https://doi.org/10.35662/unine-thesis-2699

Social influence on vocal communication in wild vervet monkeys

PhD thesis submitted to the faculty of Sciences

Institute of Biology

University of Neuchâtel, Switzerland

For the degree of PhD in Biology

within the Interuniversity Doctoral Program in Organismal Biology

by

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Defended on the 17th of September 2018

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I. General abstract

Vervet monkeys have been studied for decades, with important work on their alarm calling behaviour and cognitive capacities, but comparatively little is known about how their vocal behaviour is affected by the social environment. Signal production is always linked to costs, including attracting the attention of predators. Evolutionary theory predicts that call production must confer some type of benefit to the caller, either by favouring the caller itself or important social partners, such as kin or strongly bonded partners. Identifying the benefit, thus, becomes equivalent with identifying the call's function.

The aim of this thesis was to investigate vocal communication of wild vervet monkeys in three specific situations. First, using natural observations, I examined the general pattern of grunt production, an acoustic greeting signal produced during close dyadic encounters. I found that grunts were produced in seemingly strategic ways, by drawing the attention of valuable partners in ways that increased the caller's chances of survival in situations of elevated predation risks. Second, using natural and experimental situations, I studied the acoustic structure of screams given during agonistic interactions. I found that screams varied according to the identity and social role of signallers (aggressors vs. victims), as well as the severity of the conflict (mild vs. severe). I concluded that such information could be crucial for bystanders to take decisions as to whether or not to intervene in a fight. Finally, looking at competitive feeding situations, I examined subjects' screaming behaviour when approached by other group members as a function of their presumed social expectations. Here, in addition to suggesting an understanding of social expectations from an early age, my results also suggest that only adult females appeared to have a fully developed awareness and will to recognise and protest against other group members that committed violations of physical and social norms. In sum, my results demonstrated that the social environment affected vervet monkey call production in three different social situations, highlighting the importance of the social context when studying animal communication.

My results have some wider implications, also regarding the evolution of human language. Humans routinely make use of vocal behaviour to inform ignorant recipients of relevant external events, suggesting that research on audience-awareness, and social influence on vocal communication more generally, is essential in making progress in understanding human evolution. Finally, I discuss my findings in light of possible future investigations, such as the use of multi-modal signals, call combinations and deceptive signalling.

"The single biggest problem in communication is the illusion that it has taken place."

George Bernard Shaw

II. General introduction

2.1 Social cognition

Animals living in groups face several challenges when interacting with conspecifics. Beside adapting their behaviours according to their environments (e.g. terretrial vs. arboreal: Clutton-Brock and Harvey 1977), individuals should also adapt their behaviours according to their own physical and social characteristics (e.g. sex and age: Lusseau and Newman 2004), to the ones of other group members (e.g. peer migration: Cheney and Seyfarth 1983), as well as to the quality of their dyadic relationships (e.g. 'friendship': Seyfarth and Cheney 2012). Some hypotheses thus suggest that large brains have evolved as a consequence of the needs for individuals to possess advanced cognitive skills permitting them to know their social position within a group, to predict interactions with or between other group members and to behave in socially appropriate ways ('Social intelligence hypothesis': Jolly 1966, 'Machiavellian intelligence': Byrne and Whiten 1989, 'Social brain hypothesis': Dunbar 1998). Predicting outcomes of social interactions might be beneficial in tense situations as it allows reducing competition, for example, when individuals approach feeding sites already occupied by conspecifics. In this context, social knowledge can be used to avoid aggressive higher-ranking individuals, while approaching more tolerant, related individuals (Barton and Whiten 1993). For that, individuals must possess some cognitive abilities allowing them to know their positions within the group and individually recognise characteristics of other group members (Yorzinski 2017).

2.2 Individual recognition

Individual recognition is a mechanism allowing individuals to perceive features of other group members, such as their identity, age-sex or social relationships. It is widespread in animals and can be based on chemical cues (e.g. ant queens: D'Ettorre and Heinze 2005, or male mice: Kaur, Ackels et al. 2014), visual signals (e.g. chickens: Guhl and Ortman 1953, or paper wasps: Tibbetts 2002), vocal signals (e.g. territorial passerines: Stoddard 1996, or chimpanzees: Kojima, Izumi et al. 2003) or multi-modal signals (e.g. salamanders: Davis and Ovaska 2001, or dogs: Adachi, Kuwahata et al. 2007). The production of individually distinctive signals is adaptive, allowing receivers to classify individuals in categories such as offspring, kin, mates, social partners or potential rivals, and adopt appropriate behavioural responses. For example, identifiable contact calls emitted by juvenile baboons physically separated from the rest of the group offer them safer positions by relocating their mothers (Rendall, Notman et al. 2009). Similarly, individual signatures conveyed by loud calls produced by several forest primate species also help maintaining within-group cohesion and cooperation, while mediating space between groups and thus avoiding aggressive encounters with neighbours (Waser 1977). Strong selection pressure favoured individual recognition, especially kin, as in addition to benefits close relatives by, for example, intervening to help offspring involved in conflicts (Cheney 1977), it also benefits helpers through kin selection (Hamilton 1964).

2.3 Kin selection

Kin selection increase animals' inclusive fitness by adapting their behaviours according to the needs of relatives, protecting them and increasing their survival rates (Hamilton 1964). This is crucial in dangerous situations such as when encountering predators. Offspring, due to their relatively small size and lack of experience, are more vulnerable to danger than bigger, more experienced individuals (Longland and Jenkins 1987). Consequently, it is likely that cognitive abilities that permitted signallers to adjust their behaviours according to the presence of kin would be selected for. For example, several species produce a higher rate of alarm calls when surrounded by kin compared to non-kin, suggesting that kin selection has favoured the ability to maximise calling behaviour when the benefits are high

(Zuberbühler 2006). Individuals can thus adapt their behaviours according to the audience. For example, new immigrant adult male ground squirrels not related to other group members, remained silent when encountering predators, while adult females were more likely to alarm call, especially in the presence of kin (Dunford 1977). Signallers also adapt their vocal behaviour when in presence of valuable food items, by calling more in the presence of close relatives (Hauser and Marler 1993), which has at least two possible benefits: increased access to food for both signallers and their kin, and better food defence from other rivals through alliance formation.

2.4 Social relationships

An individual's reproductive success can be affected by its social relationships within a group (Cheney, Seyfarth et al. 1986). Closely bonded individuals, or 'friends', typically spend more time together, grooming each other at higher rates and supporting one another more during aggressive interactions than non-friends (Smuts 2017). Food calls of wild chimpanzees, for example, are not produced spontaneously when discovering food, but are selectively emitted towards important social partners (Schel, Machanda et al. 2013). Sharing strong bonds with non-relatives can help individuals to increase survival through increased cooperation (Berghänel, Ostner et al. 2011) and predator defence (Micheletta, Waller et al. 2012). For instance, listeners are more likely to respond to recruitment alarm calls produced by friends than by individuals with whom they share weaker bonds (Kern and Radford 2016). However, in order to form and maintain such bonds, individuals must encounter each other regularly, recognise individually other group members, remember past interactions and adjust their social behaviour accordingly (Trivers 1971).

2.5 Third-party relationships

Sophisticated cognitive skills allow animals to recognise not only their own social relationships with conspecifics, but also relationships between other group members, so called third-party relationships (Silk 1999). By observing interacting individuals, a third member not involved in the interaction, gains social knowledge that is highly beneficial to get a better understanding of the social structure of a group, driving individuals to behave in socially appropriate ways. Transitive inference, that is, deducing features of an individual from observing several social relationships (e.g. knowing that A>B and B>C helps to infer that A>C), is a mechanism that allows individuals to make some reasoning about the social status of other group members by observing third-party relationships, without having to interact directly with every single individual from a group (Cheney, Seyfarth et al. 1986). Although cognitively demanding, this ability has been demonstrated in many social animals ranging from fish (e.g. *Astatotilapia burtoni*: Grosenick, Clement et al. 2007), to birds (e.g. pinyon jays: Bond, Kamil et al. 2004), and mammals (e.g. rats: Davis 1992), but most studies have been realised with primates (e.g. chimpanzees: Gillan 1981, squirrel monkeys: McGonigle and Chalmers 1992, lemurs: MacLean, Merritt et al. 2008, rhesus monkeys: Gazes, Chee et al. 2012).

2.6 Social expectations

Knowing the social status of other group members, i.e., dominance ranks and friendships, is indeed useful as it allow individuals to have some social expectations that can be used in alliance formations. For example, male bonnet macaques use this knowledge to recruit specific allies that are higher-ranking than both themselves and their opponents, which increases their likelihood of winning agonistic interactions (Silk 1999). Similarly, hamadryas baboon males adapt their behaviours and refrain from taking over females that share strong bonds with their rivals, thus demonstrating knowledge of others' friendship (Bachmann and Kummer 1980). As individuals sometimes redirect aggression to third-parties following a fight (Cheney and Seyfarth 1989), especially towards relatives of opponents (Engh, Siebert et al. 2005), it is also beneficial for bystanders to initiate reconciliation between interacting individuals in order to decrease further risks of attacks (De Waal and Waal 2007).

Furthermore, social expectations also help to maintain cooperative partners as they dictate how one individual should behave, and ‘punish’ individuals that do not follow the rules (Yamamoto and Takimoto 2012). While following social rules in a group is adaptive, insofar as individuals with similar behavioural patterns generally cooperate better than individuals who do not coordinate their activities (Fehr, Fischbacher et al. 2002, Senigaglia, de Stephanis et al. 2012), it could also be costly for individuals in the presence of individuals that do not follow social rules, commonly called ‘free-riders’. By not behaving in predictable ways, free-riders can potentially damage public goods, such as enjoying defended resources without participating in territorial conflicts with neighbouring groups (Nunn and Deaner 2004). Consequently, punishing these individuals helps to maintain cooperation in a group by forcing them to behave in what others perceive as socially acceptable (Fehr and Fischbacher 2004b).

Experiments with captive animals demonstrated that some species have a sense of ‘fairness’ and protest in situations where their expectations are not met. Inequity aversion, that is, the reaction of individuals towards inequitable outcomes such as getting food rewards of lower value than partners, has been demonstrated in several species ranging from rhesus monkeys (Wechkin, Masserman et al. 1964) to capuchins (Brosnan and De Waal 2003), long-tailed macaques (Massen, Van den Berg et al. 2012), chimpanzees (Brosnan, Schiff et al. 2005), dogs (Range, Horn et al. 2008), rats (Oberliessen, Hernandez-Lallement et al. 2016) and some bird species including crows and ravens (Wascher and Bugnyar 2013). To my knowledge, however, studies looking at the reactions of individuals when social expectations are violated remain scarce with only one study showing some vocal protest by semi-captive bonobos towards unexpected aggressions (Clay, Ravaux et al. 2016). In addition, to get insights into how the social environment can influence vocal communication in signallers, investigating vocal protests when expectations are violated also allows researchers to get better understanding on what signallers know about the social structure of their group.

2.7 Audience effects

Knowing the identity, physical and social characteristics of other group members has important consequences, as the mere presence of bystanders around an individual already influences its behaviour (Zuberbühler 2008). Such ‘audience effects’ are widespread across species (e.g. cockroaches: Zajonc, Heingartner et al. 1969, chickens: Evans and Marler 1994, Siamese fighting fishes: Matos and McGregor 2002, meerkats: Townsend, Rasmussen et al. 2012, humpback whales: Dunlop 2016) and contexts (e.g. predator encounter: Karakashian, Gyger et al. 1988, conflict: Slocombe and Zuberbuhler 2007, copulation event: Townsend and Zuberbuhler 2009, food discovery: Schel, Machanda et al. 2013).

To date, non-human primates have been a focus for a great deal of research into audience effects due to their rich and complex social systems, e.g. red-bellied tamarins (Caine, Addington et al. 1995), Thomas langurs (Wich and Sterck 2003), capuchin monkeys (Coyne 2010), rhesus macaques (Overduin-de Vries, Massen et al. 2012), chimpanzees (Crockford, Wittig et al. 2012) or bonobos (Clay and Zuberbühler 2012). While some studies looked at audience effects using gestural communication, such as orang-utans adjusting the use of gestures to reach non-accessible food items according to different degrees of experimenters’ understanding (Cartmill and Byrne 2007), most of them imply the use of vocal signals, with call production varying according to the absence or presence of specific individuals. For example, cockerels increase food calling in the presence of familiar females and decrease call production in the presence of males (Marler, Dufty et al. 1986). Although the presence of socially important partners usually favour call production (Slocombe, Kaller et al. 2010b), the presence of alpha individuals can also have inhibitory effects (Laporte and Zuberbühler 2010). Individuals might also vocalise strategically according to their social position relative to other group members: while low-ranking individuals should refrain from calling in the presence of an audience to avoid attracting powerful individuals around valuable resources (reducing feeding competition), high-ranking individuals should increase their call production to signal food possession, attract important social partners and help maintaining group cohesion (Clark 1993).

2.8 Vocal communication

The production of vocal signals is one of the most effective ways to attract attention and convey information in animals living in dense habitats, where visual cues are not always efficient. One suggested function has been for callers to directly influence receivers through specific acoustic features, for example by acoustic features that increase the attention level of listeners, or features that are perceived as repellent and aversive, such as calls with chaotic spectral features (Owren and Rendall 2001). One popular theory is Morton's motivational-structural rules (1977) that describe the general pattern of acoustic variation in animal calls according to the context of production. While vocalisations produced during hostile situations tend to be of low frequency with a broadband frequency range, vocalisations produced in friendly or fearful situations are often tonal with high frequencies (Morton 1977). Another theory that focuses on differences in the acoustic structure of vocal signals is on presumed underlying emotional states in animals (Briefer 2012). A key component is the notion of 'valence', that is, whether a situation is perceived as positive or negative. This is predicted to be linked to the call's energy distribution and frequency spectrum whereas arousal, reflecting the situation's intensity, should be linked to fundamental frequency, duration and rate of calling (Mendl, Burman et al. 2010, Briefer 2012). Consequently, by paying careful attention to calls' acoustic properties, listeners can extract crucial information about the caller's presumed emotional state and adapt their behaviour accordingly.

Calls are also important for individuals to recognise others by their voice through individual signatures (e.g. whistles of bottlenose dolphins: Sayigh, Tyack et al. 1990, eight call types of wild western gorillas: Salmi, Hammerschmidt et al. 2014, barks and roars of black howler monkeys: Briseño-Jaramillo, Estrada et al. 2015, bark-howls of dingoes: Déaux, Charrier et al. 2016). In addition to identity, listeners might extract physical attributes of signallers, such as age, sex or body size (e.g. Fitch 1997, Briefer and McElligott 2011), or hormonal levels (e.g. Wada 1982, Charlton, Keating et al. 2011). Furthermore, information concerning the social position of signallers can also be encoded in vocal signals, such as their social rank (e.g. Kitchen, Seyfarth et al. 2003, Fischer, Kitchen et al. 2004) and friendships (e.g. Snowdon and Elowson 1999, King, Harley et al. 2014). Finally, listeners might also extract information about the general context of call production (e.g. Fischer, Hammerschmidt et al. 2002, Crockford, Gruber et al. 2018), as well as a situation's urgency (e.g. Manser 2001, Fichtel and Hammerschmidt 2002). Appropriate responses from listeners increase signallers' fitness, either directly by receiving support or indirectly via kin selection (Hamilton 1964). Consequently, evolution favoured 'honest vocal signals' that encode specific information related to emotional states of signallers or peculiar external events.

2.9 Vervet monkeys

Vervet monkeys are one of the most studied Old World Monkeys due to their interesting social structure, complex communication system and developed cognitive skills.

2.9.1 Taxonomy

Formerly described as *Cercopithecus spp.*, the taxonomy of vervet monkeys is under constant revision (Grubb, Butynski et al. 2003). Nowadays, they are considered as *Chlorocebus spp.* (Turner, Schmitt et al. 2018) and at least seven species are recognised. Here, we studied vervet monkeys from South Africa, *Chlorocebus pygerythrus pygerythrus*, which are the biggest vervet species showing the least sexual dimorphism (Turner, Schmitt et al. 2018). Adult males are bigger than females (Horrocks 1986), reaching an average full body size at around 5.69kg, compared to an average full body size at around

4.09kg for females (Turner, Schmitt et al. 2018). Females give birth once per year, with seasonal births varying across study sites, but usually ranging from September to February (Arseneau, Taucher et al. 2015, Young, McFarland et al. 2017). Infants are born black with pink faces and colours change gradually to reach adult coloration at the age of 12 weeks old (Lee 1984). Adults have yellow to greenish coats with black faces, hands and feet, and bluish skin on their abdomens. Adult males also have coloured genital parts, i.e., bright blue scrotums and red penises that can be used as visual cues signalling dominance, that is, the 'Red, White and Blue display' (Struhsaker 1967a, Rowe 1996).

2.9.2 Habitat & territory

Being present in more than 39 African nations, vervet monkeys are one of the most abundant and widespread of all African monkeys (Struhsaker 1967b, Cardini, Jansson et al. 2007, De Jong and Butynski 2012). Inhabiting large parts of sub-Saharan Africa, ranging from Senegal to Ethiopia and along the East coast from Eritrea down to South Africa (Turner, Schmitt et al. 2018), they can adapt easily to different environments, including tropical rainforests, mangrove swamps, lowland and mountainous forests, thorn and scrub forests, grassland and savannah environments (Struhsaker 1967b). However, water being an important limiting resource, there is an apparent preference for riverine environment (Fedigan and Fedigan 1988, Enstam and Isbell 2007, Mercier 2011). Although the territory size of vervet groups depends on the composition and distribution of the vegetation and other socio-ecological factors, such as group size (Fedigan and Fedigan 1988), it can vary from 0.1km to a few square kilometres (Struhsaker 1967b), with an average size of 1.6km^2 in our study site (Mercier 2011). Being opportunistic omnivores, they have successfully adapted to "human disturbed" habitats, i.e., agricultural areas and touristic places, and can even become a major pest in areas where they are forced into close proximity with humans (Barret, Brown et al. 2006).

2.9.3 Social structure

Vervet monkeys live in relatively stable and heterosexual groups composed of multi-male, multi-female groups, with an adult sex ratio of 1.5 females to 1 male (Fedigan and Fedigan 1988). Group size can vary from approximately five to 76 individuals (Fedigan and Fedigan 1988), with a mean of 33 individuals in our study groups (Eichenberger 2017). Adults being responsible of the cohesive unit in a group, a minimum of two adults are needed to maintain a group (Isbell, Cheney et al. 1991). Groups can sometimes fusion with neighbouring groups when only one adult is left (Isbell, Cheney et al. 1991). When group size is increasing, however, intragroup competition might lead to natural fissions, events rarely reported in the literature but observed a few times in our field site (van de Waal, van Schaik et al. 2017). Interactions with neighbouring groups are usually conflictual, especially in overlapping territories, due to intergroup competition to access valuable food resources or intensely used territory areas (Arseneau-Robar, Taucher et al. 2017). Apart from these rare fusion/fission events, migrations occur regularly within this species (Cheney and Seyfarth 1983), usually during the mating season from April to June (Henzi and Lucas 1980, Sobrino 2018). While males emigrate from their natal groups when reaching sexual maturity (at around four years old) and change social groups several times throughout their lifetimes to avoid inbreeding (Struhsaker 1967c), females are philopatric and remain in their natal group throughout their lives (Cheney and Seyfarth 1992). Females thus share strong bonds with their close relatives that last for their whole lives, bringing them support when involved in agonistic interactions through powerful coalitions that are necessary to maintain social positions in a group (Cheney and Seyfarth 1980). Matrilineal kinship units are thus considered as the most important social structure in vervet monkey groups (Cheney and Seyfarth 1992).

Dominance relationships differ according to the sex of individuals. Males have unstable linear hierarchies that are mainly based on their fighting abilities (Cheney and Seyfarth 1992). The rank of young males depend on that of their mothers' when remaining in their natal group, but relates to their physical conditions when migrating to new groups, getting highest ranking when fully grown up and experienced at around six to ten years old (Henzi and Lucas 1980). Although females can improve the social status of preferred partners (Young, McFarland et al. 2017), males need to maintain their social rank by outperforming new challenging immigrants. In contrast to males, females have clear linear dominance hierarchies that are relatively stable over time due to coalitionary support received by close relatives (Fairbanks and McGuire 1986). Female hierarchies are organised according to matrilines, with offspring inheriting the rank of their mothers (Cheney and Seyfarth 1992), and the youngest offspring of a matriline getting the highest rank (Cheney and Seyfarth 1980). Juvenile females usually keep their social rank through their lifetime. Rank reversals between matrilines can occur in rare cases, for example when a large family challenges a smaller but higher-ranking one, as it's also the case in female baboons (Samuels, Silk et al. 1987). While males, being bigger than females, are dominant over females in one-to-one interactions, female coalitions are dominant over any male (Cheney and Seyfarth 1992), demonstrating the importance of social relationships in this species.

2.9.4 Cognitive abilities

Vervet monkeys living in large socially structured groups have evolved advanced cognitive skills allowing them to face various social challenges when interacting with other group members, as well as with neighbouring groups. Results from playback experiments demonstrated, for example, that individuals could recognise juveniles through their voice alone, with males and females responding more strongly to playbacks of screams produced by their (potential) offspring compared to the ones produced by unrelated juveniles (Cheney and Seyfarth 1980, Hauser 1986). Besides demonstrating flexible behavioural responses to individually distinctive signals, adult females can also recognise third-rank relationships. 'Control' females, i.e., unrelated adult females that participated in the playback experiments, looked towards the mother of the screaming juvenile rather than the juvenile itself, suggesting an ability to identify mother-offspring relationships (Cheney and Seyfarth 1980). Although third-party rank relationships seem well developed in adult females, they differ according to the age-sex class of individuals (Borgeaud, Alvino et al. 2015). Furthermore, audience effects in vervet monkeys have been shown with captive individuals in a predatory context (Cheney and Seyfarth 1985). While physical and social features of signallers influenced their alarm calling behaviour, with high-ranking individuals alarm calling at higher rates than low-ranking ones (Cheney and Seyfarth 1981), natural observations of free-ranging vervet monkeys also revealed that alarm call production of vervet monkeys is under voluntary control, with low-ranking individuals potentially withholding information upon detecting predators (Cheney and Seyfarth 1981).

Other playback experiments showed that alarm calling depended on the social context. For example, females alarm called at a higher rate when in the presence of their own offspring than in the presence of unrelated juveniles, whereas males were more likely to call in the presence of females than in the presence of other adult males (Cheney and Seyfarth 1985). Audience effects have also been shown in their social interactions, such as when individuals trade grooming for tolerance from higher-ranking individuals (Borgeaud and Bshary 2015), with lower tolerance in the presence of higher-ranking bystanders (Borgeaud, Schnider et al. 2017). Recent studies also demonstrated that females remembered actions of other group members, by 'rewarding' (with social grooming) cooperative males that were active during fights with neighbouring groups and 'punishing' (with aggression) males that did not participate (Arseneau-Robar, Taucher et al. 2016). Similarly, males also punished females that were promoting between-group fights, a possible mechanism that would help avoiding conflict escalation and decreasing the intensity of ongoing aggressive encounters (Arseneau-Robar, Müller et al. 2018).

2.9.5 Communication

The description of vervet monkey cognitive skills has been possible thanks to extensive work on their vocal system. The vocal repertoire of vervet monkeys was first described using 36 spectrographically and/or audibly distinct sounds produced in several contexts such as while encountering other group members or neighbouring groups, during the first phase of group progression, while being separated from other individuals, during agonistic interactions or while encountering predators (Struhsaker 1967a). Alarm calls are by far the most studied vocalisations in this species (Seyfarth and Cheney 1980, Cheney and Seyfarth 1981, Cheney and Seyfarth 1985, Price and Fischer 2013). Individuals from all age-sex classes produce distinct vocalisations depending on the type of predators encountered. ‘Leopard alarm calls’ are produced towards dangerous terrestrial mammals such as leopards, servals or caracals, ‘eagle calls’ are emitted when encountering several species of raptors (e.g. crowned or martial eagles) and ‘snake calls’ are produced towards dangerous snakes (e.g. black mamba or Mozambique spitting cobra). The emergence of acoustically distinctive alarm calls in this species is likely a consequence of the different escaping strategies required in response to the hunting techniques used by the predators. Vervet monkeys respond appropriately to different alarm call types by running up in trees for leopard calls, scanning the air/running into bushes for eagle calls and standing up bipedal for snake calls (Seyfarth, Cheney et al. 1980a; *see QR codes at the end of Appendix 1 from chapter 1 to watch their reactions during playback experiments of leopard and snake alarm calls*). Since their alarm calls are used to denote different external events and generate appropriate escaping behaviour, they have first been described as being “functionally referential signals” (Macedonia and Evans 1993). However, vervet monkeys also use alarm calls in other non-predatory contexts such as during aggressive encounters (Price, Wadewitz et al. 2015), thus violating one assumption of referential signalling. As a consequence, their referential nature has since been debated (Wheeler and Fischer 2012, Price and Fischer 2013). Beside alarm calls, few studies have investigated other call types, including the various grunt vocalisations produced during greeting interactions or when moving into open areas (Cheney and Seyfarth 1982, Seyfarth and Cheney 1984a, Seyfarth and Cheney 1986), and agonistic screams (Cheney and Seyfarth 1980, Hauser 1986).

Grunts have been described as short duration, low-pitched and pulsatile vocalisations that can be produced by individuals of all age-sex classes ('Woof'; Struhsaker 1967a). They are usually produced once or twice, are sometimes answered by other nearby individuals, and commonly serve to initiate group movement. However, individuals also grunt when approaching higher-ranking individuals, when approaching subordinates, when watching individuals crossing open areas or when detecting the presence of another group (Cheney and Seyfarth 1982). While all these calls sound similar to human ears, subtle difference in their acoustic structure allow individuals to differentiate between at least four different grunt types, suggesting that they might also be used to refer to specific events in their external world (Cheney and Seyfarth 1982). Listeners react differently upon hearing different grunt types. For example, grunts produced towards subordinates elicit movement away from the speaker, probably due to the simulated arrival of a higher-ranking individual, a pattern not found when hearing grunts produced towards higher-ranking individuals. Consequently, by examining in which context individuals grunt and observing how listeners react, one can get an understanding on the functional use of these vocalisations. However, despite few studies realised in the 80’s investigating the referential signalling aspect of vervet monkey grunts (Cheney and Seyfarth 1982), their acoustic features (Seyfarth and Cheney 1984a) and their vocal development (Seyfarth and Cheney 1986), not much work has been done on these vocalisations.

2.10 Aim of this research

Although vervet monkeys have been well studied over the past decades, relatively little work has been conducted on the social influence on their vocal communication. Apart from the effect of the presence of kin or mates, especially in predatory contexts and with captive animals, it remains largely unknown if other physical and social attributes of individuals (e.g. social rank or friendship) can influence the production of vocal signals in other contexts. As such, the aim of this study was to investigate the mechanisms underlying the vocal behaviour of wild vervet monkeys by examining how individuals adapt their signalling behaviours according to the presence, identity and social role of other group members in three different situations: when encountering other group members, during agonistic interactions and when social expectations are violated.

In the first chapter, I used natural observations to describe the general pattern of vocal greetings during dyadic encounters between group members. As vocalisations produced by an individual might target specific individuals, I investigated whether signallers could adapt their call production according to the identity of their partners. By doing so, signallers could get different advantages such as getting an increased tolerance from higher-ranking individuals by signalling submission, avoiding conflicts with reconciliatory signals, receiving more grooming from relatives that help to strengthen their bonds, and improving the coordination and so the cooperation in a group, which can be crucial when facing dangerous predators. Consequently, I used model selection theory to investigate the functional aspect of their greeting signals. If greeting signals are produced to express the social position of individuals as it is the case in wild chimpanzees (Laporte and Zuberbühler 2010), greeting calls in vervet monkeys are expected to be more common in male-male interactions due to their relative unstable hierarchy. In contrast, if greetings are used to test social bonds as in male Guinea baboons (Whitham and Maestripieri 2003), I expected more greeting exchanges between females that share strong bonds due to their relatedness. However, if greeting signals help reducing the level of aggression (de Waal and Roosmalen 1979), one would expect all individuals to produce a greater proportion of calls targeted at the most aggressive individuals in a group, especially after fights occurred to repair relationships. Finally, I expected all individuals to use greeting signals to improve social coordination, as all signallers would benefit from living in a social, cohesive and cooperative group. Results showed that the production of wild vervet monkey grunts is under voluntary control, with all individuals producing greeting calls, but targeting only adult males. As greetings were produced mainly near rivers where most of predator encounters occurred, I suggested a new functional use of these signals, that is, to reduce predation risks by increasing the attentional state of adult males, which are the most active individuals against predators. Results from this first chapter thus demonstrated vervet monkeys ability to recognise the physical power of individuals, and adapt their signalling behaviour accordingly.

In the second chapter, I analysed the acoustic structure of another vocalisation, i.e., the screams that are produced during agonistic interactions. I examined whether individuals could modify the properties of their calls according to their socio-ecological environment. Since agonistic interactions do not occur frequently in wild vervet monkeys, I recorded their screams both during natural observations as well as opportunistically around several experiments involving valuable food that is highly contested. Wild chimpanzees screams have been shown to vary according to the social role of signallers (victims vs. aggressors: Slocombe and Zuberbuhler 2005), conflict severity (mild vs. severe: Slocombe and Zuberbuhler 2007), and audience composition (Slocombe and Zuberbuhler 2007), with call exaggeration happening only if a higher-ranking bystander was present. Playback experiments further demonstrated that these acoustic cues were salient to receivers, who showed stronger responses to stimuli of severe than mild aggressions (Slocombe, Townsend et al. 2009). Apart from studies demonstrating individual signatures in vervet monkey screams that listeners could extract to adjust their behavioural responses (Cheney and Seyfarth 1980, Hauser 1986), little is known on the information encoded in their screams. Consequently, based on well-established animal communication theories, I investigated: 1) whether vervet monkeys can alter the acoustic features of their screams depending on their social role and conflict severity and 2) the potential functions of screams according to the age-sex class and social status of signallers. If these vocalisations are used to recruit help, it would be beneficial for the caller to convey information about the nature of the ongoing event. Since it would be more beneficial for victims to recruit help, especially juveniles involved in severe fights, one would expect them to produce distinct vocalisations from aggressors. However, if signallers are bigger and higher-ranking than their opponents, screams can then be used to directly repel them by advertising potential conflict escalation. Results from acoustic analyses showed that victim screams were longer and higher-pitched than aggressor screams, and screams produced in severe conflicts had higher entropy than screams emitted during mild conflicts. Differences in acoustic variations between screams produced in various contexts are also in line with the potential dual use of screams, that is, by victims to recruit help from bystanders and by aggressors to repel their opponent. Consequently, results from this second chapter demonstrated the ability of vervet monkeys to recognise and adapt their signalling behaviour according to some social characteristics of other group members.

The third and last chapter allowed me to go one-step further, that is, to investigate more advanced cognitive skills by examining vervet monkeys' ability to recognise 'cheaters', defined here as individuals that do not follow social expectations. To do so, I looked at their vocal reactions when approached by individuals that are not entitled to do so, either because of their physical and/or social characteristics. Bigger and higher-ranking individuals should indeed benefit from better access to food resources due to their stronger fighting abilities or higher social status, respectively. Protests against violations of social expectations has been demonstrated in several species in captivity, for example, with individuals refusing to participate in experiments if their partners received better food rewards for the same task (Brosnan and De Waal 2003). Similarly, semi-captive bonobos vocally protested by varying the acoustic structure of their screams depending on whether or not aggression was perceived as justified by victims (Clay, Ravaux et al. 2016). Due to their rich social system, vervet monkeys are an interesting species to investigate reactions to violations of social expectations. As offspring inherit the rank of their mothers, they can acquire high social status despite their relatively small sizes. Due to these contingencies, vervet monkey groups are structured along at least three social rules: (1) yield to anyone who is physically superior, (2) yield to anyone who is higher-ranking, (3) yield to anyone in the same matriline who is younger and has the second highest rank in the matriline due to the increased support received from mothers. Consequently, I studied the screaming responses of subjects that were feeding when approached by individuals from different age-sex classes. Results showed effects of body size and social rank differences, although patterns were mediated by the subjects' age-sex class, with juveniles protesting more when approached by bigger opponents and adults reacting during violations of physical power, i.e., approached by smaller individuals. As all individuals also reacted in stronger ways when approached by lower than higher-ranking individuals (i.e., violations of social power), results from this last chapter suggest an early understanding of social rules in this species. However, time is probably needed to develop appropriate cognitive abilities as young subjects first reacted to violations of physical characteristics (visual cues easily detectable) before being able to recognise and protest against violations of social power at a later stage through social knowledge acquired by experience.

Overall, results from my thesis show that the vocal behaviour of wild vervet monkeys is influenced by their social environment, with signallers adapting their call production according to the presence, identity and social role of surrounding individuals. Furthermore, it confirms the evolution of advanced cognitive skills in this species allowing individuals to adjust their behavioural responses according to their socio-ecological environment through the understanding of their social positions compared to the ones of other group members. This also highlights the importance of including social factors in vocal communication studies.

III. Chapter 1 - Vervet monkeys greet adult males during high-risk situations

Manuscript published in Animal Behaviour, Volume 132, October 2017, Pages 229-245, https://doi.org/10.1016/j.anbehav.2017.07.021

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Received 13 November 2016
Initial acceptance 19 January 2017
Final acceptance 12 June 2017
MS number 16-00988R

3.1 Abstract

Many animal species produce ritualized signals during dyadic encounters but the functions of such 'greeting' behaviour vary considerably, or is often unknown. One established function is to acknowledge existing dominance relationships. At the same time, call rates often increase during social tension, suggesting additional functions, such as to appease higher-ranking individuals, or to maintain spatial proximity and friendly relations. For vervet monkeys, *Chlorocebus pygerythrus*, vocal behaviour has been studied extensively, but little research has been devoted to calls given during encounters between two individuals, i.e. grunts. Here, we examined how individual and relationship features affected the vocal greeting behaviour of wild vervet monkeys in different ecological and social situations. We used an information theory approach to investigate the functional hypotheses of vervet monkeys' vocal greeting signals. We found little support for the main functions proposed in the literature, that is, to signal submission, to avoid conflicts, to test social bonds or to coordinate group activity. Results supported the use of grunts to signal benign intent, and we found that grunts were mostly given to closely bonded males near rivers, suggesting that vervet monkeys use vocal greeting signals to recruit individuals in situations of danger to reduce predation risks.

Keywords: *Chlorocebus pygerythrus*; greeting signal; predation risk; recruitment signal; vocal communication

3.2 Introduction

Living in groups involves both costs and benefits. Benefits can be derived from decreased predation risk, for example due to safety in numbers, predator confusion, decreased vigilance costs or cooperative defence (Krause and Ruxton 2002). Costs can emerge due to competition and increased time demands for social activities, such as the maintenance of social bonds, to the detriment of other essential activities, such as foraging (Lehmann, Korstjens et al. 2007, Majolo, de Bortoli Vizioli et al. 2008). Animals thus have to balance the costs incurred from living in groups and the benefits from their interactions with other group members.

One way by which group-living animals can manage their social relations is by performing ritualized behaviours during close encounters, which have been termed greetings (Hall 1962, Brown 1967). Greeting signals appear in various modalities, which include vocalisations (e.g. red-bellied woodpeckers, *Centurus carolinus*: (Kilham 1961); bottlenose dolphins, *Tursiops truncatus*: (Quick and Janik 2012); African wild dogs, *Lycaon pictus*: (Estes and Goddard 1967); African elephants, *Loxodonta africana*: (Poole 2011); mantled howlers, *Alouatta palliata*: (Dias, Rodriguez Luna et al. 2008) chimpanzees, *Pan troglodytes*: (Laporte and Zuberbühler 2010)), but also facial expressions, affiliative gestures and a variety of postures (e.g. lesser black-backed gulls, *Larus fuscus*: (Brown 1967) wild boars and warthogs, *Sus scrofa* and *Phacochoerus aethiopicus*: (Frädrich 1974) spotted hyaenas, *Crocuta crocuta*: (East, Hofer et al. 1993) baboons, *Papio* sp.: (Smuts and Watanabe 1990, Whitham and Maestripieri 2003) spider monkeys, *Ateles geoffroyi*: (Aureli and Schaffner 2007)).

Although greeting signals are relatively widespread in group-living animals, their exact function has remained mostly unclear. The current literature suggests five main functions to explain why animals signal to each other during close-range encounters. First, the 'benign intent hypothesis' posits that individuals use greeting signals in socially tense situations (e.g. around food resources or when outcomes of interactions are unpredictable) to signal willingness to interact in a friendly way (Bauers 1993, Silk 1996, Silk, Cheney et al. 1996, Silk 2000, Katsu, Yamada et al. 2014). For instance, wild female baboons use vocal signals to communicate benign intent when approaching mothers to increase the likelihood of affiliative contacts, especially with infants (Silk, Seyfarth et al. 2016).

Second, the 'conflict management hypothesis' posits that individuals use greeting signals to avoid conflicts and repair their relationships after agonistic interactions (de Waal and Roosmalen 1979). Reconciliatory grunts, for example, are produced by female baboons to encourage friendly approaches between former opponents (Cheney and Seyfarth 1997). During fusion events, spider monkeys and mantled howlers also use greeting signals, such as embraces, sniffs, throat rumbles, clucks or a variety of postures, presumably as a strategy to avoid conflicts (Aureli and Schaffner 2007, Dias, Rodriguez Luna et al. 2008).

Third, according to the 'signal submission hypothesis' individuals use greeting signals to acknowledge existing dominance relationships by advertising their inferior social status, which then increases social tolerance from higher-ranking individuals (de Waal 1986). This has been documented in wolves and dogs, *Canis lupus* sp. (Schenkel 1967), spotted hyaenas (East, Hofer et al. 1993) and rhesus macaques, *Macaca mulatta* (de Waal and Luttrell 1985). Another well-studied example is the pant-grunt of chimpanzees, produced by low-ranking individuals when encountering higher-ranking ones (Laporte and Zuberbühler 2010).

Fourth, the 'social coordination hypothesis' posits that individuals use greeting signals to increase group cohesion and to coordinate joint activities, which can have fitness benefits in terms of reducing predation risk (e.g. synchronized swimming of long-finned pilot whales, *Globicephala melas*: (Senigaglia, de Stephanis et al. 2012) or cooperative hunting (e.g. African wild dogs: (Estes and Goddard 1967). Similarly, male capuchins, *Cebus apella*, produce 'sirena' screams to increase social coordination with allies when encountering other groups (Lynch Alfaro 2008) and Hamadryas baboons, *Papio hamadryas*, use a ritualized form of presenting to recruit males to cooperate with them against rivals in getting access to females (Abegglen 1984). Observations on wild chimpanzees and crested macaques, *Macaca nigra*, showed that individuals produce lip-smacks, a nonvocal but audible behaviour in which the lips moved repeatedly during face-to-face encounters, when approaching other group members to elicit affiliative interactions, such as grooming (Micheletta, Engelhardt et al. 2013a, Fedurek, Slocombe et al. 2015a).

Fifth, the 'social bond testing hypothesis' posits that individuals use greeting signals to assess the quality of their social relationships. Here, the idea is that greeting behaviour can vary in terms of completeness, reciprocity and symmetry depending on the strength of the interacting individuals' social bond, and thus serves as a proxy to assess their mutual affiliation (Whitham and Maestripieri 2003). Signals are often intimate or risky, such as kissing, embracing, sniffing or, for males, inspecting and touching genitals (Wang and Milton 2003), as if males are 'literally placing their future reproductive success in the trust of another male' (Smuts and Watanabe 1990, p.169). Generally, these kinds of greetings are often between closely bonded individuals (e.g. spotted hyaenas: (Smith, Powning et al. 2011); spider monkeys: (Schaffner and Aureli 2005); Tonkean macaques, *Macaca tonkeana*: (De Marco, Sanna et al. 2014); capuchin monkeys: (Matheson, Johnson et al. 1996); chimpanzees: (Okamoto, Agetsuma et al. 2001)). Such potentially dangerous signals thus appear to strengthen their existing bonds.

Vervet monkeys, *Chlorocebus pygerythrus*, live in multimale/multifemale groups and various studies on their communication system have generated insights concerning their social cognition. For example, playback experiments of screams have demonstrated that mothers distinguish their own offspring from unrelated juveniles, while bystander females can allocate juveniles to their respective mothers (Cheney and Seyfarth 1980). Other work has shown that some call types convey relatively specific meanings to recipients, as demonstrated by the monkeys' reactions to playbacks of predator-specific alarm calls (Seyfarth, Cheney et al. 1980a, but see Price, Wadewitz et al. 2015) and different grunt variants (Cheney and Seyfarth 1982).

Grunts are an acoustically heterogeneous soft call type, produced in a range of situations, which includes group progression, as well as intra- and intergroup encounters (Struhsaker 1967a). During intragroup encounters, grunts appear to function as a greeting signal, and it has been proposed that the calls signal submission and inhibit aggressive behaviours from higher-ranking group members (Struhsaker 1967a). Although vervet monkeys have been studied extensively, we are not aware of any systematic research on greeting behaviour. During pilot observations, we noted that adults often produced grunts while approaching males near rivers, where predation risk is high (see Appendix 1). Therefore, we generated a new functional hypothesis, the 'risk reduction hypothesis', which posits that greeting signals are produced in dangerous situations to group members who are most valuable in situations of danger (Krause and Ruxton 2002). In vervet monkeys, adult males are most vigilant and play the most active role in predation defence (Baldellou and Henzi 1992), but individuals should also greet closely bonded individuals who are also likely to provide support in risky situations (e.g. macaques: (Berghänel, Ostner et al. 2011, Micheletta, Waller et al. 2012) dwarf mongooses, *Helogale parvula*: (Kern and Radford 2016)).

The goal of our study was to describe the general patterns of greeting behaviours of wild vervet monkeys and examine the function of vocal signals produced in this context. To this end, we first examined individual, dyadic and ecological factors that triggered grunts during close encounters in an intragroup context. Specifically, we investigated the influence of sex, relative rank difference and strength of social bonds between interacting partners, as well as the influence of visibility (habitat type) and predation risk (i.e. close to rivers, high-risk areas where most natural predator encounters occur in our study site; Appendix 1).

Following this analysis, we used multimodel inference to explore the function of grunts produced during dyadic encounters in male vervet monkeys. We identified five predictor variables to test the six hypotheses outlined before. Two predictors described the social relationship between the interacting individuals, that is, relative rank differences ('signal submission hypothesis') and social bonds strength ('social bond testing hypothesis'). Two further predictors described the ecological situation when signalling occurred. First, being close to rivers may require coordinating movement ('social coordination hypothesis') and support by valuable group members, that is, adult males ('risk reduction hypothesis'), since predation risk is high near rivers (Appendix 1). Another predictor was the presence of contestable food ('conflict management hypothesis') which is likely to increase aggression (Isbell 1991). A final predictor described whether calls were given by the approaching individual ('benign intent hypothesis'), to signal its willingness for a peaceful interaction.

We used an information theory approach to compare a set of six competing, nonexclusive models, representing the six described functional hypotheses of greeting behaviour in animals (Table 1). This approach allowed us to compare and rank our models in terms of how well they fit the existing data (Burnham and Anderson 2003, Burnham, Anderson et al. 2011). Information theory is a viable alternative to more traditional falsification-based hypothesis testing with *P* values. Its advantage is that it produces insights into the relative importance of the different hypotheses, which are represented by different combinations of biologically relevant predictors (i.e. statistical models) that, in our case, may govern vervet monkey greeting behaviour. We created six models using combinations of the predictors and their interaction terms where appropriate to address the six hypotheses, such that each model represented one hypothesis (Table 1).

Table 1. Descriptive summary of the six tested hypotheses

Hypothesis	Description	Source
Benign intent	Promote friendly interactions and increase social tolerance	(Bauers 1993, Silk 1996, Silk 2000, Katsu, Yamada et al. 2014, Silk, Seyfarth et al. 2016)
Conflict management	Mitigate agonistic interactions and repair social relationships after conflicts	(de Waal and Roosmalen 1979, Colmenares 1990, Cheney and Seyfarth 1997, Aureli and Schaffner 2007, Dias, Rodriguez Luna et al. 2008)
Signal submission	Acknowledge existing dominance relationships, reduce aggression and increase group stability	(Schenkel 1967, de Waal and Luttrell 1985, de Waal 1986, East, Hofer et al. 1993, Laporte and Zuberbühler 2010)
Social coordination	Increase group cohesion, coordinate joint activities and benefit from antipredator group effect	(Estes and Goddard 1967, Abegglen 1984, Lynch Alfaro 2008, Senigaglia, de Stephanis et al. 2012, Micheletta, Engelhardt et al. 2013b, Fedurek, Slocombe et al. 2015a)
Social bond testing	Assess relationships quality, strengthen social bonds and increase support from closely bonded individuals	(Smuts and Watanabe 1990, Matheson, Johnson et al. 1996, Okamoto, Agetsuma et al. 2001, Wang and Milton 2003, Whitham and Maestripieri 2003, Schaffner and Aureli 2005, Smith, Powning et al. 2011, De Marco, Sanna et al. 2014)
Risk reduction	Recruit valuable individuals during risky situations and reduce both aggression and predation risks	(Baldellou and Henzi 1992, Berghänel, Ostner et al. 2011, Micheletta, Waller et al. 2012, Kern and Radford 2016)

Although we suggested this new 'risk reduction hypothesis', we give sources here to highlight the importance of valuable partners, such as adult males and closely bonded individuals, during risky situations.

3.3 Methods

3.3.1 Ethical Note

Our study was approved by the relevant local authority, Ezemvelo KZN Wildlife, and by the University of Cape Town, South Africa. The study conforms with the ASAB/ABS guidelines for the Treatment of Animals in Behavioural Research and Teaching. We used non-invasive methods of data collection to observe animals in their natural habitats, and all individuals were habituated to human observers. We identified all individuals based on physical characteristics, such as body size and shape, scars and/or broken digits.

3.3.2 Study site and species

We studied individuals in five wild groups of vervet monkeys over a year (13 March 2014–17 March 2015) in the Mawana Game Reserve in KwaZulu-Natal, South Africa (28°00.327S, 31°12.348E). Mawana is a 12 000 ha private game reserve situated in a savannah biome. Group size in our groups varied from four to over 56 individuals and their home range sizes approximated 160 ha (van de Waal, Borgeaud et al. 2013). Most of the groups contained multiple adult males and females with many juveniles. Group composition varied between groups and over time due to birth, death and migratory events (Table 2). We considered males as adult (AM) after their first migration while females were considered as adult (AF) after they had given birth for the first time.

Table 2. Composition of the groups at the beginning and end of the study period

	AM		AF		Group size		Analyses	
Group	2014	2015	2014	2015	2014	2015	General	Function
AK	3	4	9	10	33	42	-	X
BD	3	9 (7)	7	12 (5)	45	56 (12)	X	X
IN	1	1	3	3 (2)	4	5 (2)	X	-
KB	3	1	4	5	24	21	-	X
NH	4	7 (4)	10	12 (5)	48	53 (9)	X	X

AM and AF correspond to the number of adult males and females, respectively, and group size corresponds to the total number of individuals present within each group, including juveniles, in March 2014 and 2015. Numbers in parentheses correspond to the number of focal animals used in each group in March 2015. A cross in the last two columns represents the groups we used for each analysis as we used focal data from three groups to analyse the general pattern of vervet monkeys' greeting behaviour while we used all-occurrence data from four groups to investigate the functions of grunts.

3.3.3 Behavioural definitions

We defined an encounter as an approach between a focal animal and a partner within 5 m. An encounter ended whenever one of the participants moved beyond this distance. During these close encounters, individuals could interact in friendly or aggressive ways, or not interact at all. Since the vocalisations produced by the focal animal during those meetings were short-distance soft calls of low frequency with a guttural acoustic quality, we classified them as grunts, although they occasionally graded into higher-pitched signals of longer duration (Struhsaker 1967a, see Appendix 2). Since we examined social encounters during dyadic interactions, no other monkeys were present in the 5 m surrounding the two participants, thus allowing us to infer the receiver of the calls thanks to body orientation and/or gazing behaviour of the signaller. We defined vocal encounters as dyadic interactions during which the focal individual produced at least one grunt, in contrast to silent encounters during which no call was produced.

3.3.4 Data Collection

General

We collected focal animal data (Altmann 1974) from 23 well-habituated individuals (12 AF and 11 AM) belonging to three of the five study groups (BD, IN and NH; Table 2) over 8 months (9 May 2014–3 January 2015, total = 206 h of focal data collected between 0515 and 1730 hours, mean = 9.0, range 6.1–19.0). During focal follows, we collected dyadic encounter data on an all-occurrence basis, specifying whether greeting signals were produced or not. For each encounter, we also collected whether it occurred close to rivers (GPS data) and the habitat type (satellite imagery by Google Earth v7.1.5.1557; 8 July 2016; https://www.google.com/earth/). Relevant social information, such as the identity of all individuals present within 10 m of the focal animal were also collected using instantaneous sampling every 15 min (see Tables A2, A3, A4 and A5 in Appendix 3; Altmann 1974). We considered two data points as independent if one of the partners changed, or if two consecutive encounters with the same participants were separated by at least 10 min.

Function

Although vervet monkeys sometime produce nonvocal signals, such as body presentations, lip-smacks or various postures during close encounters, we focused on the most obvious signals produced during dyadic interactions, the grunts. Here, we defined the caller as the individual producing a vocal signal while facing and/or looking at another specific individual, the receiver. We focused on the greeting behaviour of adult males because females rarely produced grunts and because their calls were often barely audible. In addition, to collect dyadic encounter data between males within 5 m, we also recorded all-occurrence data of such vocal interactions between two males in four of the five study groups (AK, BD, KB and NH; Table 2) between 13 March 2014 and 17 March 2015 (see Tables A3 and A4 in Appendix 3). Although we might have missed some vocal encounters, we are confident that our data reflect the general patterns of male greeting behaviour.

Interobserver Reliability

We insured interobserver reliability by first completing an identification test, during which each observer had to correctly recognize all individuals three times in a row within 30 s. Second, we calculated interobserver reliability on instantaneous samples on the focal animal collected simultaneously by two observers (i.e. main activity, height, distance to refuge, position in group, group spread, distance to nearest neighbour and the number of neighbours in 10 m). We considered our behavioural data to be collected reliably if the proportions of agreement observed between two observers were significantly different from those expected by chance (Cohen's kappa, S.M.–M.C.: $k = 0.63$, $P < 0.001$, $N = 79$; S.M.–E.C.: $k = 0.58$, $P < 0.001$, $N = 60$; S.M.–J.M.d.B.: $k = 0.81$, $P < 0.001$, $N = 60$; (Cohen 1960). Although we had somewhat low Cohen's kappa values they are still considered fair if ranging from 0.4 to 0.6 and good if between 0.6 and 0.8 (Watkins and Pacheco 2000).

Dominance status

We determined dominance ranks of adults based on the outcomes of dyadic agonistic interactions collected ad libitum and during focal animal sampling using Elo-rating (Neumann, Duboscq et al. 2011). By continuously updating each individual's rating after each conflict, Elo-ratings of individuals allow the monitoring of dominance status over time by reflecting the competitive abilities of each individual while taking into account the social dynamics of a group during a desired timescale. We defined losers of dyadic dominance interactions as those individuals ending the interaction by showing submissive behaviours and/or retreating, while the other individuals were defined as winners. From individual Elo-ratings, we calculated pairwise differences for all dyads. We standardized Elo-ratings of each dyad according to three sex combinations (male/male, female/female, female/male), thus allowing comparisons of standardized differences of each dyad type (see Appendix 4). Although absolute differences could help us understand the influence of the social rank of a specific individual on its greeting behaviour (e.g. investigating whether grunts are produced by low- versus high-ranking individuals), we used relative differences between two individuals as we were interested in examining the influence of small versus large real rank differences between two participants on their vocal greetings. Ratings were calculated with *k* = 100 (Neumann, Duboscq et al. 2011), using the 'EloRating' package version 0.43 (Neumann and Kulik 2014).

Social Bonds

To quantify the strength of social bonds between pairs of individuals we calculated the dyadic composite sociality index (DSI; Appendix 3; Silk, Cheney et al. 2013). This index, based on the composite sociality index (Sapolsky, Alberts et al. 1997), generates a score reflecting the strength of dyadic affiliative relationships. For its calculation, we used three social behaviours: grooming bouts per observation time (continuously sampled during focal follows), nearest neighbour (i.e. the closest individual of the focal animal based on instantaneous samples collected every 15 min) and proximity (i.e. all individuals within 10 m of the focal animal based on instantaneous samples collected every 15 min). The average DSI value across all dyads in a group by definition equals one. Larger values indicate stronger than average bonds and values between zero and one indicate lower than average bonds (Silk, Cheney et al. 2013). Calculations were carried out using the 'socialindices' package version 0.46-7 (Neumann 2016).

3.3.5 Statistical Analyses

General

We used focal data to describe the general greeting behaviour of vervet monkeys, that is, which focal animals vocalized towards which partners. We analysed 316 clear dyadic interactions between all adults, involving 23 focal individuals (12 AF and 11 AM) and 46 partners (28 AF and 18 AM). We used a generalized linear mixed model (GLMM, Baayen, Davidson et al. 2008) fitted with a binomial structure and logit-link function. We used the vocal behaviour of the focal animal as a response variable, that is, whether it produced a grunt or not (Yes=1/No=0). We added six predictor variables describing the individuals involved, the relationship between them and the ecological situation in which an encounter occurred (Table 3; see Appendix 5).

Table 2. Description of the predictors used to examine the general pattern of greeting signals

Predictors	Description	Scale
Sex focal	Sex of the focal individual	Categorical (Male/Female)
Sex partner	Sex of the partner participating in the dyadic encounter with the focal animal	Categorical (Male/Female)
Elo-rating difference	Relative Elo-rating difference between the two participants, a bigger score difference indicating a larger rank difference	Numerical (standardized across dyad type)
Social bond strength (DSI)	Score describing the strength of the social bond between the two participants, a bigger score indicating a stronger relationship	Numerical (log-transformed)
Close to rivers	Whether the encounter occurred close to rivers, i.e. within 100 m of the riverbed	Categorical (Yes/No)
Habitat closed	Whether the encounter occurred in a closed habitat, defined by a vegetation cover >75%	Categorical (Yes/No)

In addition to the six fixed effects, we included both the identity of the focal animal and its partner as random intercepts to control for repeated measurements. After checking for collinearity between variables using variance inflation factors (maximum VIF = 1.1), we calculated Cook's distances to look for influential individuals (Nieuwenhuis, te Grotenhuis et al. 2012). We identified five potentially influential individuals that accounted for a total of 49 encounters during which no greeting signals were produced (one female and two males as focal individuals; two female partners). However, as their removal resulted in only minor changes in parameter estimates, which did not affect our conclusions, we present results on our full data set. Moreover, although graphical analyses of residuals (using half-normal plots) revealed one observation as an outlier, we decided not to remove it, as it concerned an adult male grunting towards the second highest-ranking female, while all other greeting signals were produced towards adult males. In conclusion, although we are aware of the high variation in our model, caused by influential individuals, we decided to run and interpret it to obtain first insights into a rare but socially important behaviour, vocal greeting in wild vervet monkeys.

Function

We used behavioural data during adult male dyadic vocal encounters to examine the functions of grunts. To this end, we built one specific model for each of the six hypotheses, which included a combination of the five predictors, plus their interaction terms when necessary (Table 4).

Table 3. Description of the five predictors used to examine the potential functions of grunts

Predictors	Rank difference	Social bond strength (DSI)	Presence of food	Whether initiator called	Close to rivers
Description	Relative Elo-rating difference between participants, bigger values indicating larger rank difference	Strength of relationship between two participants, bigger scores indicating stronger relationships	Whether at least one of the partners was feeding	Whether the individual approaching (initiating the interaction) produced a greeting call	Whether the encounter occurred close to rivers (within 100 m of the riverbed)
Scale	Numerical	Numerical (log-transformed)	Categorical (Yes/No)	Categorical (Yes/No)	Categorical (Yes/No)
Benign intent			X[1]	X[1]	
Conflict management	X	X	X		
Signal submission	X		X		
Social coordination	X[1, 2, 3]	X[1, 4, 5]	X[2, 4]		X[3, 5]
Social bond testing		X	X		
Risk reduction		X		X	X

We used a quadratic term for rank difference in the conflict management model (see section 'Function' in 'Statistical Analysis' for details). Identical superscripts for the benign intent and the social coordination models indicate interaction terms.

(1) For the 'benign intent hypothesis', we included the presence of food as a predictor variable as it increases the risk of social tension (Isbell 1991). This was because, in other work, we had noticed that providing rich food dramatically increased aggression rates in our groups (E. van de Waal, personal observations). Thus, we expected more grunts around valuable food. We also included whether the initiator called, that is, whether the individual actively approaching was grunting or not, as we expected initiators to call more frequently to show their peaceful intention (Bauers 1993). Finally, we added the interaction term between both predictors since initiators should be more interested in reducing tension during feeding.

(2) For the 'conflict management hypothesis', we included rank difference as a predictor variable as conflicts are more likely to escalate between males of similar rank (Smith and Parker 1976), between which we expected more greeting signals. Consequently, we used a quadratic term in this model as we expected grunting to be common if rank differences were close to zero, but not if rank differences were very negative or very positive. We also included the strength of the social relationship between the two participants, as it is more important to repair relationships after conflicts with valuable partners. This has already been demonstrated by reconciliation rates in chimpanzees, which are higher between philopatric males which form strong alliances than between females which have weaker bonds (de Waal 1986). We thus expected closely bonded individuals to produce more greetings to strengthen their valuable relationships. Finally, we included the presence of food as a predictor

variable, as we expected grunt production to increase in these socially tense situations to reduce the risk of aggression.

(3) For the ‘signal submission hypothesis’, we included rank difference as a predictor variable as acknowledging existing dominance relationships should increase social tolerance (de Waal 1986). We expected more greetings between animals of similar dominance status as it might be advantageous for those individuals to avoid ambiguities, and thus to reduce the risk of conflict escalation (Smith and Parker 1976). We also included the presence of food in this model, as social ranks influence access to food, with dominants often monopolizing valuable items (e.g. red deer stags, *Cervus elaphus*: (Appleby 1980) rainbow trout, *Salmo gairdneri*: (Metcalfe 1986) vervet monkeys: (Whitten 1983)). Consequently, we expected greetings to be especially important in the presence of food, when competition was high.

(4) For the ‘social coordination hypothesis’, we included two social and two ecological variables. First, we included rank difference in the model mainly because, in vervet monkeys, higher-ranking individuals are more likely to initiate group progressions (Baldellou 1991) and should therefore produce more greetings. Second, we included social bond strength as a predictor variable because closely bonded partners are more likely to benefit from close proximity (Senigaglia, de Stephanis et al. 2012) and should produce more calls than individuals with weaker bonds. Third, we included the presence of food, as increased grunt production during feeding may help to optimize spacing and minimize competition (Gros-Louis 2004). Finally, we added close to rivers as a fourth predictor variable, as grunts should increase social cohesion in high-predation areas (Appendix 1; Krause and Ruxton 2002). We thus expected an increased calling rate near rivers. In addition to these four main predictors, we also added interaction terms that appeared meaningful to us (Table 4). We expected all individuals to call in risky situations (presence of food or predators) to benefit from decreased risks. However, we expected higher-ranking individuals, playing central roles as group leaders, to produce more greetings in peaceful environments (absence of valuable resources and low predation risk), or while moving into open areas, to enhance social cohesion and synchronize activities, as lower-ranking individuals were more likely to follow their movement (Cheney and Seyfarth 1992). Similarly, despite all individuals benefitting from increased fitness by remaining near closely bonded partners, we expected higher-ranking individuals to produce more greetings when interacting with nonfriends to incite them to synchronize activity. Finally, we expected closely bonded individuals to produce more greetings in peaceful situations, that is, in the absence of food and predators.

(5) For the ‘social bond testing hypothesis’, we included social bond strength and the presence of food as predictor variables, since closely bonded partners should produce more greetings than individuals with weaker bonds (Whitham and Maestripieri 2003). Since the presence of food increases the risk of aggression (Isbell 1991), we expected increased call production around food resources, as social bond testing might be especially important in these socially tense situations.

(6) For the ‘risk reduction hypothesis’, we included social bond strength as support from bystanders, such as cooperative defence against potentially dangerous males or predators, increases with bond strength (Berghänel, Ostner et al. 2011, Micheletta, Waller et al. 2012). Individuals with strong bonds should produce more greeting signals. We also included whether the initiator called as a predictor variable, as initiating an interaction in dangerous situations helps to decrease predation risk by increasing vigilance (Brown 1999). We thus expected individuals approaching partners (initiators) to call more frequently than individuals being approached. As, in our study area, most predator encounters occurred near rivers (Appendix 1), we finally added close to rivers as a last predictor variable. Individuals should increase grunt production mainly in these dangerous areas to attract individuals and benefit from group-related antipredator effects (Krause and Ruxton 2002).

After removing incomplete data (missing identity of one or both participant(s), e.g. due to unfavourable observation conditions), we analysed 53 vocal encounters in 25 dyads. Our modelling strategy here focused on whether or not we observed a greeting signal in any given dyad under different conditions. Similar to Kulik et al (2012), we restructured our data set to include each dyad (*N* = 58 possible dyads) once in each of our different combinations of predictor variables (resulting in *N* = 752 data points; see Appendix 5 for details on the methods used to restructure the initial data set). To account for repeated data for each dyad introduced by this procedure, we added dyad identity as a random intercept in each model, in addition to caller identity, receiver identity and group identity. We then scored for each of these possibilities whether we observed a greeting (Yes=1/No=0), which served as the response variable in the models. Hence, our models assessed under which conditions greetings were more likely to occur and thus be observed.

We used Akaike's information criterion corrected for small sample size (AICc; Burnham, Anderson et al. 2011) to rank our models according to how likely they were given our data (for an example of a study using similar methods see (Duboscq, Romano et al. 2016). We considered the model having the smallest AICc value as the one explaining best our observations, with all other models having an increasing AICc score having relative weaker explanatory value. One of the principles of AICc (and similar information criteria; Grueber, Nakagawa et al. 2011) is that it represents a trade-off between model fit and complexity. Better fit is invariably achieved by increasing the number of predictors in a model, but comes at the cost of increasing complexity. However, AICc includes a 'penalty' term that increases the value of AICc if more predictors are added to a model (Anderson 2008). Given two models with the same fit but with different numbers of predictors, the AICc will be smaller for the model with fewer predictors, that is, for the same fit, the less complex model will be ranked better.

Inference from such model comparisons can be drawn in multiple ways. First, differences in AICc (ΔAICc) values between two models can be used to assess plausibility of the lower-ranked model. For example, models with ΔAICc values larger than about 15 will be dismissed by most as implausible compared to the higher-ranked model (Anderson 2008). Despite this, Anderson (2008, p.85) explicitly advised against using ΔAICc values for creating artificial cutoff points. More intuitively, standardized model weights express the probability that a given model is the best among those in the set of models tested (Anderson 2008) and thus allow for a more gradual examination of evidence for or against specific models. Note that any comparison of multiple models in this framework is relative, not absolute, that is, if a model is identified as the best model, this model is the relative best one in the candidate set (Anderson 2008). Possible models that were not included in the candidate set might be better still (i.e. with smaller AICc) than the best model in the candidate set.

For each model, we used generalized linear mixed models (GLMM; Baayen, Davidson et al. 2008) fitted with a binomial structure and logit-link function. We used whether we observed a greeting signal within a dyad as the response variable, but for ease of discussion, we refer to it as whether one individual produced at least one grunt (Yes=1/No=0). We entered caller and receiver identity, as well as dyad as random intercepts to control for repeated measurements. We also added group identity as a random intercept to avoid bias due to group size and composition. Predictor variables and their interactions differed between models (Tables 1 and 4; Appendix 5). Model assumptions (maximum VIF = 1.0, homogeneity of residuals using half-normal plots and Cook's distances) were tested on a full model including all five predictors. Since all assumptions were satisfied without any influential cases, we considered all simpler models to be suitable for analysis (A. R. Slobodeanu, personal communication, 5th July 2016).

All tests were performed using R v3.3.1 (Team 2016) with the glmer function, lme4 package v1.1.11 (Bates, Mächler et al. 2015) and the MuMIn package v1.15.6 (Barton 2016).

3.4 Results

During close social encounters grunts were produced in only 20 of 384 dyadic interactions (5.2%) during 206 h of focal follows (Fig. 1; mean call rate = 0.1/h, mean duration of encounter = 4.30 min, range 0.03–66.00 min; see Table A5 in Appendix 3).

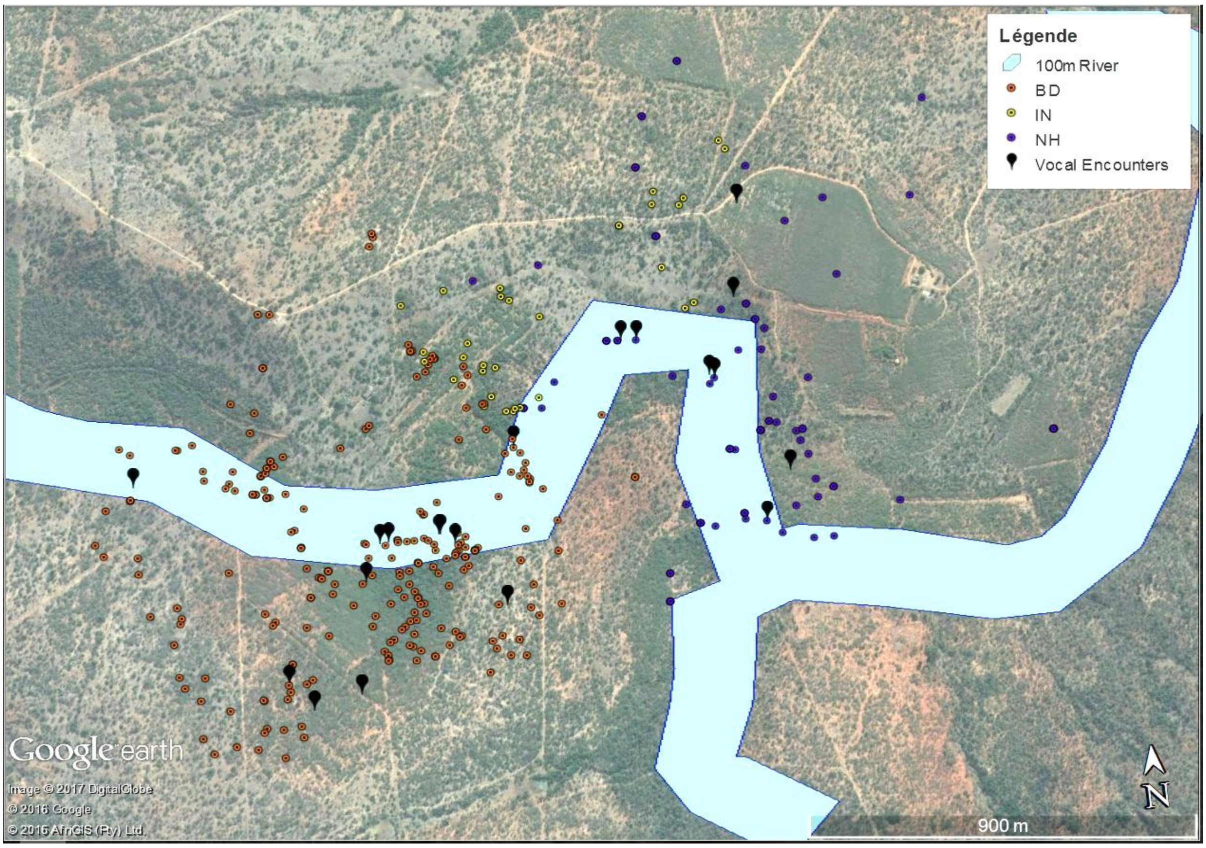

Fig 1. Map showing the location of dyadic encounters collected during focal follows according to groups (orange = BD, yellow = IN, dark violet = NH) and whether a grunt was produced (vocal encounters in black and silent ones in colours). The blue polygon represents the variable close to rivers, i.e. areas within 100 m of the riverbed. Source: 'Mawana' 28°00'25.07"S and 31°11'47.07"E. Google Earth, version 7.1.5.1557, 8 July 2016, available at https://www.google.com/earth/.

General

We analysed 316 complete observations of dyadic encounters to examine the general pattern of vervet monkeys' greeting behaviour (Table 5). A likelihood ratio test revealed a significant difference between the full and null models ($\chi^2_6 = 14.68$, $P = 0.023$), suggesting that our full model was more informative than the corresponding null model.

Table 5. Results of the GLMM testing social and ecological factors affecting grunt production

	Estimate	SE	*Z*	CI	*P*
Intercept	-8.24	2.03	-4.07	-12.22 to -4.27	4.72e-05
Sex focal (Male)	0.81	0.94	0.86	-1.04 to 2.66	0.391
Sex partner (Male)	3.80	1.36	2.81	1.15 to 6.46	0.005
Elo-rating difference	-0.01	0.42	-0.02	-0.83 to 0.81	0.983
Social bond strength (DSI)	-0.10	0.41	-0.24	-0.90 to 0.71	0.814
Close to rivers (Yes)	1.12	0.69	1.62	-0.23 to 2.47	0.105
Habitat closed (Yes)	0.53	0.87	0.61	-1.18 to 2.23	0.546

CI = 95% confidence intervals using Wald method; test levels of categorical predictors are given in parentheses.

Although both males and females vocalized, grunts were almost exclusively produced towards adult males (95%; Table 5, Fig. 2; the exception was one male greeting a high-ranking female). There was no influence of the sex of the focal animal, the social relationship between participants (rank difference and social bond strength) and habitat visibility. However, grunts tended to be more likely to occur near rivers (Fig. 1; 12% of encounters near rivers were vocal but away from rivers only 4% of encounters were vocal).

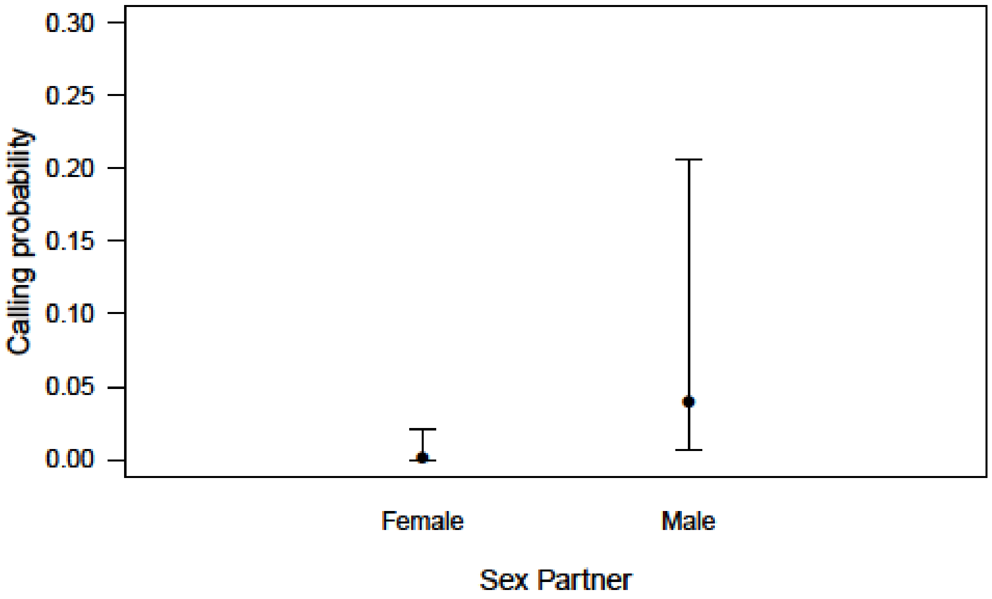

Fig 2. Effect of the sex of the partner on grunt production by the focal animal. Model estimates are shown with associated 95% confidence intervals.

Function

We analysed 53 vocal dyadic encounters between adult males collected during both focal and ad libitum sampling (Appendix 3). The model comparison is summarized in Table 6 and detailed model results are presented in Tables A10–A15 in Appendix 5.

Table 6. Results of multimodel inference

Models	*K*	AICc	ΔAICc	Weight
Risk reduction	3	292.3	--	0.896
Benign intent	3	296.6	4.3	0.104
Signal submission	2	313.4	21.2	0.000
Social bond testing	2	314.3	22.0	0.000
Conflict management	3	314.4	22.2	0.000
Social coordination	9	318.9	26.6	0.000

The six models represent the six hypotheses about the functions of vervet monkeys' greeting signals. We sorted models by their AICc scores. K = number of terms included; AICc = Akaike's information criterion corrected for small sample size; ΔAICc= difference in AICc scores between the model with the lowest AICc and the following one; weight = model probabilities.

Comparison of model weights and AICc differences between the six models indicated highest support for the 'risk reduction hypothesis' and the 'benign intent hypothesis' (Table 6). The risk reduction model, including whether the initiator called, the strength of social bonds and close to rivers as variables, had the highest model probability (0.90) of being the best model among the six we compared. The second-best model in our set, the benign intent model, which included the presence of food and whether the initiator called as predictors, had a model probability of 0.10 (Table 6). The remaining four models (Table 6) had a combined probability of less than 0.01. These results suggest that vervet monkeys' greeting signals probably serve to reduce risks by communicating to other individuals in dangerous areas, such as near rivers, and, to a lesser extent, grunts might also be used to signal benign intent.

3.5 Discussion

Although a rare behaviour produced only in 5.2% of dyadic encounters, both male and female vervet monkeys produced vocal signals when approaching other group members. However, with one exception, only interactions with male partners triggered these vocalisations. Results from the analysis of focal data of close dyadic encounters (Table 5, Appendix 3) suggested little to no influence of the social relationship between participants, indicating that greeting signals were produced between individuals independently of their rank difference or social bond strength. Despite results on the influence of ecological variables not being statistically significant, vervet monkeys tended to greet each other more often near rivers, where predation risk was high (Fig. 1; Appendix 1).

One possibility to explain the rarity of vervet monkey grunts is that individuals may use other, nonvocal signals for the same purpose, which might differ between the sexes. For example, to establish friendly relationships, females may perform other behaviours, such as socially targeting grooming (van de Waal, Spinelli et al. 2013) or infant handling (Fruteau, van de Waal et al. 2011). Since males have less stable dominance relationships than females, which have to be re-established after each migration event (Cheney and Seyfarth 1992), they may have evolved additional mechanisms to deal with this challenge. During social interactions, subordinate vervet monkeys produce grunts as part of 'Red, White and Blue' displays, i.e. a dominant individual exposes his red peri-anus, white medial pelage stripes and blue scrotum to a subordinate, who responds with a submissive posture and grunting (Struhsaker 1967a). This visually based ritualized display, used during close dyadic encounters, appears to help males in acknowledging dominance relations, as they are performed by dominants in front of subordinates who respond by crouching and vocalizing. The behavioural difference between males and females might thus explain why males exchanged most of the greeting signals. However, visual signals might be less useful in risky areas where predator attacks occur rapidly and unexpectedly. In these circumstances, it seems more beneficial to interact vocally, especially if signals function to recruit others to antipredator behaviour in low-visibility areas, such as riverine forests. Acoustically inconspicuous grunts may be especially useful in these situations, as they minimize the risk of being detected by predators.

Overall, our results most strongly supported the ‘risk reduction hypothesis’ and, to a lesser degree, the ‘benign intent hypothesis’. The former suggests that vervet monkeys should call preferentially while approaching socially important partners when predation risk is high (i.e. near rivers; Appendix 1), while the latter suggests that calling might be used by initiators to mitigate social interactions during socially tense situations, such as near valuable food resources. We found only little support for the four remaining hypotheses, suggesting that, unlike chimpanzees (Laporte and Zuberbühler 2010), vervet monkeys from our studied groups do not use greeting signals to acknowledge dominance or as a conflict management tool, as shown in baboons (Colmenares 1991a, Colmenares 1991b). Also, vervet monkeys do not seem to grunt to reinforce social relationships, as shown in male Tonkean macaques (De Marco, Sanna et al. 2014) and, finally, grunts do not appear to increase social cohesiveness, coordinate activity or promote cooperation between group members, as shown in African wild dogs (Estes and Goddard 1967).

Results from the general analysis are also in line with the ‘risk reduction hypothesis’ (including three predictor variables: whether the initiator called, close to rivers and social bond strength), indicating that calls function to recruit valuable partners during danger to reduce predation risks since grunts were preferentially produced to adult males (Table 5). Adult males usually lead in group progressions, and the alpha male plays an essential role in these initiations (Baldellou 1991). During risky river crossings, adult and subadult males are usually both at the front and back of the group (Bodin 2015). Moreover, males are more vigilant and more active during predator encounters than females (Baldellou and Henzi 1992). Following Hamilton’s (1971) model of the selfish herd, this suggests that more vulnerable individuals, being in a central position, benefit from increased protection thanks to the ideal location of those peripheral males. The increased rates of grunts directed mainly towards adult males might be the result of callers seeking to encourage males to occupy these important spatial positions. However, future studies investigating the behaviour of receivers will be necessary to further validate the ‘risk reduction hypothesis’, in particular, the prediction that support to signallers increases after grunt production during close encounters in situations of danger, for example by deterring predators or forming coalitions to repel potential rival males.

Although not significant, we found grunt production more likely when two individuals encountered each other near rivers (Fig. 1, Table 5). Wild vervet monkeys often cluster as a cohesive group before crossing rivers (S. Mercier, personal observations). Individuals arriving early at crossing locations wait for other group members to arrive and this is likely to cause social tension among them, which in turn might increase their calling rate. Vervet monkeys might thus produce greeting signals to reduce the risk of injury by increasing tolerance and reducing conflicts before river crossings. Results from a recent study showed that wild female baboons produce grunts to signal peaceful interactions, especially when encountering unpredictable partners (Silk, Seyfarth et al. 2016). Similarly to spider monkeys, which use embraces to reduce aggression risk during fusion events (Aureli and Schaffner 2007), vervet monkeys might use greeting signals to reduce social risks due to agonistic interactions during socially tense situations, such as while waiting before crossing rivers.

Despite results from the general analysis showing little to no influence of strength of the social relationship between the two interacting individuals on grunt production in our studied groups, we included social bond strength as another predictor variable of our risk reduction model. Social bonds generally enhance cooperation between individuals (Berghänel, Ostner et al. 2011), and it has been shown, for instance in male baboons, that closely bonded partners produce more greetings than other individuals having weaker bonds (Whitham and Maestripieri 2003). In addition to increasing social coordination with allies, as male capuchins do when encountering other groups for example (Lynch

Alfaro 2008), greeting signals in vervet monkeys might help to maintain social bonds, which is likely to be of special importance in risky situations, such as near rivers (Micheletta, Waller et al. 2012, Kern and Radford 2016).

Our study has several limitations. First, although we used a 10 m distance during the pilot study to define an encounter, reducing it to 5 m helped to improve the quality of the data due to better visibility and more reliable identification of individuals. However, individuals sometimes gave greeting signals over much greater distances, so the reported call rates are probably underestimates. For the all-occurrence data, we only focused on vocal encounters (without a distance criterion) but we had to exclude many of them because of identification problems due to low visibility or a lack of clarity about whom the signaller was trying to address.

Second, multimodel inference relies on the validity of the models compared (Anderson 2008, Burnham, Anderson et al. 2011). This approach ranks models relative to each other. It is possible that we overlooked a relevant hypothesis or incorrectly specified models such that they did not address the hypotheses properly. Regardless of these pitfalls, we are convinced that the advantages of multimodel inference outweigh these potential drawbacks. Future studies can build upon the models we presented here and refine them if necessary to allow further insights into the functions of greeting calls in particular, and signals more generally.

Often close social interactions involve a range of signals, sometimes a mixture of vocal and nonvocal ones. Greetings have been well documented in baboons as they use sequential combinations of different patterns (facial, vocal, postural, manipulatory and locomotory) to assess their relationships, and thus negotiate their status without fighting (Colmenares 1990). For instance, baboons can use facial displays, such as ear flattening or grimaces to signal willingness to interact in a friendly way, while simultaneously accompanying some of their greetings with vocalisations uttered by one or both participants (Colmenares 1991a, Colmenares 1991b). Several species of macaques also use combinatorial signals. For example, facial displays such as lip smacking are combined with different vocalisations when engaging in positive social interactions (Partan 2002, De Marco, Cozzolino et al. 2011, Micheletta, Engelhardt et al. 2013a). In chimpanzees, 74% of pant-grunts are produced in conjunction with other communicative signals, such as facial expressions or gestures, directed at specific individuals (Taglialatela, Russell et al. 2015). However, each participant might use specific signals. Wolves and dogs, for example, use different signals according to their social rank. While the alpha individual produces vocal signals when approaching the pack, subordinates greet with several forms of submissive postures, such as lying on the back or ‘nose-push’ gestures (Schenkel 1967).

Although vervet monkeys use multimodal signals when encountering each other, for example by combining grunts with ‘Red, White and Blue’ displays (Struhsaker 1967a), we only focused on the vocal channel, mainly because the frequency of social encounters involving only two individuals within 5 m was low. Nevertheless, animals might communicate flexibly by using different signals in specific contexts to convey different messages. For instance, ‘contest hoots’ produced by bonobos, *Pan paniscus*, to challenge males are used in combination with different type of gestures, which provide extra cues on the forthcoming social interaction. In this species, soft gestures were more likely to be produced during friendly play, whereas rough ones often preceded agonistic interactions (Genty, Clay et al. 2014). Consequently, future studies should focus on multimodal signals to deepen our understanding of the complexity of such social rituals.

Another way a signaller can gain flexibility during communication is to use the same signal for different functions, and our findings may be an example. For example, it is possible that during close encounters subjects mainly signalled benign intent to potentially aggressive males, while over greater distances the same calls might function to increase vigilance from others. Another example of the multifunctionality of a signal is the use of different forms of ritualized greetings in Hamadryas baboons, to signal submission, avoid conflicts and form alliances (Fraser and Plowman 2007). Similarly, spotted hyaenas also use greetings for two main purposes: to reinforce social bonds and to effectively communicate cooperative affiliations (Smith, Powning et al. 2011). Further detailed investigations on this vocal signal, including acoustic analysis, multimodal signalling and contextual variations, might reveal additional functions than the use of greetings by vervet monkeys to recruit individuals in dangerous situations and to signal willingness to interact in friendly ways.

3.6 Acknowledgments

We are grateful to K. van der Walts for allowing us to conduct research at Mawana Game Reserve as well as A. Driescher and A. van Blerk for managing the Inkawu Vervet Project. We thank the IVP team members for their support in the field. Ezemvelo KZN Wildlife provided us permission to conduct our research on wild vervet monkeys in South Africa. E.W. was funded by the Swiss National Science Foundation (P300P3_151187) and Society in Science–Branco Weiss Fellowship. This work was funded by the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013) / ERC grant agreement no. 283871 and the Swiss National Science Foundation (Project 310030_143359). We thank A.R. Slobodeanu for statistical advice as well as P. Fedurek and C. Stephan for interesting discussions. We are grateful for the constructive comments of two anonymous referees, which greatly improved the manuscript.

3.7 Data Availability

We archived our data and code in a publicly available repository (Mercier, Neumann et al. 2017; https://figshare.com/s/259509e0b8b29fe81b90, doi:10.6084/m9.figshare.4203339), following best practices (White, Baldridge et al. 2013, Roche, Kruuk et al. 2015).

3.8 Supplementary materials

Appendix 1: Predator encounter analysis

We used ad libitum data on all predator encounters collected between 18 February 2013 and 30 January 2016 by trained researchers to investigate the spatial distribution of predator encounters. We used GPS data from 172 predator encounters collected on seven groups (AK, BD, CR, IN, KB, LT, NH) for which the predator had been seen and the species identified. We divided predators into three main categories (Seyfarth, Cheney et al. 1980a) and considered the following species: snakes (boomslang, *Dispholidus typus*, Mozambique spitting cobra, *Naja mossambica*, black mamba, *Dendroaspis polylepis*, puff adder, *Bitis arietans*, and python, *Python natalensis*), eagles (martial eagle, *Polemaetus bellicosus*, tawny eagle, *Aquila rapax*, African hawk eagle, *Aquila spilogaster*, and brown snake eagle, *Circaetus cinereus*) and mammals (black-backed jackal, *Canis mesomelas*, caracal, *Caracal caracal*, and serval, *Leptailurus serval*). We considered predator encounters to be near rivers if they were within 100 m from the riverbed using satellite imagery (by Google Earth v7.1.5.1557; 8 February 2014; https://www.google.com/earth/, Table A1, Fig. A1).

Table A1. Distribution of predator encounters according to their proximity to rivers (*N*=172)

Close to rivers	Eagle	Mammal	Snake
Yes	50	12	38
No	28	23	21
Total encounters	78	35	59

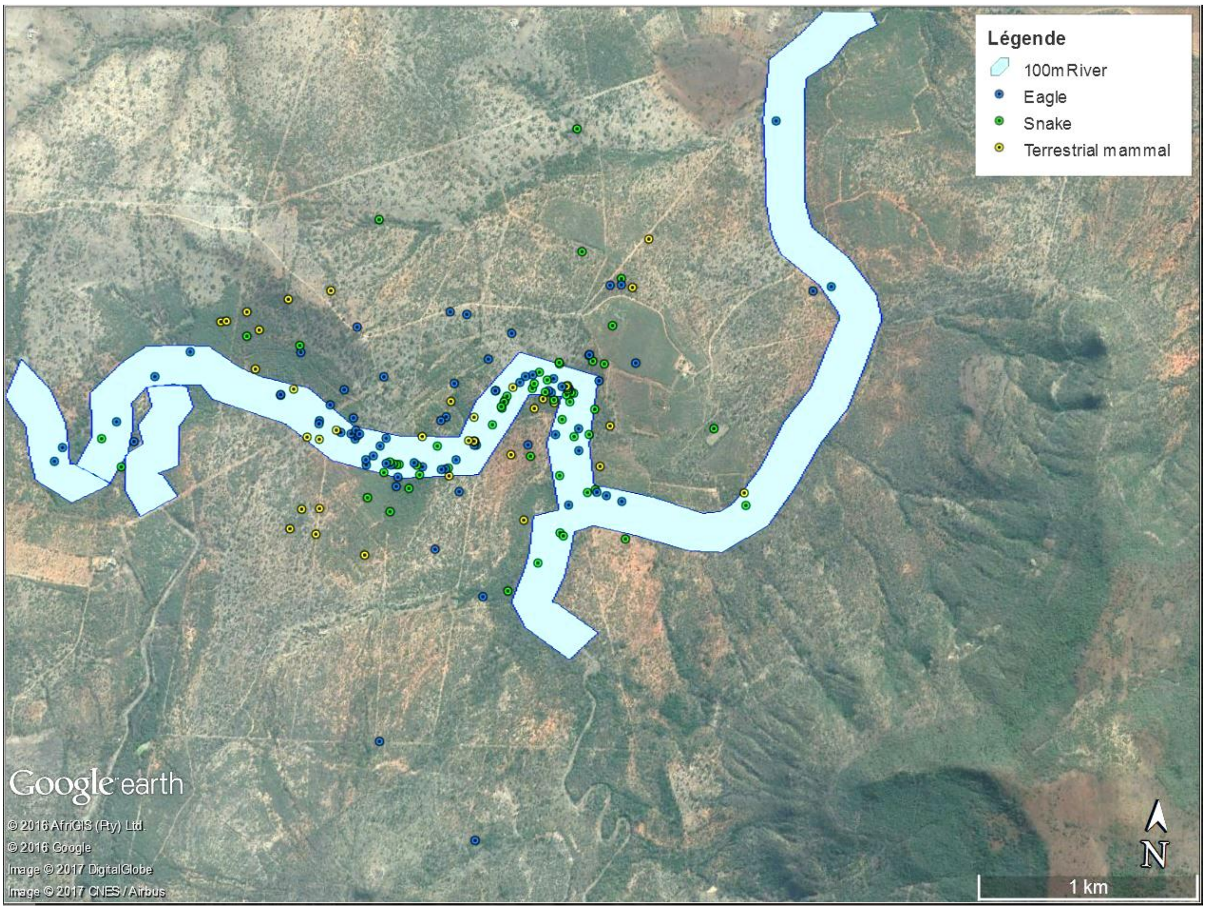

Fig A1. Map showing the location of predator encounters (yellow = terrestrial mammal, green = snake, blue = eagle) according to their distance from rivers (i.e. considered as near rivers when points are in the blue polygon representing 100 m from the riverbed). Source: 'Mawana' 27°59'41.89"S and 31°10'14.26"E. Google Earth, version 7.1.5.1557, 8 February 2014, available at https://www.google.com/earth/.

Although vervet monkeys encountered all predator types, encounters with snakes (34%) and eagles (46%) were more frequent than encounters with mammalian predators (20% including jackals 19%, caracals 0.5% and servals 0.5%; Pearson's chi-square test: $X^2_2 = 8.58$, $P = 0.014$). The field site is part of a private reserve used for hunting and the population of carnivores is managed to maintain sufficient game for hunting. Both eagles and snakes were encountered more frequently near rivers than terrestrial mammals, which appeared to be more common away from rivers (Table A1, Fig. A2; three-sample test for equality of proportions without continuity correction: $X^2_2 = 10.28$, $P = 0.006$). Consequently, we considered areas near rivers being dangerous as they corresponded to areas in which encounters with the more common predator types were more frequent.

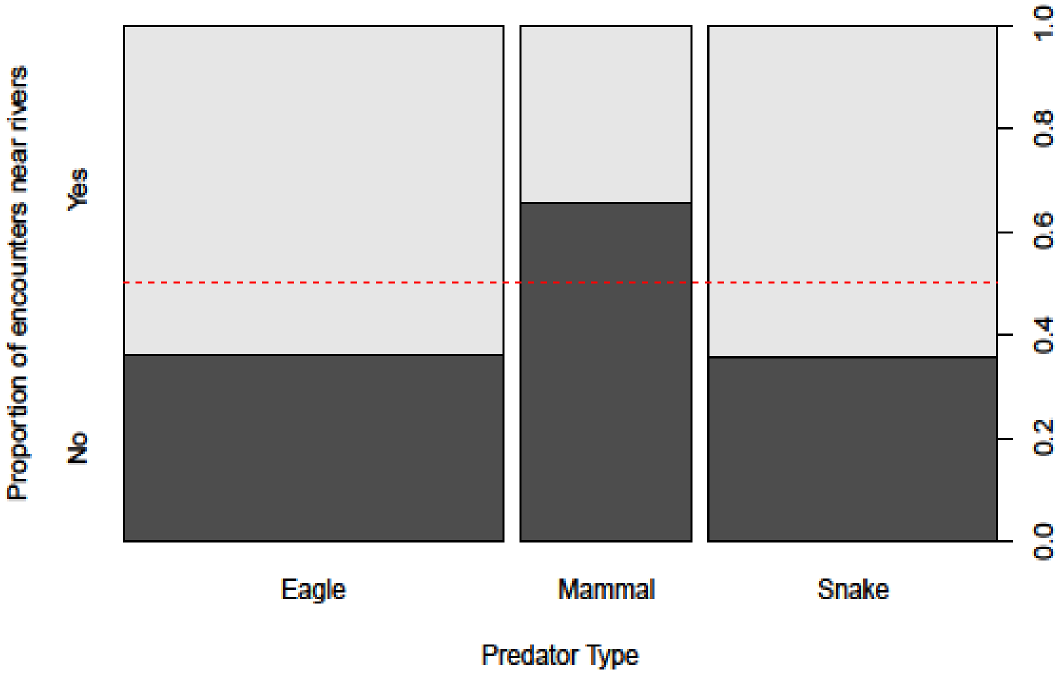

Fig A2. Mosaic plot of predator type encounters according to proximity to rivers (Yes when close to rivers, No otherwise). The horizontal dashed line represents predator encounters if randomly distributed across rivers.

QR codes of vervet monkeys' reactions upon hearing their own alarm calls produced towards two kinds of predators: leopard (left) and snake (right). These videos were filmed by the BBC for their documentary 'Monkey Planet' (https://www.bbc.co.uk/programmes/p01s0z7y) during playback experiments conducted by S. Mercier.

Appendix 2: Acoustic analysis

We recorded all vocalisations produced by the focal animal, its partner or any neighbouring individuals opportunistically during the study period using a Marantz digital recorder PMD661 (sampling rate of 44.1 kHz, resolution 24 bits) and a Sennheiser unidirectional microphone MKH416. Recordings were then transferred to a computer and spectrograms were extracted using a fast Fourier transformation (time steps = 1000, frequency steps = 500, Gaussian window shape, window length = 0.05 ms and dynamic range = 70 dB) in PRAAT 5.4.13 (www.praat.org). We classified a vocalisation as a grunt if it was produced by an individual while another identified group member was approaching or being approached by the signaller. These calls of short duration had a guttural acoustic quality, and were either produced once or several times in sequences (Fig. A3; Struhsaker 1967a).

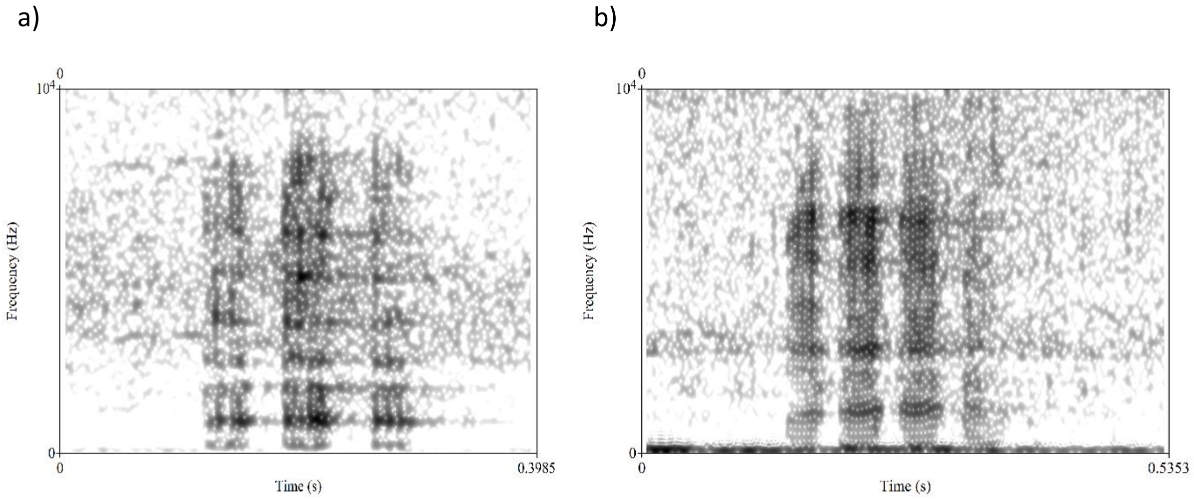

Fig A3. Spectrograms of grunts produced by (a) a male and (b) a female during a close dyadic encounter between two adults.

Appendix 3: Observational data

Table A2. Data collected during instantaneous sampling of our focal animals every 15min

Variable	Description
Date	Date of the day
Group	Identity of the group to which the focal individual belongs
Focal individual	Identity of the focal individual
Nearest adult neighbour	Identity of the nearest adult neighbour of the focal individual
Nearest juvenile neighbour	Identity of the nearest juvenile neighbour of the focal individual. For mothers, infants were not recorded as nearest neighbours unless no other juvenile neighbours were present within 10 m
No. and ID neighbours in 10 m	Number and identities of all the neighbours present within 10 m of the focal animal
Remarks	Anything of interest (e.g. if target individual was crossing the river at the time of sampling)

Table A3. Observation time and number of encounters collected on each focal from three groups

Group	Focal identity	Sex	Observation time (h)	No. of encounters
BD	Ouli	Female	7.52	16
BD	Asis	Female	10.72	25
BD	Mooi	Female	6.55	14
BD	Numb	Female	7.50	14
BD	Riss	Female	8.43	20
BD	Oku	Male	7.65	20
BD	Lek	Male	10.68	28
BD	Ham	Male	7.47	31
BD	Neu	Male	6.25	20
BD	Zur	Male	8.85	28
BD	Tor	Male	9.17	23
BD	Che	Male	7.90	15
IN	Wiet	Female	7.83	16
IN	Bemi	Female	11.55	16
NH	Pari	Female	7.5	9
NH	Pret	Female	7.42	1
NH	Upps	Female	10.73	2
NH	Xaix	Female	7.75	16
NH	Bogo	Female	6.12	11
NH	Can	Male	8.25	17
NH	Ert	Male	19.08	13
NH	Gov	Male	13.00	14
NH	LSk	Male	8.5	15
	Total	Female	99.62	160
	Total	Male	106.82	224
	Total	All	206.47	384

Table A4. Data collected during an encounter between two individuals, i.e. an approach within 5 m

Variable	Description
Date	Date of the day
Group	Identity of the group to which the focal individual belongs
GPS location	GPS location of the focal individual when an encounter occurred
Focal individual	Identity of the focal individual
ID partner	Identity of the partner, i.e. individual approaching or being approached within 5 m of the focal individual
Approaching individual	Identity of who is approaching the other one, i.e. who initiates the encounter (Focal, Partner, Both or Unknown)
No. and ID of neighbours in 10 m	Number and identities of all the neighbours present within 10 m of the focal animal
Vocalisation produced	Whether vocalisations were produced
- ID caller	Identity of the caller
- Type	Type of vocalisation produced (e.g. grunts, aggressive calls, screams)
- Duration	Duration (s) of the first vocalisation produced (<10 s, 11–30 s, 31–60 s, >60 s, unknown)
- Resume calling	Whether the caller resumes calling after 5 s of silence (Yes/No)
- Vocalisation recorded	Whether the vocalisations were recorded (Yes/No)
- Track number	Number of tracks on which the vocalisations were recorded
Other signals produced	Whether other nonvocal signals were produced (Yes/No)
What signal?	Description of any other signal produced (e.g. lip smacking or submissive postures)
Interaction	Whether the type of interaction between individuals was Neutral (if there was no interaction), Affiliative (if they entered into contact in a friendly way, i.e. sitting in contact or grooming) and Agonistic (if some aggressive behaviours were produced by either individual, such as stare, attack or chase)
Description	Ad libitum description of what happened during the encounter and any other interesting facts

Table A5. Encounter rate and grunt production of all focal individuals that produced at least one signal

Focal identity	Group	Sex	Elo-ratings	Encounter rate (per h)	Grunt production (per h)	Partner identities (Age/Sex class; Elo-ratings)
Bogo	NH	Female	740	1.80	0.16	Ert (AM;1432)
Pari	NH	Female	974	1.20	0.13	Gov (AM;1195)
Mooi	BD	Female	1001	2.14	0.15	Che (AM;1008)
Xaix	NH	Female	1344	2.06	0.26	Gov (AM;1198) Ert (AM;1432)
Upps	NH	Female	1903	0.19	0.09	Gov (AM;1050)
Pret	NH	Female	NA	0.27	0.22	Gov (AM;1048)
LSko	NH	Male	787	1.76	0.12	Can (AM;876)
Tor	BD	Male	866	2.51	0.22	Che (AM;995) Ham (AM;815)
Lek	BD	Male	1034	2.71	0.70	Jag (AM;NA) Oku (AM;761) Prin (AF;1527) Art (AM;850)
Neu	BD	Male	1084	3.20	0.16	Ham (AM;857)
Ert	NH	Male	1401	0.68	0.10	Gov (AM;1051)
Average female				1.17	0.15	
Average male				1.64	0.23	
Average all				1.44	0.20	

Focal individuals are sorted by sex and Elo-ratings. We could not calculate the Elo-rating of Pret as she became an adult during our study period (by giving birth to her first infant) and we did not have enough agonistic interactions to extract an Elo-rating for the day we observed her greeting Gov.

Appendix 4: Friendship and dominance

Friendship

We used the dyadic composite sociality index (DSI) to assess the social bond strength of dyads (see also Silk, Altmann et al. 2006, c.f. Silk, Cheney et al. 2013). We calculated the DSI of each dyad of focal individuals by using the frequency of three social behaviours of focal animals over the study period: grooming bouts per observation time (continuously sampled during focal follows), nearest neighbour (i.e. closest individual of the focal animal based on instantaneous samples collected every 15 min) and proximity (i.e. all individuals present within 10 m of the focal animal based on instantaneous samples collected every 15 min). These data allowed us to quantify the strength of social bonds between two individuals using the following equation from Silk, Cheney et al. (2013):

$$DSI_{xy} = \frac{\frac{Gxy}{G} + \frac{Pxy}{P} + \frac{Nxy}{N}}{3}$$

Here, $\frac{Gxy}{G}$ corresponds to the number of grooming bouts in which the dyad xy participated divided by the mean number of grooming bouts for all dyads in the group G. $\frac{Pxy}{P}$ corresponds to the number of instantaneous samples in which xy were in proximity to each other (i.e. within 10 m) and one of them was the focal individual divided by the mean number of instantaneous samples of proximity for all dyads involved in the study P. And $\frac{Nxy}{N}$ corresponds to the number of instantaneous samples in which xy were nearest neighbours of each other (i.e. closest individuals) and one of them was the focal individual divided by the mean number of instantaneous samples of nearest neighbours for all dyads involved in the study N. The rates of the three behaviours were corrected for the observation time and co-residency of dyads. The average DSI value across all dyads in a group by definition equals one. Larger values indicate stronger than average bonds and values between zero and one indicate lower than average bonds (Silk, Cheney et al. 2013). Calculations were carried out using the 'socialindices' package (Neumann 2016).

As the calculation of the DSI included grooming, a nonaggressive physical contact used to maintain social relationships (van de Waal, Spinelli et al. 2013), it limits our possibilities to distinguish between two functional hypotheses that could operate for the 'social bond testing hypothesis': individuals use greetings to establish social bonds or individuals greet because they share strong bonds. Although it is an interesting topic for future studies, we unfortunately do not have the data enabling us to disentangle these two hypotheses. However, we do not think that this is a major issue as we were interested in the more general prediction of the 'social bond testing hypothesis', which is that vervet monkeys use greeting signals to strengthen their social bonds.

Dominance

We used ad libitum dyadic agonistic interactions between adults to establish the dominance hierarchy of vervet monkeys using Elo-rating (Neumann, Duboscq et al. 2011). For each observed dyadic dominance interaction, we defined the loser as the individual ending the interaction by showing submissive behaviours and/or retreating (Table A6), while the other individual was defined as the winner. Only complete data were included in the analyses, that is, when the identities of both individuals were known and their winner/loser status could be assigned without ambiguity. At least one winner and/or loser's behaviour presented in Table A6 had to occur during an agonistic interaction to define the winner/loser status of both individuals with certitude, even though some other behaviours might have been produced by one or both opponents (for example approaching, looking for support or screaming).

Table A6. List of behaviours used to describe the social role of both individuals involved in a conflict

Social role	Behaviour	Definition
Aggressor	Aggression calls	Low pitch vocalisations, such as chutter and bark (Struhsaker 1967a)
	Attack	Forward motion of the body towards an opponent
	Bite	Grabbing an opponent with the mouth
	Chase	Running after an opponent who is fleeing
	Grab	Holding an opponent with the hand
	Hit	Slapping an opponent with the hand
	Monopolize	Restraining access to other individuals from a valuable resource
	Stare	Popping up the eyelids towards an opponent
	Take place	Displacing an opponent and taking his/her place
Victim	Avoid	Moving head or body away from an aggressor
	Crawl	Bowing down to an aggressor while looking at him/her
	Flee	Running away from an aggressor as he/she is chasing
	Jump aside	Jumping to the side to avoid an aggressor
	Retreat	Moving without running away from an aggressor

Since we were interested in examining the effects of dominance status difference between two individuals rather than individual dominance status, we defined three dyad types according to the sex of the dyad members: male–male, female–female and mixed dyads including interactions between all adults (male–female and female–male). We then extracted Elo-ratings of each dyad member for each day of data collection (see Fig. A4). We standardized their Elo-ratings within each dyad type by scaling the Elo-rating differences between the focal animal and its partner to a mean of zero and a standard deviation of one. Doing so allowed us to compare standardized differences of each dyad type (i.e. a difference of 100 is similar across the three dyad types when comparing the social rank difference of pure male, pure female or mixed-sex interactions). Ratings were calculated with *k* = 100 (Neumann, Duboscq et al. 2011), using the EloRating package version 0.43 (Neumann and Kulik 2014).

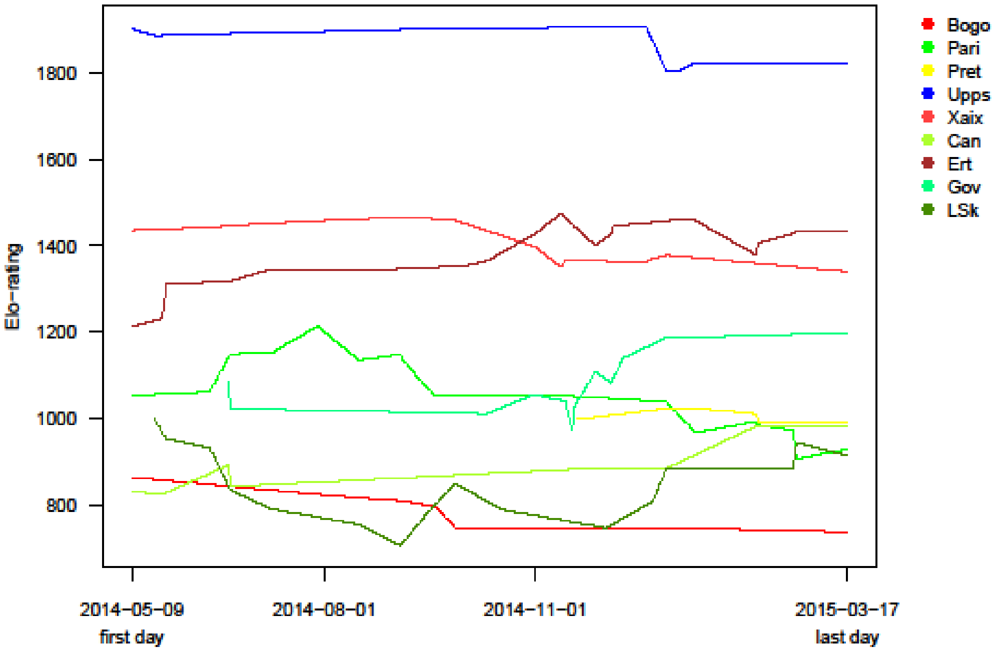

Fig A4. Elo-ratings of focal animals from the NH group over the entire study period (five adult females: Bogo, Pari, Pret, Upps, Xaix; four adult males: Can, Ert, Gov, LSk). An initial rating of 1000 was assigned to immigrant males and adult females (after giving birth for the first time). The figure shows how Elo-ratings change through time according to single agonistic interactions: the ratings of winners increase while the ratings of losers decrease.

Appendix 5: Statistical analyses

General analysis

Although 384 encounters were collected during focal follows, we only analysed 316 encounters (17.7% incomplete data removed) involving 23 well-habituated individuals (12 AF and 11 AM) belonging to three of five study groups (BD, IN and NH) over 8 months (9 May 2014–3 January 2015). We excluded 101 observations that were collected on juveniles because we did not collect data to establish their dominance status or friendships.

We built a generalized linear mixed model fitted by maximum likelihood using Laplace approximation (Bolker, Brooks et al. 2009) with a binomial error structure and logit link function ("glmer" provided by the package "lme4"; Bates, Mächler et al. 2015). We used this model to describe the general greeting behaviour of vervet monkeys, that is, under which condition greetings were produced. Whether the focal individual produced a grunt during an encounter served as a response variable in our model. We introduced six variables to check the influence of both individual characteristics (focal and partner sex), characteristics of the relationship between the two interacting individuals (standardized rank difference and DSI reflecting social bonds strength) and two relevant ecological factors (close to rivers and habitat type). We included both the identity of the focal animal and its partner as random intercepts to control for repeated measurements. We transformed numerical explanatory variables when necessary to approximate symmetric distributions of our predictor variables (i.e. we log-transformed DSI).

Function analysis

We focused on the greeting behaviour of adult males because females rarely produced grunts and because their calls were often barely audible. Here, we defined the caller as the individual producing a vocal signal and the receiver as the individual responding to it. In addition to collecting dyadic encounter data between males within 5 m, we also recorded all-occurrence data of such vocal interactions between two males in four of five study groups (AK, BD, KB and NH; Table 2) between 13 March 2014 and 17 March 2015 (Table A4; Appendix 3). We collected 891 dyadic interactions, from which we excluded 338 observations involving females and juveniles (focal data excluded: 229 adult females, nine juvenile females, 28 juvenile males; partner data excluded: 28 adult females, 14 juvenile females, 30 juvenile males) and 14 observations from the LT group as no social data were collected on this group (meaning we could not calculate rank difference and social bond strength). We excluded a further 96 observations for which we could not identify at least one of the participants and 89 observations during which we were not confident on the identity of the caller (our study focused on calls produced by the focal animal only). We also removed data from unhabituated males (defined by the number of days present in the study group prior to data collection, and whether the male had been seen in other habituated groups previously) to avoid observation bias as habituated males were more likely to be observed than shyer ones remaining at the periphery. We excluded 27 observations from nine unhabituated males from three groups (one in AK, five in BD and three in NH). As we wanted to investigate the function of greeting signals, we kept only male–male dyadic interactions during which grunts were produced, thus excluding 243 observations where no vocal signals were produced and five encounters during which calls other than grunts were produced (mostly aggression calls).

As a result, we analysed greetings occurring between 25 male dyads. Since some individuals were more vocally active than other group members, some dyads were observed greeting more often than others (mean = 3.16 vocal encounters per dyad, range 1–18). Consequently, we transformed the response variable into a binomial structure, that is, whether a greeting signal was produced at least once in a given situation in a specific dyad (Table A7).

Table A7. Number of males, male–male dyads and observed greetings in the four study groups

Group	No. of adult males	No. of male–male dyads	No. of male–male dyads observed greeting	No. of greeting calls produced
AK	4	6	2	7 (4)
BD	9	36	12	21 (18)
KB	4	6	5	39 (20)
NH	5	10	6	12 (11)
Total	22	58	25	79 (53)

Two males migrated from one study group to another during the study period and were counted twice in the total number of adult males as they participated in encounters in both groups. Numbers in parentheses in the last column represent the number of greetings used for the function analysis after modifications to get a binomial structure, i.e. considered as Yes=1 for an observed greeting as soon as at least one vocal signal was produced within a dyad and No=0 if males from a dyad have never been observed greeting.

Our modelling strategy here focused on whether we observed a greeting signal in any given dyad under different conditions. We used Kulik et al.'s (Kulik, Muniz et al. 2012) approach to create an expanded table (see Table A8; see also Genty, Neumann et al. (2015) for another example). We first selected all the males that were present at least 1 day in our studied groups as potential subjects. We then created a table including all dyads that could potentially have interacted with each other. . Since both males from any dyad could have been either the caller or the receiver, we represented the dyad twice in our table, thus already doubling the amount of data. We then assumed that encounters of each dyad could potentially occur in all combinations of our conditions. In other words, we expanded our data table containing all the observations we could have made using all the dyads in all conditions. For instance, by including the categorical variable close to rivers, we again doubled the size of the data set as we assumed that encounters of each dyad could have happened either close to rivers (Yes=1) or away from them (No=0). Consequently, by adding two more categorical variables, caller approached (Yes=1/No=0) and feeding involved (Yes=1/No=0), we multiplied the amount of data by four. However, we took care to remove all self-dyads and males that were not co-residents in one group during the study period. We then added information on the social relationship between the two males involved in the dyad, that is, their rank difference as well as their social bond strength. At this stage, we also also removed all unhabituated to avoid biased observations towards bolder males. Finally, we added the response variable whether a grunt was observed in a dyad at least once or not (Yes=1/No=0), thus again doubling the amount of data. With this method, each dyad (N=58 possible dyads) in which a greeting could potentially have been observed, was represented multiple times according to different combinations of predictor variables. However, each dyad was represented only once for each specific condition, such as for example ‘close to rivers = Yes’, ‘caller approached = Yes’ and ‘feeding involved = No’. Moreover, in addition to the identity of both males, we also included group and dyad as random intercepts in all our models to avoid pseudoreplication. As a result, we analysed a restructured data set with 752 data points that represent the conditions under which a greeting could have potentially occurred, from which we observed 53 (about 7%), that is, we observed a male producing a grunt towards another male under specific circumstances. In addition to investigating what individuals do, examining under which conditions individuals do not do it also helps us understand the functional aspects of this behaviour.

Table A8. The nine steps needed to obtain the restructured data set

1. Select participating males	We considered every male present in a studied group at least 1 day during the study period in the analysis
2. Create dyads	We created all the possible male–male dyads (e.g. if group size is four males, then there are six possible dyads, see Table A7)
3. Assign caller/receiver	We represented each dyad twice, with caller/receiver roles reversed
4. Add predictive variables	We added the following three predictors: close to rivers = whether greetings occurred <100 m of riverbed (Yes/No); caller approached = whether the caller was initiating the encounter by actively approaching another male (Yes/No); feeding involved = whether at least one of the participants was feeding (Yes/No)
5. Take only co-resident males	We excluded all self-dyads (i.e. the same male being the caller and receiver as that was not possible) as well as all dyads composed of males that were not co-residents in one group during the study period
6. Add Elo-rating difference	We obtained a rank difference for a specific dyad by subtracting the average Elo-rating of the receiver during the study period from that of the caller. Negative values thus mean callers are lower-rated than receivers whereas positive values indicate that callers are higher-rated than receivers
7. Add social bond strength (DSI)	We added the dyadic composite social index (Silk, Cheney et al. 2013) for a dyad by looking at the time two individuals spend grooming, in close proximity (<10 m) or as nearest neighbours of each other using focal data
8. Exclude unhabituated subjects	We excluded all the males considered as not well habituated based on their tenure in the group, on their presence in another studied group before their immigration into their current group and the number of days they were seen in the group during the study period to avoid habituation bias, as bold individuals might be observed more frequently than shyer ones
9. Add response variable	We added whether a grunt between two adult males was observed at least once (Yes=1/No=0) under the conditions specified by the different combinations of outcomes of our predictor variables to examine the functions of greeting signals (see Table A9 for further illustration)

Table A9. Example of restructured data set used for the function analysis

Caller	Receiver	Close to rivers	Caller approached	Feeding involved	No. of days of co-residence	Elo-rating difference	DSI	Observed greeting
Art	Lek	No	No	No	67	-223	5.140	0
Art	Lek	No	No	Yes	67	-223	5.140	0
Art	Lek	No	Yes	No	67	-223	5.140	1
Art	Lek	No	Yes	Yes	67	-223	5.140	0
Art	Lek	Yes	No	No	67	-223	5.140	0
Art	Lek	Yes	No	Yes	67	-223	5.140	0
Art	Lek	Yes	Yes	No	67	-223	5.140	0
Art	Lek	Yes	Yes	Yes	67	-223	5.140	0
Lek	Art	No	No	No	67	223	5.140	0
Lek	Art	No	No	Yes	67	223	5.140	1
Lek	Art	No	Yes	No	67	223	5.140	0
Lek	Art	No	Yes	Yes	67	223	5.140	1
Lek	Art	Yes	No	No	67	223	5.140	1
Lek	Art	Yes	No	Yes	67	223	5.140	1
Lek	Art	Yes	Yes	No	67	223	5.140	0
Lek	Art	Yes	Yes	Yes	67	223	5.140	1

DSI: dyadic composite social index. The last column represents our response variable, that is, whether we observed at least one greeting between both participants under specific conditions (Yes=1 and No=0).

Table A9 is an excerpt from our data set and illustrates this approach. It depicts a specific dyad (Art/Lek). Art was the caller and Lek the receiver in the first half of the table, whereas their roles were reversed in the second part. Three further combinations are depicted: close to rivers (i.e. within 100 m of the riverbed), caller approached (i.e. whether the caller was the individual actively approaching the partner) and feeding context (i.e. whether some feeding behaviour was involved). In this example, we observed one greeting between Art/Lek that took place away from rivers (close to rivers = No), where Art, who was the caller, approached (caller approached = Yes) and during which no feeding was involved (feeding involved = No, see line 3 in Table A9). In contrast, we did not observe a greeting between Art/Lek that took place away from rivers (close to rivers = No), where Art, who was the caller, approached (caller approached =Yes) and during which some feeding was involved (feeding involved = Yes) as we never observed Art greeting in a feeding context while approaching Lek away from rivers (line 4 in Table A9). In contrast to Art who we observed producing a grunt in only one of the eight possible conditions, we observed Lek greeting Art under five specific circumstances out of the eight possible (lines 10, 12, 13, 14, 16 in Table A9).

Table A10. Results of the GLMM testing the benign intent hypothesis

	Estimate	SE	*Z*	CI
Intercept	-3.24	0.73	-4.44	-4.67 to -1.81
Presence of food (Yes)	0.34	0.41	0.82	-0.47 to 1.15
Whether initiator called (Yes)	-1.47	0.56	-2.61	-2.58 to -0.37
Interaction Presence of food (Yes)*Whether initiator called (Yes)	-0.56	0.78	-0.71	-2.10 to 0.98

CI = 95% confidence intervals using Wald method; test levels of categorical predictors are given in parentheses.

Table A11. Results of the GLMM testing the conflict management hypothesis

	Estimate	SE	*Z*	CI
Intercept	-3.72	0.62	-5.96	-4.94 to -2.50
Rank difference	-0.58	0.33	- 1.75	-1.22 to 0.07
Rank difference (quadratic)	0.19	0.19	0.99	-0.19 to 0.57
Social bond strength (DSI)	0.49	0.35	1.41	-0.19 to 1.17
Presence of food (Yes)	0.17	0.34	0.50	-0.49 to 0.83

CI = 95% confidence intervals using Wald method; test levels of categorical predictors are given in parentheses.

Table A12. Results of the GLMM testing the signal submission hypothesis

	Estimate	SE	Z	CI
Intercept	-3.62	0.63	-5.72	-4.86 to -2.38
Rank difference	-0.63	0.37	-1.71	-1.36 to 0.09
Presence of food (Yes)	0.17	0.34	0.50	-0.49 to 0.83

CI = 95% confidence intervals using Wald method; test levels of categorical predictors are given in parentheses.

Table A13. Results of the GLMM testing the social coordination hypothesis

	Estimate	SE	*Z*	CI
Intercept	-3.99	0.65	-6.17	-5.26 to -2.72
Rank difference	-0.91	0.45	-2.00	-1.80 to -0.02
Social bond strength (DSI)	0.82	0.56	1.48	-0.27 to 1.92
Presence of food (Yes)	0.47	0.39	1.22	-0.29 to 1.23
Close to rivers (Yes)	0.47	0.37	1.27	-0.25 to 1.20
Interaction Rank difference*Social bond	0.27	0.36	0.74	-0.44 to 0.98
Interaction Rank difference*Presence of food	0.64	0.33	1.91	-0.02 to 1.29
Interaction Rank difference*Close to rivers (Yes)	-0.10	0.32	-0.31	-0.72 to 0.52
Interaction Social bond strength*Presence of food (Yes)	-0.27	0.49	-0.55	-1.24 to 0.70
Interaction Friendship*Close to rivers (Yes)	-0.13	0.48	-0.27	-1.08 to 0.82

CI = 95% confidence intervals using Wald method; test levels of categorical predictors are given in parentheses.

Table A14. Results of the GLMM testing the social bond testing hypothesis

	Estimate	SE	*Z*	CI
Intercept	-3.52	0.61	-5.73	-4.73 to -2.32
Social bond strength (DSI)	0.55	0.35	1.58	-0.13 to 1.24
Presence of food (Yes)	0.17	0.33	0.50	-0.49 to 0.82

CI = 95% confidence intervals using Wald method; test levels of categorical predictors are given in parentheses.

Table A15. Results of the GLMM testing the risk reduction hypothesis

	Estimate	SE	*Z*	CI
Intercept	-3.28	0.69	-4.75	-4.63 to -1.93
Social bond strength (DSI)	0.59	0.38	1.57	-0.15 to 1.34
Whether initiator called (Yes)	-1.77	0.42	-4.18	-2.60 to -0.94
Close to rivers (Yes)	0.56	0.36	1.56	-0.14 to 1.26

CI = 95% confidence intervals using Wald method; test levels of categorical predictors are given in parentheses.

IV. Chapter 2 - Correlates of social role and conflict severity in vervet monkeys agonistic screams

First submission in PLOS ONE on February 2018.
Revised manuscript submitted in PLOS ONE on the 8th of August 2018.

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4.1 Abstract

Screams are acoustically distinct, high-pitched and high-amplitude calls, produced by many social species. Despite a wide range of production contexts, screams are characterised by an acoustic structure that appears to serve in altering the behaviour of targeted receivers during agonistic encounters. In chimpanzees, this can be achieved by callers producing acoustic variants that correlate with their identity, social role, relationship with the targeted recipient, composition of the audience and the nature of the event. Although vervet monkeys (*Chlorocebus pygerythrus*) have been studied for decades, not much is known about their agonistic screams. Here, we examined agonistic screams produced by wild vervet monkeys to investigate the degree to which the callers' social role and conflict severity affected the acoustic structure of their calls. We found that screams were individually distinct, with victim screams being longer and higher-pitched than aggressor screams, and screams produced in severe conflicts (chases, physical contact) having higher entropy than screams during mild conflicts. We discuss these findings in terms of their evolutionary significance and suggest that acoustic variation might serve to reduce the aggression level of opponents, while simultaneously attracting potential helpers.

<u>Keywords</u>: aggression, alliance formation, audience effect, non-human primate, recruitment signal, vocal communication

4.2 Introduction

Many species of animals produce acoustically distinct screams in a range of contexts. These calls are usually high-pitched and of maximum amplitude within a species' vocal repertoire (e.g. Macaques, *Macaca spp.*: Gouzoules and Gouzoules 2000). As a result, screams often travel over considerable distances to serve different functions, such as repelling aggressors (e.g. tree shrew, *Tupaia belangeri*: Binz and Zimmermann 1989) or predators (e.g. European starling, *Sturnus vulgaris*: Hogstedt 1983), recruiting allies (e.g. pigtail macaque, *Macaca nemestrina*: Gouzoules and Gouzoules 1990), advertising copulations (e.g. New Guinea singing dog, *Canis hallstromi*: Koler-Matznick, Brisbin et al. 2003) or facilitating group fusions (e.g. dwarf mongoose, *Helogale parvula*: Rubow, Cherry et al. 2017). Despite their universal acoustic characteristics, in some species it has been found that screams are characterised by substantial between-context variation, particularly with regards to duration, pitch and proportion of tonal and noisy components (Cleveland and Snowdon 1982, Gouzoules, Gouzoules et al. 1984).

A number of theories have been put forward to explain general patterns of acoustic variation in animal calls. First, Morton's motivational-structural rules (1977) state that vocalisations emitted during hostile and aggressive situations tend to be low frequency, harsh sounds with a broadband frequency range (large inter-quartile range and high entropy), with harshness being positively related to non-linear acoustic phenomena (NLP; Fitch, Neubauer et al. 2002). In contrast, calls produced in friendly interactions or when the caller is fearful tend to be tonal and high frequency (1977). Similar arguments have been made for differences in urgency with signallers producing longer calls at higher rates in urgent contexts compared to other situations (Seyfarth and Cheney 2003a).

Second, a related argument has been made by Owren & Rendall (1997, 2001) who suggested that the primary function of vocal signals is to directly influence the behaviour of receivers through specific acoustic features. For example, chaotic spectral sounds with sharp onsets and dramatic fluctuations in both frequency and amplitude are likely to increase attention levels and other inner states in receivers, and may become aversive when repetitive (Owren and Rendall 2001, Rendall, Owren et al. 2009). To humans, such acoustic structures tend to be intrinsically 'unpleasant' (Arnal, Flinker et al. 2015), suggesting the same may be the case for animals (Owren and Rendall 2001). Another important feature of animal calls are non-linear phenomena (Fitch, Neubauer et al. 2002), which include frequency jumps, bi-phonation, sub-harmonics and deterministic chaos (see Wilden, Herzel et al. 1998 for further descriptions). While sub-harmonics and chaotic segments appear to prevent habituation (Blumstein and Recapet 2009), bi-phonation appears to signal the caller's physical condition (e.g. in chimpanzee, *Pan troglodytes schweinfurthii*, pant hoots: Riede, Arcadi et al. 2007) and facilitate individual recognition (e.g. dhole, *Cuon alpinus*, yap-squeaks: Volodina, Volodin et al. 2006).

Third, Briefer (2012) argued that vocalisations might be good indicators of emotional states in animals, where emotion is defined in terms of valence and arousal (Mendl, Burman et al. 2010). Valence (whether a situation is perceived as positive or negative) is thought to mainly be linked to energy distribution and frequency spectrum, while arousal (reflecting situations' intensity) is thought to be linked to fundamental frequency, duration and rate of calling, produced by differences in respiration (Briefer 2012). More specifically, calls produced in situations of high arousal should therefore be high frequency, high amplitude, noisy, long and produced at high rates.

While the previous theories all focus on the eventual dissuasive effects of screams on opponents, thanks to the general obnoxious acoustic characteristic of these calls (Berryman 1976, Owren and Rendall 1997), another function concerns the potential to attract helpers (Fedurek, Slocombe et al. 2015b). Interfering in ongoing aggression is likely to be very costly for bystanders, suggesting that listeners may require specific information before deciding whether to intervene or not (Slocombe, Townsend et al. 2009). In particular, screams' variation should provide reliable identity cues and describe the on-going event in sufficient details so that potential third-party helpers can intervene only when beneficial, such as to support kin involved in severe fights. Indeed, several studies on a range of species have shown that screams differ according to caller identity, including, for example, European starlings (Chaiken 1992), white-faced capuchins, *Cebus capucinus* (Digweed, Fedigan et al. 2007) or vampire bats, *Phyllostomidae* family (Carter, Logsdon et al. 2012). Crucially, playback experiments in several primate species have demonstrated that listeners adjust their support according to the identity of the caller, suggesting that they attend to the identity features of the calls (e.g. squirrel monkey, *Saimiri sciureus*: Symmes and Biben 1985, Barbary macaque, *Macaca sylvanus*: Hammerschmidt and Fischer 1998, or Japanese macaque, *Macaca fuscata*: Shizawa, Nakamichi et al. 2005). For example, rhesus monkeys, Macaca mulatta, respond more strongly to playbacks of screams by kin than unrelated individuals (Fugate, Gouzoules et al. 2008).

Similarly, there is evidence in some primates that screams conveys the type of event, another essential piece of information for bystanders (caller's social role: aggressor vs. victim; conflict severity: mild vs. severe). For example, Geoffroy's spider monkeys, Ateles geoffroyi, produce screams with lower fundamental frequencies as aggressors than as victims as well as during severe than mild conflicts (Ordóñez-Gómez, Dunn et al. 2015). In chimpanzees, screams also differ in duration and spectral structure according to the social role of signallers (Slocombe and Zuberbuhler 2005), and receivers adapt their support according to whether victims are involved in mild or severe conflicts (Slocombe, Townsend et al. 2009). Moreover, nearby listeners react appropriately according to the nature of agonistic events, by using a combination of acoustic cues and their general social knowledge (Slocombe, Kaller et al. 2010a).

Like other primates, vervet monkeys often produce screams in a variety of contexts, particularly during social conflicts (Struhsaker 1967a; S1 Table). Screams can be accompanied by facial expressions that range from partially closed to widely open mouths with exposed teeth (Struhsaker 1967a), probably reflecting differences in the severity of conflicts. Using playback experiments, Hauser (1986) argued that adult listeners attend to identity cues present in infant screams. Furthermore, females discriminate between screams of their own and unrelated juveniles, with bystander females looking towards the mothers of call providers, suggesting third-party knowledge of mother-offspring dyads (Cheney and Seyfarth 1980). Whether the acoustic structure of vervet monkey screams differs according to the social role of signallers and conflict severity has, to our knowledge, not yet been addressed.

The aim of this study was to describe the structure of all high-pitched calls produced by wild vervet monkeys during agonistic interactions. We selected 15 common acoustic parameters and tested whether part of the variation could be predicted by the social role of signallers (aggressor vs. victim) and conflict severity (mild vs. severe). First, in line with previous theories, we expected screams produced by victims to be higher pitched and contain more NLP than the ones produced by aggressors. Second, we predicted that victims of mild aggressions would emit screams that would be shorter, higher-pitched, more tonal and given at lower rates than screams produced by victims of severe aggressions (see S2 Table for detailed predictions). As identity cues are important if calls are directed at third-party bystanders, we investigated whether screams were individually distinct and, crucially, whether the social role of signallers and/or conflict severity affected the rate of support obtained by signallers.

4.3 Methods

4.3.1 Ethical note

All animals have been fully habituated to the presence of human observers and did not show any signs of disturbance related to researchers. We used standard ways of collecting natural behavioural data for this study and received approval by Ezemvelo KZN Wildlife, the governmental organisation in charge of Kwa-Zulu Natal wildlife conservation and biodiversity, and the University of Cape Town, South Africa. Furthermore, all field experimental protocols of feeding experiments ran by other researchers were carried out in accordance with the relevant guidelines and regulations, which also have been approved by Ezemvelo KZN Wildlife, as well as by the Ethics Committee of the School of Psychology and Neuroscience, University of St Andrews.

4.3.2 Study site and species

The study took place in the Savannah biome of the Mawana Game Reserve, a private farm of 12’000 hectares in KwaZulu-Natal, South Africa (S28°00.327; E031°12.348) and base of the Inkawu Vervet Project (IVP). Subjects were 28 wild individuals, belonging to two wild groups of vervet monkeys: Ankhase (AK; one adult female and one juvenile male) and Baie Dankie (BD; eight adult females, seven juvenile females and 11 juvenile males, see S3 Table for detailed descriptions of call providers). Although group size varied over time due to births, deaths and migrations, both groups contained multiple males (defined as adults after their first migratory event, but excluded from analyses as they rarely scream), females (defined as adults after they gave birth for the first time) and juveniles.

4.3.3 Data collection

We recorded scream vocalisations over four years (17.07.12 – 06.11.2015, see S3 Table for detailed number of calls, bouts and events used for analyses). Recordings were made with a Marantz PMD661 (sampling rate of 44.1 kHz, resolution 24 bits) and a Sennheiser MKH416 microphone and stored as wav files. Recordings were based on ad libitum sampling, that is, any call observed during natural conflicts or during conflicts following food provisioning experiments carried out as part of other research, using four different experimental methods (‘box’ experiment: subjects had to retrieve food from a closed container (Borgeaud and Bshary 2015), ‘jingle’ experiment: conditioned subjects were rewarded following individualised acoustic cues (Arseneau-Robar, Müller et al. 2016), ‘corn’ experiment: large plastic containers with corn were provided for the entire group to feed on (van de Waal, Borgeaud et al. 2013, van de Waal, van Schaik et al. 2017), ‘vervetable’ experiment: subjects had to copy a demonstrator’s object manipulations to access a small amount of food (van de Waal, Claidiere et al. 2015)). Conflicts occurred in all four experimental conditions.

For any conflict, we recorded the context (observation vs. experiment), caller and recipient identity and behaviour (feeding vs. not feeding), social role (aggressor vs. victim), conflict severity (mild vs. severe), any third-party interventions (yes vs. no), GPS location, weather condition, audience size (i.e. number of individuals present within 10m of the interaction) and, if possible, audience identity.

4.3.4 Definitions

Screams

We defined a scream as any call that was high-pitched, shrill-sounding and produced during an agonistic event (see S1 Table for screams’ production in vervet monkeys and S4 Appendix for details on acoustic data). Although the mean scream intervals in our dataset was 0.5s (measured from spectrograms created in Praat version 5.4.13 (Boersma 2006), www.praat.org), we coded a scream as a distinct utterance if it was separated by at least 0.3s of silence from another scream. To reduce the problem of non-independency of data, we selected calls from different bouts or events whenever possible (see S3 for detailed information of the number of events, bouts and screams used for each call provider). We excluded all aggressive calls, such as barks, grunts and any unclassifiable vocalisations (Struhsaker 1967a).

Conflict

We defined conflict as an agonistic interaction that started when an individual approached another one in a threatening way, i.e., performing at least one of the aggressive behaviours described in Table 1, and lasted until both opponents resumed normal activities. While such events sometimes started without specific signalling (e.g., one individual displacing another one silently), we measured event duration from the onset of the first and offset of the last screams produced during the event using oscillograms and spectrograms created in Praat (Boersma 2006) using a Fast Fourier Transformation (Hanning window shape, window length = 0.01s, number of time steps = 1000, number of frequency steps = 500 and dynamic range = 40dB). We classified events as separate from each other if there was a change in partner identities or if there were separated by an interval of at least 30s without any agonistic behaviour. Screams were typically emitted in bouts, which we defined as different stages of the conflict distinct from each other when either the social role of signallers or the severity of the conflict changed (S4 Appendix).

Table 1. Description of the aggressive behaviours determining conflict severity

Aggression	Conflict	Risk of injury	Aggressive behaviour
Mild	Non-directed	Low	Approach, aggression calls, monopolise
Mild	Directed	Low	Stare, attack, displace
Severe	Chase	High	Chase
Severe	Physical contact	High	Hit, grab, bite

Modified from Slocombe and Zuberbuhler (2007)

Conflict severity

Similarly to the study on wild chimpanzees' screams (Slocombe and Zuberbuhler 2007), we distinguished two types of agonistic interactions according to conflict severity. We considered a conflict being of mild aggression if the risk of injuries resulting from the conflict was low, while a severe aggression could generate potential harm either through direct physical contact, or through accidental injuries resulting from an escaping or chasing behaviour (Table 1). While some behaviours were clearly directed at targeted opponents (e.g. stare, chase, physical contact), others were not directed but provoked reactions in nearby conspecifics, such as approaching a feeding spot, which could trigger screams from feeding individuals.

Social role of signallers

During agonistic interactions, individuals could take two basic social roles: aggressor or victim. We defined individuals as aggressors if they performed at least one of the following behaviours: stare, monopolise, attack, displace, chase, hit, grab, bite or produce aggressive calls. We classified individuals as victims if they performed at least one of the following behaviours: avoid, retreat, jump aside, crawl, flee, look for support or redirect the aggression on another individual, including humans (see S5 Table for a detailed ethogram). However, the social role of an individual might change during a single event, as for example when a victim being chased by an aggressor redirects the aggression towards a new victim, thus becomes an aggressor, or by recruiting support from bystanders that help the victim to chase away the initial aggressor. In such cases of role switching, we defined the different stages of conflicts as separate bouts (S4 Appendix).

Support

Support was defined as an individual entering an already ongoing conflict and behaving aggressively towards one of the two opponents. We recorded whether or not support occurred during each conflict (see S5 Table for a detailed ethogram). Whenever possible, we collected the identity of all animals involved.

4.3.5 Acoustic analyses

We only subjected screams to acoustic analyses if they were of good quality (low background noise, no clipped sounds or reverberation noise) and if the required contextual information was available. We tried to match screams exchanged between the same two individuals during the same period (or with minimal time intervals) in different contexts (observation vs. experiment). This was to control for potential effects of opponent identity or developmental effects. As adult males rarely produced screams, we excluded them from analysis.

Following visual inspection of the spectrograms we excluded 19.8% of the recording due to poor recording quality following above criteria. The resulting dataset then included N=513 screams from 122 bouts and 98 events produced by 28 individuals of all age-sex classes, except adult males. We excluded a further N=103 screams due to incomplete observations and N=104 screams because some acoustic parameters could not be reliably extracted from these recordings, resulting in a final dataset of N=306 screams from 121 bouts and 98 events produced by 28 individuals (see S3 Table for details and S4 Appendix for acoustic data). We selected 15 acoustic parameters to describe the screams' acoustic properties and the temporal structure of their bouts (nine parameters at the call level and six at the bout level; Table 2). We chose commonly used parameters that allowed us to make clear predictions on screams variation according to the social role of signallers and conflict severity (S2 Table). We were unable to use fundamental and formant frequencies due to the noisy acoustic components often present in vervet monkey screams. Temporal parameters were extracted from spectrograms and oscillograms created in Praat (Boersma 2006). All other acoustic parameters were extracted from spectrograms and spectral slices (see S4 for examples) created with Seewave (Sueur, Aubin et al. 2008) and tuneR packages (Ligges 2013) in R version 1.0.143 (Team 2016) using the following settings: sampling rate of 44.1 kHz, 16 bits accuracy, Fast Fourier Transformation with 512 samples, Hanning window and 90% overlap.

Table 2. Definitions of the 15 selected acoustic parameters for this study

Parameters	Definitions
CALL LEVEL	
Scream duration (s)	Duration of one scream, described as a continuous vocal unit along a time axis on the spectrogram that is not interrupted by more than 0.03s of silence
Peak frequency (kHz)	Frequency taken from the spectral slice at which maximum acoustic energy occurs in the entire scream
Coefficient of frequency variation *	Coefficient of frequency variation representing the range of frequency variation around the mean
Coefficient of frequency modulation	Coefficient of frequency modulation representing frequency changes over time
Absolute transition onset (Hz)	Frequency at which maximum acoustic energy occurs at the middle of the scream minus the one occurring at the beginning of the scream
Absolute transition offset (Hz)	Frequency at which maximum acoustic energy occurs at the end of the scream minus the one occurring at the middle of the scream
Frequency quartile 50 (Hz)	Frequency quartile that divides the scream into two frequency intervals of equal energy (corresponding to 50-50%)
Inter-quartile range (Hz)	Inter-quartile range representing the difference of the frequency quartile of 25% and 75% (corresponding to Q25-Q75)
Shannon entropy	Measure of the uniformity of the power spectrum, with white noise having an entropy value of 1 and pure tone having an entropy value of 0
BOUT LEVEL	
Bout duration (s) *	Duration of one bout, described as a specific stage of a conflict in which the social role of signallers and the conflict severity is stable
Number of screams	Total number of screams emitted by the signaller within a single bout
Average scream duration (s)	Average duration of all screams produced by one individual within a bout
Scream intervals (s) *	Average duration of the intervals between the screams produced by one individual within a bout
Scream rate (number of screams/s)	Rate of screams produced by one individual within a bout delivered per time unit
Percentage of screams with NLP (%)	Percentage of screams emitted in a bout containing at least one of the four following forms of NLP: frequency jumps, sub-harmonic segments, bi-phonation or chaotic segments

** Parameters excluded due to high correlations or failure to reach symmetrical distribution, leading to analyses using 12 acoustic parameters (eight at the call level and four at the bout level; S2)*

4.3.6 Inter-observer reliability

We tested for inter-observer reliability of behavioural and acoustic data using Cohen's Kappa method (1960). First, two observers coded behavioural sequences of agonistic interactions recorded in the field to obtain a proportion of agreement for the number of bouts within the conflict, the social role of signallers and conflict severity (SM-EW, Cohen's Kappa, number of bouts: N = 50 i.e. 49% of all data, k = 0.88; social role: N = 63 i.e. 49% of all data, k = 0.90; severity: N = 63 i.e. 54% of all data, k = 0.87). Second, two observers annotated 20 raw recordings (i.e. 14% of all data, see Fig S1. for an example of annotated recording) in Praat to then compare the resulting text grids allowing us to obtain a Cohen's Kappa value for five acoustic parameters: duration of event (counted as an agreement if differences in measurement were <1s), total number of screams produced within a bout, average duration of screams produced in a bout (counted as an agreement if differences in measurement were <0.3s), proportion of screams of good quality and percentage of screams presenting at least one form of NLP (SM-ED, Cohen's Kappa, N = 20 recordings, event duration: *k* = 1.00; number of screams: *k* = 0.88; scream duration: *k* = 0.84; analysable screams: *k* = 0.82; NLP: *k* = 0.70, see S6 Appendix for detailed protocol used to test for inter-observer reliability).

4.3.7 Statistical analyses

Context and caller identity

We initially performed fully crossed permutated discriminant function analyses (pDFA) using an R script provided by R. Mundry to investigate whether context (i.e. screams recorded during natural follows vs. during feeding experiments) affected call and bout related acoustic parameters while controlling for individual variation (Mundry and Sommer 2007). We then tested whether screams were individually distinct using a discriminant function analysis (DFA). We used the jack-knifed method, which derives discriminant functions from a subset of the data (classification success) and uses those to classify the remaining observations (cross-validation success). We selected on average 51.7% calls per individuals from datasets to maintain a balanced training set, and obtained mean classification and cross-validation successes using 100 randomly selected samples. We evaluated the success of the procedures by comparing the success rates obtained to the success rates obtained on 1000 permutated datasets, where calls were randomized across individuals. This comparative approach allows obtaining expected classification rates, which pertain directly to the dataset investigated, rather than relying on a theoretical distribution (see Déaux, Charrier et al. 2016 for more details on the methods). Data were transformed to reach approximate symmetrical distribution when needed and scaled (mean = 0 and s.d. = 1). We checked multi-collinearity among variables using correlation matrices and highly correlated variables (i.e. when > 0.80) were excluded from pDFAs and DFAs. We excluded the coefficient of frequency variation variable as it was highly correlated to Q50, and bout duration as it was highly correlated to both the number of screams and screams rate. Furthermore, we excluded scream intervals as transforming this parameter did not help to reach symmetrical distribution, and due to its correlation with both bout duration and scream rate. For the DFAs on caller identity, we used a crossed design with fully balanced dataset, to control for the participation of each individual in social role and severity, which reduced dramatically our sample size (resulting in N = 4 and N = 8 individuals for caller identity at the call and bout levels respectively). We thus re-ran these analyses to check for the robustness of our analyses with an increased sample size using an incomplete crossed design (increasing to N = 24 individuals and N = 13 individuals for caller identity at the call and bout levels respectively).

Social role of signallers and conflict severity

To investigate whether the social role of the signaller and conflict severity influenced the acoustic characteristics of screams, we performed a series of linear mixed models fitted by restricted maximum likelihood (REML) with Laplace approximation, normal or lognormal distributions and logit-link function (LMER; Bates, Mächler et al. 2015). We used each acoustic parameter as the response variable (leading to 12 GLMMs) and three fixed effects: social role of signallers (binary: aggressor vs. victim), conflict severity (binary: mild vs. severe) and their interaction. We included caller identity as a random effect to control for repeated measures, thus avoiding pseudo-replication (Waller, Warmelink et al. 2013). We then checked for homogeneity of the data and the distribution of residuals using graphical analyses of residuals (using bwplots, density plots, qqplots and binned plots) and checked for influential individuals and outliers, removing them only if necessary (that is, if it helped to reach approximate symmetrical distribution and did not affect our results). Consequently, we removed a total of six outliers and one influential individual (one outlier for the coefficient of frequency modulation, one outlier for the absolute transition offset, one influential individual (Alsi) for the frequency at quartile 50, one outlier for the Shannon entropy, one outlier for the number of screams and two outliers for the percentage of NLP).

Support

As one suggested function of agonistic screams is to recruit support, we used a generalized linear mixed model (Baayen, Davidson et al. 2008) fitted with a binomial structure and logit-link function to examine the influence of the social role of signallers and conflict severity on the occurrence of support during conflicts. We used the occurrence of support as the response variable, that is, whether a third-party individual intervened on behalf to one of the interacting monkey (binary: yes vs. no). We tested three predictor variables: social role of signallers (aggressor vs. victim), conflict severity (mild vs. severe) and their interaction. To control for repeated measurements, we included caller identity and context of production (using four levels: natural observations with and without feeding individuals and experiments involving and not involving valuable food items) as random intercepts. After checking for collinearity between variables using correlation matrices (all <0.80), we looked at the normality of residuals and the presence of outliers using graphical analyses of residuals (using half-normal plots and binnedplots).

Correcting for multiple testing

Although we ran the analyses on different datasets (all response variables were different), we extracted all acoustic parameters from the same recordings. Since we used a total of 12 linear models, each of them generating one p-value for each of the three fixed effects, we obtained a total of 36 p-values that we adjusted using the false discovery rate (BH method (Benjamini and Hochberg 1995)). Although less conservative that the more traditional Bonferroni correction (Wallenstein, Zucker et al. 1980), this method is applicable when researchers base their overall decision of the influence of a factor on multiple inferences, as it is the case here since we examined the influence of social role of signallers and conflict severity based on their effect on 12 acoustic features. This method controls both the expected proportion of falsely rejected hypotheses (FDR), and in a weak sense, the more traditional family-wise error rate (FWER), and is thus widely accepted.

All analyses were performed in R version 3.4.2 (Team 2016) using RStudio Version 1.1.383 and arm (Gelman, Su et al. 2016), car (Fox and Weisberg 2011), effects (Fox 2003), faraway (Faraway 2016), ggpubr (Kassambara 2017), lattice (Sarkar 2008), lme4 (Bates, Mächler et al. 2015), MASS (Venables and Ripley 2002), Matrix (Bates and Maechler 2017), MuMIN (Barton 2016) and RVAideMemoire packages (Hervé 2018).

4.4 Results

Context of production

Using 187 screams from 13 individuals, we could not discriminate screams according to the context of production at the call level, i.e., whether calls were given under natural situations of scramble competition or experimental situations of contest competition during artificial feeding events (pDFA crossed design: 74.2% expected calls correctly classified compared to 76.5% calls correctly classified, $P = 0.46$; cross-validation: 51.7% expected calls correctly cross-classified compared to 55.9% calls correctly cross-classified, $P = 0.21$). Similarly, using 102 bouts from 15 individuals, we could not discriminate bouts according to the context of production (pDFA crossed design: 54.4% expected calls correctly classified compared to 55.2% calls correctly classified, $P = 0.77$; cross-validation 50.7% expected calls correctly cross-classified compared to 40.8% calls correctly cross-classified, $P = 0.88$).

Caller identity

Since we could not discriminate screams according to the context of production, we pooled our data together for subsequent analyses. Using a fully balanced dataset with regards to the social role of signallers and conflict severity, we found that screams were individually distinctive at the call level (DFA crossed design, N = 4 individuals, N = 82 screams: 50.7% expected calls correctly classified compared to 66.3% calls correctly classified, *P* = 0.02; cross-validation: 24.9% expected calls correctly cross-classified compared to 47.2% calls correctly cross-classified, *P* = 0.002). Even when using an increased sample size (by using an unbalanced crossed design), screams could be discriminated according to the identity of the caller (DFA incomplete crossed design, N = 24 individuals, N = 301 screams: 33.6% expected calls correctly classified compared to 48.7% calls correctly classified, *P* = 0.002; cross-validation: 4.1% expected calls correctly cross-classified compared to 12.6% calls correctly cross-classified, *P* < 0.001). However, screams could not be discriminated between individuals at the bout level (DFA crossed design, N = 8 individuals, N = 61 bouts: 36.6% expected bouts correctly classified compared to 43.3% bouts correctly classified, *P* = 0.211; cross-validation: 12.5% expected bouts correctly cross-classified compared to 13.6% bouts correctly cross-classified, *P* = 0.504), including when we increased the sample size (DFA incomplete crossed design, N = 13 individuals, N = 85 bouts: 26.4% expected bouts correctly classified compared to 38.6% bouts correctly classified, *P* = 0.006; cross-validation: 7.4% expected bouts correctly cross-classified compared to 12.7% bouts correctly cross-classified, *P* = 0.096). Detailed results can be found in supplements (S7 Appendix).

Social role of signallers: aggressor vs. victim

Results from linear models showed that two out of the eight acoustic parameters tested at the call level were influenced by the social role of signallers (duration and Q50; Table 3 and S8 Appendix). We found that victims produced longer screams and had a higher Q50 than aggressors (Fig 1). In line with these results, we found that victims produced on average longer screams in a bout than aggressors (Fig 2, Table 4 and S9 Appendix). However, the percentage of NLP did not differ according to the social role of signallers.

Table 3. Results of linear models on the effect of social role and conflict severity at the call level

	Number of individuals and number of screams	Social role (binary: aggressor vs. victim)	Severity (binary: mild vs. severe)	Social role : Severity	R^2m - R^2c
Duration (s) *Estimate*		0.50	0.30	-0.25	
SD		0.13	0.15	0.20	0.07 - 0.09
T value	26	3.92	1.94	-1.24	
CI 95%	306	0.25 to 0.76	-0.00 to 0.60	-0.65 to 0.15	
P		< 0.001	0.123	0.215	
adjusted p		< 0.001 ***	0.316	0.407	
Peak frequency (kHz) *Estimate*		-0.12	-0.29	0.09	
SD		0.20	0.24	0.32	0.01 – 0.40
T value	26	-0.60	-1.18	0.28	
CI 95%	306	-0.50 to 0.27	-0.77 to 0.19	-0.54 to 0.72	
P		0.590	0.141	0.782	
adjusted p		0.732	0.317	0.828	
Coefficient of frequency modulation *Estimate*		0.04	0.19	-0.34	
SD		0.16	0.19	0.25	
T value	26	0.26	1.01	-1.35	

	CI 95%	305	-0.27 to 0.35	-0.18 to 0.57	-0.84 to 0.15	0.01 – 0.30
	P		0.443	0.993	0.176	
	adjusted p		0.612	0.993	0.372	
Absolute transition onset (Hz)	*Estimate*		-0.23	0.08	0.18	
	SD		0.15	0.19	0.25	0.01 – 0.10
	T value	26	-1.49	0.42	0.74	
	CI 95%	306	-0.53 to 0.07	-0.29 to 0.44	-0.30 to 0.67	
	P		0.186	0.132	0.459	
	adjusted p		0.372	0.317	0.612	
Absolute transition offset (Hz)	*Estimate*		-0.17	0.21	0.10	
	SD		0.15	0.18	0.24	0.02 – 0.13
	T value	26	-1.15	1.17	0.42	
	CI 95%	305	-046 to 0.12	-0.14 to 0.57	-0.37 to 0.57	
	P		0.253	0.023	0.676	
	adjusted p		0.434	0.104	0.737	
Q50 (Hz)	*Estimate*		0.06	0.03	0.06	
	SD	25	0.04	0.04	0.06	
	T value	298	1.72	0.66	0.96	0.05 – 0.19
	CI 95%		-0.01 to 0.13	-0.06 to 0.12	-0.06 to 0.17	
	P		0.003	0.036	0.336	
	adjusted p		0.022 *	0.118	0.550	
IQR (Hz)	*Estimate*		0.02	0.01	-0.03	
	SD		0.02	0.03	0.04	
	T value	26	0.88	0.33	-0.80	0.003 – 0.15
	CI 95%	306	-0.03 to 0.07	-0.05 to 0.07	-0.11 to 0.04	
	P		0.632	0.671	0.425	
	adjusted p		0.737	0.737	0.612	
Shannon entropy	*Estimate*		0.005	0.03	0.05	
	SD		0.02	0.02	0.03	
	T value	26	0.30	1.57	2.11	0.10 – 0.31
	CI 95%	305	-0.03 to 0.04	-0.01 to 0.07	0.004 to 0.11	
	P		0.035	< 0.001	0.035	
	adjusted p		0.118	< 0.001 ***	0.118	

*Significant results are represented by * when adjusted p-values < 0.05, ** <0.01 and *** < 0.001. R^2m corresponds to the variance explained by the fixed effects (marginal); R^2c corresponds to the variance explained by both the fixed and random effects (conditional). These numbers help to describe the amount of variation explained by the different factors included in the models.*

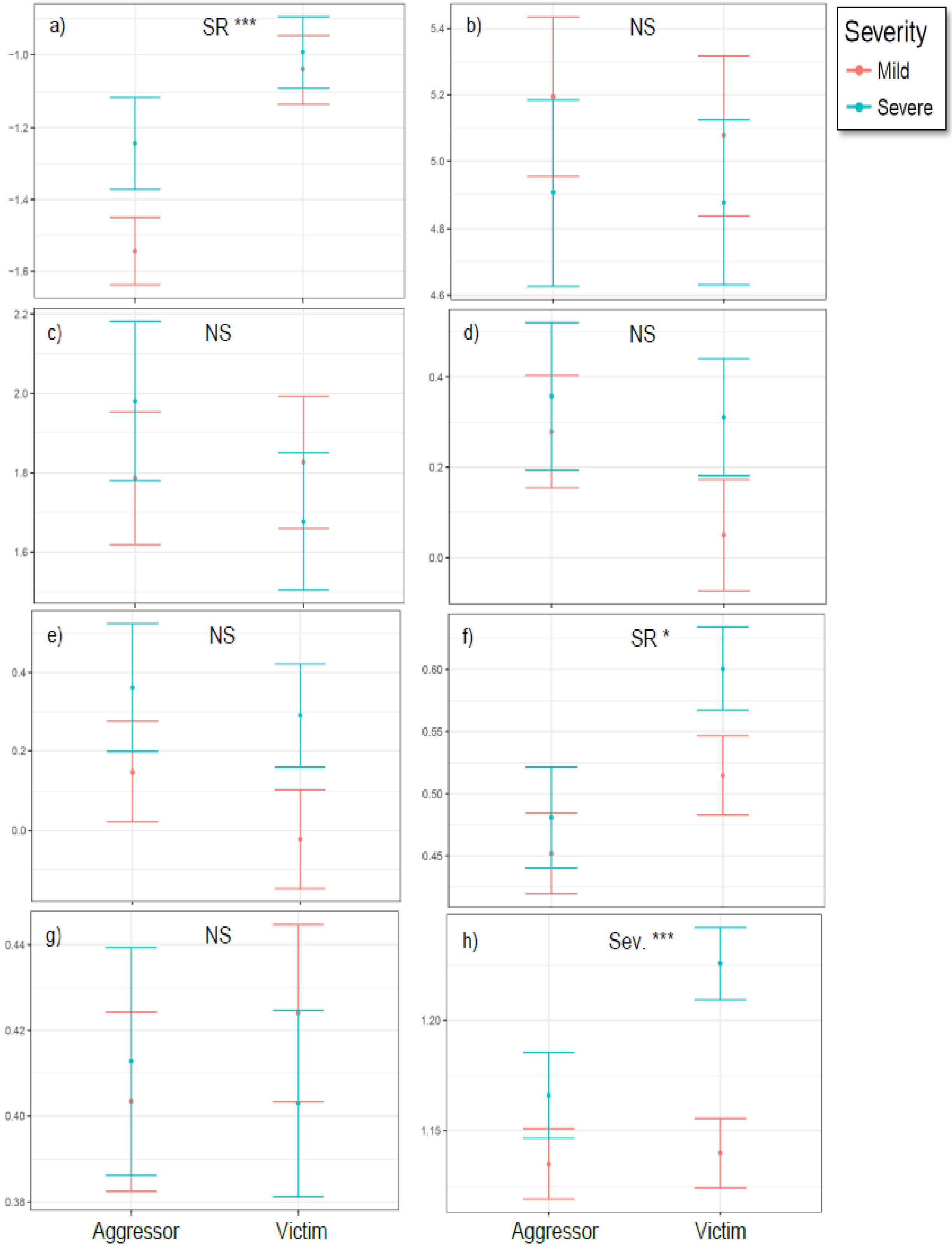


Fig 1. Effect plots displaying results from GLMMs at the call level of eight parameters varying according to the social role of callers (SR: aggressor vs. victim) and conflict severity (Sev: mild in orange vs. severe in blue): a) scream duration (s), b) peak frequency (kHz), c) coefficient of frequency modulation, d) absolute transition onset (Hz), e) absolute transition offset (Hz), f) frequency at quartile 50 (Hz), g) interquartile range (Hz) and h) Shannon entropy. While dots represents the predicted mean of the parameters (previously transformed when necessary and scaled), bars represent standards errors. Significant results are represented by * when adjusted p-values < 0.05, ** <0.01 and *** < 0.001.

Table 4. Results of linear models on the effect of social role and conflict severity at the bout level

		Number of individuals and number of bouts	Social role (binary: aggressor vs. victim)	Severity (binary: mild vs. severe)	Social role : Severity	R^2m - R^2c
Number of screams	*Estimate*		0.02	0.34	-0.43	
	SD		0.22	0.28	0.36	
	T value	28	0.09	1.19	-1.19	0.02
	CI 95%	120	-0.41 to 0.45	-0.22 to 0.89	-1.13 to 0.28	–
	P		0.433	0.670	0.235	0.25
	adjusted p		0.612	0.737	0.421	
Average scream duration (s)	*Estimate*		0.39	0.47	-0.15	
	SD		0.16	0.20	0.26	
	T value	28	2.51	2.33	-0.57	0.14
	CI 95%	121	0.09 to 0.70	0.07 to 0.87	-0.65 to 0.36	–
	P		0.007	0.002	0.569	0.18
	adjusted p		0.036 *	0.018 *	0.732	
Scream rate (number of screams/s)	*Estimate*		0.08	-0.76	0.51	
	SD		0.20	0.26	0.33	
	T value	28	0.42	-2.94	1.55	0.09
	CI 95%	121	-0.31 to 0.48	-1.27 to -0.25	-0.14 to 1.15	–
	P		0.088	0.005	0.122	0.19
	adjusted p		0.264	0.030 *	0.316	
NLP (%)	*Estimate*		-0.03	0.18	0.11	
	SD		0.08	0.10	0.12	
	T value	28	-0.42	1.79	0.91	0.11
	CI 95%	119	-0.18 to 0.12	-0.02 to 0.39	-0.13 to 0.35	–
	P		0.857	< 0.001	0.361	0.37
	adjusted p		0.881	< 0.001 ***	0.565	

*Significant results are represented by * when adjusted p-values < 0.05, ** <0.01 and *** < 0.001. R^2m corresponds to the variance explained by the fixed effects (marginal); R^2c corresponds to the variance explained by both the fixed and random effects (conditional). These numbers help to describe the amount of variation explained by the different factors included in the models.*

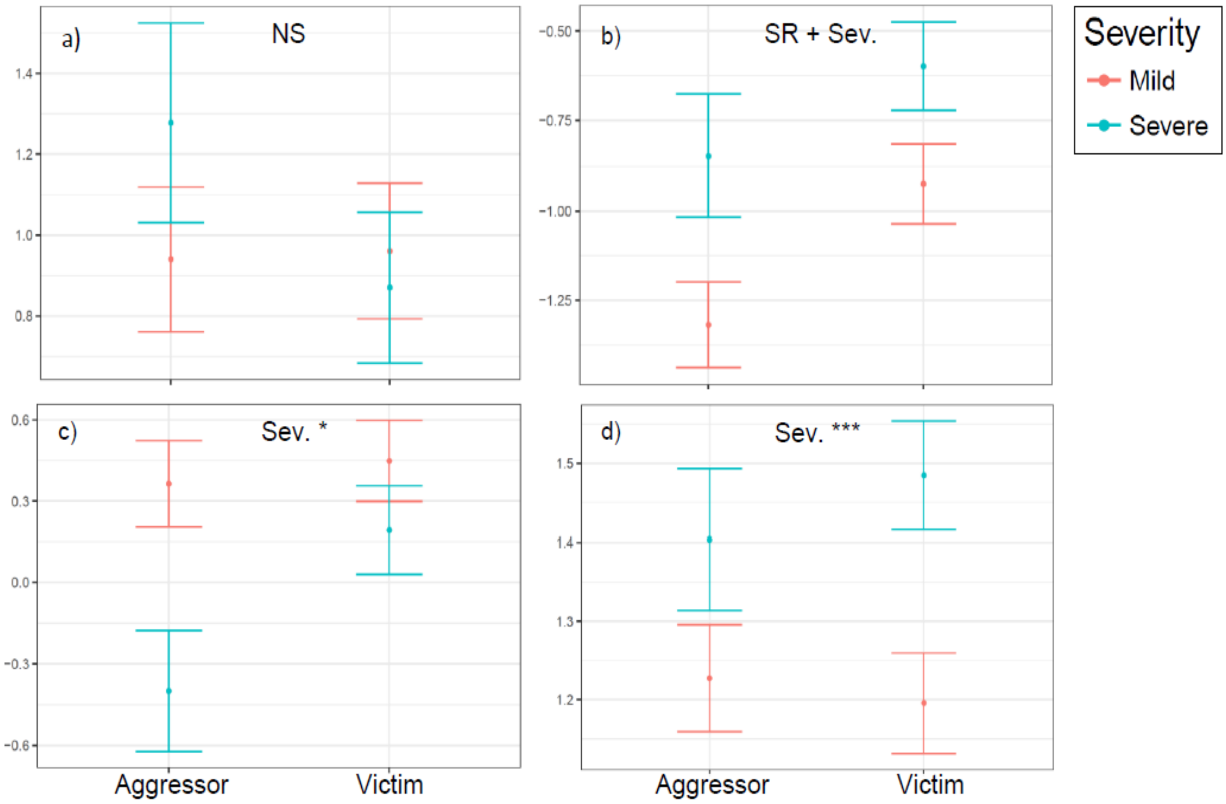


Fig 2. Effect plots displaying results from GLMMs at the bout level of four parameters varying according to the social role of callers (SR: aggressor vs. victim) and conflict severity (Sev: mild in orange vs. severe in blue): a) number of screams, b) average scream duration (s), c) scream rate (number of screams/s) and d) percentage of NLP (%). While dots represents the predicted mean of the parameters (previously transformed when necessary and scaled), bars represent standards errors. Significant results are represented by * when adjusted p-values < 0.05, ** <0.01 and *** < 0.001.

Conflict severity: mild vs. severe

Results from linear models showed that one of the eight acoustic parameters tested at the call level was influenced by conflict severity (Shannon entropy; Table 3 and S8 Appendix). We found that screams produced during severe aggressions had higher entropy (i.e. were noisier) than the ones produced during mild conflicts (Fig 1). In line with these results, screams produced during severe fights were on average longer in a bout and contained more NLP than the ones produced by individuals facing mild aggressions (Table 4 and S9 Appendix). However, screams were produced at lower rates during severe conflicts (Fig 2).

Support

We used 114 bouts involving 28 callers to investigate the occurrence of support during conflicts according to the social role of signallers (aggressor vs. victim) and conflict severity (mild vs. severe). Supporters intervened in 22 of 114 bouts (19.3%) following scream production. Results from a linear model showed that both factors influenced the probability of obtaining support (Table 5 and S10 Appendix), with aggressors receiving more support than victims, especially during severe fights (Fig 3).

Table 5. Results of a linear model showing the effect of social role and conflict severity on the occurrence of support offered at the bout level

		Number of individuals and number of bouts	Social role (binary: aggressor vs. victim)	Severity (binary: mild vs. severe)	Social role : Severity	R^2m - R^2c
Number of support	*Estimate*		-1.88	2.63	-3.05	
	SD	28	0.90	1.07	1.69	0.03
	Z value	114	-2.07	2.47	-1.81	–
	CI 95%		-3.65 to -0.10	0.54 to 4.71	-6.36 to 0.26	0.06
	P		0.038 *	0.014 *	0.071	

*Significant results are represented by * when adjusted p-values < 0.05, ** <0.01 and *** < 0.001. R^2m corresponds to the variance explained by the fixed effects (marginal); R^2c corresponds to the variance explained by both the fixed and random effects (conditional). These numbers help to describe the amount of the variation explained by the different factors included in the models.*

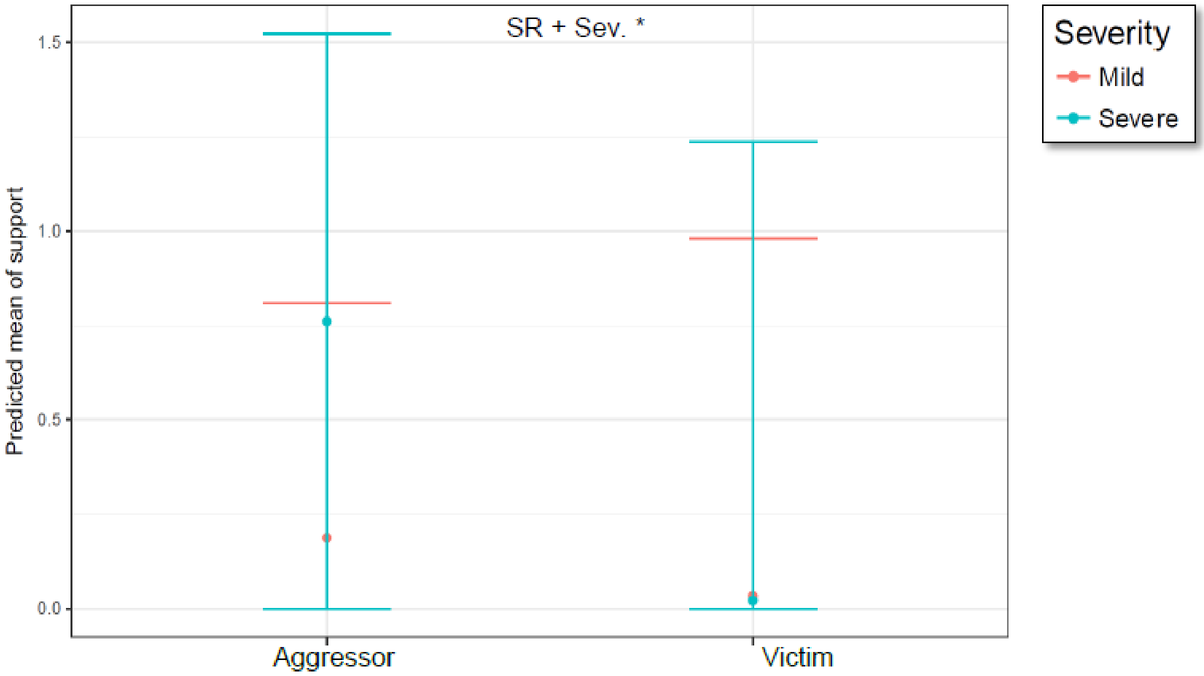


Fig 3. Effect plots displaying results from a GLMM showing the effect of the social role of callers (SR: aggressor vs. victim) and conflict severity (Sev: mild in orange vs. severe in blue) on the occurrence of support at the bout level. While dots represents the predicted mean of the support, bars represent standards errors. Significant results are represented by * when p-values < 0.05.

4.5 Discussion

This study aimed to explore how acoustic variation in wild vervet monkey agonistic screams varies according to the social role of signallers (aggressor vs. victim), as well as conflict severity (mild vs. severe). Using pDFAs, we could not discriminate screams according to the context of production (natural observation vs. feeding experiment). However, results from DFAs showed that screams were individually distinct at the call, but not the bout level, as the observed classification and cross-validation successes were significantly better than expected by chance. Results from GLMMs showed that six of 12 acoustic parameters measured varied with the social role of signallers and/or conflict severity. Furthermore, we found that both factors also influenced the amount of support signallers received, providing some preliminary support for the hypothesis that receivers were able to perceive these acoustic cues.

Results from pDFAs showed that screams could not be discriminated according to the context of production (given during natural or experimentally induced conflicts). However, screams could be discriminated according to caller identity, albeit only at the call but not at the bout level (S7 Appendix). This supports previous studies, which describe individual recognition based on screams (Cheney and Seyfarth 1980), which seems to be a common feature in animals (e.g. Barbary macaques (Fischer 2004) and gorilla, *Gorilla gorilla* (Salmi, Hammerschmidt et al. 2014) but see also (Byrne 1982) for information usually conveyed in primate vocalisations and (Yorzinski 2017) for a review of vocal individual recognition across species). At the call level, we found that scream classification was predominantly based on frequency parameters, i.e. peak frequency, coefficient of frequency modulation and energy distribution at quartile 50 (S7 Appendix). These results, which mirror those found in other primate species (Rendall 2003, Price, Arnold et al. 2009), fit within the established pattern describing frequencies and formant dispersion as good indicators of caller identity as they are inversely proportional to the length of the vocal tract of an individual (Sommers, Moody et al. 1992, Fitch 1997, Owren and Rendall 2001). However, results from DFAs were not significant at the bout level, meaning that bouts could not be discriminated between individuals. This is unsurprising as we could expect temporal parameters, such as number of screams and scream rate used here at the bout level, to relate more to the nature of the ongoing event (e.g. conflict severity) than to the identity of callers, which already influenced some frequency parameters at the call level.

Results from GLMMs showed that screams produced by victims were longer (using both scream duration at the call level and average scream duration at the bout level) and were higher-pitched (higher Q50) than aggressor screams. Furthermore, screams produced during severe conflicts were longer (using average scream duration at the bout level), had higher entropy and a higher percentage of NLP than screams during mild conflicts. However, in contrast to predictions, screams during severe conflicts were produced at lower rates than screams produced in mild conflicts, when no chasing or physical contact were involved (Tables 3 & 4 and Fig 1 & 2; S8 & S9 Appendices). This is in agreement with the Morton's motivational structural rules (Morton 1977) and Briefer's hypothesis (Briefer 2012), which both predict that calls produced during hostile situations, i.e. when individuals are aggressors (negative valence), should be of low frequency, having a broadband frequency range (represented here by a high entropy) with a high percentage of NLP. Furthermore, screams produced during high arousal situations, reflected here by conflicts of severe intensity, were expected to be longer. Interestingly, however, both theories predicted them to be produced at higher rates compared to individuals facing less urgent contexts (Seyfarth and Cheney 2003a), but here we found the opposite pattern, a result also found in wild chimpanzees (Slocombe and Zuberbuhler 2007). One explanation may be that, during severe fights, individuals engage more in physical behaviours, such as being chased/chasing opponents, or fighting behaviours when biting or wrestling (Fischer, Hammerschmidt et al. 2002). These intense behaviours might affect directly the respiratory system of signallers, and thus reduce their ability to call at high rates.

The acoustic characteristics of vervet monkey screams relate to both the social role of the signallers and to the severity of a conflict, suggesting that they could provide cues for nearby listeners to assess the nature of the ongoing event. Agonistic calls of other primates, such as Geoffroy's spider monkeys (Ordóñez-Gómez, Dunn et al. 2015) or chimpanzees (Slocombe, Kaller et al. 2010a), also differ according to the caller's social role and conflict severity and playback experiments have confirmed that such cues can be salient to receivers and help bystanders to adapt their responses to intervene only when necessary, that is, to support kin that are involved in severe aggressions (Fugate, Gouzoules et al. 2008). In line with this, chimpanzees sometimes exaggerate their screams, by increasing call duration and altering two frequency parameters when they were victims of severe attacks, but they did so only when a higher-ranking individual than the opponent was present in the audience, an apparently efficient modification as this helped them to recruit more support than non-exaggerated calls (Slocombe and Zuberbuhler 2007).

Since we restricted our study to agonistic screams, i.e., produced during agonistic events, other functional hypotheses of primate screams (e.g., to repel predators, advertise copulation or facilitate group fusion) could be excluded (Hogstedt 1983, Koler-Matznick, Brisbin et al. 2003, Rubow, Cherry et al. 2017). In agonistic contexts, however, screams could function in two mutually non-exclusive ways, i.e. to repel aggressors (e.g. several primates: Todt 1988, tree shrews: Binz and Zimmermann 1989) and to recruit allies (e.g. pigtail macaques: Gouzoules and Gouzoules 1990, bonnet macaques, *Macaca radiata*: Silk 1999, dwarf mongooses: Rubow, Cherry et al. 2017). A good illustration of vocalisations fulfilling both functions are chimpanzees calling as victims during conflicts, both to recruit support from bystanders, and to repel their opponent (Fedurek, Slocombe et al. 2015b).

In line with Owren & Rendall hypothesis (Owren and Rendall 1997, Owren and Rendall 2001), our data support the idea that vervet monkey screams are multi-functional. We found that victims produced longer screams that were more piercing (higher Q50) and had more noisy components (high entropy and percentage of NLP) during severe conflicts than aggressors. These characteristics make the calls sound harsher and may help making signallers unappealing targets, ultimately leading to a cessation of negative events by repelling the aggressor (Rendall, Owren et al. 2009). Specifically, the presence of high percentage of NLP may signal aggressive motivation (Riede, Arcadi et al. 2007) and directly affect listener physiology (Owren and Rendall 1997), leading to avoidance (Owren and Rendall 2001, Rendall, Owren et al. 2009). Simultaneously, the roughness of screams due to NLP can also prevent habituation (Townsend and Manser 2011, Karp, Manser et al. 2014), signal the physical condition of signallers (Riede, Arcadi et al. 2007) and facilitate individual recognition (Volodina, Volodin et al. 2006). These characteristics could thus also help to increase the attentional state of third-party listeners (Owren and Rendall 2001), and provide crucial cues necessary to increase signallers' chances of obtaining support.

Although further playback experiments are needed to test the dual-functional hypothesis, research on screams produced by juvenile vervet monkeys in Amboseli National Park in Kenya suggest that these calls may be efficient in recruiting support, as mothers approached and threatened opponents on a mean of 22% of conflicts involving their screaming offspring (Cheney and Seyfarth 1980). In our study, we also found that 19.3% of screams produced during fights obtained support from bystanders. Importantly, results from GLMMs showed that both the social role of signaller and conflict severity influenced the number of times support was received, with aggressors receiving more supports than victims, especially during severe fights (S10 Appendix). While we cannot exclude the possibility that nearby listeners visually assessed the interaction, in some cases future supporters were unable to see the conflict, suggesting that they relied on the calls' acoustic characteristics when taking a decision as to whether or not to intervene.

In our study, aggressors received more support than victims, a finding that is somewhat surprising as victims would benefit to get more help than aggressors due to their potential higher risks of injuries, when being bitten for example. However, this is in line with recent experimental evidence showing that vervet monkeys primarily support the higher-ranking individual in a conflict, which is usually the aggressor (Borgeaud and Bshary 2015). Nonetheless, it should be noted that this could be an artefact of frequent roles switching during conflicts: individuals screaming for help may start as victims but, as soon as they received aid, effectively become aggressors by chasing away their opponents due to the coalitionary support they received.

Vervet monkeys tend to form coalitions with kin and when outranking their opponents (Struhsaker 1967c). Since aggressors were more likely to receive support than victims, especially during severe fights, it is unlikely that victims screamed to recruit help but to either repel opponents (Owren and

Rendall 2001, Rendall, Owren et al. 2009, Arnal, Flinker et al. 2015) or to signal submission. In doing so, victims might avoid further escalation, and further support for aggressors. Victims often crouch or expose their teeth when facing their opponents, suggesting they are mainly motivated to indicate subordination to reduce further aggression (de Waal and Luttrell 1985, Flack and de Waal 2007, Waller and Cherry 2012, Beisner and McCowan 2014). Vervet monkey screams, in other words, are likely to serve different functions, depending on the social role of the signallers.

4.6 Conclusions

We demonstrated that variation in six out of 12 parameters of screams could be predicted by the social role of signallers and/or conflict severity, showing that the acoustic properties of screams have the potential to affect receivers' behaviours in specific ways. While non-linearities and the presence of noisy components in scream production might create an aversive response in opponents, variation in duration and frequency-related parameters might help signallers to recruit aid from nearby listeners. However, it would be interesting to examine other factors, such as the social rank of signaller (Fischer, Kitchen et al. 2004), social relationships among dyads (Gouzoules, Gouzoules et al. 1984) or the presence of particular social partners (Slocombe and Zuberbuhler 2007), as these variables may also influence screams' acoustic characteristics. Future studies on the potential effects of these social and other environmental factors will help to better understand the functions and mechanisms of vervet monkey screams' production.

4.7 Acknowledgements

Many thanks go to K. van der Walts and his family for permissions to conduct research at Mawana Game Reserve, as well as the local managers of the Inkawu Vervet Project, A. Driescher and A. van Blerk. We are grateful to all researchers working at IVP for their help in the field. Ezemvelo KZN Wildlife provided us permission to conduct our research on wild vervet monkeys in South Africa. Finally, special thanks go to C. Neumann, S. Binning and R. Slobodeanu for interesting discussions and statistical advice, as well as to two anonymous reviewers and the editor for their constructive comments, which greatly improved the manuscript.

4.8 Funding

This work was funded by the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013) / ERC grant agreement n° 283871 and the Swiss National Science Foundation (Project 310030_143359). EW was funded by the Swiss National Science Foundation (P300P3_151187 and 31003A_159587) and the Branco Weiss Fellowship - Society in Science.

4.9 Data availability

Our data and codes will be publicly available upon acceptance (https://figshare.com/s/564f7ee3778c7bb413c7; DOI: 10.6084/m9.figshare.5413975; Mercier, Déaux et al. 2018). We used figshare as a public repository following best practices (White, Baldridge et al. 2013, Roche, Kruuk et al. 2015).

4.10 Supplementary materials

S1. Vervet monkey screams

In order to study the influence of social role of signallers and conflict severity on the acoustic structure of vocal signals produced by wild vervet monkeys, we focused on all high-pitched calls produced during agonistic encounters, categorised by Struhsaker as squeals, chutter-squeals, squeal-screams and screams (Table S1, 1967). However, for more clarity, we grouped all those signals occurring during agonistic encounters under “screams” and we did not take into account all other scream-like vocalisations produced by this species in other contexts in our study.

Table S1. Description of different types of screams produced by vervet monkeys

Context	Call types	Acoustic features	Main callers	Bystanders reaction
Agonistic encounters	Squeals	Uniform, tonal calls	Adult females and juveniles	Support caller
	Chutter-squeals	Mixed phases with tonal and non-tonal calls		
	Squeal-screams	Non-tonal sounds superimposed by tonal band		
	Screams	Non-tonal shrill-sounding calls		
Mating	Anti-copulatory squeal-screams	Resemble squeal-screams	Adult and sub-adult females	Move away from females, copulation inhibited
Approach of a “strange” male	Screams	High-pitched shrill-sounding calls	Infants	Approach and retrieval from mothers, males moving away
Weaning	Weaning squeals	Compound units, ultrasonic portions in calls	Infants	Mothers refusing nursing, moving away from infants
	Weaning screams	Non-tonal calls		
Separation from the rest of group	Lost squeals	Mix of tonal and non-tonal portions intermingled with lost rrr and lost Rrah	Infants	No obvious reaction apart from mothers sometimes facilitating reunion by locating and retrieving their infants
	Lost screams	Similar to weaning screams and intermingled with lost squeals and lost rrr		

modified from Struhsaker (1967a)

S2. Detailed predictions

Table S2. Predictions of the influence of the social role of signallers (aggressor vs. victim) and conflict severity (mild vs. severe) on 15 selected acoustic parameters

Parameters	Predictions	References
CALL LEVEL		
Scream duration (s)	Longer call in urgent context: victim > aggressor severe > mild	Slocombe and Zuberbuhler (2005), Slocombe and Zuberbuhler (2007), Taylor and Reby (2010)
Peak frequency (kHz)	Lower peak frequency sound when hostile and low-urgency context: victim > aggressor severe > mild	Morton (1977), Slocombe and Zuberbuhler (2005), Slocombe and Zuberbuhler (2007), Taylor and Reby (2010), Walter and Schnitzler (2017)
Coefficient of frequency variation *	Rapid fluctuation evokes attention: victim > aggressor severe > mild	Morton (1977), Tooze, Harrington et al. (1990), Owren and Rendall (2001), Briefer (2012), Déaux, Clarke et al. (2016)
Coefficient of frequency modulation	Rapid fluctuation evokes attention: victim > aggressor severe > mild	Morton (1977), Tooze, Harrington et al. (1990), Owren and Rendall (2001), Briefer (2012), Déaux, Clarke et al. (2016)
Absolute transition onset (Hz)	Sound rising in frequency indicates lower hostility: victim > aggressor severe > mild	Morton (1977), Slocombe and Zuberbuhler (2005), Slocombe and Zuberbuhler (2007)
Absolute transition offset (Hz)	Sound decreasing in frequency indicates higher hostility: victim < aggressor severe > mild	Morton (1977), Slocombe and Zuberbuhler (2005), Slocombe and Zuberbuhler (2007)
Frequency quartile 50 (Hz)	Higher frequency quartile sound when submissive: victim > aggressor severe > mild	Morton (1977), Taylor and Reby (2010), Déaux, Charrier et al. (2016), Walter and Schnitzler (2017)
Inter-quartile range (Hz)	Tonal sound (represented by a lower inter-quartile range) when fearful: victim < aggressor severe > mild	Morton (1977), Briefer (2012), Déaux, Charrier et al. (2016), Walter and Schnitzler (2017)
Shannon entropy	Noisy call (high-entropy) produces aversive response: victim > aggressor severe > mild	Morton (1977), Gouzoules, Gouzoules et al. (1984), Ordóñez-Gómez, Dunn et al. (2015)
BOUT LEVEL		
Bout duration (s) *	Longer in urgent context: victim > aggressor severe > mild	Morton (1977), Slocombe and Zuberbuhler (2007), Taylor and Reby (2010)
Number of screams	Higher in high intensity situation: victim > aggressor severe > mild	Rendall (2003), Bastian and Schmidt (2008), Taylor and Reby (2010), Clay, Ravaux et al. (2016)

Average scream duration (s)	Longer in urgent context: victim > aggressor severe > mild	Morton (1977), Slocombe and Zuberbuhler (2005), Slocombe and Zuberbuhler (2007), Taylor and Reby (2010)
Scream intervals (s) *	Shorter in urgent context: victim > aggressor severe > mild	Morton (1977), Rendall (2003), Bastian and Schmidt (2008), Taylor and Reby (2010), Briefer (2012)
Scream rate (number of screams/s)	Higher in high arousal situation: victim > aggressor severe > mild	Seyfarth and Cheney (2003a), Seyfarth and Cheney (2003b), Taylor and Reby (2010), Briefer (2012)
Percentage of screams with NLP (%)	Higher in high arousal situation: victim > aggressor severe > mild	Riede, Arcadi et al. (2007), Blumstein and Recapet (2009), Townsend and Manser (2011), Clay, Ravaux et al. (2016)

** Parameters excluded due to high correlations or failure to reach symmetrical distribution, leading to analyses using 12 acoustic parameters (eight at the call level and four at the bout level).*

S3. Call providers

Table S3. Description of call providers, number of events, bouts and screams recorded for each individual and their participation in our study, i.e. whether we recorded their screams in both contexts (natural observations vs. feeding experiments), social role (aggressor vs. victim) and severity (mild vs. severe), as well as whether we used them in call and/or bout analyses.

Caller	Age	Sex	Gp	Number of events	Number of bouts	Number of screams	Both contexts (observations vs. experiments)	Both social role (aggressor vs. victim)	Both severity (mild vs. severe)	Used for call analyses	Used for bout analyses
Hlek	A	F	AK	1 (2)	1 (2)	2 (4)	No	Yes	No	X	√
Hwa	Juv	M	AK	2	2	8	No	Yes	No	√	√
Asis	A	F	BD	2 (6)	3 (7)	4 (10)	Yes	Yes	No	X	√
Enge	A	F	BD	8	9	31	Yes	Yes	Yes	√	√
Heer	A	F	BD	1	2	2	No	Yes	No	√	√
Miel	A	F	BD	4	4	21	Yes	Yes	Yes	√	√
Mooi	A	F	BD	5 (7)	5 (7)	15 (24)	Yes	Yes	Yes	√	√
Ouli	A	F	BD	6	9	22	Yes	Yes	Yes	√	√
Pann	A	F	BD	3	3	10	No	Yes	Yes	√	√
Riss	A	F	BD	3	3	11	No	Yes	Yes	√	√
Aapi	Juv	F	BD	2 (3)	2 (4)	17 (34)	Yes	Yes	Yes	√	√
Alsi	Juv	F	BD	3	3	13	No	Yes	Yes	√	√
Hipp	Juv	F	BD	6	8	33	Yes	Yes	Yes	√	√
LBlind	Juv	F	BD	2 (3)	5 (6)	22 (23)	No	Yes	Yes	√	√
Nies	Juv	F	BD	8	8	27	Yes	Yes	Yes	√	√
Piep	Juv	F	BD	6	9	29	Yes	Yes	Yes	√	√
Potj	Juv	F	BD	2	2 (3)	3 (48)	No	Yes	Yes	√	√
Afr	Juv	M	BD	5 (7)	8 (10)	25 (36)	Yes	Yes	Yes	√	√
Bul	Juv	M	BD	3	3	7	No	No	Yes	√	√
Nok	Juv	M	BD	3	3	10	No	Yes	Yes	√	√
Ogi	Juv	M	BD	5 (6)	6 (7)	36 (38)	Yes	Yes	Yes	√	√
Onb	Juv	M	BD	3	5	32	Yes	Yes	Yes	√	√
Poe	Juv	M	BD	2 (4)	2 (4)	12 (25)	Yes	Yes	Yes	√	√
Roo	Juv	M	BD	4	5	58	No	Yes	Yes	√	√
Spo	Juv	M	BD	4 (7)	5 (8)	19 (50)	Yes	Yes	Yes	√	√
Vak	Juv	M	BD	3 (4)	3 (4)	18 (22)	Yes	Yes	Yes	√	√
Wol	Juv	M	BD	1	2	11	No	Yes	No	√	√
Wur	Juv	M	BD	1	2	15	No	Yes	No	√	√
Total				*98 (49)*	*122 (62)*	*513 (314)*	*N = 15 ind*	*N = 27 ind*	*N = 22 ind*	*N = 26 ind*	*N = 28 ind*

Numbers in brackets represent the number of data excluded from the analyses due to poor signal to noise ratio. A tick mark (√) in the last two columns indicates that calls produced by an individual have been used for the concerned analyses, while a cross mark (X) indicates that we had to exclude calls from an individual due to bad quality or lack of samples.

S4. Acoustic data

Sound inspection in Praat

After selecting raw recordings of good quality from a maximum of individuals in as many situations as possible, i.e., recorded during both contexts (natural observation vs. experiment), in both social roles (aggressor vs. victim) and in both conflict severity (mild vs. severe), we inspected sounds and created corresponding text grids (Table S4) in Praat 5.4.13 (Boersma 2006, www.praat.org), using a Fast Fourier Transformation (Hanning window shape, window length = 0.01s, number of time steps = 1000, number of frequency steps = 500 and dynamic range = 40dB). When possible, we also selected screams that opposed the same two individuals during the same period (or with minimal time intervals) in different contexts in order to obtain a balanced dataset minimizing potential differences due to external factors, such as identities of opponents or recording day. Comparisons of text grids created by two different observers (Fig S1 and S2) allowed us to test for inter-observer reliability on acoustic data using Cohen's method, making sure that data were extracted in a reliable way (1960; see S6).

Table S4. Description of the main steps used to annotate recordings, which allowed us to extract events, bouts and calls, for which precise acoustic parameters could be measured

Main steps	Praat commands
Open original recording (wav file)	Open - Read from file…
Select sound and create the appropriate TextGrid	Annotate – To TextGrid…
Define all tiers names	Remplace "Mary John bell" by tiers used for the study, i.e. here "Context Event Bouts Calls Type NLP PreSuffix Breaks", leaving blank the second question concerning the point tiers
Edit the TextGrid	Select both the sound and the corresponding TextGrid and click on "View & Edit"
Annotate Tiers	- **Context**: define whether the vocalisations were recorded during natural observations (OB) or during feeding experiments (Exp), adding more details when possible on the precise context, i.e. the behaviour of the caller or the kind of experiment involved - **Event**: delimit starting and ending point in order to obtain the duration of an event (EventDuration) - **Bouts**: delimit starting and ending point of each bout, allowing us to get the number of bouts and their duration (NbBout and BoutDuration), and noting down the event type for each bout, i.e., whether the signaller was aggressor or victim and whether the conflict was of mild or severe aggression. - **Calls**: delimit starting and ending point of each vocal unit, separated by other ones by at least 0.03s of silence, and noting the call type produced when known such as screams, aggressive calls, grunts or NA if not clear. In order to keep only calls of good quality for the analyses, we also noted here whether the calls were of bad quality (BadSc), clipped (ClippedSc), if some other individuals were calling simultaneously during a chorus (ChorSc), or if there was a lot of background noise such as birds (Sc-B), insects (Sc-I) or humans (Sc-H).

	Consequently, only screams with clear annotations (sc) were extracted and used in further analyses. - **Type**: define the social role of the signaller and conflict severity for each call, using the four following categories: aggressor of mild conflict (AscM), agressor of severe aggression (AscS), victim of mild conflict (VscM) and victim of severe fight (VscS). - **NLP**: define whether some irregularities occur within each call, indicating when possible the kind of NLP encountered: frequency jumps (FJ), sub-harmonics (SH), deterministic chaos (DC), periodic window (PW) and bi-phonation (BP; Fig S2) - **PreSuffix**: define whether a prefix and/or suffix was observed at the beginning and/or end of each call respectively - **Breaks**: define whether a break (B), i.e. a silence of less than 0.03s, occurred within each call
Save the TextGrid	Save TextGrid as text file, making sure to keep exactly the same name for the TextGrid and the corresponding sound file

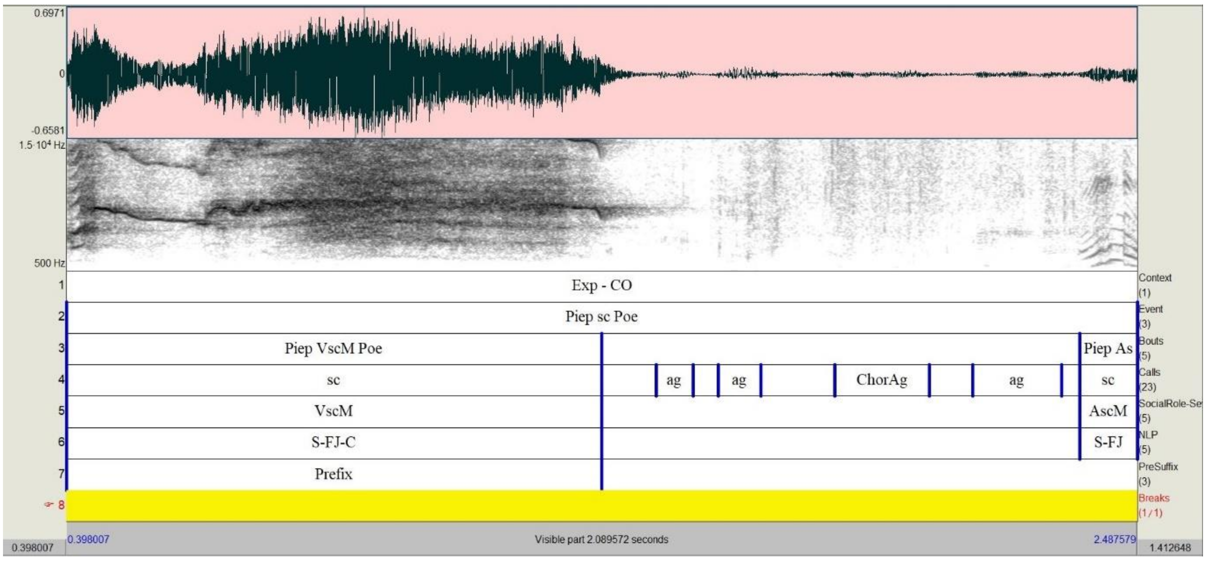


Fig S1. Example of a raw recording recorded around an experiment with its corresponding annotated text grid (in order to make the last scream more visible, we adapted here the settings in Praat to 60dB). While a victim of a mild conflict screamed at the beginning of the event (left side), the social role changed, and the signaller became an aggressor of a mild conflict who again screamed at the end of the event (right side). As this social role switching defined a new bout, we thus analysed here one event containing two bouts and two screams (one scream in each bout). Note: we also defined new bouts, not only when the social role switched, but also when the severity of the conflict changed.

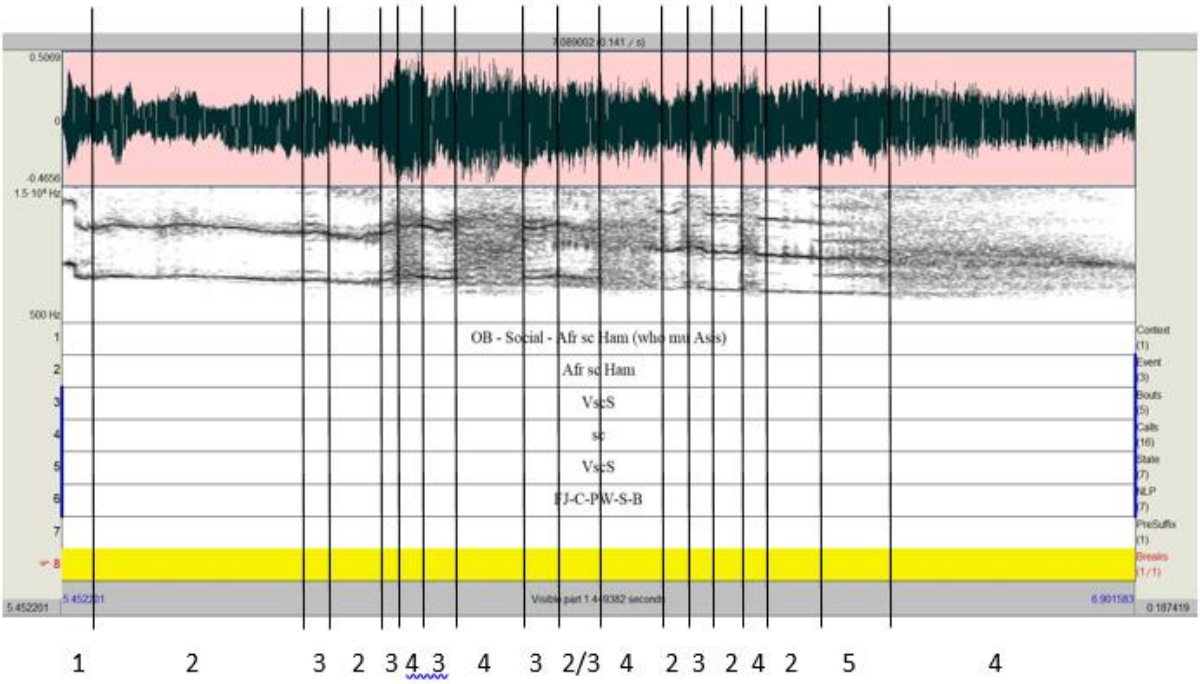
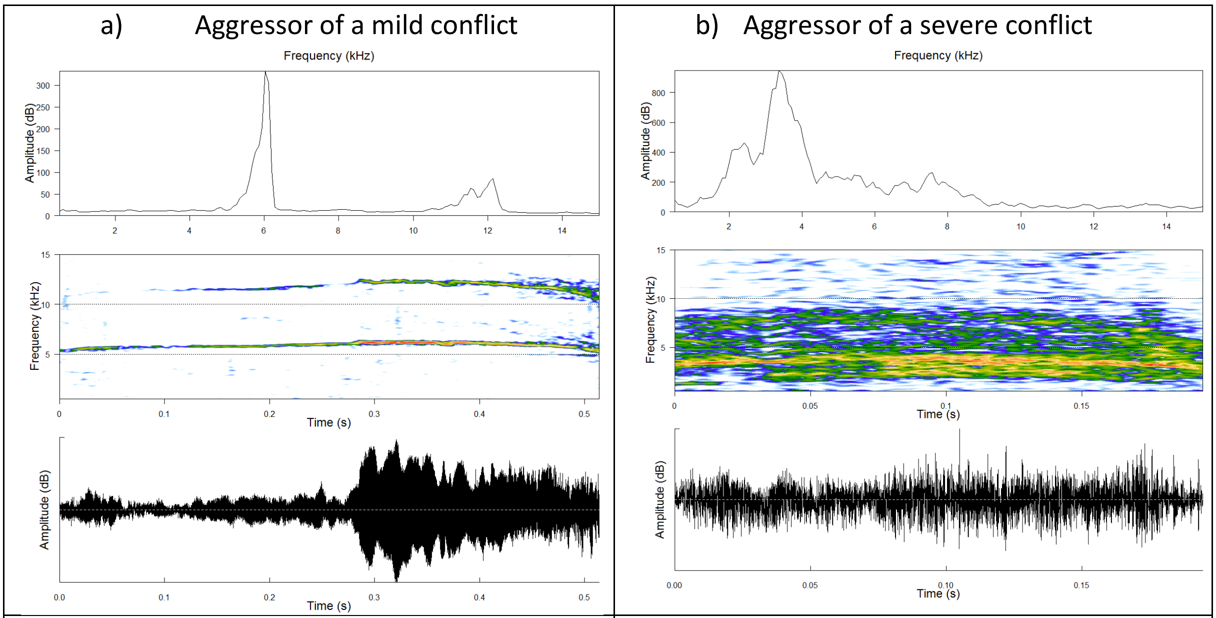


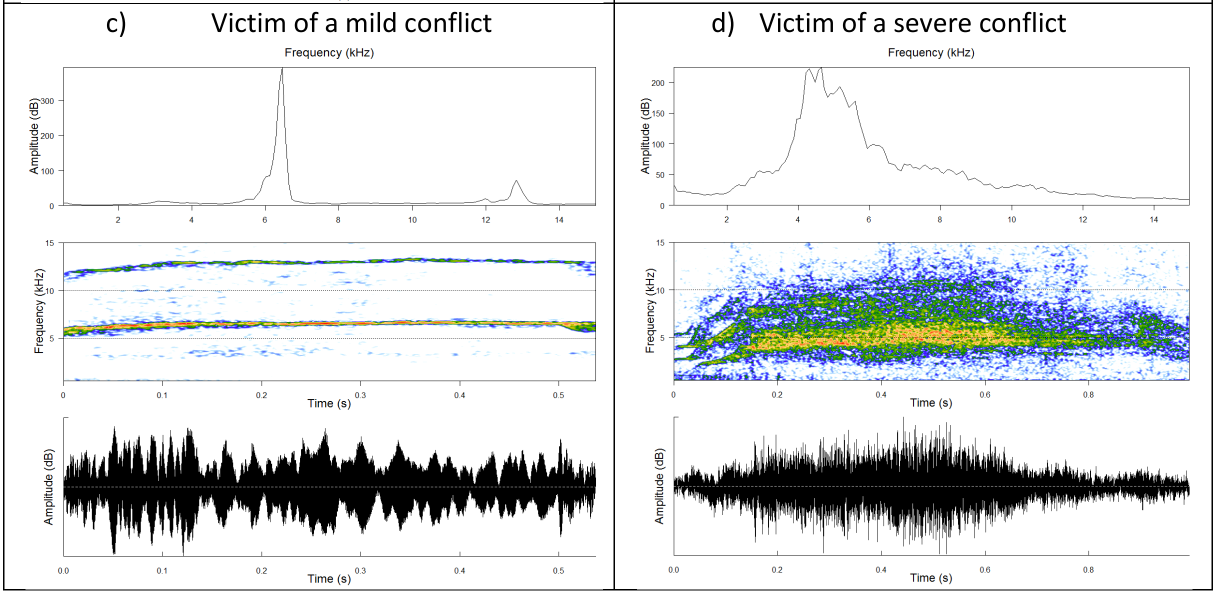
Fig S2. Example of a spectrogram and its corresponding annotated text grid showing non-linear phenomena found in a scream produced by a juvenile male vervet monkey when being victim of a severe conflict. Different numbers at the bottom of the figure represent the different classes of NLP: 1) frequency jumps, 2) periodic window, 3) sub-harmonics, 4) deterministic chaos and 5) bi-phonation.

Acoustic parameters extraction in R

As we were unable to use fundamental and formant frequencies due to the noisy acoustic components often present in vervet monkey screams, we selected 15 acoustic parameters that described the acoustic properties of their screams and the temporal structure of their bouts (nine parameters at the call and six at the bout level; Table 2 and S2). While temporal parameters were extracted from spectrograms and oscillograms created in Praat 5.4.13 (Boersma 2006, www.praat.org) using a Fast Fourier Transformation (Hanning window shape, window length = 0.01s, number of time steps = 1000, number of frequency steps = 500 and dynamic range = 40dB), all other acoustic parameters were extracted from spectrograms and spectral slices (Fig S3) with the following settings: sampling rate of 44.1 kHz, 16 bits accuracy, Fast Fourier Transformation with 512 samples, Hanning window and 90% overlap using Seewave (Sueur, Aubin et al. 2008) and tuneR packages (Ligges 2013) in R version 1.0.143 (Team 2016).


a) Aggressor of a mild conflict

b) Aggressor of a severe conflict


c) Victim of a mild conflict

d) Victim of a severe conflict

Fig S3. Example of spectrograms, oscillograms and spectral slices obtained using R of screams produced by different individuals in all event types (social role and conflict severity).

S5. Detailed ethogram

Table S5. Ethogram of the behaviours used to define the social role of signallers

Social Role	Behaviour	Code	Description
Aggressor	Aggressive calls	ag	Producing aggressive vocalisations
	Attack	at	Forward motion of the body towards the opponent, often combined with stare (st.at)
	Bite	bi	Biting another individual, often combined with grab (gb.bi)
	Chase	ch	Running after another individual who is fleeing
	Displace	tp	Individual takes the place of another who retreats, usually combined with approach (ap.tp)
	Grab	gb	Grabbing another individual with the hand and/or the mouth
	Hit	hi	Hitting another individual
	Monopolise	mo	Keeping a valuable item such as food away from other interested individuals
	Stare	st	Popping up the eyelids, exposing the white above the eyes, often combined with attack (st.at)
Victim	Avoid	av	Stopping previous behaviour or moving the head or body away from an aggressor
	Crawl	cr	Crouching down while facing an aggressor
	Flee	fl	Running away from an aggressor that is chasing
	Frustration hop	fh	Jumping on the spot while looking at an individual usually monopolising a valuable resource, often while screaming and combined with standing up
	Jump aside	ja	Jumping aside from the opponent
	Leave	le	Walking away from an aggressor
	Look for support	lo	Looking around for support while being threatened by an aggressor
	Redirect	re	Performing some aggressive behaviours after being a victim, targeting a third uninvolved individual that is becoming the new victim
	Retreat	rt	Quickly leaving the proximity of another individual, without running and/or moving large distances
	Stand up	su	Standing up during a conflict, often following a crawl and combined with frustration hop and screams

S6. Inter-observer reliability tests

Behavioural data

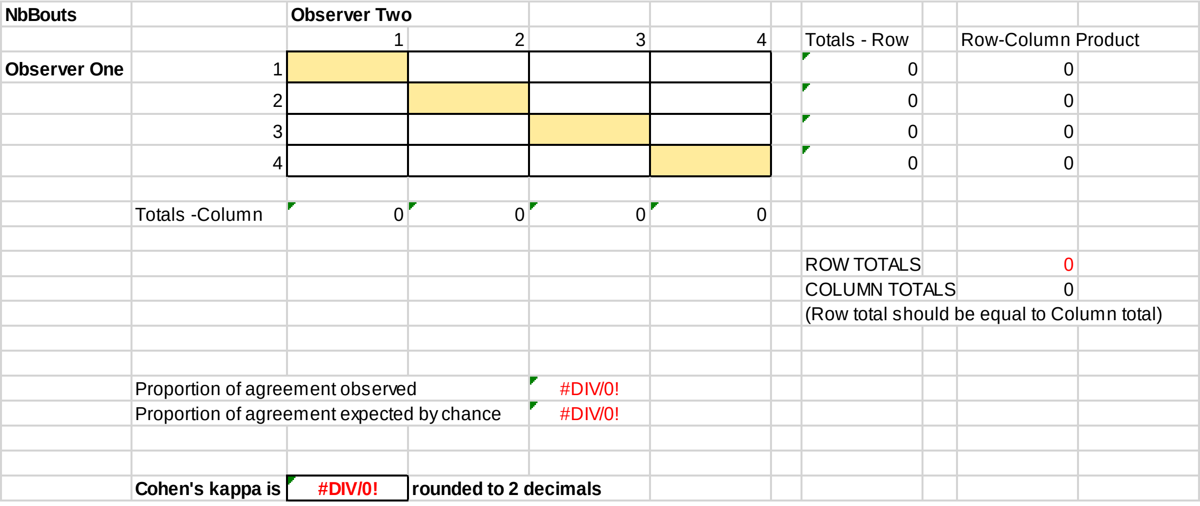
For each event included in a row (S6 Table), two observers (SM & EW) specified independently for each bout (ranging from one to three), the social role of signallers (aggressor vs. victim) as well as the conflict severity (mild vs. severe) when clear (NA if we could not determine it precisely) using one of the following categories:

- A = scream produced by an aggressor of an aggression
- V = scream produced by a victim of an aggression
- M = scream produced during a mild aggression
- S = scream produced during a severe aggression

Table S6. Example of dataset to be filled independently to calculate Cohen's Kappa

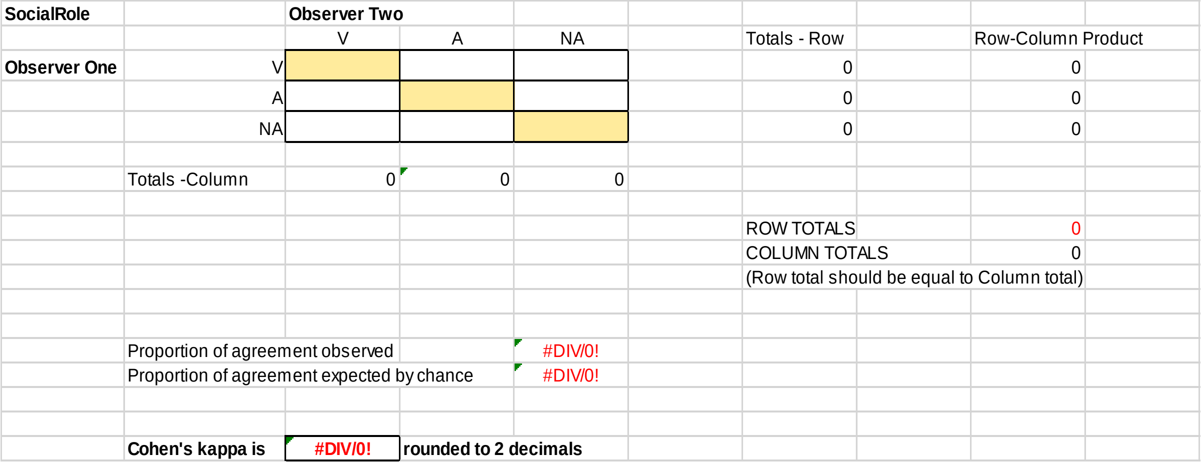
Behavioural description	BOUT 1		BOUT 2		BOUT 3		BOUT 4		NbBouts
	SR1	Sev1	SR2	Sev2	SR3	Sev3	SR4	Sev4	
Afr voc.sc Heer rt									
Afr st.sc.vo Tor rt									
distr call seq afrikans against									
Nok aps c.rt Ogi st.at									
Miel st.gb.bi Nies ja.sc									

We then compared the data sheets from the two observers in order to observe the percentage of agreement between both researchers, thus making sure that we collected data in the same way, suggesting that they were meaningful for analyses. We calculated Cohen's Kappa (Cohen 1960) by comparing the percentage of correct agreement observed with the one expected by chance for the number of bouts defined by each researcher for each event (Fig S4), as well as for the social role of signallers (Fig S5) and the conflict severity (Fig S6) for each bout. We used an average of 50.7% of the data to calculate Cohen's Kappa score and accepted data as correctly collected if the scores reached a minimum of 80% agreement between the two observers.



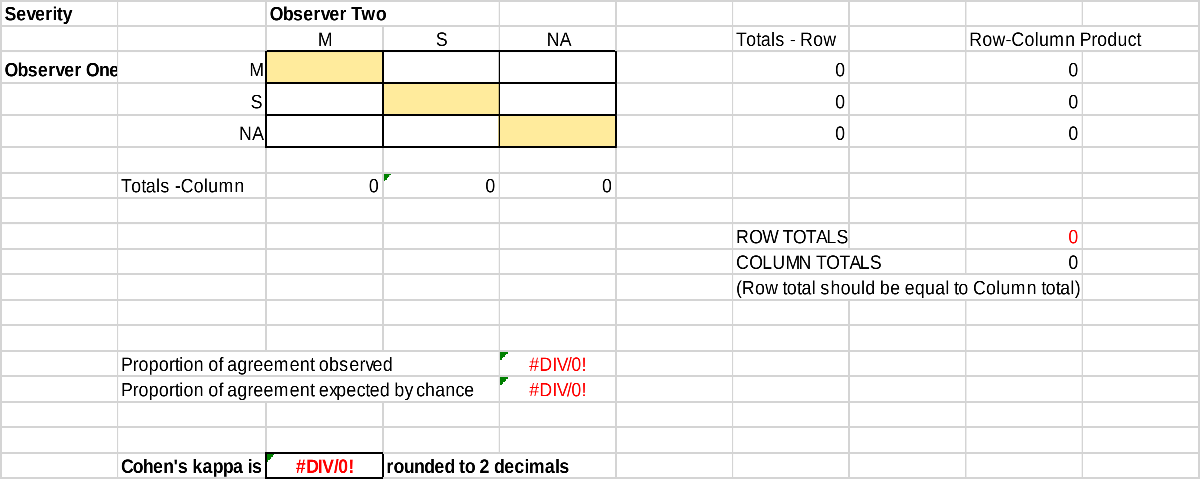
NbBouts		**Observer Two**					
		1	2	3	4	Totals - Row	Row-Column Product
Observer One	1					0	0
	2					0	0
	3					0	0
	4					0	0
	Totals -Column	0	0	0	0		
						ROW TOTALS	0
						COLUMN TOTALS	0
						(Row total should be equal to Column total)	
	Proportion of agreement observed			#DIV/0!			
	Proportion of agreement expected by chance			#DIV/0!			
	Cohen's kappa is	**#DIV/0!**	**rounded to 2 decimals**				

Fig S4. Picture of datasheet prepared to calculate the Cohen's Kappa for the number of bouts observed in events. We calculated proportion of agreement observed as the sum of each diagonal cells corresponding to correct agreement (i.e. yellow cells) divided by the sum of each total row (i.e. Totals- Row 1+2+3+4), while we calculated proportion of agreement expected by chance as the sum of the multiplication Totals-Column*Totals-Row (i.e Row-Column Product) divided by the multiplication of Row-Totals + Column-Totals.



SocialRole		Observer Two						
		V	A	NA		Totals - Row		Row-Column Product
Observer One	V					0		0
	A					0		0
	NA					0		0
	Totals -Column	0	0	0				
						ROW TOTALS		0
						COLUMN TOTALS		0
						(Row total should be equal to Column total)		
	Proportion of agreement observed			#DIV/0!				
	Proportion of agreement expected by chance			#DIV/0!				
	Cohen's kappa is	#DIV/0!	rounded to 2 decimals					

Fig S5. Picture of datasheet prepared to calculate the Cohen's Kappa for the social role of signallers for each bout observed in events. We calculated proportion of agreement observed as the sum of each diagonal cells corresponding to correct agreement (i.e. yellow cells) divided by the sum of each total row (i.e. Totals- Row V+A+NA), while we calculated proportion of agreement expected by chance as the sum of the multiplication Totals-Column*Totals-Row (i.e Row-Column Product) divided by the multiplication of Row-Totals + Column-Totals.



Severity		Observer Two						
		M	S	NA		Totals - Row		Row-Column Product
Observer One	M					0		0
	S					0		0
	NA					0		0
	Totals -Column	0	0	0				
						ROW TOTALS		0
						COLUMN TOTALS		0
						(Row total should be equal to Column total)		
	Proportion of agreement observed			#DIV/0!				
	Proportion of agreement expected by chance			#DIV/0!				
	Cohen's kappa is	#DIV/0!	rounded to 2 decimals					

Fig S6. Picture of datasheet prepared to calculate the Cohen's Kappa for conflict severity for each bout observed in events. We calculated proportion of agreement observed as the sum of each diagonal cells corresponding to correct agreement (i.e. yellow cells) divided by the sum of each total row (i.e. Totals- Row M+S+NA), while we calculated proportion of agreement expected by chance as the sum of the multiplication Totals-Column*Totals-Row (i.e Row-Column Product) divided by the multiplication of Row-Totals + Column-Totals.

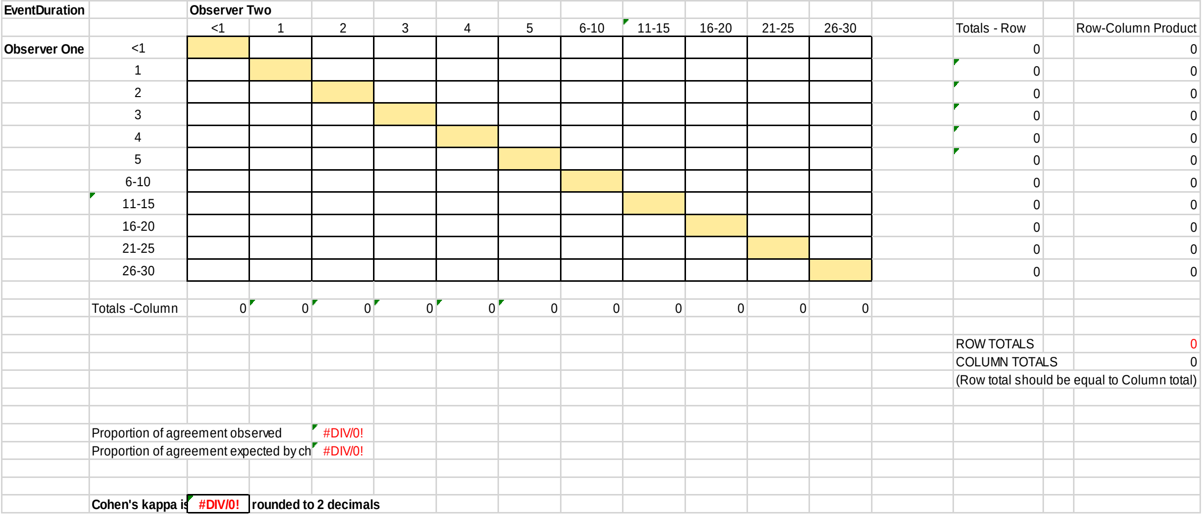
Acoustic data

For each recording, two observers (SM & ED) annotated corresponding text grids independently in Praat in order to define precisely the starting and ending points of each "Event", "Bouts" (ranging from one to four) and "Calls" (ranging from one to over 20, see Fig S1. in S4 Appendix for an example of annotated TextGrid of a recording). Each observer had then to complete an excel table (S7 Table) in order to obtain some relevant measurements, i.e. the duration of the event (Event duration), the total number of screams produced in the event (Nb screams), the mean duration of screams in an event (Sc duration), the number of screams of good quality that can be used for further analyses (Analysable screams, excluding screams annotated as bad quality or for which there was a lot of background noise), and the percentage of screams including NLP within the event (NLP% corresponding to (number of screams with NLP/total number of screams within an event)*100). Please note that as we usually had a single event per recording, researchers in the field starting a new recording after each conflict, we did not assess inter-observer reliability on this parameter.

Table S7. Example of dataset to be filled independently to calculate Cohen’s Kappa

Wav File	Event duration (s)	Nb screams	Sc duration (s)	Analysable screams	NLP (%)
Afr_VscM_Neu_17nov14					
Afr_AscM_Tor_5jul14					
Afr_sc_Unk_17jul12					
Afr_Asc_Ham_7Aug14					
Afr_Vsc_Che_18-juil-14					

The comparison of those data sheets filled up by the two observers allowed us to observe directly whether some bias due to an observer could be made while describing agonistic interactions, using the percentage of agreement between both researchers. To make sure that we collected the data in similar way, suggesting that they were meaningful for analyses, we calculated Cohen’s Kappa (Cohen, 1960) by comparing the percentage of correct agreement observed with the one expected by chance for each measure, as for example here shown for the duration of the event (Fig S7). Although we accepted an interval of one second to define the duration of the event, we had to agree within 0.03s for screams’ durations as by definition, a silence of at least 0.03s allowed us to distinguish two separated screams. We used 14% of the data to calculate Cohen’s Kappa score and accepted data as correctly collected if the scores reached a minimum of 70% agreement between the two observers.



EventDuration		**Observer Two**												
		<1	1	2	3	4	5	6-10	11-15	16-20	21-25	26-30	Totals - Row	Row-Column Product
Observer One	<1												0	0
	1												0	0
	2												0	0
	3												0	0
	4												0	0
	5												0	0
	6-10												0	0
	11-15												0	0
	16-20												0	0
	21-25												0	0
	26-30												0	0
	Totals -Column	0	0	0	0	0	0	0	0	0	0	0		

ROW TOTALS 0

COLUMN TOTALS 0

(Row total should be equal to Column total)

Proportion of agreement observed #DIV/0!

Proportion of agreement expected by ch #DIV/0!

Cohen's kappa is #DIV/0! rounded to 2 decimals

Fig S7. Picture of datasheet prepared to calculate the Cohen’s Kappa for the duration of event obtained from annotated text grids of recordings. We calculated proportion of agreement observed as the sum of each diagonal cells corresponding to correct agreement (i.e. yellow cells) divided by the sum of each total row (i.e. Totals- Row), while we calculated proportion of agreement expected by chance as the sum of the multiplication Totals-Column*Totals-Row (i.e. Row-Column Product) divided by the multiplication of ROW-TOTALS + COLUMN-TOTALS.

S7. Results from DFAs on caller identity

DFA on caller identity at the call level – conservative approach

(using a balanced dataset with N = 4 individuals & N = 82 screams)

Prior probabilities of groups

Afr	Ogi	Onb	Piep
0.171	0.293	0.305	0.232

Proportion of trace

LD1	LD2	LD3
0.508	0.290	0.203

Group means

Callers	Duration	PF	CoFm	Onset	Offset	Q50	IQR	Sh
Afr	0.007	-0.063	-0.563	-0.440	-0.791	-0.157	-0.109	-0.117
Ogi	-0.245	0.397	-0.270	0.180	0.007	-0.108	-0.383	-0.260
Onb	-0.080	-0.574	0.520	-0.203	0.243	-0.222	-0.043	0.005
Piep	0.411	0.301	0.072	0.364	0.255	0.544	0.621	0.409

Coefficients of linear discriminants

Parameters	LD1	LD2	LD3
Duration	-0.262	0.052	0.648
PF	-0.800	-0.207	-0.320
CoFm	0.979	0.113	-0.301
Onset	-0.198	-0.270	-0.225
Offset	0.348	-0.654	-0.443
Q50	0.680	-0.783	-0.353
IQR	-0.241	-0.495	0.718
Sh	-0.013	0.478	0.392

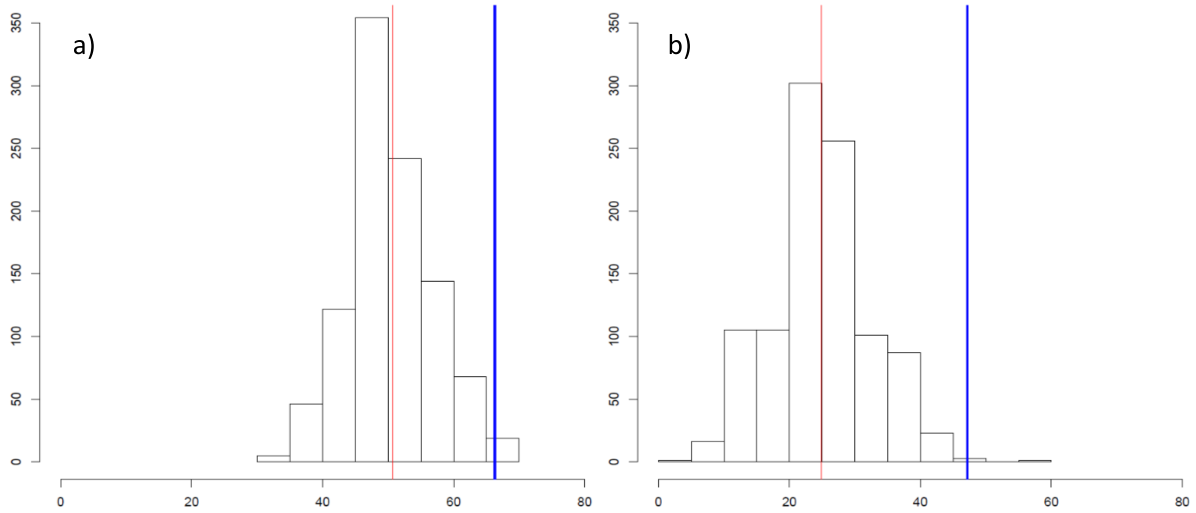


Fig S8. Histograms showing the frequency of classification rates from DFAs (%) at the call level with a balanced dataset using a) correct classification and b) correct cross-classification. While red bars correspond to the expected percentage of correctly classified, respectively cross-classified calls, blue bars represent the mean percentage of correct classified and cross-classified calls obtained from real dataset.

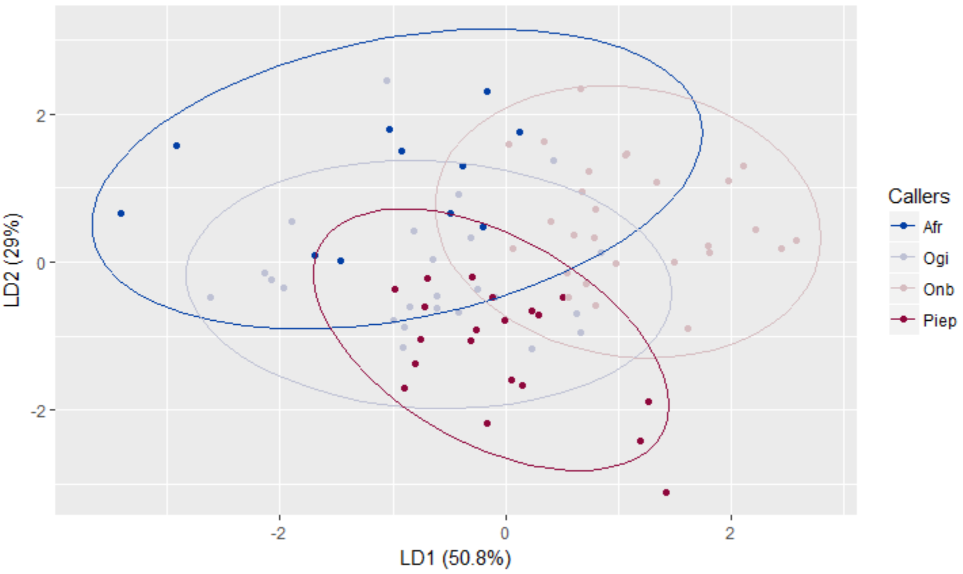


Fig S9. Graph showing first and second discriminant component scores resulting from an analysis of 82 screams produced by four individuals, represented by the different colours. Both axes represent the percentage of the variance explained by the first and second discriminant functions, respectively.

DFA on caller identity at the call level – incomplete crossed design

(using an incomplete crossed design with N = 21 individuals & N = 301 screams)

Prior probabilities of groups

Aapi	Afr	Alsi	Bul	Enge	Hipp	Hwa	LBlind	Miel	Mooi	Nies	Nok
0.030	0.047	0.027	0.020	0.050	0.043	0.017	0.056	0.056	0.037	0.050	0.020
Ogi	Onb	Ouli	Pann	Piep	Poe	Riss	Roo	Spo	Vak	Wol	Wur
0.080	0.083	0.033	0.027	0.063	0.017	0.030	0.106	0.027	0.037	0.017	0.030

Group means

Callers	Duration	PF	CoFm	Onset	Offset	Q50	IQR	Sh
Aapi	-0.167	0.522	0.097	-0.479	-0.471	0.681	1.082	0.671
Afr	-0.072	0.170	-0.465	-0.254	-0.575	-0.081	0.146	0.013
Alsi	0.406	0.569	-0.506	0.293	-0.459	1.178	0.322	0.839
Bul	0.499	0.785	-1.299	-0.142	-0.351	0.567	-0.306	0.153
Enge	0.084	-0.959	0.122	-0.429	-0.181	-0.217	-0.382	0.404
Hipp	-0.370	0.359	-0.123	0.262	0.072	0.253	0.025	0.080
Hwa	-0.126	-0.587	-0.803	-0.689	-0.375	-0.148	-0.646	0.140
LBlind	-0.005	0.945	0.690	0.477	0.380	-0.108	0.368	-0.519
Miel	-0.084	-0.083	0.269	0.465	0.588	0.052	0.062	0.352
Mooi	0.258	-1.094	-0.330	-0.183	-0.511	-0.476	-0.118	-0.151
Nies	-0.044	-0.207	-0.264	-0.025	0.205	0.167	-0.537	0.318
Nok	0.204	-0.615	-0.299	-0.917	-0.997	-0.492	-0.275	-0.168
Ogi	-0.299	0.654	-0.183	0.389	0.197	-0.029	-0.140	-0.133
Onb	-0.151	-0.366	0.580	-0.008	0.426	-0.151	0.214	0.138
Ouli	-0.179	-0.367	-0.594	0.094	-0.030	-0.060	-0.483	-0.424
Pann	-0.267	-0.058	-0.259	0.234	0.593	0.159	-0.341	0.465
Piep	0.291	0.553	0.147	0.580	0.438	0.669	0.905	0.553
Poe	0.787	0.766	0.074	-0.315	0.472	0.529	0.703	0.703
Riss	-0.331	-0.925	0.470	-0.120	-0.654	-0.652	-0.562	-0.268
Roo	0.226	-0.634	0.701	-0.041	0.065	-0.572	0.179	-0.428

Spo	-0.568	-0.883	0.373	-0.533	0.105	-0.452	-0.271	-0.070
Vak	0.963	0.525	-0.061	-0.048	-0.182	-0.142	-0.444	-0.258
Wol	-0.267	-0.395	-1.894	-1.126	-0.516	-0.081	-0.599	-1.276
Wur	-0.779	1.061	-0.631	-0.462	-1.001	0.578	-0.376	-0.747

Coefficients of linear discriminants

Parameters	LD1	LD2	LD3	LD4	LD5	LD6	LD7	LD8
Duration	0.290	-0.105	-0.139	0.893	0.407	0.174	0.027	-0.428
PF	-1.134	0.374	-0.311	0.253	0.380	-0.661	0.257	0.251
CoFm	0.385	0.742	0.380	-0.191	-0.325	-0.631	-0.032	-0.541
Onset	-0.058	0.100	0.338	0.119	0.202	0.333	-1.031	0.196
Offset	-0.126	0.332	-0.001	-0.484	0.488	0.554	0.684	-0.098
Q50	-0.193	-0.476	0.696	-0.764	-0.831	0.495	-0.150	-1.222
IQR	-0.196	0.219	0.021	0.538	-0.570	0.663	0.126	0.531
Sh	0.289	0.587	-1.400	0.014	0.276	-0.592	-0.081	0.474

Proportion of trace

LD1	LD2	LD3	LD4	LD5	LD6	LD7	LD8
0.389	0.216	0.112	0.092	0.073	0.060	0.033	0.025

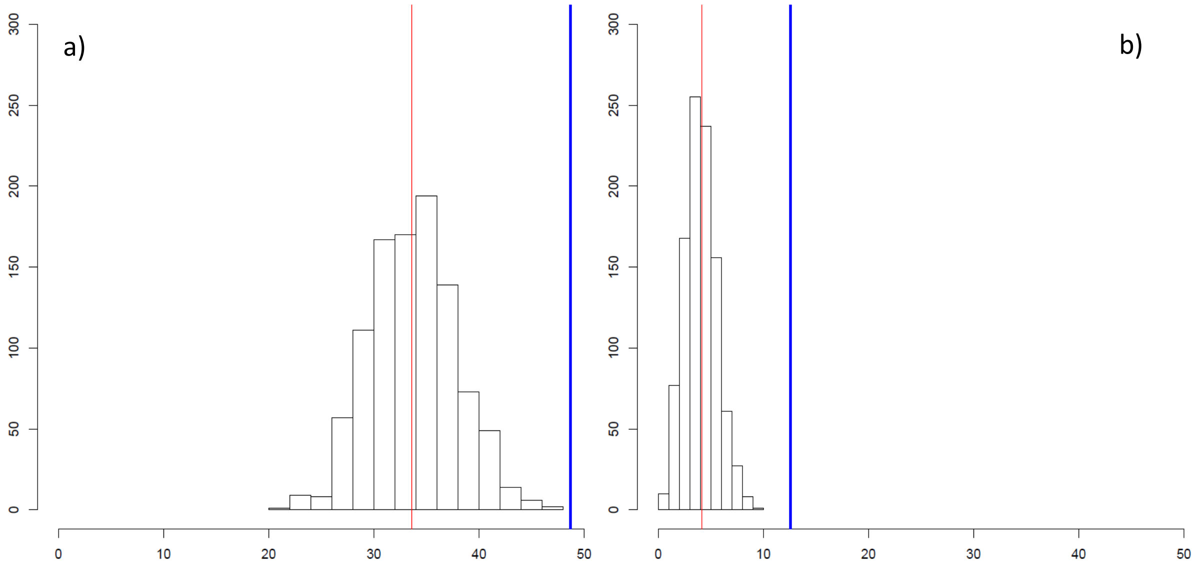


Fig S10. Histograms showing the frequency of classification rates from DFAs (%) at the call level with an incomplete crossed-design using a) correct classification and b) correct cross-classification. While red bars correspond to the expected percentage of correctly classified, respectively cross-classified calls, blue bars represent the mean percentage of correct classified and cross-classified calls obtained from real dataset.

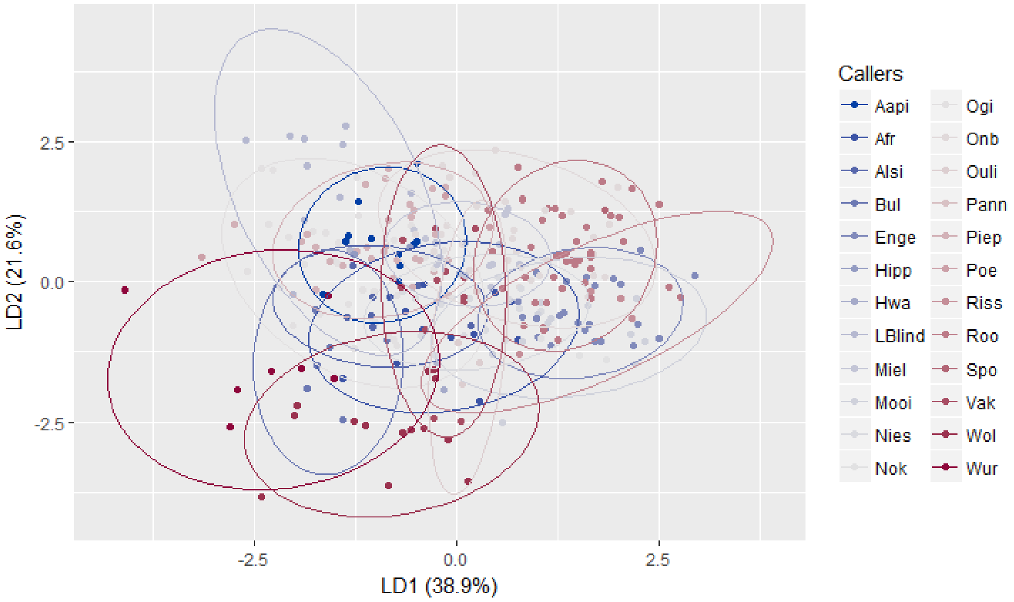


Fig S11. Graph showing first and second discriminant component scores resulting from an analysis of 301 screams produced by 21 individuals, represented by the different colours. Both axes represent the percentage of the variance explained by the first and second discriminant functions, respectively.

DFA on caller identity at the bout level – conservative approach

(using a balanced dataset with N = 8 individuals & N = 61 bouts)

Prior probabilities of groups

Afr	Enge	Hipp	Nies	Ogi	Onb	Ouli	Piep
0.131	0.148	0.131	0.131	0.098	0.082	0.131	0.148

Group means

Callers	NbSc	ScDuration	ScRate	NLP
Afr	-0.155	0.472	-0.577	0.437
Enge	0.006	-0.165	0.492	0.504
Hipp	0.357	-0.470	0.057	-0.029
Nies	-0.445	0.386	0.055	-0.010
Ogi	0.593	-0.293	-0.431	0.009
Onb	0.677	0.023	-0.273	0.161
Ouli	-0.365	-0.478	0.668	-0.984
Piep	-0.237	0.427	-0.234	-0.079

Coefficients of linear discriminants

Parameters	LD1	LD2	LD3	LD4
NbSc	0.389	0.894	0.360	0.917
ScDuration	-0.060	-0.227	0.989	1.056
ScRate	-0.517	0.742	1.217	0.574
NLP	0.910	0.144	0.389	-0.444

Proportion of trace

LD1	LD2	LD3	LD4
0.506	0.285	0.174	0.036

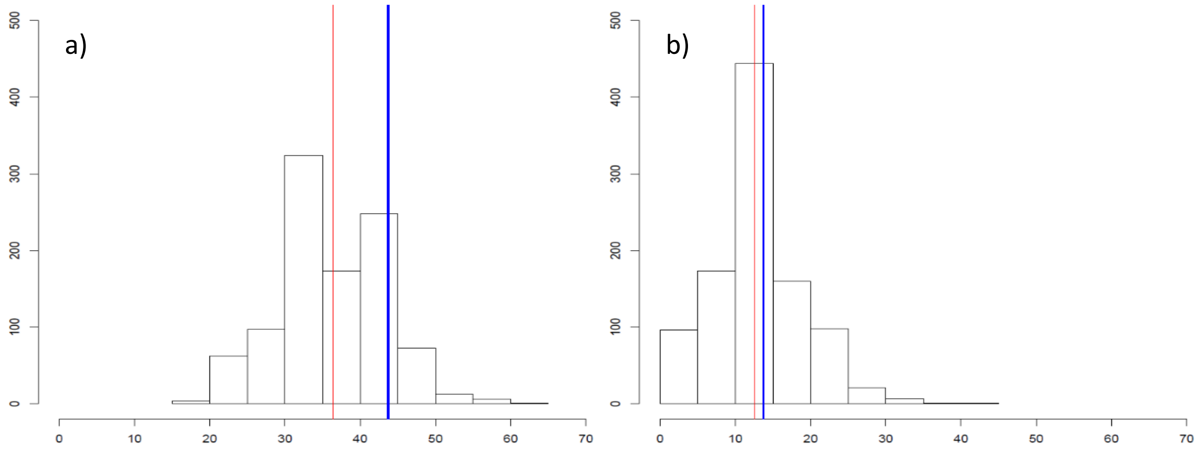


Fig S12. Histograms showing the frequency of classification rates from DFAs (%) at the bout level with a balanced dataset using a) correct classification and b) correct cross-classification. While red bars correspond to the expected percentage of correctly classified, respectively cross-classified calls, blue bars represent the mean percentage of correct classified and cross-classified calls obtained from real dataset.

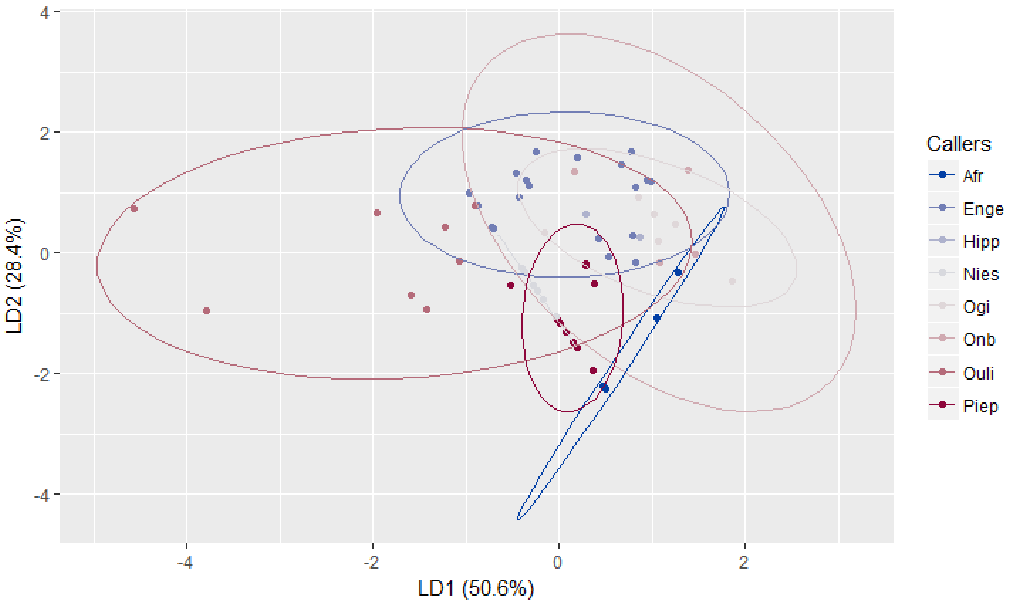


Fig S13. Graph showing first and second discriminant component scores resulting from an analysis of 61 bouts produced by eight individuals, represented by the different colours. Both axes represent the percentage of the variance explained by the first and second discriminant functions, respectively.

DFA on caller identity at the bout level – incomplete crossed design

(using an incomplete crossed design with N = 13 individuals & N = 85 bouts)

Prior probabilities of groups

Afr	Enge	Hipp	LBli	Miel	Mooi	Nies	Ogi	Onb	Ouli	Piep	Roo	Spo
0.094	0.106	0.094	0.059	0.047	0.059	0.094	0.071	0.059	0.094	0.106	0.059	0.059

Group means

	NbSc	ScDuration	ScRate	NLP
Afr	-0.313	0.481	-0.688	0.530
Enge	-0.146	-0.150	0.492	0.599
Hipp	0.216	-0.452	0.012	0.052
LBlind	0.008	0.083	0.331	0.404
Miel	0.602	-0.287	0.010	-0.114
Mooi	-0.588	0.552	-0.370	0.364
Nies	-0.613	0.397	0.010	0.072
Ogi	0.461	-0.276	-0.527	0.091
Onb	0.547	0.037	-0.352	0.247
Ouli	-0.529	-0.460	0.686	-0.928
Piep	-0.397	0.437	-0.310	0.000
Roo	1.403	0.019	-0.213	-0.260
Spo	0.159	-1.476	0.878	0.091

Coefficients of linear discriminants

Parameters	LD1	LD2	LD3	LD4
NbSc	1.053	0.464	0.614	0.035
ScDuration	-0.046	0.284	1.373	0.462
ScRate	0.718	-0.410	0.885	0.893
NLP	0.163	0.779	-0.571	0.614

Proportion of trace

LD1	LD2	LD3	LD4
0.379	0.311	0.193	0.117

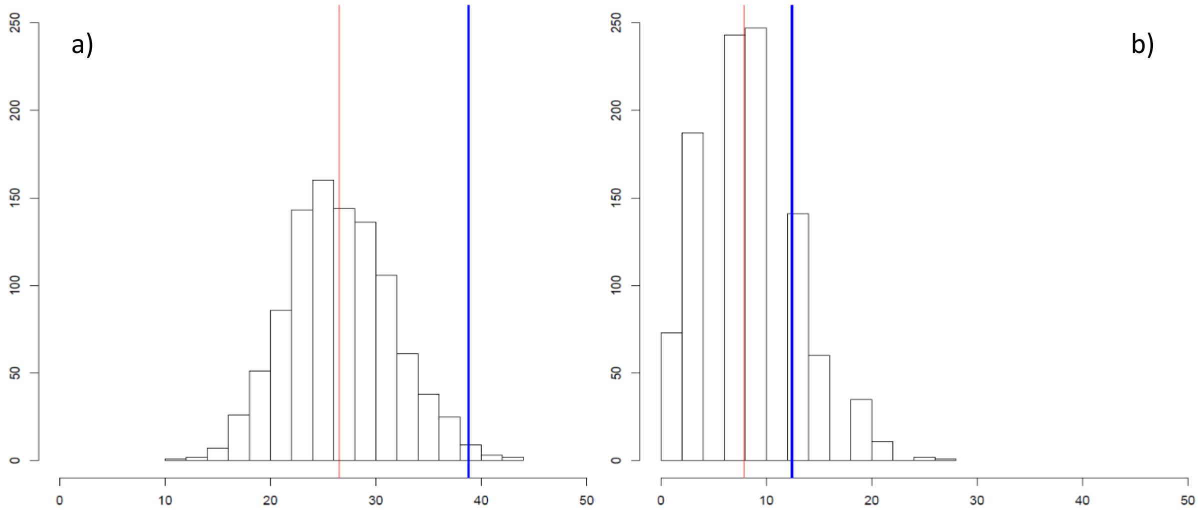


Fig S14. Histograms showing the frequency of classification rates from DFAs (%) at the bout level with an incomplete crossed-design dataset using a) correct classification and b) correct cross-classification. While red bars correspond to the expected percentage of correctly classified, respectively cross-classified calls, blue bars represent the mean percentage of correct classified and cross-classified calls obtained from real dataset.

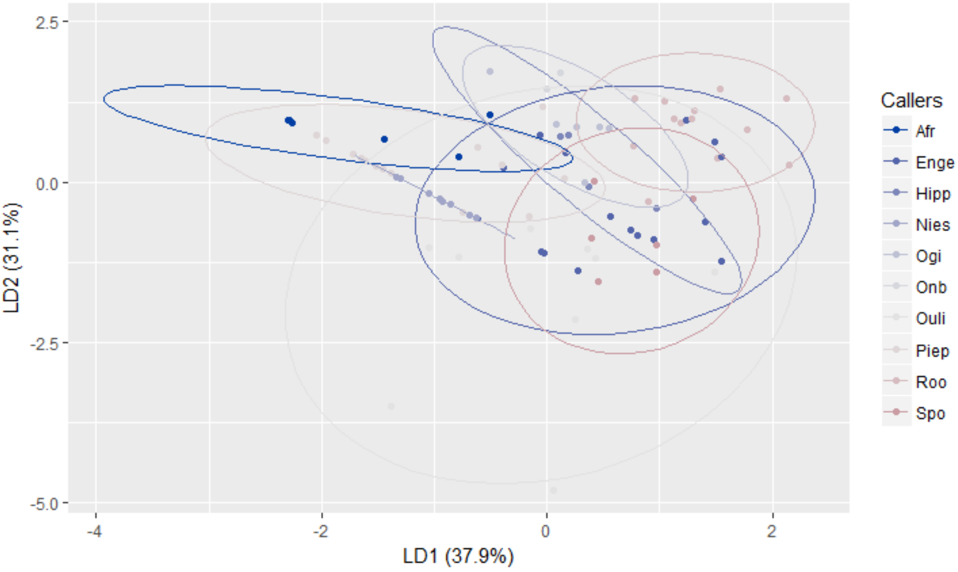


Fig S15. Graph showing first and second discriminant component scores resulting from an analysis of 85 bouts produced by 13 individuals, represented by the different colours. Both axes represent the percentage of the variance explained by the first and second discriminant functions, respectively.

S8. Detailed results of the analyses at the call level

Permutated Discriminant Function Analyses

We used 187 screams produced by 13 individuals to investigate whether contexts (screams recorded during natural follows vs around experiments) affected nine call related acoustic parameters: scream duration, peak frequency, coefficient of frequency variation, coefficient of frequency modulation, absolute transition onset, absolute transition offset, frequency quartile 50, inter-quartile range and Shannon entropy. However, we had to exclude the coefficient of frequency variation from further analyses due to its high correlation with Q50. Results from pDFAs showed that we could not discriminate screams according to the context of production (51.46% expected calls correctly cross-classified compared to 56.64% calls correctly cross-classified, *P* = 0.14). Similarly, we used 82 screams produced by four individuals to investigate whether callers' identity affected the same acoustic parameters. Results from pDFAs showed that we could not discriminate screams according to individuals (38.11% expected vs 41.00% calls correctly cross-classified, *P* = 0.36). To reproduce those two results, please visit Figshare (Mercier, Déaux et al. 2018).

Linear Mixed Models

As context nor individuals affected our acoustic parameters in significant ways, we thus used screams produced in both contexts and by all individuals for further analyses, leading to a dataset of 306 screams produced by 26 individuals. We performed 12 linear mixed models fitted by restricted maximum likelihood (REML) with Laplace approximation, normal or lognormal distributions and logit-link function (LMER; Bates, Mächler et al. 2015) for each acoustic parameter, using the later one as the response variable and three fixed effects: social role of signallers, conflict severity and their interaction. We included caller identity as a random effect to control for repeated measures. We then checked for homogeneity of the data and the distribution of residuals using graphical analyses of residuals (using bwplots, qqplots and binned plots) and checked for influential individuals and outliers, removing them only when necessary (if it did help to reach approximate symmetrical distribution and did not affect our results). For more details, please see Figshare (Mercier, Déaux et al. 2018).

Duration

REML criterion at convergence: 772.4
Number of observations: 306
Number of callers: 26

Scaled residuals	Min	1Q	Median	3Q	Max
	-2.25092	-0.66352	0.00772	0.72648	2.48457

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.01446	0.1202
	Residual		0.70181	0.8377

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
R^2m = 0.06991508
R^2c = 0.08868550

Table S8. Results from the linear mixed model testing variation found in scream duration

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	-1.544	0.094	-16.388	-1.728	-1.359	NA	NA
Social role (Victim)	0.504	0.128	3.924	0.252	0.756	0.000	0.000
Severity (Severe)	0.301	0.155	1.944	-0.003	0.604	0.123	0.316
Social role : Severity	-0.253	0.204	-1.241	-0.652	0.147	0.215	0.407

Peak frequency

REML criterion at convergence: 1040.3
Number of observations: 306
Number of callers: 26

Scaled residuals	Min	1Q	Median	3Q	Max
	-3.0905	-0.5078	-0.0101	0.4418	3.6646

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.9614	0.9805
	Residual		1.4694	1.2122

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
R2m = 0.006999794
R2c = 0.399735245

Table S9. Results from the linear mixed model testing variation found in peak frequency

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	5.194	0.241	21.577	4.722	5.666	NA	NA
Social role (Victim)	-0.117	0.197	-0.592	-0.503	0.269	0.590	0.732
Severity (Severe)	-0.288	0.244	-1.181	-0.767	0.190	0.141	0.317
Social role : Severity	0.089	0.322	0.277	-0.542	0.721	0.782	0.828

Coefficient of frequency modulation

REML criterion at convergence: 888.7
Number of observations: 305
Number of callers: 26

Scaled residuals	Min	1Q	Median	3Q	Max
	-2.8114	-0.4838	-0.0638	0.5645	2.6638

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.3907	0.6251
	Residual		0.9250	0.9618

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
$R^2m = 0.007102547$
$R^2c = 0.301966099$

Table S10. Results from the linear mixed model testing variation found in coefficient of frequency modulation

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	1.786	0.167	10.674	1.458	2.114	NA	NA
Social role (Victim)	0.040	0.156	0.256	-0.266	0.346	0.443	0.612
Severity (Severe)	0.194	0.193	1.009	-0.183	0.572	0.993	0.993
Social role : Severity	-0.343	0.254	-1.353	-0.841	0.154	0.176	0.372

Absolute transition onset

REML criterion at convergence: 874.2
Number of observations: 306
Number of callers: 26

Scaled residuals	Min	1Q	Median	3Q	Max
	-2.17937	-0.70185	-0.05813	0.82880	1.97223

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.0867	0.2944
	Residual		0.9462	0.9727

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
R^2m = 0.01355634
R^2c = 0.09635839

Table S11. Results from the linear mixed model testing variation found in absolute transition onset

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	0.279	0.124	2.240	0.035	0.523	NA	NA
Social role (Victim)	-0.229	0.153	-1.494	-0.529	0.071	0.186	0.372
Severity (Severe)	0.078	0.187	0.420	-0.287	0.444	0.132	0.317
Social role : Severity	0.183	0.246	0.741	-0.300	0.666	0.459	0.612

Absolute transition offset

REML criterion at convergence: 854.2
Number of observations: 305
Number of callers: 26

Scaled residuals	Min	1Q	Median	3Q	Max
	-2.14931	-0.79368	-0.03636	0.72633	2.18083

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.1156	0.3400
	Residual		0.8803	0.9383

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
R^2m = 0.01998765
R^2c = 0.13374769

Table S12. Results from the linear mixed model testing variation found in absolute transition offset

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	0.149	0.127	1.175	-0.099	0.397	NA	NA
Social role (Victim)	-0.172	0.149	-1.149	-0.465	0.121	0.253	0.434
Severity (Severe)	0.213	0.182	1.170	-0.144	0.570	0.023	0.104
Social role : Severity	0.101	0.241	0.417	-0.372	0.573	0.676	0.737

Frequency quartile 50

REML criterion at convergence: -0.1
Number of observations: 298
Number of callers: 25

Scaled residuals	Min	1Q	Median	3Q	Max
	-2.56541	-0.58947	-0.03483	0.59440	3.09249

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.008463	0.0920
	Residual		0.050925	0.2257

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
$R^2m = 0.05290242$
$R^2c = 0.18787291$

Table S13. Results from the linear mixed model testing variation found in frequency quartile 50

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	0.452	0.032	13.912	0.388	0.516	NA	NA
Social role (Victim)	0.063	0.037	1.720	-0.009	0.135	0.003	0.022
Severity (Severe)	0.029	0.044	0.656	-0.058	0.116	0.036	0.118
Social role : Severity	0.057	0.059	0.961	-0.059	0.172	0.336	0.550

Inter-quartile range

REML criterion at convergence: -254.5
Number of observations: 306
Number of callers: 26

Scaled residuals	Min	1Q	Median	3Q	Max
	-2.65639	-0.61020	-0.00952	0.56861	3.00418

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.003707	0.06088
	Residual		0.021925	0.14807

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
$R^2m = 0.003245867$
$R^2c = 0.147396829$

Table S14. Results from the linear mixed model testing variation found in inter-quartile range

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	0.403	0.021	19.331	0.362	0.444	NA	NA
Social role (Victim)	0.021	0.024	0.876	-0.026	0.067	0.632	0.737
Severity (Severe)	0.009	0.029	0.325	-0.047	0.066	0.671	0.737
Social role : Severity	-0.031	0.038	-0.798	-0.105	0.044	0.425	0.612

Shannon entropy

REML criterion at convergence: -485.9
Number of observations: 305
Number of callers: 26

Scaled residuals	Min	1Q	Median	3Q	Max
	-3.2286	-0.6105	0.1047	0.6628	2.1111

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.002958	0.05439
	Residual		0.009815	0.09907

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
R^2m = 0.1017186
R^2c = 0.3097735

Table S15. Results from the linear mixed model testing variation found in Shannon entropy

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	1.135	0.016	71.760	1.104	1.166	NA	NA
Social role (Victim)	0.005	0.016	0.297	-0.027	0.036	0.035	0.118
Severity (Severe)	0.031	0.020	1.568	-0.008	0.070	0.000	0.000
Social role : Severity	0.055	0.026	2.113	0.004	0.106	0.035	0.118

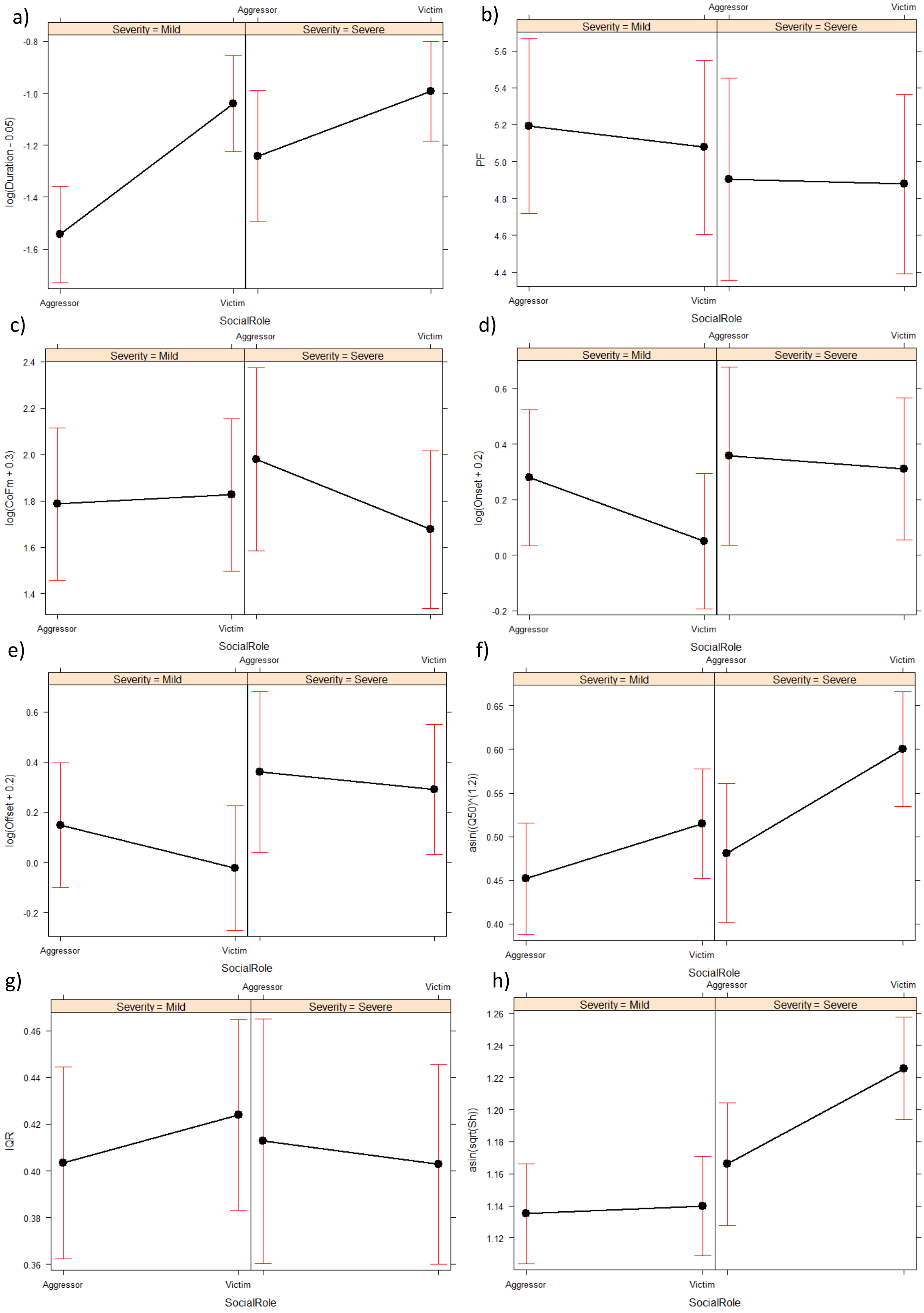


Figure S16. Effect plot showing the influences of both social role and severity on eight acoustic parameters tested at the call level: a) scream duration, b) peak frequency, c) coefficient of frequency modulation, d) absolute transition onset, e) absolute transition offset, f) frequency quartile 50, g) inter-quartile range and h) Shannon entropy.

S9. Detailed results of the analyses at the bout level

Permutated Discriminant Function Analyses

We used 102 bouts of screams produced by 15 individuals to investigate whether contexts (screams recorded during natural follows vs around experiments) affected six bout related acoustic parameters: bout duration, number of screams, average scream duration, scream intervals, scream rate and percentage of screams with NLP. However, we had to exclude bout duration from further analyses due to its high correlation with the number of screams and scream rate. Furthermore, we removed scream intervals, as we did not reach approximate symmetrical distribution, thus violating the assumption of normality. Results from pDFAs showed that we could not discriminate bouts according to the context of production (50.53% expected calls correctly cross-classified compared to 42.21% calls correctly cross-classified, *P* = 0.88). Similarly, we used 53 bouts of screams produced by seven individuals to investigate whether callers' identity affected the same acoustic parameters. Results from pDFAs showed that we could not discriminate bouts according to individuals (19.60% expected vs 16.48% calls correctly cross-classified, *P* = 0.58). To reproduce those two results, please visit Figshare (Mercier, Déaux et al. 2018).

Linear Mixed Models

As context nor individuals affected our acoustic parameters in significant ways, we thus used bouts of screams produced in both contexts and by all individuals for further analyses, leading to a total dataset of 121 bouts produced by 28 individuals. We performed five linear mixed models fitted by restricted maximum likelihood (REML) with Laplace approximation, normal or lognormal distributions and logit-link function (LMER; Bates, Mächler et al. 2015) for each acoustic parameter, using the later one as the response variable and three fixed effects: social role of signallers, conflict severity and their interaction. We included caller identity as a random effect to control for repeated measures. We then checked for homogeneity of the data and the distribution of residuals using graphical analyses of residuals (using bwplots, qqplots and binned plots) and checked for influential individuals and outliers, removing them only when necessary (if it did help to reach approximate symmetrical distribution and did not affect our results). For more details, please see Figshare (Mercier, Déaux et al. 2018).

Number of screams

REML criterion at convergence: 333.7
Number of observations: 120
Number of callers: 28

Scaled residuals	Min	1Q	Median	3Q	Max
	-1.6095	-1.0258	0.1121	0.6100	2.6156

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.1570	0.3962
	Residual		0.8132	0.9018

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
$R^2m = 0.01578851$
$R^2c = 0.17503317$

Table S16. Results from the linear mixed model testing variation found in the number of screams

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	0.940	0.179	5.265	0.590	1.290	NA	NA
Social role (Victim)	0.020	0.219	0.092	-0.409	0.449	0.433	0.612
Severity (Severe)	0.337	0.283	1.192	-0.217	0.891	0.670	0.737
Social role : Severity	-0.427	0.360	-1.189	-1.132	0.277	0.235	0.421

Average scream duration

REML criterion at convergence: 254.1
Number of observations: 121
Number of callers: 28

Scaled residuals	Min	1Q	Median	3Q	Max
	-2.52352	-0.63077	-0.00547	0.63659	2.74987

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.02567	0.1602
	Residual		0.43593	0.6603

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
R^2m = 0.1365090
R^2c = 0.1845231

Table S17. Results from the linear mixed model testing variation found in average scream duration

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	-1.319	0.120	-11.027	-1.553	-1.084	NA	NA
Social role (Victim)	0.395	0.157	2.507	0.086	0.703	0.007	0.036
Severity (Severe)	0.475	0.203	2.325	0.074	0.870	0.002	0.018
Social role : Severity	-0.147	0.258	-0.569	-0.652	0.359	0.569	0.732

Scream rate

REML criterion at convergence: 314.3
Number of observations: 121
Number of callers: 28

Scaled residuals	Min	1Q	Median	3Q	Max
	-3.2131	-0.5790	-0.0291	0.4921	2.4527

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.09065	0.3011
	Residual		0.69591	0.8342

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
R^2m = 0.08553756
R^2c = 0.19093051

Table S18. Results from the linear mixed model testing variation found in scream rate

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	0.364	0.159	2.288	0.052	0.676	NA	NA
Social role (Victim)	0.084	0.201	0.420	-0.310	0.479	0.088	0.264
Severity (Severe)	-0.764	0.260	-2.942	-1.272	-0.255	0.005	0.030
Social role : Severity	0.509	0.329	1.548	-0.136	1.153	0.122	0.316

NLP

REML criterion at convergence: 92.4
Number of observations: 119
Number of callers: 28

Scaled residuals	Min	1Q	Median	3Q	Max
	-2.4953	-0.6171	0.2825	0.6914	1.2967

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	0.03921	0.1980
	Residual		0.09315	0.3052

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
R^2m = 0.01355634
R^2c = 0.09635839

Table S19. Results from the linear mixed model testing variation found in NLP

	Estimate	Std. Error	T value	CIL	CIU	*P*	Adjusted *P*
(Intercept)	0.364	0.159	2.288	1.094	1.361	NA	NA
Social role (Victim)	0.084	0.201	0.420	-0.181	0.118	0.857	0.881
Severity (Severe)	-0.764	0.260	-2.942	-0.017	0.369	0.000	0.000
Social role : severity	0.509	0.329	1.548	-0.129	0.354	0.361	0.565

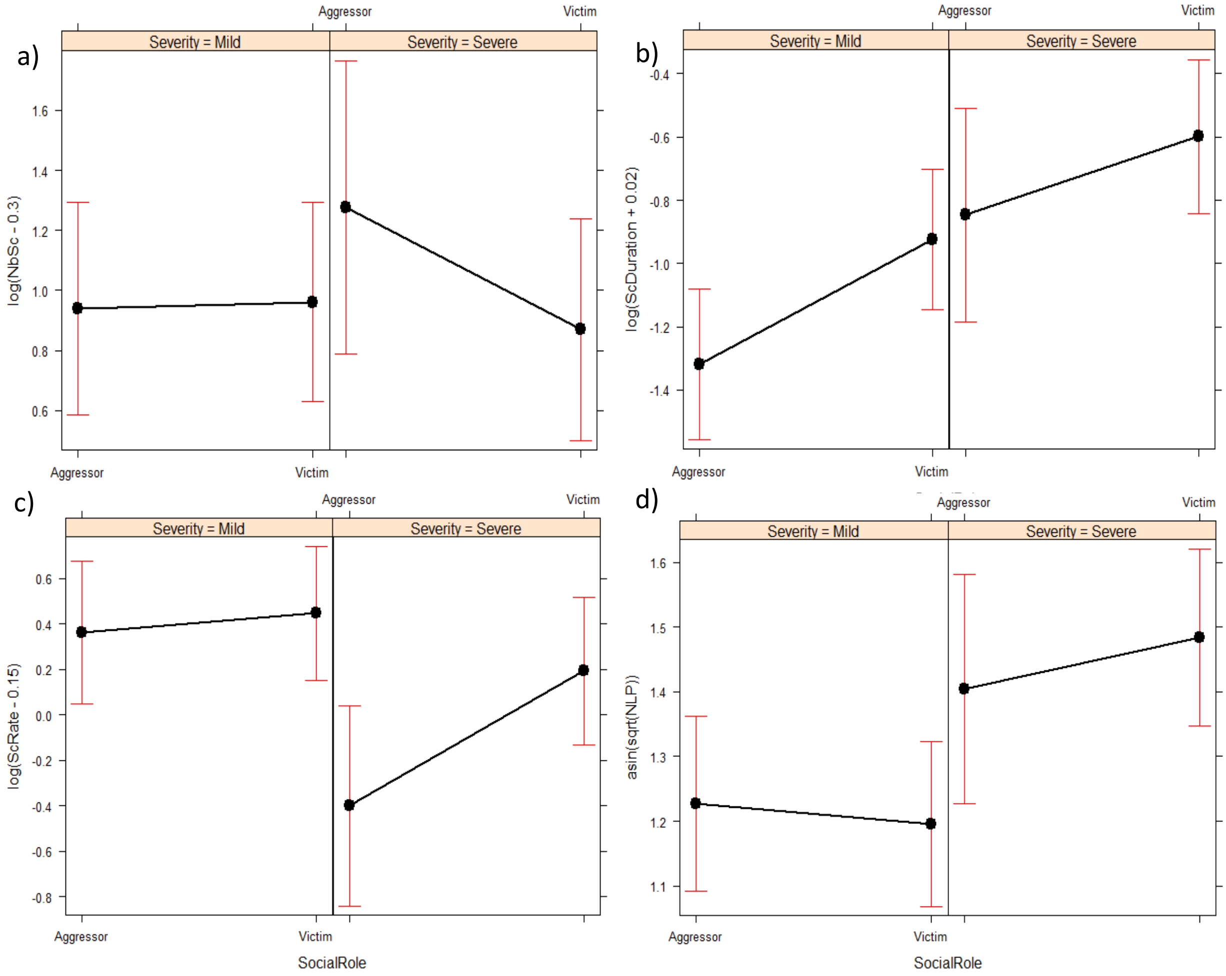


Fig S17. Effect plot showing the influences of both social role and severity on four acoustic parameters at the bout level: a) number of screams, b) average scream duration, c) scream rate and d) percentage of non-linear phenomena.

S10. Detailed results of the support analysis

Linear Mixed Models

We used 114 bouts of screams produced by 28 individuals to perform a generalized linear mixed model (GLMM; Baayen, Davidson et al. 2008) fitted with a binomial structure and logit-link function to examine the influence of the social role of signallers (aggressor vs. victim) and conflict severity (mild vs. severe) on the number of support received. We used the later one as the response variable and three fixed effects: social role of signallers, conflict severity and their interaction. We included both caller identity and context of production (using six levels: observation, observation without food, observation with food involved, experiments, experiments without food and experiments with food involved) as random effects to control for repeated measures, thus avoiding pseudo-replication (Waller, Warmelink et al. 2013). After checking for multicollinearity (all r < 0.80), we then checked for homogeneity of the data and the distribution of residuals using graphical analyses of residuals (using bwplots, qqplots and binned plots) and checked for influential individuals and outliers, not removing any of them. For more details, please see Figshare (Mercier, Déaux et al. 2018).

Number of support

AIC	BIC	logLik	deviance	df.resid
91.3	107.7	-39.6	79.3	108

Number of observations: 114
Number of callers: 28

Scaled residuals	Min	1Q	Median	3Q	Max
	-1.3756	-0.3557	-0.1694	-0.1272	4.8190

Random effects	Groups	Name	Variance	Std. Dev.
	Caller	(Intercept)	1.124	1.06
	Context	(Intercept)	0.000	0.00

R squared values (R^2m = marginal R^2 explained by fixed effects only and R^2c = conditional R^2 explained by both fixed and random effects):
$R^2m = 0.04692823$
$R^2c = 0.07073086$

Table S20. Results from the GLMM testing variation found in the number of support

	Estimate	Std. Error	Z value	CIL	CIU	*P*
(Intercept)	-1.468	0.621	-2.365	-2.685	-0.252	NA
Social role (Victim)	-1.875	0.904	-2.073	-3.647	-0.102	0.038
Severity (Severe)	2.626	1.065	2.466	0.539	4.714	0.014
Social role : Severity	-3.052	1.690	-1.806	-6.364	0.260	0.071

V. Chapter 3 - Early understanding of social expectations in wild vervet monkeys

First submission in Sciences Advances on August 2018.

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5.1 Abstract

Some primates appear to predict outcomes of conflicts based on physical and social features of their opponents. Individuals sometimes protest vocally when expectations are violated, but little is known about how this ability is acquired. We studied vervet monkeys due to their peculiar social structure with offspring inheriting their mothers' social status. We investigated subjects' reactions when expectations were violated, for example, when approached by a physically smaller but socially higher-ranking opponent. Overall, we found that subjects screamed at higher rates when approached by lower than higher-ranking individuals. However, reactions varied between age/sex classes with juveniles protesting more when approached by bigger and higher-ranking opponents, while adults protested more when expectations were violated. Furthermore, while juvenile males screamed most against violations of physical norms, subadult males reacted more against social ones. Our results thus suggest an early understanding of social expectations in this species.

5.2 Introduction

Human social interactions are governed by norms; mental constructs of what are considered acceptable and unacceptable social interactions. These norms are based on shared beliefs and perceived as socially enforced rules dictating how members of a society ought to behave (Fehr and Fischbacher 2004a). Social norms regulate almost every aspect of human life, including trivial matters such as how to consume food (Higgs 2015) or beverages (Perkins 2002). Social norms are stratified and usually confined to specific groups of individuals, such as family units, religious communities or larger cultural organizations, such as nation states, with significant differences across such groups (Fehr and Fischbacher 2004a). Adhering to social norms can be adaptive, insofar as individuals with similar behavioural patterns generally cooperate better than individuals who do not coordinate their activities. At the same time, following social norms can be costly for individuals, which favours free-riders that disregard social rules and, in doing so, prevent cooperation and damage public goods. Humans tend to respond aggressively when encountering free-riders in order to impose costs and, in doing so, render norm-breaking behaviour more costly. Since such policing behavior is usually also costly for the enforcing individual, it has been termed ‘punishment’ (Fehr and Fischbacher 2004b).

Animal social behaviour is also governed by rules that lead individuals to behave in what others perceive as socially acceptable ways. Social interactions are usually determined by biological factors, such as the sex, age or body size of the interacting individuals. Age and body size are often related, a visible physical manifestation of fighting capacity when accessing resources such as food, sleeping sites or mates (Gaillard, Festa-Bianchet et al. 2000). The ability to compare one’s own body size with that of an opponent is adaptive because it will help individuals to lower the risks of injuries in case of conflict escalations.

In most group-living animals, social interactions are additionally governed by dominance relations, which determine who has priority of access in competitive situations, with higher-ranking individuals having better access to limited resources than lower-ranking ones. For example, highest-ranking red deer stags have privileged access over food (Appleby 1980). As better access to resources reduces food consumption time, higher-ranking individuals also benefit from increased time they can dedicate to other essential activities, such as vigilance (Hegner 1985) or grooming (Tiddi, Aureli et al. 2012). However, to maintain high social status, dominant individuals need to control subordinates’ behaviour and, if necessary, respond aggressively towards ‘cheating’ individuals that violate the rules (Cummins 1999). Thereby, lower-ranking individuals developed different strategies to mitigate the aggressive behaviour of higher-ranking ones, for example, by retreating from approaches and so avoiding interactions, by using visual and/or vocal signals of submission (Laporte and Zuberbühler 2010), or by behaving in socially expected ways. In primates, an individual’s rank can also be a social asset, as individuals choose their grooming partners based on rank by preferring higher over lower-ranking individuals (Newton-Fisher and Kaburu 2017).

In vervet monkeys, males and females have separate dominance hierarchies, which is likely to lead to different social expectations depending on the individuals’ age-sex class and social position (Cummins 1999). The male hierarchy is based on fighting abilities and, due to frequent migration events, is relatively unstable (Cheney and Seyfarth 1992). In contrast, the female hierarchy is relatively stable, possibly reinforced by the fact that related females support each other during conflicts, which effectively results in a system of maternally inherited social ranks (Cheney and Seyfarth 1992). High-ranking males have prioritized access to females and thus better mating opportunities than low-ranking ones, while high-ranking females have prioritized access to food and water resources (Cheney and Seyfarth 1992). Moreover, the female propensity to form alliances renders them more powerful than males, despite males being bigger than females (Turner, Schmitt et al. 2018). One peculiar consequence of this system is that the youngest individual of a matriline not only inherits his/her mother's matrilineal rank, but also obtains the highest rank within the matriline (Cheney and Seyfarth 1992), leading to a negative relationship between body size and social rank.

Due to these contingencies, vervet monkey groups are structured along at least three social rules: (1) yield to anyone who is physically superior, (2) yield to anyone who is a member of a higher-ranking matriline, (3) yield to anyone younger in the same matriline. Evidently, rules 1 and 2 are often in accordance with one another, whereas rules 1 and 3 are always in conflict. Our main questions in this study are, first, whether social interactions among vervet monkeys are governed by these rules and, in case they are broken, will they vocally protest towards 'cheaters'? Second, at what period in their development will they give precedence to individuals based on their social rather than physical power?

There is a sizable literature on how primates react to violations of social expectations, but most studies have been realised in captivity. A famous example comes from feeding experiments with capuchin monkeys trained to exchange tokens for food rewards (Brosnan and De Waal 2003). One finding was that individuals protested (by refusing to participate) if their partner received a better food reward than they did for the same task. Follow-up studies then demonstrated the importance of additional factors, such as the amount of effort provided (van Wolkenten, Brosnan et al. 2007) or the relationship between the partners (Brosnan, Schiff et al. 2005). Nevertheless, the argument has been made that primates have some sense of 'fairness', insofar as they have some understanding of what is considered 'normal', and that individuals protest if such norms are violated. A recent example are bonobos, with individuals protesting with screams that were acoustically different depending on whether or not aggression was perceived as justified by victims (Clay, Ravaux et al. 2016). In the wild, studies of social expectations in animals remain scarce. In vervet monkeys, foraging behaviour appears to be subject to somewhat arbitrary rules, with infants learning from their mothers what foods to eat or to avoid, similar to immigrant males who will even learn to feed against their own preference, in alleged attempts to follow group norms (van de Waal, Borgeaud et al. 2013).

Our aim was to examine how vervet monkeys, occupied with feeding, responded when approached in non-aggressive ways by individuals that were younger, smaller, or lower-ranking than themselves. The focus was particularly on competitive feeding situations where two variables were in conflict with one another, such as being approached by a smaller but higher-ranking individual. As dependent variable, we analysed subjects' screaming responses. Primates use screams as attention getters to enlist support from other group members (Cheney and Seyfarth 1980), but also to directly dissuade aggressors, presumably due to the inherently aversive acoustic nature of screams (Owren and Rendall 2001). Yet, we are not aware of any work on how individuals use screams when social expectations are violated and how this behaviour develops. Screaming behaviour, in other words, provides somewhat of a window into the individuals' minds. In this sense, our study was designed to get an insight into how vervet monkey social cognition develops across the different age/sex classes.

We predicted that, individuals should produce more screams in situations when its expectations are violated, that is, when approached by an individual that is not entitled to do so, due to its age, size or social rank. In contrast, we expected subjects to retreat silently and non-aggressively when approached by individuals that adhered to the social rules, for instance, because they were bigger and higher-ranking. In addition, we predicted age and sex differences in the relative importance of the social rules. In particular, we predicted females to scream more when approached by lower-ranking individuals, as social power is more important to females than males (Hausfater, Altmann et al. 1982). In contrast, we predicted males to scream more when approached by smaller individuals, as physical power is more important to them than to females (Cheney, Seyfarth et al. 1986). Finally, we expected age effects with younger individuals responding less strongly to violations of social norms than older individuals, due to hypothesis that cognitive capabilities develop and that immature individuals need time to learn social norms and their violations.

5.3 Results

We addressed our research questions by analysing the data in three complementary ways, i.e., by using non-parametric statistics, generalised linear modelling and simulations.

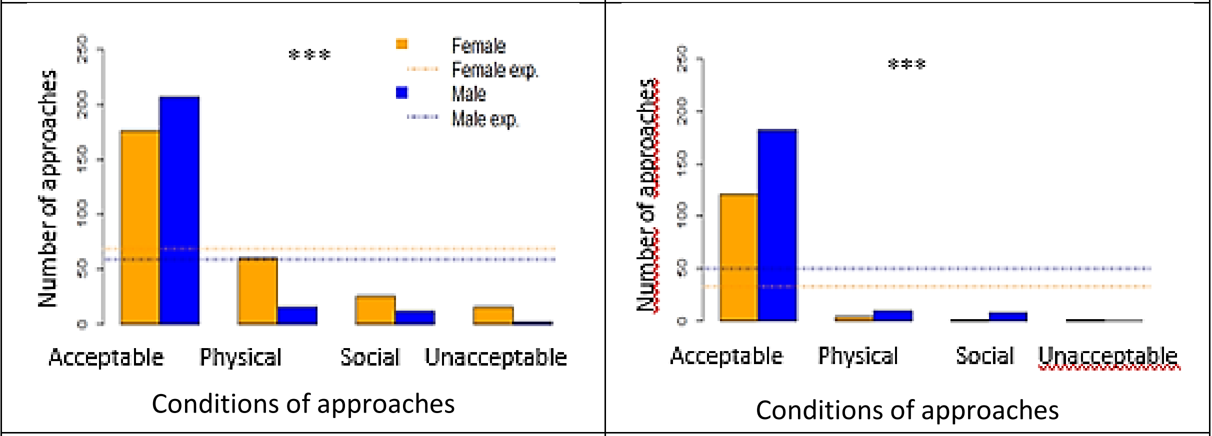
Analysis strategy 1: Age-sex classes comparisons

Approaches

The overall number of approaches was not randomly distributed with approaches by bigger and higher-ranking individuals (acceptable approaches) being more frequent than expected (‘acceptable’: 75% - 383/511; ‘physical violations’ when approached by smaller individuals: 14.7% - 75/511; ‘social violations’ when approached by lower-ranking individuals: 7% - 36/511; ‘unacceptable’ when approached by both smaller and lower-ranking individuals: 3.3% - 17/511, N = 511, Fisher's exact test for count data, p-value < 0.001, Fig. 1). However, the number of approaches also differed according to the subjects’ sex and age, with juvenile males and subadult females being approached more often in ‘acceptable’ conditions than juvenile females and subadult males, respectively. Interestingly, juvenile males did not elicit approaches by smaller and lower-ranking individuals (‘unacceptable’ approaches), and subadult females did not elicit approaches by similar sized but lower-ranking individuals (social violations), as well as by smaller and lower-ranking individuals (‘unacceptable’ approaches). In adult females, surprisingly, the number of approaches was highest in conditions of physical violations, i.e., when approached by smaller but higher-ranking individuals. Unfortunately, it was not possible to look at the number of ‘acceptable’ approaches in this age class as adult females could not elicit approaches by bigger individuals than themselves.

OVERALL
(N = 511; females: N = 276; males: N = 235)

JUVENILES – 1-2 years old ♀ / 1-3 years old ♂
(N = 325; females: N = 127; males: N = 198)



SUBADULTS – 3-4 years old ♀ / 4-5 years old ♂
(N = 99; females: N = 62; males: N = 37)

ADULT FEMALES
usually mothers >5 years old (N=87)

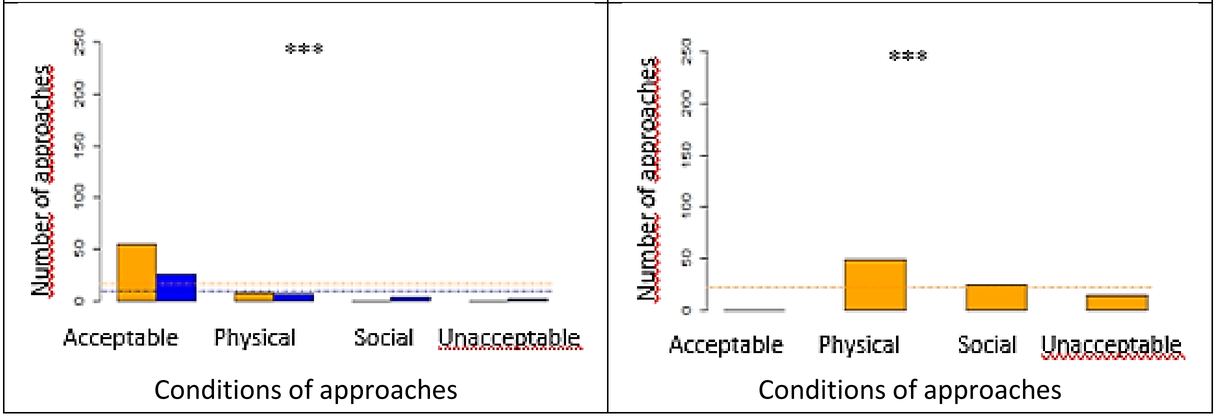


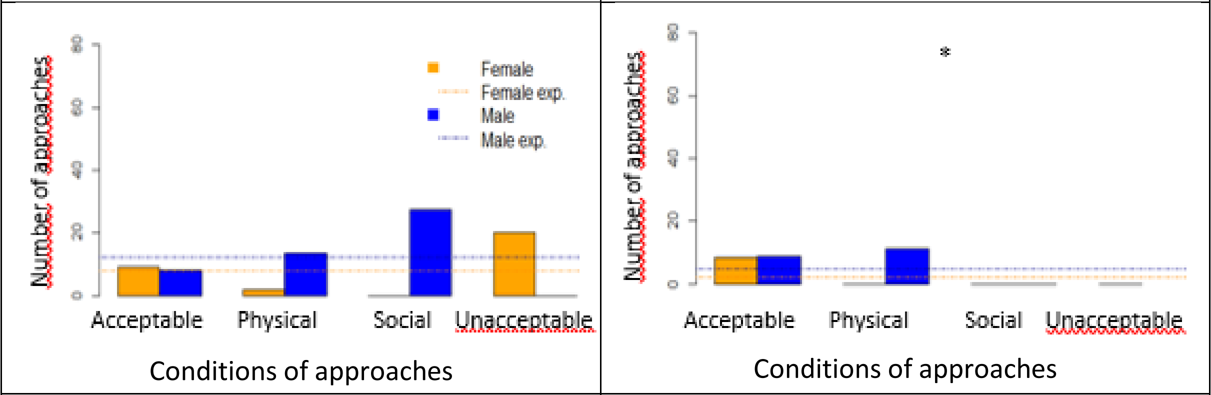
Fig. 1. Bar plots showing the number of approaches attained by subjects of different sex and age. Approaches were: 1) 'acceptable' if approached by a bigger and higher-ranking individual, 2) a 'physical violation' if approached by a smaller but higher-ranking individual, 3) a 'social violation' if approached by a similarly sized but lower-ranking individual and 4) 'unacceptable' if approached by a smaller and lower-ranking individual. Dashed lines indicate expected values if number of approaches were randomly distributed across the four conditions in females (orange) and males (blue). Significant results are represented by * if p-values < 0.05, ** if < 0.01 and *** if < 0.001.

Communication during approaches

Overall screaming was distributed randomly across the different age-sex classes (4-sample test for equality of proportions without continuity correction, $\chi^2 = 4.8151$, df = 3, p-value = 0.186, Fig. 2), but pairwise comparisons revealed several differences, explained hereafter.

OVERALL (N = 511, scream rate = 8.2%; females: N = 276 with 7.3% screams; males: N = 235 with 9.4% screams)

JUVENILES – 1-2 years old ♀ **/** 1-3 years old ♂ (N = 325, scream rate = 8.3%; females: N = 127 with 7.9% screams; males: N = 198 with 8.6% screams)



SUBADULTS – 3-4 years old ♀ **/** 4-5 years old ♂ (N = 99, scream rate = 11.1%; females: N = 62 with 9.7% screams; males: N = 37 with 13.5% screams)

ADULT FEMALES (N=87, scream rate = 4.6%)

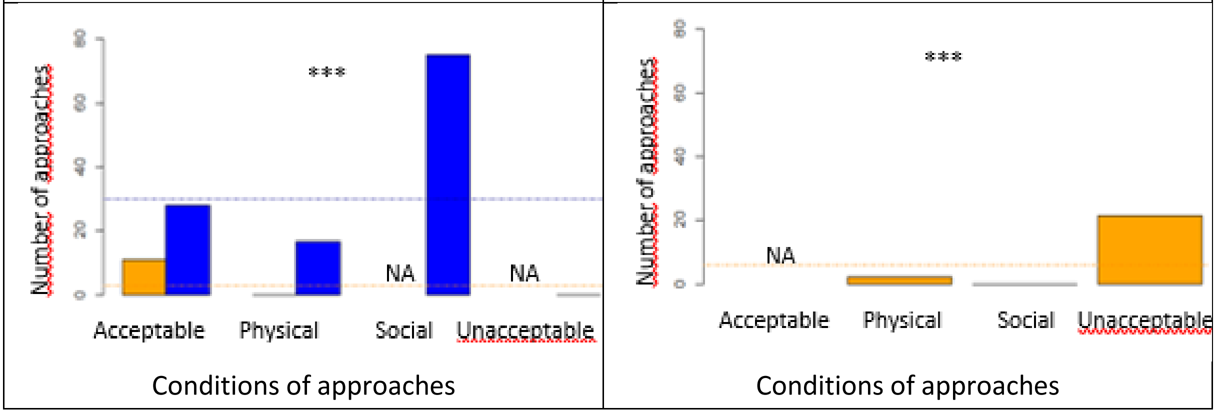


Fig. 2. Bar plots showing the percentage of screams produced by subjects of different sex and age. Approaches were: 1) 'acceptable' if approached by a bigger and higher-ranking individual, 2) a 'physical violation' if approached by a smaller but higher-ranking individual, 3) a 'social violation' if approached by a similarly sized but lower-ranking individual and 4) 'unacceptable' if approached by a smaller and lower-ranking individual. Dashed lines indicate expected values if number of approaches were randomly distributed across the four conditions in females (orange) and males (blue). Significant results are represented by * if p-values < 0.05, ** if < 0.01 and *** if < 0.001.

If controlling for sex, we did not find a significant difference in subjects' screaming responses (2-sample test for equality of proportions without continuity correction, $\chi^2 = 0.159$, df = 1, p-value = 0.69), with males and females screaming at similar rates (12.2% vs. 7.7%). However, if controlling for age, we found a significant difference in subjects' screaming responses (3-sample test for equality of proportions without continuity correction, $\chi^2 = 8.0356$, df = 2, p-value < 0.02), with subadults screaming at the highest rate (22.9%), followed by adult females (7.8%) and juveniles (4.1%).

As predicted, adult females screamed most in 'unacceptable' conditions, i.e., if approached by smaller and lower-ranking individuals ($\chi^2 = 17.567$, df = 2, p-value < 0.001). Surprisingly, however, female subadults and juveniles screamed most in 'acceptable' situations, i.e., if approached by bigger and higher-ranking individuals than any physical and social conditions (subadults: $\chi^2 = 4.8446$, df = 1, p-value < 0.03; juveniles: $\chi^2 = 9.9622$, df = 3, p-value < 0.02). Unfortunately, they did not elicit approaches by lower and smaller individuals, preventing us from looking at their reactions in some conditions of norm violations. Although this result seems meaningless, we highlight its implication in the discussion.

No data were analysed for adult males due to their special status related to their dispersal behaviour. Subadult males screamed most in response to ‘social violations’, i.e., if approached by lower-ranking individuals of similar size ($\chi^2 = 53.107$, df = 3, p-value < 0.001), whereas juvenile males screamed most in response to ‘physical violations’, i.e., if approached by smaller but higher-ranking individuals ($\chi^2 = 8.0639$, df = 2, p-value < 0.02).

Analysis strategy 2: Generalized linear mixed models

We analysed all approaches, including the ones that did not fall into one of the four previously described conditions (acceptable, physical violation, social violation and unacceptable), such as when approached by individuals that were bigger but lower-ranking (N=89) or that were similar in size but higher-ranking (N=528). Consequently, we analysed N=1,128 approaches by N=108 initiators to N=147 subjects belonging to 57 different matrilines from three different groups (Table S1). Results from a generalized linear mixed model with a binomial error structure and a logit-link function showed that subjects’ screaming responses were influenced by three factors: subject age, size and social rank differences between subjects and initiators (‘Dyadic rank’, Table 1), as well as the interaction between age and size difference (Figs. 3 & 4).

Table 1. Results of the GLMM testing individual and dyadic characteristics of approaches affecting subjects’ screaming responses.

	Estimate	SE	Z	CI	*P*
Age	-1.504	0.493	-3.053	-1.30 to -0.30	0.002 **
Size difference (similar)	-0.736	0.232	-3.173	-15.80 to -1.00	0.028 *
Size difference (smaller)	-2.726	1.238	-2.202	-20.11 to 0.60	0.193
Dyadic rank (lower-ranking)	-2.661	2.047	-1.300	0.37 to 3.57	0.003 **
Age:Size difference (similar)	1.922	0.652	2.946	0.26 to 2.82	0.015 *
Age:Size difference (smaller)	0.717	0.295	2.428	-0.08 to 3.64	0.078
Age:Dyadic rank (lower-ranking)	0.787	0.447	1.761	-1.05 to 0.60	0.494
Size difference (similar): Dyadic rank (lower)	-0.211	0.309	-0.684	-6.64 to 3.44	0.749
Size difference (smaller): Dyadic rank (lower)	0.402	1.259	0.320	-6.95 to 8.24	0.547

*CI = 95% confidence intervals using bootstrap method; test levels of categorical predictors are given in parentheses. Significant results are represented by * if p-values < 0.05, ** if < 0.01 and *** if < 0.001.*

Younger subjects screamed at higher rates than older ones, and they were all producing more screams when approached by lower compared to higher-ranking individuals (Figs. 3 & 4). However, there was an interaction effect between subject age and size difference, with younger subjects screaming more when approached by bigger initiators than older ones, and older subjects screaming more when approached by smaller initiators (Fig. 4). Scream rates were comparable when approached by similarly sized or smaller individuals.

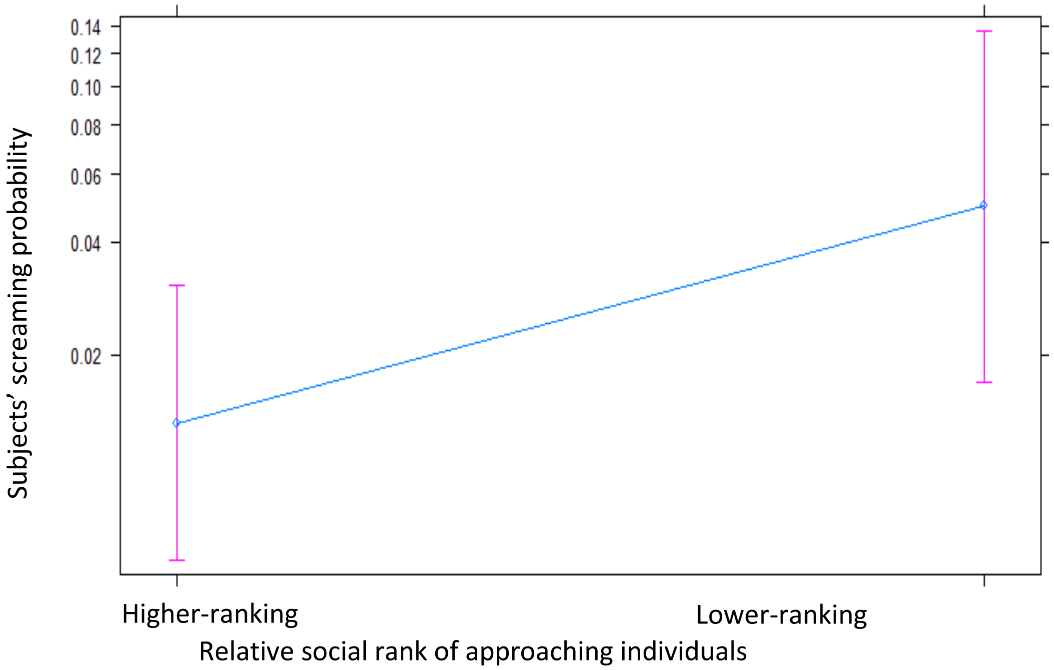


Fig. 3. Effect plot showing the influence of social rank differences on screaming responses.

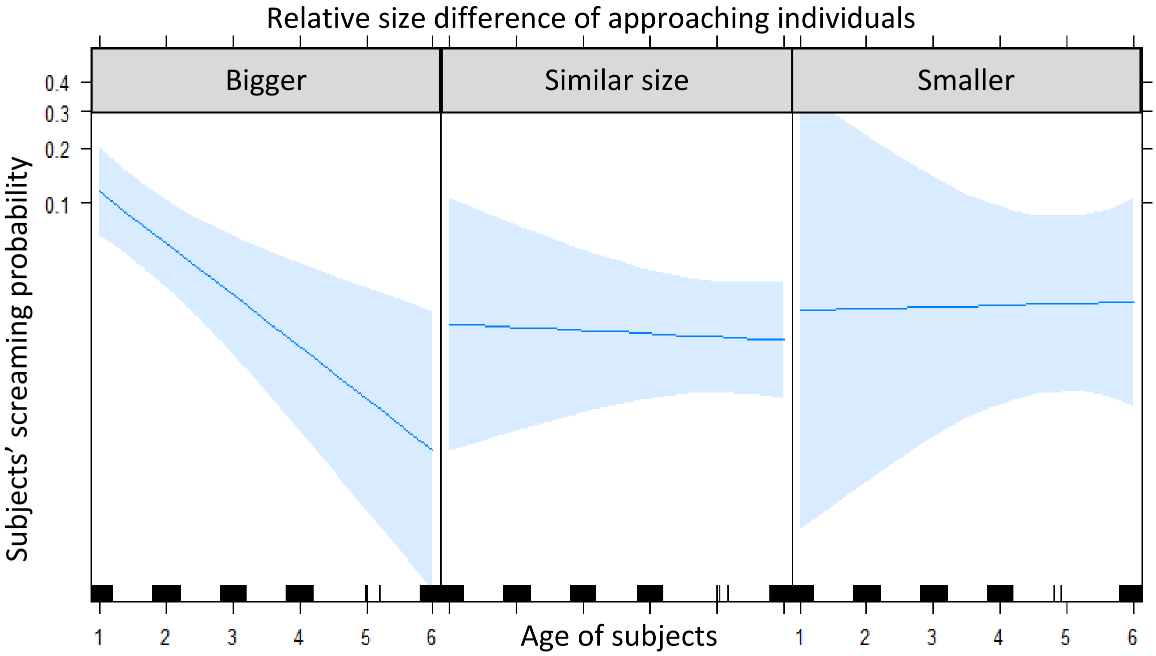


Fig. 4. Effect plot showing the influence of subject age and size difference on screaming responses.

Analysis strategy 3: Simulations

In the final analysis, we simulated four data sets representing four possible functions: (1) random screaming, (2) violation of physical power (approached by smaller individual), (3) violation of social power (approach by lower-ranking individual) and (4) reacting to 'unacceptable' conditions (approach by smaller and lower-ranking individual).

Euclidean distances between actual and simulated datasets for screaming responses showed an age effect. Juveniles and subadults were closer in Euclidean distance compared to their simulated size data sets (juveniles: 0.085; subadults: 0.062, Table S8), while adult females were closer in distance to their simulated rank data set (0.032).

5.4 Discussion

We explored whether vervet monkeys had something akin to social norms, evidenced by data showing that eventual violations by others were perceived and acted upon. To address this, we studied subjects' screaming responses when approached by other group members whose sex, size and social rank could differ from their own. We carried out three analyses, based on direct comparisons, linear mixed modelling and simulation data.

Analysis 1: Frequency data

Overall, we found that 'acceptable' approaches, i.e., by bigger and higher-ranking group members, were more frequent than expected, while norm violations were relatively infrequent, suggesting that monkeys adhered to basic rules defined by physical and social power when interacting with each other.

Although subjects screamed in all four conditions, their vocal responses developed in specific ways. Adult females screamed almost exclusively when approached in 'unacceptable' ways, i.e., by smaller and lower-ranking individuals, suggesting they took into account both the physical and social power of their opponents. This is in line with results from adult chimpanzees, who modify the acoustics of their screams to increase the likelihood of receiving support only if higher-ranking individuals are present in the audience (Slocombe and Zuberbuhler 2007), suggesting a similar but more advanced type of triadic awareness.

Our results were different for juvenile and subadult vervet monkey females, however, who screamed most when approached by bigger and higher-ranking individuals, i.e., in what we considered 'acceptable' conditions. Although it was not possible to evaluate their screaming responses during 'unacceptable' approaches (smaller and lower-ranking individuals) as we never observed approaches under these conditions, they did not react to violation of physical power. One explanation for this somewhat surprising finding is that it may reflect a lack of experience or underdeveloped cognitive skills. Primate screams are thought to have a dual function, both to recruit help (Cheney and Seyfarth 1980) and to directly address and divert the attacker (Owren and Rendall 2001), but this may require more advanced levels of cognitive functioning. Older individuals are expected to be capable of operating within these two functions, but this may not be true for younger individuals who may lack the required social knowledge for a successful use of the recruitment function, that is, an understanding under which social conditions support is likely to be received. Under this hypothesis, juvenile and subadult females mainly deploy screams to avert bigger and higher-ranking opponents, whilst ignoring the screams' potential as a recruitment agent. However, it is difficult to draw firm conclusions from these findings, mainly because we had no data for two of the three conditions of norm violations, i.e., 'social' violations and 'unacceptable' conditions, as approaches by lower-ranking individuals never happened to juvenile and subadult females. In fact, this may be a relevant result demonstrating the importance of social power in females, with individuals never approaching higher-ranking females, regardless of age. Females generally may be more resolute in enforcing and maintaining their social positions via aggression and punishment of individuals that do not adhere to the social norms (Cheney and Seyfarth 1992, Fehr and Fischbacher 2004b).

For the males, we did not include adult data, due to the fact that they maintain a separate hierarchy following dispersal (Cheney and Seyfarth 1992), which prevented us from testing the social violation hypothesis. For subadult males (i.e., prior to emigration), however, we found that subjects protested mostly to social violations, i.e., if approached by lower-ranking individuals of similar size. For juvenile males, in contrast, we found that subjects reacted mostly to physical violations, i.e., if approached by higher-ranking but smaller individuals, thus revealing an interesting transition from reacting to physical to social power. As for the females, these data suggest that detecting social violations requires more experience, or more developed cognitive skills, than detecting physical violations. After their first dispersal, males acquire their own social position in the new group without any support, suggesting they rely more on physical than social power. As juveniles and subadults, however, they can still benefit from their inherited rank, which could explain why they reacted strongly to social violations as subadults in their natal group.

Analysis 2: Modelling data

For the second part of our analysis, we used generalized linear mixed models (GLMM) confirming that subjects' screaming responses were influenced by age, as well as size and rank differences relative to the opponents. Subjects screamed at significantly higher rates towards lower-ranking than higher-ranking opponents, in line with the hypothesis that monkeys vocally protested against violations of social power relations. These screaming rates decreased with an increasing age, with a significant interaction between subject age and size difference. While younger subjects screamed most when approached by bigger individuals, older subjects screamed most when approached by smaller individuals. This is in line with our previous results, which showed that only adult females were able to vocally protest in 'unacceptable' conditions.

Analysis 3: Simulation data

We finally carried out a simulation analysis, in which we compared actual screaming responses with simulated data representing four different reaction types: 1) random screams, 2) reaction to violations of physical power (most screams if approached by smaller individuals), 3) reaction to violations of social power (most screams if approached by lower-ranking individuals) and 4) reaction to violations of both physical and social powers (most screams if approached by smaller and lower-ranking individuals). Here, juvenile and subadult data showed that screaming responses were in line with the hypothesis that disrespect of physical power was most remarkable to them, whereas adult female data suggested that disrespect of social power was most important for this age-sex class.

Alternative explanations

Our study was observational, to the effect that some conditions were under-represented or, as discussed before, simply absent. Also, some encounter types were merely not possible due to ceiling effects (e.g. juveniles were by definition the smallest individuals included in the analyses and hence could never be approached by smaller individuals, in the same way that adult females were the largest individuals that could not be approached by bigger individuals). Due to the categorical nature of the size data in the first analysis, juveniles could have two size classes above them and adults two size classes below them, whereas subadults could only have one. Although a potential caveat of our analysis, it is unlikely to explain the observed functional shift in the use of screams between juveniles and adults. Despite their lack of social knowledge to use screams as a recruitment tool, juveniles probably produced screams when approached by bigger and higher-ranking individuals, whereas adult females probably produced screams as a tool to repel opponents (Owren and Rendall 2001), and thus punish cheaters that are violating social expectations.

In addition to perceived violations of social expectations, it is likely that a number of other factors further affected subjects' screaming behaviour. First, the quantity and quality of food consumed might generate different motivational states in subjects and this may further influence the intensity of the reactions. As already shown in capuchins (Brosnan and De Waal 2003), vervet monkeys may also show higher rates of vocal protest if high-value food items are potentially available. High-ranking male chimpanzees also produce more pant-hoots than low-ranking ones (Mitani and Nishida 1993), suggesting that individual ranks might be another factor influencing screaming responses. Similarly, social rank might influence vocal protest in vervet monkeys as higher-ranking individuals might have to deal more often with violation of social power than lower-ranking ones (due to a higher number of individuals being lower-ranking than themselves compared to low-ranking individuals). Furthermore, high-ranking signallers usually receive more support than lower-ranking ones upon screaming (Borgeaud and Bshary 2015). Finally, we could also expect relatedness to influence their vocal protest, with subjects screaming less when approached by kin than when approached by unrelated individuals due to increased tolerance towards kin around food resources, independently of their age, size or respective rank (Smith 1964).

5.5 Conclusion

Using three different analysis strategies, results consistently showed the importance of three predictors: subject age, size difference and social rank difference between interacting individuals. Screaming decreased with age, and we found age-sex differences in how individuals deployed this vocal signal across different conditions. While juvenile females screamed when approached by bigger and higher-ranking individuals (‘acceptable’), juvenile males screamed most when physical power was violated (i.e., when approached by smaller individuals). However, subadult males reacted mainly to violations of social power (i.e., when approached by lower-ranking individuals). Finally, adult females reacted to violations of both physical and social powers, i.e., when approached by smaller and lower-ranking individuals. Our results further suggest a dual function in vervet monkey screams, with juveniles mainly screaming due to their potentially high arousal states when approached by powerful individuals, which consequently help to receive support from relatives, and adults most likely screaming for the purpose of directly repelling their opponents and advertising readiness to escalate an aggressive interaction if norms are violated. Furthermore, our results suggest an early understanding of social expectations, as individuals reacted at an early age to violations of physical power. Time and experience, however, seem needed to develop cognitive skills that allow older individuals to vocally protest when social power, a knowledgeable feature of opponents, is also violated.

5.6 Materials and Methods

5.6.1 Experimental Design

Study site and species

The study took place at the Inkawu Vervet Project, located in the Mawana Game Reserve, a private farm of 12’000 hectares in KwaZulu-Natal, South Africa (S28°00.327; E031°12.348). Subjects were 231 individuals (N = 30 adult females and N = 201 juveniles, from which 27 females became adults during the study period) belonging to three groups of vervet monkeys (AK: N=62 individuals; N=14 matrilines; BD: N=88 individuals, N=24 matrilines; NH: N=81 individuals; N=9 matrilines; see Table S1). Although group size varied due to births, deaths and dispersals, all groups contained multiple males (defined as adults when reaching average full body size at around 5.69kg in their sixth year; Turner, Schmitt et al. 2018), females (defined as adults when reaching average full body size at around 4.09kg in their fifth year; Turner, Schmitt et al. 2018), subadults (three to four years old females and four to five years old males), juveniles (one to two years old females and one to three years old males), and infants (less than one year old). We excluded adult males from analyses, due to the fact that they maintain a separate hierarchy (Cheney and Seyfarth 1992), and infants, due to the fact that they are dependent on their mothers.

Data collection

We used ad libitum, scan and focal long-term data (Altmann 1974) in all three groups collected by a large number of observers (N=116) over a period of seven years (9th November 2010 - 9th February 2018; Altmann 1974). Inter-observer reliability was ensured by each observer obtaining reliability training to collect long-term data by the project manager or a senior researcher. This included both faultless identification of individuals and reliability tests for behavioural data.

Ethical note

All animals have been fully habituated to the presence of human observers and did not show any signs of disturbance related to researchers. We used standard data collection methods for behavioural data (Altmann 1974). Field experiments consisted of providing artificial feeding opportunities, which was carried out in accordance with the ethical ASAB/ABS guidelines for the use of animals in research. Local permission was given by Ezemvelo KZN Wildlife, the governmental organisation in charge of Kwa-Zulu Natal wildlife conservation and biodiversity.

Dyadic interactions

We described dyadic interactions performed by individuals actively approaching subjects using four types. First, individuals can approach subjects without performing any other aggressive behaviours (Approach). Second, they can approach in aggressive ways using mild aggressive behaviours such as staring, producing aggressive vocalisations (barks) or attacking their opponents (Mild). Third, they can chase their targets by running after them while potentially also performing other aggressive behaviours (Chase). Finally, they can approach in aggressive ways using severe aggressive behaviours involving physical contacts such as biting, fighting, grabbing or hitting, also potentially chasing them or performing other aggressive behaviours (Severe).

Aggression data

Out of the 15,635 dyadic interactions, 11,401 composed the fight data set as they were clearly aggressive (removing 3,849 non-aggressive approaches, composing the approach data set and 385 cases in which information was missing). In order to calculate the social ranks of all individuals from a group, we excluded all cases for which we did not have clear outcomes, i.e., interactions in which we did not have clear winners (defined as the most aggressive individuals in an interaction) or clear losers (defined as the most submissive ones, usually ending up conflicts by moving away from aggressors; N = 40). Therefore, we used 11,361 agonistic interactions to calculate the yearly I&SI rank-order of all adult females using the Elo-Rating package for R (Neumann and Kulik 2014; see S2 for detailed protocols). As common in primates, and especially suggested in vervet monkeys (Cheney and Seyfarth 1992), we assumed that juveniles took similar rank as their mother, with the younger sibling within a matriline having the highest rank. Following recent recommendations (Newton-Fisher 2017), we included prior knowledge by adapting initial values for all new matrilines to give new adult females the rank just below their mother, using the average Elo-score of their mother and the next adult female in the hierarchy. Furthermore, we also varied the outcomes of win-loss interactions according to conflict intensity using different K values for displace, mild aggression, chase or severe aggression (see S2 for more details). Consequently, we allocated social ranks to all offspring belonging to a matriline, from the highest-ranking matriline to the lowest-ranking one, excluding adult males as they have a separate hierarchy based mainly on their fighting abilities (Cheney and Seyfarth 1992).

Approach data

We collected 3,849 approaches in which we did not observe any other sign of aggressiveness than individuals merely approaching subjects. However, we restricted this data set to feeding contexts (excluding N = 1,812 data), both when individuals were naturally feeding and when they were feeding during experiments involving high-quality food items such as corn or apples. This allowed us to create specific competitive situations where subjects occupied feeding were being approached by individuals, thus facilitating the investigation of their vocal responses when approached by other group members of different size and social rank. We removed all interactions occurring in 2010 as we did not have enough interactions for this year to allow good estimation of their social rank order since data collection started in November (N = 13). Although we used results from genetic analyses performed by other researchers to confirm relatedness between some individuals (Eichenberger 2017), we had to exclude 318 data from 15 individuals of unknown mothers (N = 30 interactions from six individuals in AK; N = 150 interactions from six individuals in BD & N = 138 interactions from three individuals in NH). We also restricted our data set to adult females and their juveniles to investigate the influence of females' hierarchy, thus excluding adult males including young immigrants (N = 542 interactions) and infants (N = 36 interactions; Figshare).

Number of approaches and scream proportions

In order to get an overall view of the occurrence of approaches and screaming responses from subjects, we separated these 1,128 non-aggressive approaches into four conditions (Table 2) according to violations of social expectations when subjects were approached by: 1) bigger and higher-ranking individuals ('Acceptable' as following 'normal' social expectations), 2) smaller and higher-ranking individuals (violation of subjects' physical power as bigger individuals should have better access over food resources than smaller ones), 3) similar size and lower-ranking individuals (violation of subjects' social power as higher-ranking individuals should have better access over food resources than lower-ranking ones), and 4) smaller and lower-ranking individuals ('Unacceptable' as violating both subjects' physical and social power). We thus excluded here all approaches that did not fall into one of these four conditions (N = 617) to keep clear and interpretable situations. As subjects' age and sex might influence their screaming responses, we also examined how the number of approaches and scream proportions of subjects varied between juvenile males and females, subadult males and females and adult females.

Table 2. Description of the four conditions describing the type of approaches.

Approaches	Description	Initiators characteristics
Acceptable	Approaches following 'normal' social expectations	Bigger and higher-ranking
Physical power	Approaches violating subjects' physical power	Smaller and higher-ranking
Social power	Approaches violating subjects' social power	Similar size and lower-ranking
Unacceptable	Approaches violating both physical and social powers	Smaller and lower-ranking

Simulations

In order to test four functional hypotheses explaining why vervet monkeys screamed while being approached by different individuals when feeding, we created a life history of a random but realistic group of vervet monkeys similar to our population (see S3 for further details) and we simulated four data sets representing their screaming behaviour in four specific conditions described in the supplements.

5.6.2 Statistical analyses

Number of approaches and scream proportions

We used four conditions of approaches (Table 2) to examine the frequency of different types of approaches as well as the corresponding subjects' screaming proportions according to violations of social expectations. We used Fisher's exact tests for count data to examine whether the number of approaches differed according to the types of approaches and proportion tests to examine whether the screaming proportions of subjects differed according to the types of approaches. We also used proportion tests to investigate differences between female and male subjects, as well as between subjects of different age classes.

Influence of size and social rank differences

We analysed 1,128 approaches from 108 initiators and 147 subjects of all age-sex classes (excluding adult males and infants) to investigate the influence of size and social rank differences on the screaming responses of subjects. In addition to using the age and sex of subjects, we added age difference between interacting individuals and used that as proxy of body sizes. Females giving birth once a year to juveniles that are growing regularly until reaching adulthood (Cheney and Seyfarth 1992, Turner, Schmitt et al. 2018), we assumed that similar aged individuals were also of similar sizes, with older individuals thus being bigger (except for all adult females having similar sizes) and younger individuals being smaller (except for all infants having similar sizes but being excluded). This allowed us to add their size difference (using categories: smaller, similar or bigger). We also added their social rank difference using the rank numbers defined by the I&SI method previously described (see S1 & S2). We defined subjects as higher-ranking than initiators if their rank difference was positive (alpha individual getting the rank number one), and lower-ranking if it was negative. Please note that since we gave every individual a specific social rank according to their place within matrilines, individuals could not have the same rank. Finally, we added the predictor of interest for this study, i.e., whether subjects produced at least one scream during those dyadic approaches (Figshare).

We used a generalized linear mixed model fitted by maximum likelihood (Laplace Approximation, GLMM: Kuznetsova, Brockhoff et al. 2015) with a binomial error structure and logit-link function. We used the screaming response of subjects as a response variable, that is, whether they produced at least one scream or not (categorical, Yes = 1/No = 0). We added four predictor variables describing individual features of subjects (age using continuous variable and sex using categorical variable, male/female), as well as dyadic characteristics (size difference using three categories: smaller/similar/bigger and social rank difference using two categories: lower/higher-ranking; Figshare), and five biologically meaningful interactions (age:size, sex:size, age:rank, sex:rank and size:rank). We included both the identity of subjects and initiators as random intercepts to control for repeated measurements. Then, we used an automatic simplification of the model, which extracted the best model by ranking all possible models according to their AICc and using the averaged coefficients of the 23 best models to get the final model (Figshare). Our full model thus contained three predictors (age, size difference and dyadic rank) and all possible two-way interactions. Although subjects' sex might be an important factor, we unfortunately could not include it as we could not run separate models for female and male subjects due to missing observations (some cases just never happened, e.g. subadult males being approached by smaller or lower-ranking individuals), leading to models that failed to converge. We then checked for homogeneity of the data and the distribution of residuals using graphical analyses of residuals (using bwplots, xyplots, qqplots and binned plots) and checked for outliers. Although graphical analyses of residuals revealed some outliers, we decided not to remove them as they concerned less than five percent of observations. However, to confirm robustness of our results, we performed a bootstrap check of the confidence intervals.

Simulations

We compared the observed screaming responses of subjects with four simulated ones, representing how would vervet monkeys react under four specific conditions: 1) screaming randomly (control), 2) screaming more when approached by smaller initiators (reacting to violations of physical features expectations, size), 3) screaming more when approached by lower-ranking initiators (reacting to violations of social rank expectations, rank) and 4) screaming more when approached by individuals that were both smaller and lower-ranking (violating both physical and social expectations, mixed; Table S7). For that, we combined all screaming responses from subjects of different ages into a data frame and calculated Euclidean distances to compare their similarities, with smaller numbers representing more similar data sets.

All analyses were performed in R version 3.4.2 (Team 2016) using RStudio Version 1.1.447 and ade4 (Dray and Dufour 2007), arm (Gelman, Su et al. 2016), car (Fox and Weisberg 2011), effects (Fox 2003), EloRating (Neumann, Duboscq et al. 2011), lmerTest (Kuznetsova, Brockhoff et al. 2015), and MuMIn packages (Barton 2016).

5.7 Acknowledgments

General: We thank K. van der Walts and his family for permission to conduct research at Mawana Game Reserve, as well as the local managers of the Inkawu Vervet Project, A. Driescher and A. van Blerk. We are grateful to all researchers working at IVP for their help in the field. Ezemvelo KZN Wildlife provided permission to conduct research.

Funding**:** This work was funded by the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013) / ERC grant agreement n° 283871 and the Swiss National Science Foundation (Project 310030_143359). EW was funded by the Swiss National Science Foundation (P300P3_151187, 31003A_159587, and PP00P3_170624) and a Branco Weiss Fellowship - Society in Science.

Author contributions**:**
SM: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Validation, Visualization, Writing – Original draft preparation
MW: Data curation, Validation, Visualization, Writing – Review and Editing
EW: Methodology, Project administration, Funding acquisition, Resources, Writing – Review and Editing
KZ: Supervision, Conceptualization, Methodology, Project administration, Funding acquisition, Writing – Review and Editing

Competing interests**:** The authors declare that there are no competing interests.

Data and materials availability**:** Our data and code will be publicly available upon acceptance on Figshare (https://figshare.com/s/b312309f8ae996a784e9).

5.8 Supplementary materials

S1. Matrilines

Females, being the philopatric sex in vervet monkey, remain in their natal group and form the social core of the group, while males disperse throughout their life in different groups (Cheney and Seyfarth 1992). Each group is composed of several matrilines, defined as an adult female with all her offspring, and several adult males (Table S1). Vervet monkeys give birth to infants once a year (birth season: September to December) that are growing regularly until reaching adulthood. As it was not possible to get real measurements from this wild population, we used age of individuals as a proxy of their body sizes, with all individuals born in the same year having similar sizes. We defined adults as all individuals reaching their full body sizes, i.e., at approximately five years old for females (4.09kg) and six years old for males (5.69kg, Turner, Schmitt et al. 2018). Consequently, we determined new matrilines whenever a female turned five years old, as she reached adult size at this age. However, we also determined new matrilines whenever a female gave birth for her first time even if this later one did not reach five years old yet, as their body sizes following pregnancy were thus comparable to adults' ones.

Table S1. Description of all matrilines from the three studied groups.

Gp	AF	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	Nb of Matrilines	Nb of Offspring
AK	Gaga[1]	Gov	Ghan	Gugu	Giy	Gele	Gagb	Ginq	Ga	X		4	16
	Ghan					Gho	-	Ghid	Gh	X			
	Gugu							Gubh	Gu	Guny	Gud		
	Gele										Godu		
	Ula[1]				Ubu	Unw	X					1	2
	Hamb[1]	Hele	Hlek	Hib	Hwa	Hol	Hama	Hum	X			3	10
	Hele					Hey	-	X					
	Hlek					Hlo	-	Hlu	X				
	Nko[1]			Ndon	Ngu	Nyo	-	Nyan	Nk	Nge	Nak	2	10
	Ndon							Ndi	Ndaw	-	Ndik		
	Isil[1]		Inhl	Ifu	Idwa	Iji	Ilon	Ihl	Is	X		3	10
	Inhl						Inkw	Int	-	X			
	Idwa								Id	X			
	Mamo[1]		Mna	Mvu	Modj	Mun	Mba	Mat	Ma	-	Moya	1	8
BD	Ouli[1]				Ogi	Onb	-	Obe	Oort	-	Obse	1	5
	Prin[1]			Pann	Poe	Piep	Potj	Ples	Puol	X		4	10
	Pann							Pa	Pap	-	Pan		
	Piep										-		
	Potj										Pom		
	Asis[1]			Afr	Akk	Alsi	Aapi	Ass	Add	-	-	1	6
	Haki[1]		Enge	Heer	Haa	Hipp	X					4	10
	Enge							Eina	-	-	-		
	Heer							Hei	Has	Honj	Hee		
	Hipp									Hibi	-		
	Mooi[1]			Miel	Mo	Mevr	-	Mee	X			2	7
	Miel							Mi	Midd	-	Mij		
	Snor[1]		Gese	-	Spo	Siel	-	Safa	-	-	Sari	3	9
	Gese							Gaa	-	-	Gd		
	Siel									Si	Sirk		
	Numb[1]		Namn	Nies	Nok	Nurk	-	Nooi	Nirt	-	Nu	3	9
	Nies							Ni	X				
	Nurk										Nws		
	Riss[1]				Roo	Rak	-	Rede	Rate	-	Rust	1	5
	Kaik[1]		Don	Kie	Koni	Ka	X					1	4

	Dagg[1]			Dwe	-	Da	X					1	2
	Wiet[1]			Wol	Watn	Wur	Wiea	X				1	4
	Bemi[1]					Bul	Be	X				1	2
	Vrou[1]				Vak	Vul	-	X				1	2
NH	Gene[1]			Guy	Gaya	Gar	Gla	Gran	-	Guat	-	2	9
	Gaya								Gala	Gabi	Gan		
	Upps[1]				Ulu	-	Uji	Umt	Ula	-	Ura	1	5
	Xaix[1]			Xox	Xer	Xian	Xala	Xiny	-	X		3	7
	Xian									Xia			
	Xala										Xal		
	Pari[1]		Pret	-	Pue	-	-	-	-	X		2	6
	Pret						Prai	Pro	Pru	-	Pye		
	Zara[1]		Zur	Zee	Zio	Zhe	Zan	-	Zhu	X		1	6
	Bogo[1]			Bras	Bam	Boga	Bos	Bela	Bari	X		2	7
	Bras								Bri	X			
	Troi[1]		Tor	Tun	Tal	Tir	-	Tou	Tro	X		1	6
	Jaka[1]			Jink	Jun	Jill	Jix	Jed	Joha	X		2	8
	Jink							Ji	Jia	X			
	Laus[1]		Lhas	-	Lom	La	X					2	4
	Lhas							Lima	X				
	Roma[1]			Rio	Reva	Rhe	Renn	Riy	Rosl	Raba	Rioj	2	10
	Reva								Rey	-	Rev		
	Yaou[1]					Yoog	-	Ya	X			1	2

[1] *Adult females since the beginning of the study, even if they did not have offspring when the study started (09.11.2010). While a cross (X) indicates that the matriarch died, the dash (-) indicates that she did not have offspring during a specific year. We indicated males with a three letters' code and female with four letters' code. Individuals with two letters were thus unfortunately not sexed before they disappeared. Despite we used genetic data to confirm some of the relatedness between individuals (Eichenberger 2017) especially at the beginning of the study, we excluded 10 juvenile males (not presented in this table) as their mother was not known and we could thus not calculate their social ranks (AK: SMA & Oku; BD: Gro, Ert, Bab, Bin & LSk; NH: Qui, Ist & Neu).*

Although this table shows all the matrilines of the three studied groups over the entire study period, we looked at yearly group composition in order to see its evolution and stability through time (Figshare). This allowed us to extract the age, and thus corresponding body size, of all individuals that grew up during the study period for each year, and to adapt their social ranks according to all individuals present in the group at these specific times (see S2 for methods to calculate their social ranks). However, we decided to look at group composition on the 1st of August, i.e., before the beginning of the birth season, to exclude infants that were dependent from mothers and include all individuals from juveniles that were turning one year old (i.e., when they were already travelling and feeding independently from their mothers) to adults.

1. Ankhase

We used data from 27.01.2011 until 29.11.2017 to extract the yearly average Elo-scores of all adult females initially present in AK (N = 6 females, N = 229 agonistic interactions; Figshare), making sure to create new matrilines whenever a female gave birth for the first time or turned five years old (N = 7: Hele, Ghan, Hlek, Inhl, Gugu, Ndon, Idwa). Despite we used genetic data to confirm some of the relatedness between individuals (Eichenberger 2017) especially at the beginning of the study, we excluded two juvenile males (not presented in this table) as their mother was not known and we could thus not calculate their social ranks (SMA & Oku).

2. Baie Dankie

We used data from 09.10.2010 until 22.01.2018 to extract the yearly average Elo-scores of all adult females initially present in BD (N = 14 females, N = 1015 agonistic interactions; Figshare), making sure to create new matrilines whenever a female gave birth for the first time or turned five years old (N = 9: Aapi, Enge, Gese, Heer, Hipp, Miel, Pann, Potj, Siel). Despite we used genetic data to confirm some of the relatedness between individuals (Eichenberger 2017) especially at the beginning of the study, we excluded five juvenile males (not presented in this table) as their mother was not known and we could thus not calculate their social ranks (Gro, Ert, Bab, Bin & LSk).

3. Noha

We used data from 08.12.2010 until 02.02.2018 to extract the yearly average Elo-scores of all adult females initially present in NH (N = 10 females, N = 890 agonistic interactions; Fighsare), making sure to create new matrilines whenever a female gave birth for the first time or turned five years old (N = 8: Gaya, Jink, Lhas, Pret, Renn, Reva, Xala, Xian). Despite we used genetic data to confirm some of the relatedness between individuals (Eichenberger 2017) especially at the beginning of the study, we excluded three juvenile males (not presented in this table) as their mother was not known and we could thus not calculate their social ranks (Qui, Ist & Neu).

S2. ISI rank order

As female vervet monkeys are known to have stable and linear hierarchy (Cheney and Seyfarth 1992), we used the I&SI method (De Vries 1998) to calculate their social ranks thanks to the Elo-Rating package using R version 0.46 (Neumann, Duboscq et al. 2011, Neumann and Kulik 2014, Newton-Fisher 2017). However, we first verified the linearity index of the hierarchy of each group by using the Landau's index *h* (Table S2), which indicates non-linear hierarchies if $h = 0$ and linear ones if $h = 1$ (Appleby 1983). We also checked whether chance contributed to the apparent linearity by running a statistical X^2 test, which justify arranging members of a group into a rank-order only if the test is significant at $\alpha = 0.05$.

Table S2. Yearly linearity Landau's indexes *h* of each studied group.

Group	Year	Landau's index *h*	X^2 test (p-value)
AK (18.01.11 – 08.02.18)	2011	0.600	0.259
	2012	0.857	0.042
	2013	0.492	0.063
	2014	0.600	0.009
	2015	0.409	0.027
	2016	0.423	0.017
	2017	0.479	0.008
	2018	0.396	0.014
BD (09.11.10 – 09.02.18)	2011	0.257	0.039
	2012	0.349	0.006
	2013	0.419	0.002
	2014	0.435	0.001
	2015	0.271	0.001
	2016	0.271	0.002
	2017	0.269	0.001
	2018	0.206	0.001
NH (11.11.2010 – 08.02.2018)	2011	0.441	0.053
	2012	0.618	0.007
	2013	0.727	0.001
	2014	0.622	0.002
	2015	0.426	0.012
	2016	0.363	0.001
	2017	0.351	0.002
	2018	0.277	0.003

Although three of the results from the χ^2 tests were not significant at $\alpha = 0.05$, we think that this was due to the lack of data for the first year (as we extracted interactions only after few months of data collection). Furthermore, we think that non-significant results could also be due to changes in the group composition following deaths, dispersals or new matrilines as this affected group composition, which in turn influenced the linearity index. However, we think that there is no major issues assuming linear hierarchies in our population and we thus considered our population to follow the well-described general social structure of wild vervet monkeys (Cheney and Seyfarth 1992).

After that, we first determined the yearly rank order between all adult females present within a group by creating win/lose matrices on the 1st of August of each year (excluding 2010 which started in November) using the Elo-rating package (Neumann and Kulik 2014). We appropriated the highest ranks to the alpha female (rank number one). We then determined the rank order of all offspring following the well-established rules that the younger offspring in a matriline gets the highest-rank, due to support obtain from mother (Cheney and Seyfarth 1992). Consequently, we offered the rank number two to the youngest offspring of the alpha female, rank number three to her second youngest offspring, and we did so until all her offspring got a rank number. We next offered the following rank number to the second adult female (determined by the I&SI rank-order), also offering following ranks to her offspring in a similar way, i.e., giving highest rank (corresponding to smaller numbers) to her youngest offspring. Consequently, we offered the last social rank to the older offspring of the lowest-ranking female, with its rank number corresponding to the number of individuals present in the group (excluding adult males as those ones have a separate hierarchy based on their fighting abilities; Cheney and Seyfarth 1992).

To obtain win/lose matrices of all initial adult females (i.e., the ones already present at the beginning of the study), and thus their I&SI rank order, we extracted the Elo-scores using all interactions from the fight dataset and we assigned them a somewhat random starting value of 1000 (no prior knowledge at the beginning of the study, all females being equal). Elo-rating is an interesting tool for that as it recalculates Elo-scores of all females through time, allowing demographic changes to occur (Neumann, Duboscq et al. 2011). However, as we used well-established theories on their social structure, such as daughters inheriting the social position of their mother (Cheney and Seyfarth 1992), we then adapted the initial value of all new adult female when we created new matrilines, to rank them just below their mother (Table S3, Figshare). Consequently, we calculated initial values of all new adult female by averaging the Elo-scores of their mother and the following adult female in the I&SI rank order, extracted the day a new matriline was extracted (either by giving birth for the first time, or when a female was turning five years old within few months).

Table S3. Description of all new matrilines created with initial values of all new adult females.

Group	Individual	Date	Elo-score of mother	Elo-score of next female	Initial value
AK	Hele	15.10.2012	Hamb - 1008	Nkos - 940	974
	Ghan	05.11.2012	Gaga - 1080	Hamb - 1000	1040
	Hlek	23.12.2012	Hamb - 974	Hele - 972	973
	Inhl	18.11.2013	Isil - 594	Mamo - 545	574
	Gugu	01.11.2014	Gaga - 1118	Hlek - 941	1030
	Ndon	06.11.2014	Nkos - 582	Hele - 576	579
	Idwa	18.11.2015	Isil - 251	Mamo - 190	221
	Gele*	01.08.2017	Gugu - 961	Ndon - 460	711
BD	Enge*	12.02.2014	Haki - 1383	Mooi - 1042	1213
	Gese	01.08.2014	Snor 967	Riss - 731	849
	Miel	27.10.2014	Mooi - 952	Riss - 731	842
	Heer*	31.10.2014	Enge - 1090	Gese - 1031	1061
	Pann	03.11.2014	Prin - 1495	Asis - 1488	1492
	Nies	11.11.2014	Numb - 984	Snor - 967	976
	Hipp*	01.11.2016	Heer - 1216	Enge - 1193	1205
	Piep*	18.05.2017	Prin - 1581	Asis - 1519	1550
	Nurk	01.08.2017	Numb - 865	Snor - 841	853
	Siel	01.08.2017	Snor – 841	Miel - 766	804
	Aapi	17.10.2017	Asis - 1590	Hipp - 1493	1542
	Potj*	19.10.2017	Pann - 867	Nurk - 861	864
NH	Lhas	01.11.2013	Laus – 633	Yaou - 519	576
	Pret	19.11.2013	Pari - 1239	Zara - 1163	1201
	Jink	03.11.2014	Jaka - 632	Yaou - 519	576
	Bras	01.08.2015	Bogo - 959	Jink - 942	951
	Gaya	23.10.2015	Gene - 1677	Xaix - 1388	1533
	Reva[1]	23.11.2015	Roma - 346	NA	340
	Xian*	14.11.2016	Upps - 1375	Pret - 1041	1208
	Renn[1]	16.11.2017	Roma - 574	NA	570
	Xala	18.11.2017	Xian - 988	Reva - 682	835

**Individuals for which mothers were not present anymore when they became adults. In this case, we either used the score of the mother on her last day (if <6 months), or we used the score of the closest relative, usually an older sister that had her own matriline. [1] Since the mother of these individuals was the lower-ranking one, we attributed them the rank just below their mother without averaging with another female.*

As suggested by a recent paper on Elo-Rating methods (Newton-Fisher 2017), we also varied the parameter K according to conflict severity using four categories. While non-directed threats included all non-aggressive displaces, directed threats included stares, barks and attacks. In addition, individuals could also chase their opponents while potentially using other aggressive behaviours previously described, or they could escalate conflicts into severe fights including physical contacts such as bite, fight, grab or hit (K values of non-directed threat = 175, directed threat = 200, chase = 225 and fight with physical contacts = 250). We set higher K values for severe fights involving physical contacts in order to take into account higher impacts on the evolution of Elo-scores of interacting partners involved in intense conflicts than lower impacts of milder conflicts.

S3. Simulations

In order to test four functional hypotheses explaining why vervet monkeys scream while being approached by different individuals, we created a life history of a random but realistic group of vervet monkeys similar to our population and we simulated four datasets representing their screaming behaviour in four specific conditions explained hereafter.

Life history

In order to create a group as realistic as possible, we looked at the yearly composition of our three studied groups (on the 1st of August from 2010 until 2017; see S1) and we took the mean number of individuals present in those groups, as well as the average proportion of individuals of different age-sex classes (Tables S4 & S5).

Table S4. Mean number and proportions of individuals from different age classes per group during the entire study period. Individuals were considered to have 0 year old when they were new-borns and adults when they reach five years old for females and six years old for males.

Yearly proportions of individuals per age	0	1	2	3	4	5	Adults	Mean number of individuals per group
2010	22	19	6	5	1	0	46	31
2011	22	17	16	5	4	1	35	38
2012	20	18	14	13	3	1	32	45
2013	10	20	15	15	12	0	29	44
2014	19	8	16	12	11	2	32	54
2015	15	17	8	16	12	1	30	52
2016	8	9	21	10	15	2	34	29
2017	17	7	8	17	9	4	38	33
Mean	17	14	13	12	8	1	35	41
Proportion	0.17	0.14	0.13	0.12	0.08	0.01	0.35	

** Please note that all individuals in column 5 are males, females already being included into adults.*

Table S5. Mean number and proportions of individuals from different age-sex classes per group during the entire study period. Individuals were considered to have 0 year old when they were new-borns and adults when they reach five years old for females and six years old for males.

Yearly proportions of individuals per age/sex classes	0		1		2		3		4		5	Adults	
	F	M	F	M	F	M	F	M	F	M	M	F	M
2010	40	60	56	44	17	83	0	100	0	100	0	77	23
2011	24	76	42	58	56	44	17	83	0	100	100	78	23
2012	33	67	21	79	42	58	53	47	25	75	100	65	35
2013	54	46	35	65	16	84	42	58	50	50	0	71	29
2014	45	55	54	46	35	65	16	84	44	56	100	58	42
2015	56	44	46	54	54	46	32	68	16	84	100	68	32
2016	75	25	56	44	55	45	50	50	33	67	100	70	30
2017	40	60	75	25	56	44	53	47	50	50	100	61	39
Mean	46	54	48	52	41	59	33	67	27	73	100	68	32
Proportion	0.46	0.54	0.48	0.52	0.41	0.59	0.33	0.67	0.27	0.73	1.00	0.68	0.32

** Please note that all individuals in column 5 are males, females already being included into adults.*

Consequently, we used R to create a random but realistic population composed of 41 individuals, including four new-borns (two females and two males; further excluded due to their dependency to their mother), seven one year old (four females and three males), three two years old (two females and one male), five three years old (one female and four males), zero four years old, one subadult (zero female and one male) and 16 adults (10 females and six males; Figshare).

Simulations

In order to test four functional hypotheses explaining why vervet monkeys scream while being approached by different individuals, we created four similar datasets (Table S6) in which we created random interactions between two individuals of our random group, and we specified their screaming behaviour according to the four specific conditions, representing our four hypotheses. We defined individuals actively approaching by walking towards another conspecific as being initiators, represented here using their sex, age and rank. In contrast, we defined individuals being approached while busy feeding at a food patch as being targets, also represented here with their sex, age and rank. We thus investigated the screaming behaviour of targets when approached by initiators of different ages (used as a proxy of body sizes), and different social ranks. Although we first calculated their size and rank differences using numerical variables, we then transformed it into categories (smaller/similar size/bigger and lower-ranking/higher-ranking) to make the interpretation of the analyses easier.

Table S6. Example of a simulated dataset created.

Interaction	Initiators			Targets			SizeDif	Size_dif	RankDif	Rank_dif	Targets' scream
	Sex	Age	Rank	Sex	Age	Rank					
1	M	3	35	M	2	34	1	Smaller	1	Higher	1
2	M	3	11	M	5	22	-2	Bigger	-11	Lower	0
3	M	2	16	M	0	32	2	Smaller	-16	Lower	0
4	M	0	2	F	1	21	-1	Bigger	-19	Lower	0
5	M	1	33	M	4	18	-3	Bigger	15	Higher	0
6	F	0	9	F	6	24	-6	Bigger	-15	Lower	1
7	M	1	33	M	4	18	-3	Bigger	15	Higher	1
8	M	3	11	M	0	2	3	Smaller	9	Higher	1
9	F	6	24	F	6	7	0	Same	17	Higher	0
10	M	0	32	M	2	34	-2	Bigger	-2	Lower	0

This table represents the random screaming behaviour of targets during 10 interactions when approached by initiators of different sizes and ranks (here from the control data, thus representing a random screaming behaviour by targets).

We created those interactions randomly based on the group we also created, but we then specified their screaming behaviour in four specific ways, representing four different functional hypotheses of screams' use (Table S7).

1. Control data

The first simulated dataset actually served as a control since we specified here their screaming behaviour to be random (p = 0.5), calling without any specific patterns.

2. Size data

The second dataset simulated how would a vervet monkey behave if they vocally protest when the physical abilities of targets are not respected. As bigger individuals are stronger, they can use their physical power to get access to food resources. Moreover, vervet monkeys giving birth every year to a new generation of individuals, all individuals born in the same year have similar size, and they keep on growing regularly over the years until they reach their full body sizes at approximately five years old for females (4.09kg) and six years old for males (5.69kg; Turner, Schmitt et al. 2018). Thus, it could be perceived as 'acceptable' if bigger initiators, corresponding to older ones, are approaching targets busy feeding, but it would be 'unacceptable' that smaller ones, due to their younger age, approached. Consequently, we specified targets' screaming behaviour of our random group of vervet monkey to follow this by increasing their proportion of screams produced when initiators are smaller than targets and decreasing it when initiators are bigger (scream probability = 0.75 when size difference is negative vs. p = 0.25 when positive). However, we kept a random screaming behaviour (p = 0.5) for all the interactions in which the target was approached by similar sized initiators.

3. Rank data

The third dataset simulated how would a vervet monkey behave if they vocally protest when the social ranks of targets are not respected. As higher-ranking individuals have easier access to food resources, it could be perceived as 'acceptable' if higher-ranking initiators are approaching targets busy feeding, but it would be 'unacceptable' that lower-ranking ones approach. Consequently, we specified targets' screaming behaviour of our random group to follow this by increasing their proportion of screams produced when initiators are lower-ranking than targets and decreasing it when initiators are higher-ranking (scream probability = 0.75 when rank difference is positive due to higher ranks having smaller numbers vs. p = 0.25 when negative).

4. Mixed data

In the last dataset, we simulated how would a vervet monkey behave if they vocally protest when both physical abilities and social ranks of targets are not respected. If vervet monkeys consider both characteristics, it could be perceived as ‘acceptable’ if bigger and higher-ranking initiators are approaching targets feeding at a food patch (p = 0.05), and also ‘acceptable’ if higher-ranking initiators of the same size are approaching (p = 0.25). However, it would be ‘unacceptable’ that smaller and lower-ranking ones are approaching feeding targets (p = 0.95), and also ‘unacceptable’ if lower-ranking initiators of the same size are approaching (p = 0.75). However, we let the screaming behaviour of targets to be random (p=0.5) whenever targets were approached by bigger but lower-ranking individuals or smaller but higher-ranking ones. Table S7 shows the probabilities of screams used in these four simulated datasets.

Table S7. Description of four datasets used to simulate subjects’ screaming responses.

Simulated data sets	Summary	Description	Screaming probabilities
Control	Random screaming behaviour	Screaming equally in all situations	p = 0.5
Size	Screaming more when the size power is not respected, representing violation of physical power	Screaming more when approached by smaller individuals, less when approached by bigger ones and leaving random screams if individuals have similar size	p = 0.75 when approached by smaller individuals p = 0.25 when approached by bigger individuals p = 0.5 when approached by individuals of similar size
Rank	Screaming more when the social power is not respected, reprensenting violation of social power	Screaming more when approached by lower-ranking individuals, and less when approached by higher-ranking ones. Please not that individuals could not have similar ranks according to the methods used to define their social ranks	p = 0.75 when approached by lower-ranking individuals p = 0.25 when approached by higher-ranking individuals
Mixed	Screaming more when both size and social power are not respected	Screaming more when approached by lower-ranking and smaller or similar sized individuals and less when approached by higher-ranking and bigger or similar sized individuals. However, we used random screaming behaviours when only one power was not respected, such as when approached by lower-ranking but bigger	p = 0.95 when approached by lower-ranking and smaller individuals (‘unacceptable’) p = 0.75 when approached by lower-ranking individuals of similar size (‘social’violation) p = 0.5 when approached by lower-ranking but bigger individuals or by higher-ranking but smaller individuals p = 0.25 when approached by higher-ranking individuals of

		individuals or higher-ranking but smaller ones	similar size (mostly ‘acceptable’) p = 0.05 when approached by higher-ranking and bigger individuals (‘acceptable’)

Euclidean distances

We used correlation matrices created in R with the Euclidean distances method to compare our real data with four simulated datasets (Table S7). Comparing distances of subjects from three age classes (juveniles, subadults and adult females; males being excluded) helped us to investigate which potential factor influenced most screaming responses of subjects, with smaller numbers indicating higher likelihood. Data from juveniles and subadults being closer to the size simulated dataset (smaller numbers: 0.085 and 0.062 respectively) indicate that young individuals react more against violations of physical power as their screaming behaviour were more similar to the one from the size dataset. However, adult females reacted more to violations of social power, with screaming responses being more similar to the one from the simulated rank dataset (0.032).

Table S8. Euclidean distances comparing real and simulated datasets of subjects’ screaming responses. We separated tables for three different age groups; A) juveniles, B) subadults, C) adults (females only)

A

	Control	Size	Rank	Mixed	Real
Control		0.052	0.042	0.031	0.114
Size	0.052		0.061	0.023	0.085
Rank	0.042	0.061		0.052	0.124
Mixed	0.031	0.023	0.052		0.093
Real	0.114	0.085	0.124	0.093	

B

	Control	Size	Rank	Mixed	Real
Control		0.121	0.045	0.067	0.112
Size	0.121		0.112	0.164	0.062
Rank	0.045	0.112		0.077	0.1
Mixed	0.067	0.164	0.077		0.169
Real	0.112	0.062	0.1	0.169	

C

	Control	Size	Rank	Mixed	Real
Control		0.043	0.054	0.003	0.086
Size	0.043		0.011	0.045	0.043
Rank	0.054	0.011		0.057	0.032
Mixed	0.003	0.045	0.057		0.089
Real	0.086	0.043	0.032	0.089	

VI. General discussion

6.1 Summary

The aim of this research was to investigate the social influence on vocal communication in wild vervet monkeys. Despite intensive work on their alarm calls, and on how individuals adapt their calling behaviour and responses according to their social environment in predatory contexts, other call types have been surprisingly neglected. Consequently, I examined how physical and social characteristics of group members affected individuals' vocal behaviour in three distinct situations: during dyadic greetings, in agonistic interactions and when social expectations were violated. In all cases, I found that individuals adjusted their vocal signalling behaviour according to other group members, by targeting individuals of specific age-sex classes, addressing bystanders present in the audience or protesting against specific individuals that do not follow social rules. Results, in line with previous studies, confirm that vervet monkeys possess advanced cognitive skills allowing them to recognise individuals, know their own and others' social position in the group, and adopt behaviours that maximise benefits.

6.2 First chapter: vocal greeting during dyadic encounters

In the first chapter, I used natural observations to describe the general pattern of vocal greetings during close dyadic encounters between group members. I found that vervet monkeys of both sexes grunted, but these calls targeted specifically adult males and were mainly produced in risky areas, such as near rivers where predation risk was presumably high. Results did not support any of the five most common functional hypotheses of greeting behaviour, that is, to signal submission (de Waal 1986), to avoid conflicts (de Waal and Roosmalen 1979), to signal benign intent (Silk, Seyfarth et al. 2016), to test social bonds (Whitham and Maestripieri 2003), or to improve social coordination and cooperation (Senigaglia, de Stephanis et al. 2012). Consequently, I suggested a new function for these calls: to reduce predation risks by alerting competent individuals. Adult males are the most active individuals against predators (Baldellou and Henzi 1992), likely because of their increased size and strength over any individuals from other age-sex classes (Turner, Schmitt et al. 2018). They can mob and chase away dangerous predators, which increases other individuals' survival. Thus, signallers may grunt to increase the attentional state of competent adult males, specifically in situations where predator encounters are high, as a means of decreasing predation risks. This first chapter suggests that vervet monkeys are able to perceive risk levels associated with specific locations, as well as physical characteristics of other group members, which allow them to target specific skilled individuals.

6.3 Second chapter: acoustic analyses of agonistic screams

In the second chapter, I analysed the acoustic structure of screams recorded during agonistic interactions occurring naturally or in relation to experiments involving valuable and contested food items. Similarly to chimpanzees, I found that screams produced by vervet monkeys involved in conflicts differed in their acoustic structure according to the identity of signallers (Levréro and Mathevon 2013), their social role (Slocombe and Zuberbuhler 2005) and the severity of the conflict (Slocombe and Zuberbuhler 2007). The variation in the acoustic structure was in line with predictions from one group of animal communication theories that focus on the impact of the signals' acoustic structures on behaviour (Morton 1977, Owren and Rendall 2001, Briefer 2012), as victims produced longer and higher-pitched screams than aggressors, and screams produced in severe conflicts had higher entropy than screams emitted during mild conflicts. Differences between screams produced in various contexts were also in line with the potential dual use of screams, that is, individuals calling to recruit help (Gouzoules, Gouzoules et al. 1984) and to repel their opponent (Fedurek, Slocombe et al. 2015b).

Results from this second chapter demonstrated that screams encoded information on signaller identity, social characteristics of other group members and the nature of an ongoing event. This suggests that out-of-sight listeners are able to perceive these acoustic variations, allowing them to recognise individuals involved in conflicts and to use their general social knowledge to respond in appropriate ways, for example, by intervening when close relatives are involved in severe fights (Fugate, Gouzoules et al. 2008).

6.4 Third chapter: using screams as vocal protest against violations of social expectations

In the third chapter, I investigated the extent of vervet monkey cognitive skills, by examining their abilities to recognise and react against individuals that do not follow social expectations. For that, I used three different analyses to examine the vocal reaction of feeding subjects when approached by individuals of different age-sex classes. First, I compared the number of approaches and screaming percentages across four conditions (acceptable, violation of physical power, violation of social power and unacceptable) to see under which conditions subjects of different age-sex classes were more likely to protest. Then, I used generalized linear mixed models (GLMM) to investigate which factors affected subjects screaming responses. Finally, I used Euclidean distances between real and simulated data sets to get further insight in the functional use of screams during approaches by individuals that are not entitled to do so. Results consistently showed the importance of three predictors on calling behaviour: subject age, size difference and social rank difference between the two interacting individuals. Subadults screamed at the highest rates followed by juveniles and adult females, and all individuals screamed at higher rates when approached by lower than higher-ranking individuals. However, there was an interaction effect between subject age and size difference. While juveniles screamed more when approached by bigger and higher-ranking individuals (acceptable), the opposite was true for adult females, who screamed mainly when approached by smaller and lower-ranking individuals (unacceptable). Furthermore, I found that juvenile males reacted more to violations of physical power (i.e., approached by smaller individuals), whereas subadult males reacted more to violations of social power (i.e., approached by lower-ranking individuals). These results suggest that vervet monkeys possess an early understanding of social expectations but time and experience appear needed to fine-tune these skills to react appropriately, especially towards cheaters. Possessing such advanced cognitive skills is highly beneficial as in addition to help maintaining the social position of an individual within a group, it also favours cooperation (Fehr and Gachter 2000).

6.5 Vervet monkeys in studies of vocal communication

Due to their interesting social structure and communication system (Cheney and Seyfarth 1992), vervet monkeys have been extensively studied over the past decades. Although debated (Wheeler and Fischer 2012, Price, Wadewitz et al. 2015), their alarm calls are a classic example of ‘referential signals’ in animal communication, with acoustically distinct vocalisations produced when encountering specific types of predators (Seyfarth, Cheney et al. 1980b). Research has further suggested that vervet monkeys have control over call production, because low-ranking individuals sometimes withhold information concerning the presence of a danger (Cheney and Seyfarth 1985). Moreover, ‘audience effects’ also influenced the alarm calling behaviour of adults, with males calling more in the presence of females than other males, and females increasing call rates in the presence of their offspring compared to other unrelated juveniles (Cheney and Seyfarth 1985). Individuals thus have the ability to adapt their signalling behaviour according to both their ecological and social environments. Consequently, in addition to highlight the sophisticated social knowledge that animals must possess to call adequately according to various situations, this also highlights the importance of including social factors in animal research.

Studying vocal communication is an important tool to get insights into the mind of animals, allowing us to investigate how do they perceive their own world and which underlying cognitive abilities they should possess to behave in appropriate ways. Alarm calls of vervet monkeys being referential signals suggest that they have the abilities to have mental representations of their external world, and to use their knowledge to react in adaptive ways against different threats. Apart from their alarm calls, potential referential signalling has been investigated in their grunts, calls that are produced in various social contexts (Cheney and Seyfarth 1982).

6.6 General pattern and function of grunts in vervet monkeys

The first aim of my thesis was to describe the general pattern of grunt production, restricting data collection to close dyadic encounters (i.e., when a focal was approaching/approached within 5m from a partner). Instead of focussing on their acoustic properties, I examined who called towards whom, and in which context they were more likely to do so. In line with previous work, the social bonds and social rank difference between the two interacting individuals did not influence grunt production, with grunts produced independently of 'friendships' and bi-directionally both towards lower and higher-ranking individuals (Cheney and Seyfarth 1982). Interestingly, however, I found that the sex of the partner was the factor influencing most their call production, with calls targeting specifically adult males, especially in high predation risks areas. Therefore, I proposed that vervet monkeys use grunt strategically to increase the vigilance state of competent adult males against predators (Baldellou and Henzi 1992).

This hypothesis is in accordance with previous work showing individuals grunting when watching individuals crossing open areas that are usually dangerous places for monkeys exposed to predator attacks or when initiating group movement (Cheney and Seyfarth 1982). In both cases, signallers would benefit from reduced predation risks by increasing vigilance state of bystanders and maintaining group cohesion via their grunts. In addition to perceived risk levels associated with specific locations, results from this chapter also suggest that vervet monkeys can use their general social knowledge to exploit the skills of other group members. Instead of grunting towards juveniles that lack experience towards predators and often produce mistakes when alarm calling (Seyfarth and Cheney 1980), signallers targeted experienced adults. Furthermore, they also took into consideration the physical abilities of their targets, by calling almost exclusively towards adult males that are bigger and most suitable to defend signallers against dangerous predators than any other individuals in a group (Baldellou and Henzi 1992).

Interestingly, high-ranking males were more active (by being more vigilant and alarm calling at higher rates) than low-ranking ones, especially during the breeding season (Baldellou and Henzi 1992). Consequently, all individuals seem to benefit from the situation. Individuals grunting towards adult males might benefit from an increased protection against predators, whereas anti-predator behaviours performed by males might increase their reputation and females' willingness to mate with them (Baldellou and Henzi 1992). However, while the greeting behaviour of vervet monkeys seem to follow specific rules that help to increase the fitness of signallers, males might react strategically according to the benefits they might gain. While new immigrants might increase their vigilance state upon receiving grunts during the mating season to get easier access to females, males already established in the group might increase their vigilance state when females are giving birth to increase their inclusive fitness by protecting potential offspring that are highly vulnerable (Cheney and Seyfarth 1981).

Nonetheless, playback experiments are needed to confirm that listeners are indeed more active in their anti-predator behaviours upon hearing conspecific grunting, as demonstrated in wild chimpanzees that produced intentional vocalisations to draw the attention of others (Crockford, Wittig et al. 2015). Comparing the reactions of adult males differing in their social rank and tenure in the group to playback experiments conducted at different time of the year would allow us to see whether males can use complex social strategies to react in ways that maximise their own benefits. Experiments also conducted in different locations would further allow us to investigate whether vervet monkey possess a representational map of the danger present in their territory, with potentially stronger reactions in higher predation risks areas, which would confirm an ability previously demonstrated through behavioural observations of their spatial range use (Willems and Hill 2009).

6.7 Screams: adaptive signals encoding crucial information for listeners

The second aim of my thesis was to examine whether the acoustic structure of agonistic screams vary according to specific information concerning the nature of the ongoing event. In accordance with past studies, I found that screams were individually distinctive, and their acoustic properties varied according to the social role of signallers (aggressors vs. victims) and the severity of the conflict (mild vs. severe; e.g. pigtail macaques: Gouzoules and Gouzoules 1989, chimpanzees: Slocombe and Zuberbuhler 2005, Slocombe and Zuberbuhler 2007, Geoffrey's spider monkeys: Ordóñez-Gómez, Dunn et al. 2015). Results from this second chapter confirmed that call production by vervet monkeys is under voluntary control and can encode specific information that listeners might consider in their decisions to intervene in conflicts.

Due to potential costs related to possible injuries when intervening in fights, bystanders should adapt their support to signallers only if benefits outweigh these costs, such as for example, by intervening only if kin are involved in severe conflicts (Hunte and Horrocks 1987, Fugate, Gouzoules et al. 2008). Consequently, listeners must possess sophisticated skills to recognise individuals through their voice alone, and use their general social knowledge to understand the position of signallers, as well as the quality of their relationships with both opponents and other potential bystanders. Results from playback experiments already demonstrated that adults have the ability to recognize the voice of their (potential) offspring (Cheney and Seyfarth 1980, Hauser 1986). Furthermore, results showed that adult females could also recognise mother-offspring relationships as 'control' females looked at the mother of the juveniles which screams were played back (Cheney and Seyfarth 1980). In addition to confirm individual signatures in their screams, results of my second chapter are the first ones to demonstrate acoustic variation in wild vervet monkey screams according to both social role of signallers and conflict severity, information that might be yet crucial for out-of-sight potential helpers.

Knowing third-party relationships allows individuals to predict which individuals are likely to form coalitions, an important feature to avoid potential risks of injuries due to conflict escalation (Freeman, Young et al. 2016). Consequently, bystanders might possess advanced cognitive skills to look at all individuals present in the vicinity of a conflict, to make some reasoning about which individuals might offer support to which opponent, and to do some calculations on the trade-off between costs and benefits of intervening. Nevertheless, signallers might also increase their own benefits by adapting their screaming production according to the presence and composition of the audience, as shown in white-faced capuchins (Perry, Barrett et al. 2004). Signallers could increase rates of support obtained by screaming more when specific individuals that can potentially offer agonistic support are nearby, such as higher-ranking individuals, kin or closely bonded partners. Consequently, it would be interesting to investigate whether vervet monkeys could, in addition to varying the acoustic properties of their screams, also vary their screams' production according to their social environment.

Despite being rare, rank reversals in vervet monkeys can occur, especially if a higher-ranking matriline is smaller than a lower-ranking but bigger one (Cheney and Seyfarth 1992). As maintaining social positions in the hierarchy is important for whole matrilines, bystanders should react in stronger ways when conflicts do not follow the normal social structure of a group, for example, when a higher-ranking individual is aggressed by a lower-ranking one. Results from playback experiments demonstrated that vervet monkeys indeed reacted in stronger ways when hearing stimuli simulating rank reversals (Borgeaud, van de Waal et al. 2013). By supporting higher-ranking individuals, who are usually aggressors, bystanders help to maintain the hierarchy present within a group by increasing signallers' likelihood of winning the conflict. This probably explained why I found most support to aggressors rather than to victims' screams.

Nonetheless, screams being distinct according to the social role of signallers, I suggested a potential dual use of their screams, in a similar way than wild chimpanzees do (Fedurek, Slocombe et al. 2015b). While victims might scream to recruit help (Hunte and Horrocks 1987), aggressors might use the aversive characteristics of these calls to directly repel their opponent (Owren and Rendall 1997). This suggests that signallers recognise their own position during conflicts and adapt their calling strategy accordingly, by producing distinct screams according to their need in specific situations. However, playback experiments are still missing to confirm: 1) the attribution of signallers' social role by listeners through vocal cues alone, and 2) the multi-functionality of these vocalisations, by for example, showing approaches towards the speaker to support victims busy screaming and movements away from the speaker to retreat from screaming aggressors.

Results from this second chapter might have important implications for future playback experiments. Rank reversals playback experiments commonly use aggression calls to simulate aggressors and screams to simulate victims (e.g. baboons: Bergman, Beehner et al. 2003, vervet monkeys: Borgeaud, van de Waal et al. 2013). However, if listeners perceive distinct victims and aggressors' screams, researchers should select carefully which screams to use as stimuli for their playback experiments, as subjects might otherwise react upon hearing incongruent screams rather than incongruent sequences. This also highlights the importance of running detailed acoustic analyses before conducting experiments.

6.8 Advanced social skills allow individuals to recognise and punish free-riders

The third and last aim of my thesis was to examine vocal protest of vervet monkeys during violations of social expectations. Advanced social skills allow individuals to know their social position within a group, to predict interactions with or between other group members and to behave in socially appropriate ways, potentially punishing individuals that do not follow rules. Vervet monkeys, particularly adult females, have been shown to possess some knowledge of third-party rank relationships (Borgeaud, van de Waal et al. 2013, Borgeaud, Alvino et al. 2015). Such social knowledge, i.e., knowing the dominance rank and friendships of other group members as well as remembering previous interactions, is indeed useful as it allows individuals to have some social expectations. This can be decisive in alliance formations (Seyfarth and Cheney 1984b), in dispersal amongst males (Cheney and Seyfarth 1983), or to make complex decisions such as trading grooming for tolerance (Borgeaud, Schnider et al. 2017).

Social knowledge might help individuals to detect unreliable signals produced by individuals calling inappropriately, and to potentially respond aggressively to punish these free-riders, which favours the production of 'honest signals' (Cheney and Seyfarth 1988). Vervet monkey adult males, being bigger and having better fighting abilities than any other individuals in a group (Turner, Schmitt et al. 2018), are one of the most active individuals in territory defence during aggressive intergroup encounters. In addition to helping protect their potential offspring, adult males also increase their reputations by participating in fights, which increases their mating success (Arseneau, Taucher et al. 2015). Females enforce this behaviour by offering social rewards (grooming) to cooperative males that were active during previous fights (Arseneau-Robar, Taucher et al. 2016). However, if they do not behave as expected, females punish them by being aggressive towards them, which consequently increase their future participation level (Arseneau-Robar, Taucher et al. 2016). Another example of following social rules as appropriate behaviours in a group comes from feeding experiments with four wild groups of vervet monkeys (van de Waal, Borgeaud et al. 2013). Similarly to naïve infants that learnt to forage following the behaviour of their mother (van de Waal, Bshary et al. 2014), new immigrants learnt to forage against their preference in order to follow the local norms of their new group (van de Waal, Borgeaud et al. 2013). In accordance with these studies, results from my last chapter helps to demonstrate that vervet monkeys are aware of certain social rules in a group, and can potentially react aggressively, for example by using complex social strategies (alliance formations) to punish individuals that do not follow the rules.

Furthermore, looking at the reactions of vervet monkeys, especially the ones from young but high-ranking individuals, allow us to get insight into how and when individuals react to violations of social expectations. Despite time and experience seem needed to develop appropriate advanced cognitive skills, all individuals recognised social expectations and reacted to their violations by screaming. However, controlled experiments would be needed to investigate which mechanisms allow young juveniles to acquire these abilities (e.g. what do individuals learn individually and what is socially learned), as well as which socio-ecological factors affect their vocal protest. By investigating the acoustic properties of screams produced during violations of social expectations, we could further investigate whether they can encode information on the dyadic relationship between the two interacting individuals, as shown in other primate species. For example, rhesus monkeys produce distinct screams associated with the dominance rank and matrilineal relatedness of opponents (Gouzoules, Gouzoules et al. 1984), an ability that could also be present in vervet monkeys.

Monitoring what others do and enforcing cooperative behaviours via grooming while punishing non-cooperative ones via aggression (Arseneau-Robar, Taucher et al. 2016), helps to keep stability in a group. Predictable relationships are indeed beneficial for all individuals, as they dictate who should interact with whom (Seyfarth 1980), and help to avoid competition and thus aggression (Struhsaker 1967c). However, if conflicts occur, they also dictate with whom to form alliances and towards whom to redirect aggressions (Cheney and Seyfarth 1989). Furthermore, in-depth understanding of social knowledge in a group also allow individuals to repair relationships after fights via direct reconciliation (between both opponents), simple reconciliation (between one opponent and a kin of the second one) or complex reconciliation (between two relatives of both opponents; Cheney and Seyfarth 1989). Although living in groups can be costly, via increased competition to access valuable resources for example, possessing advanced social and cognitive skills might allow vervet monkeys to balance these costs and live peacefully, benefiting from the public good created by their social life, such as reduced predation risks via the production of distinct alarm calls.

6.9 Future directions

In addition to comparative work on vocal behaviour in primates that would allow us to investigate the evolutionary roots of human language by retracing the origins of specific vocal capacities in the primate lineage, I can see three main lines for future research on animal communication.

Multi-modal signalling

While I focussed on the vocal behaviour of wild vervet monkeys, social environments of individuals might also affect other aspects of their behaviour. A mixture of vocal and non-vocal signals is often used in social lives. For example, multi-modal signals (including facial, vocal, postural, manipulatory and locomotory signals) are used by baboons to assess their relationships during greeting with other group members, and thus negotiate their status without fighting (Colmenares 1990). The fact that results from my first chapter did not support grunt production to signal submission in vervet monkeys could be explained by the use of visual signals by high-ranking males to signal dominance: the ‘Red, White and Blue displays’ (Struhsaker 1967a). In contrast, females might use social rather than vocal behaviour such as grooming, to indicate respect of the hierarchy by preferentially grooming higher-ranking partners (Seyfarth 1980). In a similar way, facial displays during screaming might also convey information to opponents. Victims of aggressive interactions might signal the intensity of conflicts by varying the position of their mouth from partially closed to widely open exposing teeth (Struhsaker 1967a). Furthermore, a study on facial expressions in canids showed that while retracted lips function to appease opponents, protruded ones serve to appear larger and is used in more aggressive contexts (Fox 1970). Consequently, it would be interesting to add other modalities in future studies and investigate under which conditions signals of different modalities are used. Furthermore, researchers could use controlled experiments to examine the efficiency of these different signals by using playback experiments to test vocal signals alone, touchscreen showing soundless videos to test visual signals alone and a combination of both to test the efficiency of multi-modal signals.

Call combinations

The second line of promising future research I can see remains on the vocal channel of animal communication. In a similar way that humans combine a specific set of sounds (words) into endless meaningful sequences (phrases), some animals demonstrated the ability to use different combinatorial mechanisms, which help to increase the complexity of their seemingly fixed vocal repertoire. For example, 12 distinct call combinations produced flexibly using four classes of combinations (e.g. repetitions and mixed call combinations) in various behavioural contexts have been observed in wild meerkats (Collier, Townsend et al. 2017). As similar combinatorial features have been demonstrated in some birds (e.g. pied babblers: Engesser, Ridley et al. 2016) and several primate species (Zuberbühler 2018), these abilities appear to be more common than previously thought. Knowing the interesting social structure of vervet monkeys and their intriguing vocal system, I find it surprising to find so little work on call combinations in vervet monkeys. With the exception of one master student who looked at three types of call sequences in vervet monkeys (distress-aggression, contact-squeak and distress-grunt: Rothacher 2013), I am not aware of any other work on this topic. Consequently, future studies should focus on the combinatorial, as well as compositional capacities of this primate species, which will probably shed light on greater vocal complexity than currently described.

Tactical deception

Finally, as studying vocal communication of animals helps to get a better understanding of their cognitive abilities, future studies focussing on the intentionality of call production can highlight other potential cognitive skills that vervet monkeys might possess. Intentional signalling has mostly been studied in apes' gestural communication (e.g. Tomasello, George et al. 1985, Leavens, Russell et al. 2005, Cartmill and Byrne 2007, Byrne, Cartmill et al. 2017). Despite being very challenging, many scientists worked together to develop an empirical approach to study intentionality in animal communication, which will allow comparative work based on future studies using similar standard methods (Townsend, Koski et al. 2017). Nonetheless, a recent article using both chimpanzees and vervet monkeys as cases studies suggested a new framework in which the authors distinguish between variation within a call type and production of different call types (Schamberg, Wittig et al. 2018). They further suggest that while signallers' arousal generate acoustic variation within a call type, the production of different call types reflect signallers' goals. Consequently, this new framework indirectly implies the presence of goal-orientated communication in most primate species, something that still has to be demonstrated in vervet monkeys.

Tactical deception is a mechanism involving behaviours that must be goal-orientated as individuals need to use specific signals to manipulate the behaviours of listeners to their own benefits. Despite being often anecdotal due to their infrequent use and subtle characteristics, several forms of deceptive tactics have been demonstrated in primates (Whiten and Byrne 1988). In a similar way that tufted capuchin monkeys use false alarm calls to reduce the effects of feeding competition (Wheeler 2009), I observed several times the production of alarm calls in inappropriate contexts. First, I observed once a young low-ranking juvenile alarm calling to a tractor when feeding in a big fruiting tree. Although this was obviously not dangerous for vervet monkeys, the production of alarm calls induced escaping responses with individuals going down to hide in bushes, except for the signaller who remained feeding in the tree. Furthermore, I observed several times an adult male, Arthur, producing leopard alarm calls when involved in conflicts with coalitionary adult females of his own group. Even if I could have potentially missed the dangerous predator walking nearby, the behaviour of this male suggested that he might have use it in a deceptive way. While females involved in the fight stopped targeting Arthur to run up into trees, Arthur remained relaxed on the ground and started auto-grooming. Consequently, these anecdotes suggest that vervet monkeys might possess the cognitive basis necessary for tactical deception, and results from such studies would be promising.

VII. Conclusion

In my thesis, I examined how physical and social characteristics of other group members affected the vocal behaviour of wild vervet monkeys in three distinct situations: during dyadic greetings, in agonistic interactions and when social expectations were violated. In accordance with previous studies demonstrating the presence of audience effects in this species, I found that individuals adjusted their vocal signalling behaviour according to other group members, which can be specific targeted individuals, bystanders present in the audience or their interacting partners. While signallers probably called selfishly to increase their own fitness, by for example reducing their predation risks with grunts targeting specifically protective adult males, their vocalisations encoded specific information on the nature of ongoing events that could also be beneficial to listeners. These acoustic cues might allow bystanders to increase the fitness of both signallers, by intervening when they are involved in severe conflicts, and themselves by increasing kin's survival. Results from my thesis thus suggest that the vocal behaviour of vervet monkeys have probably been favoured through both individual and kin selection. Furthermore, I also demonstrated that individuals recognised both physical, as well as social characteristics of other group members, and had the ability to scream when social expectations were violated. This can be crucial for animals living in group, as following social rules promotes cooperation and helps maintain the social position, not only of one individual, but of a whole matriline. Finally, results from my thesis highlight the importance of taking into account not only the ecological, but also the social environment of individuals in all studies examining animal behaviour.

“Sometimes it's not enough to know what things mean, sometimes you have to know what things don't mean.”

Bob Dylan

VIII. Acknowledgments

First of all, I would like to thank Erica van de Waal, an amazing women, friend, mother and co-supervisor that I had the chance to see growing from PhD student to Professor! In addition to introduced me to her vervet world in 2009 at Loskop Dam Nature Reserve, she also believed in me and showed me that it was feasible to live surrounded by monkeys! I had the chance to be a pioneer of her new project, IVP at Mawana Game Reserve, habituating wild vervet monkeys during my master thesis and coming back later to study them for my PhD thesis. You are a successful example for me!

I would also like to thank Klaus Zuberbühler, my great supervisor who offered me the chance to realise my dream: he paid me to travel in South Africa to run after monkeys in one of the best office I could ever have: the African Savannah! Even if I probably had the hardest time of my life ever during these last years, I would like to thank you for your support, all what you thought me directly or indirectly, and your big trust in me. Thanks to you, I managed successfully big challenges that you gave me such as creating a website, supervising students or developing a new course that I had the chance to teach directly in the field… I loved it! Thanks for all the great times we spent together in the lab and in the field, and the many interesting meetings we had, including all your crazy ideas (e.g. using a drone to scare the monkeys!).

I am very grateful to Oom Kerneels van der Walt and all his family for allowing us to conduct research on their private land, despite they probably still can’t understand why we are so interested in these monkeys! Mawana is a beautiful farm and I’m very glad I could spent more than 3 years of my life there, at Kaya Lami. I’m thankful to all South African people that I had the chance to meet, especially our lovely neighbours that definitely improved my SA stays: Elaine-Ronnie and their whole family, including Tannie Mitzi & Oom Hannes with their goats, horses, dogs, cats, fishes with whom I shared wonderful relaxing times during my days off! Many thanks also to my friends from the WATCH sanctuary Bruce & Sandi, the people from the cyber-café, the paddlers guys and all the interesting people I met at Thangami… thanks for all the delicious ‘braais’, sokkie dances, emotional times such as vervet releases and lovely trips to Sodwana!

However, this work would never have been possible without the help of the whole IVP family, including all the professors involved from the different universities: Redouan Bshary, Carel van Schaik & Andrew Whiten. Special thank to Albert & Arend, managers of IVP, which thought me a lot about fieldwork, how to react with wild (potentially dangerous) animals, poachers or bush fires, and to Barry who showed me how to become a real bush girl with the right spirit! Big thank as well to all volunteers, students, researchers, and visitors that came during my stay! I won’t cite all of them as there are over a hundred people that joined the vervet adventure by now, but I’m very grateful to all of them, especially the ones with whom I shared lots of wonderful times: Erica, Erik, Jean, Simon, Chris, Jenny, Kim, Stuart, Trevor, Jeremiah, Martina, Fui, Aurélie, Coraline, Olivier, Marion, Thomas, Sebastien, Yaëlle, Méli, Sarah, Larissa, Laurien, Lucie, Nicole, Mathieu, Alex, Sofia, Miguel, Franca, Eliane, Anouck, Fabienne, Yannick, Tobias, Jacky, Yvan, Karri, Tracy, Tom, Zach, Laura, Michele, Will, Virginie, Pooja, Denisse, Eve, Alvaro, Severyne, Kelly, Annerie, Hamdah, Jacopo, Rosie, Alessandro, Adam, Zoés and all the others! Special thanks to ‘my’ master students, even if it was a lot of work, I loved the time spent with you and you did a great job, I’m proud of you: Axelle, Laura, Morgane, Emmeline, Jade, Zoé, Manu and Tecla! Big thank also to all bachelor students that trusted me and came to SA to learn how to study wild animals, an adventure I’ll never forget!!!

Many thanks as well to all my lab mates for their help, support, constructive comments, as well as all the great times: Christ of R, Pawel, Claudia, Eloïse, Emilie, Yaëlle, Noémie, Gladez, Julie, Mélissa, Alice, Coco, Rapha, Julian, Adwait, Guillaume and all the others from the lab and other labs including

Dom & Sandra, Radu, Yvonne, Philippe, Rute, Renata, Noa & Zohar with a special thanks for your lovely drawings!

Finally, I would like to thank all my comprehensive beloved friends and family, for their great support and encouragement, and for tolerating me and my passion for primates! Big up to my special ‘monkey man’, who in addition to share my joys, was always there in the hardest times, I’m not sure how I would have done to end up this thesis without you! And to finish, as Erica would say, ‘thank you vervet much’ also to all the lovely fluffy monkeys that by sharing their lives with me, offered me challenging but so rewarding amazing times that I will never forget!

~ ~ ~ My dream became true ~ ~ ~

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