooty mangabeys called and no individuals arrived to locate the snake, suggesting that receivers responded in line with the caller's expectations.

Whether or not these patterns could be explained with more basic changes in physiological states or arousal, rather than intentionality and social awareness, will have to be further investigated. Also, given that, compared to chimpanzees, sooty mangabeys have a more cohesive social structure and foraging behaviour, it may be less necessary for them to make sure that others have seen the snake as there are so many individuals to spot the predator. With some individuals already staring at the danger, it may no longer important to keep calling because other individuals arriving will easily spot the snake. Chimpanzees forage and travel in less cohesive units, making it more paramount to make sure that others see the snake, because fewer individuals are available to know the location of the snake, thus persistence is more important.

Evolution of communication – Cooperation and competition

Evidence from audience-aware communication also comes from studies on chimpanzee aggression where victims of aggression exaggerate their screams if there are individuals in the audience that would be able to intervene (Slocombe & Zuberbühler, 2007). Here, it is important to realise that there are two basic functions of aggression. First, aggression can serve to settle disputes that arise due to direct competition over limited resources (food, space, sexual partners, etc). But many animals also use aggression as an 'education' tool, either as a response or as pre-emptive act to prevent others from refusing to cooperate. The second function, aggression as a social tool (or 'negative reciprocity'), is far less explored, especially in social mammals, although behavioural observations of retaliatory aggression are common. For questions about audience-awareness this second function is clearly more promising.

Here, my results showed that sooty mangabeys increased their aggression inside food patches, provided that they were higher in rank than their opponents, but there were additional effects that could not be explained with a basic resource competition function. For instance, aggression was more likely when high-ranking individuals were within 10m and the aggressor vocalised most of the time. As these results were mainly found in cases of mild aggression, it is possible that aggressors wanted to display their aggressive motivation in front of high-rankers, without further escalation. Related to that was the fact that most of aggressions were accompanied by vocalisations, again suggesting that aggressors were interested in getting the attention of bystanders. It is therefore possible that aggression here functioned as a pre-emptive act to lower the risk of being aggressed by higher-ranking individuals in the future, similar to what happens with redirected aggression (Ito et al., 2018)

Additionally, the sudden arrival of out-of-sight individuals in the food patch did not increase the likelihood of aggression but the opposite. Individuals were more likely to be aggressive to those already in sight, implying some long-term planning rather than impulsive reactions. Severe aggression, remarkably, was rarely observed inside food patches, suggesting that competitors specifically avoided it in such situations. Pursuing selfish goals at all costs, in other words, was actively avoided, even by individuals that would have had the means to do so. Severe aggression occurred mainly outside food patches, suggesting functions other than competition over food. Severe aggression was positively related to audience size, especially when no friends were in the audience, suggesting that aggressors were aware that they could not expect any support in the ongoing conflict.

Although we did not find any clear evidence apart from seemingly audience-aware use of aggression along the predictions of the 'social tool' hypothesis, future studies should look at the long-term effects of aggressive interactions, especially those that cannot be explained in terms of dyadic conflicts over access to resources. Predictions are that individuals that have aggressed others without direct resource competitions, should be more likely to obtain tolerance or cooperation from their victims in future interactions, regardless of whether they are competitive or otherwise.

Conclusions and future directions

My general approach was to understand how primates take their audience into account in three everyday contexts, i.e., to analyse every single social interaction in a triadic or polyadic manner, under the assumption that bystanders play an important role in the outcome of dyadic interactions. My results suggest that audience composition always plays a role, sometimes just by the number of individuals and others because of the presence of socially important members.

During snake encounters, sooty mangabeys significantly changed alarm call rates as a function of the number of nearby individuals and the presence of socially important individuals. Even though snakes are not monkey predators they can pose real threats which triggers patterns of information exchange.

In a similar manner, during intergroup conflicts mangabeys adjust aggression severity for potential social benefits when observed by higher-ranking individuals which possibly enhance the likelihood of future tolerance from them. They also refrain from severe aggression when friends are present in small audiences. These patterns suggest that they constantly monitor their audience and react in the most appropriate way depending on the situation, a finding not previously reported in monkey species.

Regarding foraging for highly appreciated foods, sooty mangabeys did not produce acoustically distinct food calls, and I have explored the reasons why this feature has not evolved in this species. Nonetheless, when finding high-quality foods, individuals did vocalise, provided they were not chased, which shows that it is not difficult for them to call when finding preferred foods. One unresolved mystery concerns the fact that the two call types recorded in this context, grunts and twitters, were also produced when traveling and establishing contact with other group members, suggesting that as soon as they find food, they want to contact others, perhaps to identify their locations. This could represent an early state of food call evolution. The behaviour complies most with the ownership advertisement function (rather than the sharing function), due to the fact that I never observed any food sharing, not even when the food could not be monopolised. Food calls as ownership signals have been found in capuchins, macaques and ravens, where food calls repel others (Bugnyar et al., 2001; Gros-Louis, 2004; Hauser & Marler, 1993).

Future studies should include fine-grained acoustic analyses of these calls to identify potential early signs of acoustic divergence of these calls, mainly grunts and twitters, compared to when they are produced in other contexts. For food calls and snake alarm calls it would be also interesting to run playback experiments simulating socially important individuals to evaluate whether these calls might be modified depending on the audience.

To conclude, this is the first time audience effects in a free-ranging monkey species have been investigated across contexts, which has produced evidence of individuals not only changing their behaviour depending on audience composition, but also how the audience was affected by their signalling and reacting accordingly. Although such field studies are difficult, they are valuable in giving a glimpse of how behaviour and cognition evolved in the wild.

My work also challenges a commonly held view that only great apes are relevant for studying cognitive evolution. Instead, the evidence I presented supports a more gradual view, i.e., that features and components of human language are already present deep in the evolutionary tree of primates and most have therefore evolved early.

Finally, all the patterns I have described are not in line with a notion of animal calls as hardwired or reflexive responses to specific stimuli, but appear to involve considerable amounts of social cognition, allowing individuals to make assessments of both ecological and social variables in ways that meet criteria of intentional signalling.

REFERENCES

Bshary, R., & Bergmüller, R. (2008). Distinguishing four fundamental approaches to the evolution of helping. *Journal of Evolutionary Biology, 21*(2), 405–420. https://doi.org/10.1111/j.1420-9101.2007.01482.x

Bugnyar, T., Kijne, M., & Kotrschal, K. (2001). Food calling in ravens: are yells referential signals?. *Animal Behaviour*, *61*(5), 949-958. https://doi.org/10.1006/anbe.2000.1668

Call, J., & Tomasello, M. eds. (2007). *The Gestural Communication of Apes and Monkeys* (New York: Lawrence Erlbaum Associates).

Clay, Z., Smith, C. L., and Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: what do these calls really mean? *Animal Behaviour 83*, 323–330. https://doi.org/10.1016/j.anbehav.2011.12.008

Crockford, C., Wittig, R., Mundry, R. & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology, 22* (2), pp. 142-146. https://doi.org/10.1016/j.cub.2011.11.053

Deshpande, A., Van Boekholt, B., & Zuberbühler, K. (2022). Preliminary evidence for one-trial social learning of vervet monkey alarm calling. *Royal Society Open Science*, *9*(8), 210560. https://doi.org/10.1098/rsos.210560

Graham, K. E., Wilke, C., Lahiff, N. J., & Slocombe, K. E. (2020). Scratching beneath the surface: intentionality in great ape signal production. *Philosophical Transactions of the Royal Society B*, *375*(1789), 20180403. https://doi.org/10.1098/rstb.2018.0403

Gros-Louis, J. (2004). The function of food-associated calls in white-faced capuchin monkeys, Cebus capucinus, from the perspective of the signaller. *Animal Behaviour*, *67*(3), 431-440. https://doi.org/10.1016/j.anbehav.2003.04.009

Hamilton, W.D. (1971). Geometry for the Selfish Herd. *Journal of Theoretical Biology. 31* (2): 295–311. https://doi.org/10.1016%2F0022-5193%2871%2990189-5

Hauser, M. D. & Marler, P. (1993). Food-associated calls in rhesus macaques (*Macaca mulatta*). 1. Socioecological factors. *Behavioral Ecology*, 4, 194e205 https://doi.org/10.1093/beheco/4.3.194

Ito, M. H., Yamaguchi, M., & Kutsukake, N. (2018). Redirected aggression as a conflict management tactic in the social cichlid fish Julidochromis regani. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1871), 20172681.

https://doi.org/10.1098/rspb.2017.2681

Kenward, B., Folke, S., Holmberg, J., Johansson, A., & Gredebäck, G. (2009). Goal directedness and decision making in infants. *Developmental Psychology*, *45*(3), 809. https://doi.org/10.1037/a0014076

Leavens, D. A., Hopkins, W. D., & Thomas, R. K. (2004). Referential communication by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *118*(1), 48. https://doi.org/10.1037/0735-7036.118.1.48

Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (Pan troglodytes). *Child Development*, *76*(1), 291-306. https://doi.org/10.1111/j.1467-8624.2005.00845.x

León, J., Thiriau, C., Bodin, C., Crockford, C. & Zuberbühler, K. (2022). Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys. *iScience 25,* 104853. https://doi.org/10.1016/j.isci.2022.104853

Mielke, A., Crockford, C., & Wittig, R. (2019). Snake alarm calls as a public good in sooty mangabeys. *Animal Behaviour. 158*, 201–209. https://doi.org/10.1016/j.anbehav.2019.10.001

Moore, R. (2016). Meaning and ostension in great ape gestural communication. *Animal Cognition*, *19*(1), 223-231. https://doi.org/10.1007/s10071-015-0905-x

Piccolo, H., Beresford, D., & Hossie, T. J. (2022). Selfish herd effects depend on prey crypsis. *Biology Letters*, *18*(10), 20220242. http://doi.org/10.1098/rsbl.2022.0242

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee alarm call production meets key criteria for intentionality. *PLoS One, 8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674

Slocombe, K. E., & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228-17233. https://doi.org/10.1073/pnas.0706741104

Tomasello, M (2010). *Why we cooperate*. Boston: Boston Review Books.

Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., ... & Manser, M. B. (2017). Exorcising G rice's ghost: An empirical approach to studying intentional communication in animals. *Biological Reviews*, *92*(3), 1427-1433.
https://doi.org/10.1111/brv.12289

Zuberbühler, K., Leon, J., Deshpande, A., & Quintero, F. (2022). Socially scripted vocal learning in primates. *Current Opinion in Behavioral Sciences, 46*, 101153.
https://doi.org/10.1016/j.cobeha.2022.101153

APPENDICES

Appendix 1

The snake models were made by the local artist Djobely et Artable, who crafted them from wood and painted them to look as closest as possible to real Gaboon and Rhinoceros Vipers. Seven different snake models were made in different positions resembling the same postures that real snakes show in the wild.

Appendix 2. Ethogram of sooty mangabeys of Taï National Park, Ivory Coast. Adapted from Range & Noë (2002).

	Abbreviation	Behaviour	Definition
Affiliative Behaviours	Co	Contact	two individuals are in contact sitting usually and don't really interact with each other
	Hu	Hug	two individuals are hugging each other (usually around the shoulders or neck)
	Hb	handle baby	individual is manipulating the baby
	Ca	carry baby without stress	individual is carrying a baby to move around (usually on the stomach but sometimes on the back)
	Mtm	mouth to mouth	individual is smelling a partner's mouth and vice versa
	Lm	lips smacking	individual is making noise by clapping its lips (usually while grooming or approaching a subordinate)
	Pl	play (general)	individual is playing (no description)
	Gr	Groom	individual is grooming a partner
	Pr	prensenting groom	individual is presenting a part of its body to be groomed (usually elbow, head or back)
	nas	non-agonistic supplant	individual is approaching another animal who is occupying a resource and replaces that individual without overt aggression
	Ap	approach	individual is approaching another animal (r<2m)
	To	Touch	individual touch a partner in a gentle way, hand on shoulder
	Ins	Inspection	Individual inspects another individual sexual parts.
	Fo	Follow	individual is following another animal
	Le	Leave	individual is leaving the proximity of another (perimeter of three meters)
	Ipl	invitation to play	initiation of play (show teeth, look upside down, quick touch before darting and jumping)
Agonistic Behaviours	Fi	Fight	two partners stand up and slap each other
	asf	attempt stealing food	individual is trying to steal another's food
	akb	attempt kidnapping baby	individual is trying to steal a mother's baby
	Bt	bared teeth	individual is showing its teeth (usually while approaching a dominant)
	Av	avoidance	individual is avoiding another individual who is approching it
	Jp	jump aside	individual jump aside to avoid a partner, an aggression, something scary
	Cr	crawl on the ground	individual is lying on the ground while looking at its aggressor
	Fl	Flee	individual is fleeing an aggressor
	Lo	look around for support	individual is searching around him for support while it is threatened by another
	cas	carry baby with stress	individual is carrying a baby to escape a stressful situation for itself or for the baby (infanticide attacks)
	St	Stare	individual is threatening (look / go forward)
	Stl	stare and lunge	individual is threatening and half attacking (go forward / backward)
	Gp	Grip	individual is gripping the other's fur
	Bi	Bite	individual is bitting
	Ch	Chase	individual is chasing another
	Sf	stealing food	individual is stealing another's food
	Tp	take place	individual takes another's place
	Kb	kidnapping baby	individual managed to steal a baby and refuse to hand it back to its mother
	Ign	ignore / turn back	individual ignore a partner's sollicitation (for grooming, mating, nursing, etc) and even can turn its back
	Sa	support aggressor	individual supports the aggressor in a conflict
	Sv	support victim	individual supports the victim in a conflict

Appendix 3. Observation time for the different focal animals including rank and sex

Name	Sex	Elo Score	Observation time (HH:MM)
Norm	**Male**	**1542**	**15:10**
Michael	**Male**	**1495**	**10:16**
Drogba	**Male**	**1405**	**3:06**
Appo	**Male**	**1217**	**8:20**
Falcao	**Male**	**1127**	**5:52**
Hilda	**Female**	**1411**	**16:02**
Agatha	**Female**	**1254**	**10:39**
Helena	**Female**	**1204**	**11:01**
Nina	**Female**	**1194**	**13:36**
Sophie	**Female**	**1160**	**6:05**
Libia	**Female**	**1090**	**13:44**
Dorothee	**Female**	**1079**	**6:10**
Odile	**Female**	**1072**	**14:10**
Lana	**Female**	**1046**	**11:29**
Ivette	**Female**	**1022**	**7:23**
Tina	**Female**	**1014**	**11:50**
Emma	**Female**	**1003**	**9:56**
Mary	**Female**	**950**	**12:35**
Fiji	**Female**	**921**	**12:26**
Lama	**Female**	**908**	**10:02**
Mona	**Female**	**906**	**19:05**
Oval	**Female**	**900**	**16:07**
Fiona	**Female**	**850**	**14:30**
Sri Lanka	**Female**	**849**	**5:53**
Elizabeth	**Female**	**830**	**16:34**

Teresa	**Female**	**761**	**11:00**
Svenia	**Female**	**754**	**11:59**
Jeanne	**Female**	**741**	**10:21**
Johanna	**Female**	**735**	**13:43**
Caterina	**Female**	**733**	**4:02**
Veronica	**Female**	**690**	**8:37**
Edith	**Female**	**626**	**9:49**
Tatiana	**Female**	**568**	**19:22**
Total			**370:56**

Appendix 4. Dyadic composite sociality index (DSI) scores calculated from socio-positive behaviours ‘approach’, ‘inspection’, ‘presenting groom’, ‘contact’, ‘groom’, ‘handle infant’ and ‘hug’. In this table we only present dyads that had a DSI score higher than 0. RT’ are the rates for each behaviour. To calculate the DSI, the interaction rates for these behaviours were collected for each dyad, and then these rates were combined to form the final DSI score, which indicates the overall strength of the relationship.

i1	**i2**	**approach**	**buttinsp**	**buttpres**	**contact**	**groom**	**handle_baby**	**hug**	**approach.rt**	**buttinsp.rt**	**buttpres.rt**	**contact.rt**	**groom.rt**	**handle_baby.rt**	**hug.rt**	**DSI**	**zDSI**
Agatha	Fiona	4	0	0	0	273	0	0	14,29	0	0	0	38,35	0	0	7,52	1,69
Agatha	Hilda	1	0	0	0	519	0	0	3,57	0	0	0	72,90	0	0	10,92	1,83
Agatha	Johanna	1	0	0	0	17	0	0	3,57	0	0	0	2,39	0	0	0,85	0,07
Agatha	Lana	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Agatha	Odile	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Agatha	Veronica	1	0	0	0	0	1	0	3,57	0	0	0	0	80,14	0	11,96	1,30
Appo	Mona	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Appo	Nina	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Appo	Odile	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Caterina	Edith	2	0	0	0	284	0	1	7,15	0	0	0	39,89	0	23,38	10,06	1,90
Caterina	Elizabeth	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Caterina	Falcao	0	0	1	0	0	0	0	0	0	24,39	0	0	0	0	3,48	0,49
Caterina	Hilda	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Caterina	Lana	2	0	0	0	10	0	1	7,15	0	0	0	1,40	0	23,38	4,56	0,94

Caterina	Mary	2	0	0	0	77	0	1	7,15	0	0	0	10,82	0	23,38	5,91	1,17
Caterina	Mona	2	0	0	0	0	0	2	7,15	0	0	0	0	0	46,75	7,70	1,55
Caterina	Odile	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Caterina	Sophie	2	0	0	0	25	0	1	7,15	0	0	0	3,51	0	23,38	4,86	0,99
Caterina	Svenia	2	0	0	1	0	0	1	7,15	0	0	10,58	0	0	23,38	5,87	1,36
Caterina	Tatiana	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Dorothee	Hilda	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Dorothee	Lama	1	0	0	0	0	1	0	3,57	0	0	0	0	80,14	0	11,96	1,30
Drogba	Emma	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Drogba	Hilda	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Drogba	Libia	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Drogba	Oval	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Edith	Falcao	0	0	1	0	0	0	0	0	0	24,39	0	0	0	0	3,48	0,49
Edith	Fiji	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Edith	Fiona	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Edith	Helena	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Edith	Jeanne	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Edith	Johanna	2	0	1	0	49	0	0	7,15	0	24,39	0	6,88	0	0	5,49	1,14
Edith	Lama	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Edith	Libia	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47

Edith	Mona	3	0	0	2	0	0	1	10,72	0	0	21,17	0	0	23,38	7,89	2,06
Edith	Sophie	1	0	0	0	55	0	0	3,57	0	0	0	7,73	0	0	1,61	0,20
Edith	Svenia	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Edith	Tatiana	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Edith	Teresa	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Elizabeth	Falcao	0	0	0	0	103	0	0	0	0	0	0	14,47	0	0	2,07	0,13
Elizabeth	Jeanne	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Elizabeth	Lana	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Elizabeth	Tatiana	2	0	0	0	16	0	0	7,15	0	0	0	2,25	0	0	1,34	0,31
Elizabeth	Teresa	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Emma	Fiji	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Emma	Fiona	1	0	0	0	0	1	0	3,57	0	0	0	0	80,14	0	11,96	1,30
Emma	Johanna	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Emma	Lama	1	0	0	0	75	0	0	3,57	0	0	0	10,53	0	0	2,02	0,27
Emma	Libia	2	0	0	1	161	0	0	7,15	0	0	10,58	22,61	0	0	5,76	1,28
Emma	Mary	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Emma	Nina	1	0	0	0	249	0	0	3,57	0	0	0	34,97	0	0	5,51	0,88
Emma	Odile	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Falcao	Fiji	0	1	0	0	74	0	0	0	43,15	0	0	10,39	0	0	7,65	0,98
Falcao	Hilda	0	0	1	0	0	0	0	0	0	24,39	0	0	0	0	3,48	0,49

Falcao	Tina	0	0	0	0	165	0	0	0	0	0	0	23,18	0	0	3,31	0,35
Fiji	Fiona	1	0	0	0	11	0	0	3,57	0	0	0	1,55	0	0	0,73	0,05
Fiji	Johanna	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Fiji	Lana	2	0	0	0	0	0	2	7,15	0	0	0	0	0	46,75	7,70	1,55
Fiji	Libia	1	0	0	0	9	0	0	3,57	0	0	0	1,26	0	0	0,69	0,04
Fiji	Mary	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Fiji	Odile	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Fiji	Oval	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Fiji	Tatiana	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Fiona	Helena	1	0	0	0	281	0	0	3,57	0	0	0	39,47	0	0	6,15	1,00
Fiona	Hilda	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Fiona	Lama	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Fiona	Lana	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Fiona	Libia	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Fiona	Michael	2	0	0	0	13	0	0	7,15	0	0	0	1,83	0	0	1,28	0,30
Fiona	Tatiana	1	0	0	0	5	0	0	3,57	0	0	0	0,70	0	0	0,61	0,03
Fiona	Tina	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Fiona	Veronica	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Helena	Lama	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Helena	Libia	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47

Helena	Nina	3	0	1	1	0	0	1	10,72	0	24,39	10,58	0	0	23,38	9,87	2,32
Helena	Sophie	1	0	0	0	112	0	0	3,57	0	0	0	15,73	0	0	2,76	0,40
Helena	Svenia	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Helena	Tatiana	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Helena	Teresa	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Hilda	Mary	1	0	0	0	160	0	0	3,57	0	0	0	22,47	0	0	3,72	0,57
Hilda	Nina	2	0	0	1	14	0	0	7,15	0	0	10,58	1,97	0	0	2,81	0,76
Hilda	Norm	2	0	0	1	26	0	0	7,15	0	0	10,58	3,65	0	0	3,05	0,80
Hilda	Sophie	2	0	0	0	52	0	0	7,15	0	0	0	7,30	0	0	2,06	0,43
Hilda	Tatiana	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Ivette	Teresa	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Jeanne	Johanna	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Jeanne	Michael	1	0	0	0	17	0	0	3,57	0	0	0	2,39	0	0	0,85	0,07
Jeanne	Sri Lanka	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Jeanne	Tatiana	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Johanna	Lama	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Johanna	Lana	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Johanna	Mary	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Johanna	Odile	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Johanna	Tatiana	3	0	0	1	68	0	0	10,72	0	0	10,58	9,55	0	0	4,41	1,19

Johanna	Teresa	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66
Lama	Lana	2	0	1	0	0	1	0	7,15	0	24,39	0	0	80,14	0	15,95	2,26
Lama	Libia	2	0	0	1	143	0	0	7,15	0	0	10,58	20,09	0	0	5,40	1,21
Lama	Mona	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Lama	Nina	3	0	0	1	299	0	0	10,72	0	0	10,58	42,00	0	0	9,04	2,00
Lama	Oval	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Lama	Tatiana	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Lama	Tina	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Lana	Libia	2	0	1	1	0	0	0	7,15	0	24,39	10,58	0	0	0	6,02	1,43
Lana	Mary	2	0	0	0	18	0	1	7,15	0	0	0	2,53	0	23,38	4,72	0,96
Lana	Michael	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Lana	Mona	1	0	0	0	195	0	0	3,57	0	0	0	27,39	0	0	4,42	0,69
Lana	Norm	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Libia	Mary	2	0	0	0	0	1	1	7,15	0	0	0	0	80,14	23,38	15,81	2,19
Libia	Odile	1	0	0	0	316	0	0	3,57	0	0	0	44,39	0	0	6,85	1,12
Libia	Svenia	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Libia	Tatiana	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Libia	Veronica	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Mary	Michael	2	0	0	0	83	0	0	7,15	0	0	0	11,66	0	0	2,69	0,54
Mary	Nina	1	0	0	0	0	0	1	3,57	0	0	0	0	0	23,38	3,85	0,66

Mary	Odile	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Mary	Tatiana	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Mary	Teresa	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Michael	Nina	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Michael	Svenia	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Mona	Svenia	1	1	0	0	0	0	0	3,57	43,15	0	0	0	0	0	6,68	0,96
Mona	Teresa	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Nina	Sophie	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Nina	Tina	1	0	0	0	0	1	0	3,57	0	0	0	0	80,14	0	11,96	1,30
Nina	Veronica	1	0	0	0	0	1	0	3,57	0	0	0	0	80,14	0	11,96	1,30
Odile	Solange	1	0	1	0	0	0	0	3,57	0	24,39	0	0	0	0	3,99	0,73
Odile	Veronica	1	0	0	1	0	0	0	3,57	0	0	10,58	0	0	0	2,02	0,47
Svenia	Tatiana	3	1	0	2	0	0	0	10,72	43,15	0	21,17	0	0	0	10,72	2,36
Svenia	Teresa	1	0	0	0	20	0	0	3,57	0	0	0	2,81	0	0	0,91	0,08
Tatiana	Teresa	2	0	0	2	0	0	0	7,15	0	0	21,17	0	0	0	4,05	1,17