Form and Function of Food-Associated Calling in the Rekambo Community of Chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon

by

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We acknowledge and respect the lək̓ʷəŋən peoples on whose traditional territory the university stands and the Songhees, Esquimalt, and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

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Abstract

An important question in human evolution is when, how, and why did our species develop language. While the gap between human and non-human communication is significant, the cognitive precursors of human language are argued to be rooted in our primate lineage. One of our closest living relatives, chimpanzees (*Pan troglodytes*), offers insight into which communicative capacities emerged before and after hominins diverged from the *Pan* lineage seven to eight million years ago. Chimpanzees possess several short- and long-distance vocalizations that serve a variety of social functions and are emitted in various contexts. Chimpanzee food-associated calls (FACs) are emitted in foraging contexts; however, these vocalizations are only produced for approximately half of all feeding events. Investigating the social and ecological contexts in which FACs are produced can shed light on the functions of these calls. This is in turn can help us understand what chimpanzees are conveying with their vocalizations. This thesis seeks to contribute to the variability in both form and function(s) observed in wild chimpanzees' FACs. This research explores if the FACs of the Rekambo chimpanzee (*Pan troglodytes troglodytes*) community in Loango National Park, Gabon function to attract conspecifics to a food patch; if callers direct FACs toward nearby individuals; and, if FACs function to promote proximity between group members. How fundamental frequency (F0) (the lowest frequency of a given sound measured in hertz (Hz)) of FACs changes over the course of a feeding event is also examined. Lastly, whether FACs function referentially is investigated by testing differences in F0 in relation to food types. Results show that the focal was more likely to food call upon arriving to a feeding event where they fed for longer with at least one other individual, potentially prolonging inter-individual proximity between group members. The F0 of FACs decreased as calling progressed throughout a feeding event, with calls emitted earlier tending to have higher fundamental frequencies than those emitted later on. Overall, these findings support the notion that FACs are influenced by social contexts, and that acoustic variation correlates to arousal. These findings align with results shown in other wild chimpanzee communities, while also providing new insight regarding acoustic properties concerning arousal while feeding. Finally, this work also adds to the growing body of literature that the function(s) of chimpanzee food calls may vary across communities.

Table of Contents

List of Tables

List of Figures

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Chapter 1: Introduction

Communication in Humans and Animals

Communication in non-human animals (hereafter referred to as ‘animals’) has been the focus of considerable scientific research and has been studied across various taxa (Clay et al., 2012; Townsend & Manser, 2013; Zuberbühler, 2017). While animals exhibit a range of sophisticated communicative behaviours, a key distinction between animals and humans is our relatively complex communication that has manifested in what is often considered a uniquely human trait: language (Fedurek & Slocombe, 2011; Townsend & Manser, 2013; Zuberbühler, 2017). With language, humans are able to represent and communicate complex and abstract thoughts, emotions, and concepts. Language enables us to communicate irrespective of modality in that it takes both non-verbal and verbal forms (Fedurek & Slocombe 2011; Fitch, 2000). Sign languages work within the visual-manual modality wherein words and concepts are expressed via manual articulations. These languages have their own grammar as well as lexicon, and are as linguistically complex as spoken languages (Goldin-Meadow & Brentari, 2017). However, much of human communication relies on verbal exchanges (Fedurek & Slocombe, 2011). Therefore, speech, which is the particular auditory-vocal medium humans use to convey language (Fitch, 2000), has been at the center of language evolution research (but see Corballis, 2010; Hewes 1973). The ability to produce speech is dependent on several anatomical and cognitive capacities, and the extent to which they are present in animals is subject to investigation (Evans & Marler, 1995; Zuberbühler, 2017).

Humans’ ability to produce speech is due to our unique vocal tract anatomy. Acoustic energy, or sound, is generated from a sound-producing source (typically the larynx) and then passes through an acoustic filter apparatus (the pharyngeal, oral, and nasal cavities) wherein specific frequencies are blocked, and others pass, eventually through the nostrils and lips to the outside environment where they are emitted as sound (Fitch, 2000; Zuberbühler, 2017). It is this filtering process that is crucial in speech production as this is where formants are modified by rapidly moving one's tongue, lips, and soft palate. It is variation in these formants that give rise to the highly salient features of speech, e.g., the audible differences between words such as 'boot', 'bought', and 'bat' (Fitch, 2000). Thus, configuration of the vocal tract (i.e., pharyngeal, nasal, and oral cavity shape) and, in particular, the position of the larynx, affects variation in the sounds that can be produced. This has overall implications for vocal control and flexibility, as well as acoustic properties (Evans & Marler, 1995; Fitch & Hauser 1995; Zuberbühler, 2017). While the morphology of the sound-producing apparatus is said to be similar across mammals, including humans, a key difference is that the human larynx is positioned lower than that of any non-human primate (hereafter referred to as 'primate'). However, whether this positioning is crucial for producing speech is debated (Zuberbühler, 2017).

Compared to humans, animals exhibit considerably less vocal control (i.e., intentionality and flexibility) over the sounds they are able to produce. For example, many primates have species-typical vocalizations which are used regardless of a particular groups' geographic location or sub-species designation (Fischer & Price, 2017; Price et al., 2014; Zuberbühler, 2017). Moreover, even after extensive teaching attempts, primates are unable to produce human-like speech sounds (Zuberbühler, 2017). It is generally agreed upon that animal communication is constrained by vocal anatomy and a lack of muscular control over anatomical features. Nonetheless, there is mounting evidence to suggest that the cognitive precursors required for speech, and thus language, are to some degree present in animals (Zuberbühler, 2017).

Communication and Social Cognition

Cognitive scientists have focused on social cognition in animals as it can help us understand how, and under what conditions, language evolved (Fedurek & Slocombe, 2011; Townsend & Manser, 2013; Zuberbühler, 2017). Social cognition refers to various mental processes that enable an individual to think about oneself and about others (Frith et al., 2008). The ability to recognize and understand others' mental states, such as desires, beliefs, thoughts, and intentions is central to human social life. This capacity allows for navigation of social relationships as it enables one to interpret, predict, and influence others' behaviour (Krupenye & Call, 2019; Messer & Gonzalez, 2019; Premack & Woodruff, 1978). Communication is an inherently social behaviour as it involves at least two individuals: a signaller and a receiver. Therefore, much of the research investigating social cognition in animals focuses on their communication. The extent to which animals can predict and influence others' behaviour based on communicative signals is indicative of their socio-cognitive capacities.

Theoretical frameworks commonly used to investigate social cognition in animal communication include functional reference and audience effects. Particular attention has been paid to functionally referential signals, which are defined as context-specific signals that function to enable receivers to predict environmental phenomena in the absence of other visual or contextual cues (Clay et al., 2012; Kalan et al., 2015; Macedonia & Evans, 1993). Animal vocalizations have historically been viewed as automatic responses to stimuli and a reflection of signallers' internal states (Clay et al., 2012). However, since the discovery that Vervet monkey alarm calls (to be discussed in more detail below) reference specific predatory threats (Seyfarth et al., 1980), considerable scientific research has been dedicated to assessing if, and to what extent, animals are capable of conveying information regarding external objects or events (Clay et al., 2012; Liebel et al., 2013; Townsend & Manser, 2013).

Macedonia and Evans' (1993) theoretical framework for classifying vocalizations as functionally referential has enabled comparative investigations concerning socio-communicative cognition in animals (Evans & Marler, 1995). According to this framework, for a vocalization to be designated functionally referential it must adhere to specific production and perception criteria. The signal must first possess a distinct acoustic structure and exhibit a tight association between signal production and the response or stimuli it elicits. Second, the signal must elicit an appropriate response from receivers to the extent that receivers respond appropriately to the signal without experiencing the actual event or object the signal is referring to (Clay et al., 2012; Macedonia & Evans, 1993). Observational and playback studies have yielded evidence for functionally referential vocalizations in various species of birds and mammals, such as Japanese great tits, *Parus major minor* (Suzuki, 2014); noisy miners, *Manorina melanocephala* (Cunningham & Magrath, 2017); black-capped chickadees, *Poecile atricapillus* (Templeton et al., 2005); ravens, *Corvus corax* (Bugnyar et al., 2005); meerkats, *Suricata suricatta* (Manser et al., 2001); and Gunnison's prairie dogs, *Cynomys gunnisoni* (Kiriazis & Slobodchikoff, 2006).

Audience effects refers to changes in individual signaling behaviour in relation to the presence of other individuals (Zuberbühler, 2008). Altering one's signal according to who is there to receive it may indicate higher cognitive abilities for two reasons. First, it suggests that senders have volitional control over the signals they produce given that they are sensitive to assessments of the audience. Second, it suggests that signalers may be aware of receivers' mental states, and that their signals have the potential to influence receiver behaviour (Coppinger et al., 2017). Thus, taking one's audience into consideration while signaling raises the possibility that the signaler might also be taking into consideration how the signal may affect a specific receiver's behaviour, and may therefore be strategically emitting the signal (Zuberbühler, 2008). In animals, Evans and Marler (1994) first described audience effects in domestic chickens (*Gallus gallus*) whereby males produced specific calls upon discovering food. Crucially, it was shown that chickens did not automatically call when encountering every food source, and instead called preferentially when hens were present. Audience aware signalling has since been shown in several species including brown-headed cow birds, *Molothrus ater* (White et al., 2002); red-legged partridges, *Alectoris rufa* (Zaccaroni et al., 2013); betta fish, *Betta splendens* (Herb et al., 2003); grey squirrels, *Sciurus carolinensis* (Leaver et al., 2007); and yellow mongooses, *Cynictis penicillata* (le Roux et al., 2008). There is also considerable evidence for functionally referential signals and audience effects in primates.

Functional Reference and Audience Effects in Primates

The gap between human and primate communicative capacities is significant; however, the cognitive precursors of language are argued to be rooted in our primate lineage. Therefore, primatologists are particularly interested in the underlying cognitive mechanisms of primate communication (Townsend & Manser, 2013; Zuberbühler, 2017). Functionally referential vocalizations have been identified for several species of primates in social, predatory, and feeding contexts (Clay et al., 2012; Townsend & Manser, 2013). Regarding social contexts, Gouzoules et al.'s (1984) playback experiments of offspring screams in Rhesus macaques (*Macaca mulatta*) have shown that screams are acoustically distinct depending on the intensity of the aggression being received and the rank of the aggressing individual. Mothers responded more strongly when their offspring's screams indicated severe aggression, as such attacks often result in injury. Mothers also responded more strongly when their offspring were being attacked by low-ranking individuals because these attacks may lead to dominance usurping in macaque matrilineal society, which can have serious implications for future reproductive output. Therefore, Gouzoules et al. (1984) posit that infant screams function referentially in that they enable mothers to make informed decisions about whether to intervene during agonistic interactions based solely on the nature of their infant's scream. Socially oriented functional reference has also been demonstrated in Chacma baboons (*Papio cynocephalus ursinus*). Chacma baboons have two sub-types of grunts: one is produced when females approach mothers of young infants (i.e., 'infant' grunts), and the other at the onset of traveling across an open area (i.e., 'move' grunts). Playback experiments showed that listeners mirrored responses that are typically observed after naturally occurring grunts. That is, when a 'move' grunt was played, listeners were more likely to grunt in response and look toward the open area. When an 'infant' grunt was played, listeners were more likely to look toward the caller and not grunt in response. However, when grunts were played in resting contexts, receivers tended to not respond appropriately according to the type of sub-grunt played. Still, the authors conclude that acoustic differences in Chacma grunts are rudimentarily referential to listeners given that most individuals responded appropriately the majority of the time (Rendall et al., 1999). While there is some evidence supporting functional reference in social situations, much of the evidence for functionally referential communication comes from predator-avoidance contexts (Clay et al., 2012; Townsend & Manser, 2012).

Functionally referential vocalizations in predator contexts serve an alert function and involve distinct alarm calls for different kinds of predators, e.g., aerial or terrestrial. In their seminal study, Seyfarth et al. (1980) identified and recorded three acoustically distinct alarm calls in Vervet monkeys (*Chlorocebus pygerythrus*). Each call corresponded to a specific predatory threat: eagle, snake, or leopard. In carrying out playback experiments with recorded alarm calls, the study found that the recordings elicited appropriate predator avoidance responses from the receiver in the absence of the predator. Upon hearing the eagle alarm call the monkeys looked to the sky, after hearing the snake alarm call the monkeys looked down to the ground, and the leopard alarm call led to the monkeys running into the trees. Evidentially, the Vervets responded as if they themselves had detected the predator. This led the authors to posit that Vervet alarm calls function referentially in that they enable individuals to escape predation. However, it is important to note that additional analyses on these Vervet alarm calls found that the acoustic structures between calls for different predators were not as distinct as they were initially presented to be (Price et al., 2015). Regardless, Seyfarth et al.'s (1980) study served as a catalyst to further investigate referentiality in primate vocalizations. Functionally referential alarm calls have since been suggested in several other species of primates, such as black-fronted titi monkeys, *Callicebus nigrifrons* (Cäsar et al., 2012); Diana monkeys, *Cercopithecus diana* (Zuberbühler et al., 1997); and Campbell's monkeys, *Cercopithecus campbelli* (Zuberbühler, 2002).

Audience effects have been described for several species of primates. Wich and Sterck (2003) have suggested that alarm calls in Thomas langurs (*Presbytis thomasi*) are directed toward an audience. In a playback experiment, the authors showed that individuals alarm-called in response to a model tiger (the predatory threat) in the presence of other group members, but not when they were alone. Audience effects in predation contexts have also been observed in Sooty mangabeys. In an experimental field study, Quintero et al. (2022) showed that individuals who first discovered a snake model called more often when they had not heard another individual call and if socially significant group members were nearby. Moreover, callers remained with the snake until other individuals arrived. The authors suggest that not only were signallers calling to inform others of a predator, but they called to inform specific (i.e., socially important) group members while also intending to influence receivers' behaviour. Evidentially, primates exhibit varying levels of cognitively complex forms of communication. Given their relatedness to humans, significant research is dedicated to better understanding communication in one of our closest living relatives, chimpanzees (*Pan troglodytes*).

Chimpanzee Communication

The first studies on wild chimpanzee behaviour began in the middle of the twentieth century, with their hunting techniques and human-like tool-use behaviours captivating researchers (Goodall, 1986). Field-based and captive studies have since highlighted the crucial role that chimpanzee communication plays in navigating their complex social worlds (Slocombe, 2022). Primatologists have endeavoured to understand the function(s) of their communicative signals, and to uncover both the proximate and ultimate mechanisms behind them. Moreover, because chimpanzees are one of our closest living relatives, they often serve as an extant model of our last common ancestor (hereafter referred to as 'LCA'). Therefore, chimpanzees can provide insight into which communicative capacities were present in the LCA, and what evolutionary changes occurred after hominins diverged from the *Pan* lineage approximately seven to eight million years ago (Langegraber et al., 2012; Zuberbühler, 2017). Cognitive underpinnings, such as whether chimpanzees are able to convey and extract referential information with their communicative signals, and whether their signals are intentional and flexible, as opposed to arousal-based reactions to environmental stimuli, have implications for our understanding of the evolution of social communication and language (Fedurek & Slocombe, 2011; Slocombe et al., 2022; Townsend et al., 2017; Zuberbühler, 2017). Chimpanzees form strong social bonds with group members and possess high levels of social and ecological intelligence. They also exhibit fluid social dynamics which may have conferred a selection pressure for more complex and flexible social relationships along with communication systems to navigate them (Aureli et al., 2008; Slocombe et al., 2010).

Communication, and particularly vocal communication, is crucial in maintaining inter-individual proximity and group cohesiveness in species with more fluid social systems. 'Fission-fusion' describes social dynamics wherein group members 'fission' into smaller subgroups and 'fusion' into larger subgroups according to resource availability, social affiliations, and reproductive strategies (Aureli et al., 2008; Bouchard & Zuberbühler, 2022). Such social dynamics are relatively rare among primates but have been recognized in spider monkeys (*Ateles sp*.), muriquis (*Brachyteles sp*.), bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and humans (*Homo sapiens*) (Aureli et al., 2008). In species which exhibit higher degrees of fission-fusion dynamics, group members are rarely all together at the same time, and therefore may have evolved specialized communicative behaviours to mediate, and maintain contact with, group members.

Chimpanzees exhibit a range of flexible and sophisticated communicative behaviours, including gestural, facial, olfactory, and multimodal signals that are fundamental to navigating the social dynamics of group living (Eckhardt et al., 2015; Liebal et al., 2014). Early studies on chimpanzee communication in the wild focused on what is arguably the most conspicuous chimpanzee vocalization: the pant hoot (discussed in detail below) (Marler & Hobbett, 1975). In captivity, early experiments concluded that chimpanzees could not be taught human-like spoken words (i.e., spoken language). Captive studies did however demonstrate that chimpanzees could learn to communicate non-verbally. The cross-fostered chimpanzee named Washoe was reported to have learned American Sign Language (ASL), and by the end of four years of training had mastered over 100 signs (Gardner & Gardner 1969). Further studies revealed that chimpanzees were capable of learning to communicate via artificial visual systems. The chimpanzee named Lana was taught to use a computer-based lexigram system wherein specific symbols correlated to particular objects or ideas. The study concluded that Lana could differentiate the individual lexigrams, as well as create grammatically correct word sequences and utterances (Rumbaugh, 1977). Given chimpanzees' manual dexterity along with the capacity to learn and apply symbols to communicate with humans, subsequent research focused on non-verbal gestures in wild populations, such as leaf-clipping and other leaf gestures (Badihi et al., 2023; Nishida, 1980) along with the grooming hand-clasp (McGrew & Tutin, 1978). However, due to their generally forested habitats, large territories, and fluid social dynamics, chimpanzees rely heavily on auditory signals to communicate (Aureli et al., 2008; Eckhardt et al., 2015; Fedurek et al., 2014). Therefore, the auditory-vocal domain has since prompted considerable scientific research.

Long-Distance Signals

Both long- and short- distance signals are part of chimpanzees' communicative repertoire. The most conspicuous chimpanzee call is the pant hoot. These complex, multi-component, long-distance vocalizations can be heard up to one kilometer away and are comprised of up to four distinct phases: introduction, build-up, climax, and let-down (Goodall, 1986; Mitani et al. 1992). Pant hoots are emitted in a variety of contexts, including, traveling, foraging, and displaying. These calls generally function to coordinate movement and facilitate cohesion between group members (Kalan & Boesch, 2018; Mitani et al., 1992; Notman & Rendell, 2005), especially among males, who are known to form close social bonds (Fedurek et al., 2014). Pant hoots are also acoustically individually distinctive and therefore serve to announce an individual's presence in an area (Mitani et al., 1992). These vocalizations also exhibit notable inter-population acoustic variation (Crockford et al. 2004; Mitani et al.,1992), thereby suggesting that these species-typical vocalizations are not as genetically or anatomically constrained as once believed. Rather, they show notable flexibility and acoustic variability, suggesting that they may even be subject to vocal learning (Crockford et al., 2004).

Chimpanzees also perform buttress drumming to communicate over long distances. Buttress drumming is when an individual uses their hands and/or feet to drum atop the buttress root of a tree producing non-vocal sounds. Buttress drumming often occurs while chimpanzees are traveling and is at times accompanied by pant-hooting. Like pant hoots, buttress drumming also functions to coordinate group travel and spacing between individuals and shows some acoustic variation between communities (Arcadi et al., 1998).

Together, pant hoots and buttress drumming appear to serve social functions in that they enable chimpanzees to coordinate social behaviours despite being separated from one another. Furthermore, because these signals are often emitted when group members are out of sight, there may be a greater need to convey additional contextual (i.e., social or ecological) information. Integrating acoustic differences into species-typical signals may be a way in which chimpanzees 'fine tune' what it is they are trying to convey. While pant hoots and buttress drumming are not considered functionally referential, they are both flexible and voluntary auditory signals, as they are acoustically variable and produced (or not) in a number of contexts.

Short-Distance Signals

Chimpanzees have an extensive repertoire of short-distance vocalizations, including ‘grunts’, ‘screams’, ‘barks’, and ‘hoos’ (Goodall, 1986). Screams are context-specific in that they are only produced during agonistic encounters. These vocalizations also appear to be sensitive to nearby audiences and serve a recruitment function. Research has shown that callers acoustically alter screams and direct them toward higher-ranked group members to solicit support during agonistic interactions (Slocombe & Zuberbühler, 2007).

‘Waa’ barks, which are also produced during agonistic interactions, have likewise been found to depend on the composition of the audience (Crockford & Boesch, 2003). Both screams and ‘waa’ barks are produced during agonistic encounters; however, screams tend to be directed toward nearby group members to recruit support, whereas ‘waa’ barks are directed toward the aggressor and serve to discourage further aggression. While screams are context-specific in that they are only produced during agnostic encounters, ‘waa’ barks appear to be more flexible as they are emitted in a variety of social and ecological contexts, including, alarm, hunting, intercommunity encounters, as well as during aggressive confrontations (Crockford & Boesch, 2003; Goodall, 1986; Leroux et al., 2023).

Chimpanzees also produce acoustically distinct and context specific ‘travel hoos’. When emitted prior to traveling, these vocalizations appear to serve a recruitment function with group members more likely to join the departure, whereas departures not accompanied by ‘travel hoos’ are less successful in recruiting others to join. Furthermore, ‘travel hoos’ are more likely to be produced in the presence of affiliative group members, suggesting that the calls may be intentionally directed toward socially significant individuals (Gruber and Zuberbühler, 2013).

Evidentially, chimpanzees possess a number of long- and short-distance signals that show some combination of functional reference and audience effects, as well as flexibility. These signals appear to enable chimpanzees to navigate the social dynamics of group living as they function to recruit particular individuals and to promote proximity between affiliative group members (Eckhardt et al., 2015). Signallers may ‘encode’ additional social or ecological information via acoustic variation. Moreover, since signals are acoustically individually distinct (Arcadi et al., 1998) receivers are able to discern *who* is calling and therefore make informed decisions about how to respond. Together, these data suggest that chimpanzee signals are socially motivated, thereby raising the possibility that they may gain social benefits by emitting, and at times acoustically altering, their vocalizations during certain social situations.

Food-Associated Calls

As previously discussed, vocalizations in both affiliative, anti-predation, and agonistic contexts appear to immediately benefit a signaller. The caller may express a desire to travel with an affiliative individual, convey a need for intervention from an ally regarding an agonistic interaction, or alert conspecifics to a predatory threat, thus increasing inclusive fitness (Townsend & Manser, 2012). Calls emitted selectively in certain contexts and targeted toward specific individuals to gain social benefits might represent a certain level of social cognition. However, in foraging contexts, social benefits conferred onto callers are not always immediately apparent.

Food-associated calls (hereafter referred to as ‘FACs’) have been identified in a number of birds and mammals, such as house sparrows, *Passer domesticus* (Elgar, 1986); ravens, *Corvus corax* (Heinrich & Marzluff 1991); naked mole rats, *Heterocephalus glaber* (Judd &

Sherman, 1996); dolphins, *Tursiops truncatus* (Janik, 2000); greater spear-nosed bats, *Phyllostomus hastatus* (Wilkinson & Boughman, 1998); and big brown bats, *Eptesicus fuscus* (Wright, 2014). Multiple species of primates also vocalize when foraging, and FACs have been identified in a number of species, such as Rhesus macaques, *Macaca mulatta* (Hauser & Marler, 1993a); spider monkeys, *Ateles geoffroyi* (Chapman & Lefebvre, 1990); capuchins, *Cebus apella nigritus* (Di Bitetti, 2003); and tamarins, *Saguinus labiatus* (Caine et al., 1995). These acoustically distinct vocalizations are emitted upon discovering, and while consuming, food (Kalan & Boesch, 2015; Goodall, 1986). FACs often function to attract conspecifics to a feeding patch, leading to larger feeding parties, which may in turn result in increased competition over valuable food resources (Chapman et al., 1995). However, in order to be evolutionarily stable, there must ultimately be benefits in attracting conspecifics to a feeding event that outweigh potential costs of increased resource competition (Fedurek & Slocombe, 2013; Kalan & Boesch, 2015; Slocombe et al., 2010).

Reciprocal Altruism

Reciprocal altruism is one theory that has been posited to explain the evolution of FACs. Trivers (1971) first proposed the theory of reciprocal altruism to explain cooperative behaviours between non-related individuals. The theory can be understood as a form of conditional cooperation wherein altruistic behaviours will be favoured by selection, but only if individuals engage with reciprocating individuals. A key aspect of reciprocal altruism is that the actor must incur a cost when conferring the benefit onto the recipient. Another crucial feature of reciprocal altruism is that individuals do not necessarily cooperate for immediate gain. Rather, there is a delay from the time the actor incurs the cost to the time they receive their benefit (Schino &

Aureli, 2009). However, over time, as partners take turns giving and receiving fitness benefits, these exchanges will directly benefit both partners. Importantly, both partners must interact repeatedly and change roles (i.e., swap actor and recipient roles), as well as be able to discriminate against nonreciprocating individuals (Gomes & Boesch, 2011; Schino & Aureli, 2010.

Several mechanisms have been proposed by which FACs may qualify as a form of reciprocal altruism. Benefits gained by a caller may include increased vigilance and protection from predators (Caine et al., 1995; Elgar, 1986); increased defence of resources and territory from other groups or species (Heinrich & Marzluff, 1991; Wilkinson & Boughman, 1998); increased effectiveness in exploiting food resources (Chapman & Lefebvre, 1990); and kin selection, wherein the caller primarily benefits their kin, thus indirectly improving the caller's own fitness (Hauser & Marler, 1993a). There is even evidence suggesting that failure to produce FACs may result in punishment, and therefore be maladaptive. A study on Rhesus macaques (*Macaca mulatta*) found that individuals who did not call upon discovering a food source were subjected to increased rates of aggression from group members (Hauser & Marler, 1993b). Similarly, it has been documented that a dominant female spider monkey (*Ateles geoffroyi*) chased a subordinate female upon discovering her eating at a large fruit tree while not food calling. Conversely, on another occasion when the subordinate female had been calling while eating, the dominant female was not aggressive toward her (Chapman & Lefebvre, 1990). At first glance, FACs are a seemingly costly behaviour in that they advertise and attract group members to food sources. However, short term costs associated with increased feeding competition may eventually be offset by longer-term social and fitness benefits acquired by food sharing.

Functional Reference, Audience Effects, and Recruitment in Primate FACS

Evidence supporting functional reference, recruitment, and audience effects in primate FACs is mixed but compelling. Using recordings of FACs, Kitzmann and Caine (2009), carried out playback experiments on Geoffroy's marmosets (*Callithrix geoffroyi*). Their study found that recorded FACs elicited higher rates of food-related behaviours than control playbacks, suggesting that receivers perceive these calls to be meaningful. In a natural foraging context, Chapman and Lefebvre (1990) found that wild spider monkeys' (*Ateles geoffroyi*) FACs functioned to attract conspecifics to a food patch. Moreover, the study found that high-ranking individuals were more likely to call, and call more frequently, when fruiting trees were large and when fruit was more abundant, suggesting that FACs function to modulate feeding-group size and minimize feeding competition.

Among non-chimpanzee great apes, FACs have been identified in gorillas and bonobos. Miglietta et al. (2021) found that FAC production in western gorillas' (*Gorilla gorilla*) was influenced by both ecological and social factors. Individuals were more likely to call when foraging on high quality foods and when food was abundant, suggesting that FACs function referentially in that they convey information about food quality and quantity. In terms of social contexts, adult females were more likely to food call, and call more, when silverbacks and offspring were not visually present. Notably, adult female FAC production had a positive effect on silverbacks and offspring joining the food patch. Therefore, the authors suggest that in addition to gorilla FACs serving a general recruitment function, they also specifically influence the recruitment of kin audience members.

Regarding bonobos (*Pan paniscus*), Clay and Zuberbühler's (2009) study demonstrated that during feeding contexts individuals produce complex call sequences composed of five distinct call types: barks, peeps, peep-yelps, yelps, and grunts. Their study found that call sequences were meaningful in that they were significantly associated with the preference for a specific type of food. Barks were almost exclusively produced for highly preferred foods; peeps were produced in higher proportions for more highly preferred foods than for medium- or low-preference foods; and peep-yelps were emitted regardless of food preference. For grunts and yelps, analyses showed a trend of increased production with decreased food preference; however, these results were not significant. While social factors, such as audience composition and receiver responses, were not investigated in this study, bonobo FACs nevertheless appear to convey information regarding food preference and quality. While the authors found acoustic variability according to food-type preference, whether such signals prompt appropriate receiver responses is still unknown.

There is mounting evidence to support the claim that primate FACs function referentially and that call production is sensitive to nearby audiences. However, whether the underlying mechanisms of these communicative exchanges are as cognitively advanced as some might suggest is debated. It has been argued that receivers reliably associating signals with specific behaviours or outcomes does not necessitate mental-state attribution (i.e., recognizing and understanding others’ mental states, such as desires, beliefs, thoughts, and intentions) or higher-order intentionality whereby signallers and receivers are aware of each other’s intentional states. Instead, it has been suggested that such signals should be regarded as goal-directed behaviour involving simple one-to-one mapping (i.e., a sound to a referent) wherein signallers consider the way in which receivers respond to signals, and receivers refer to the signal to predict signaller behaviour (Fischer & Price, 2017). Thus, it is still disputed if animals, including primates, signal with the intention to inform specific individuals about environmental phenomena (but see

Townsend et al. 2017), or if such behaviour is hardwired or simply conditioned via repeated exposure over time (Zuberbühler, 2008).

Chapter 2: Chimpanzee Food-Associated Calls

Chimpanzee Food-Associated Calls

When approaching and consuming food, chimpanzees produce acoustically distinct and highly variable vocalizations that are most often produced by males, are short in duration, and are often emitted in bouts (i.e., several one after the other) (Goodall, 1986). Chimpanzees also sometimes produced these vocalizations in combination with longer-distance pant hoots (Leroux et al., 2021). FACs are individually distinctive and are only produced for approximately half of all feeding events, suggesting they are not solely an emotional or physiological response to the presence of food (Kalan et al., 2015; Slocombe, et al., 2010).

Chimpanzee FACs adhere to Macedonia and Evans' (1993) context-specificity rule as they are produced only while foraging, thus fulfilling one important criterion of functionally referential signals (Marler, 1976). At the same time, chimpanzee food calls exhibit notable variation in acoustic structure as they grade from low-pitched grunts to high-pitched barks (Goodall, 1986). This is important given that acoustic properties are known to correlate with internal states. Particular attention has been paid to fundamental frequency (F0), which is the lowest frequency of a given sound and is measured in hertz (Hz) (i.e., the number of oscillations per second). F0 is considered an indicator of arousal with lower frequencies associated with hostility and aggression, and higher frequencies with fear or appeasement (Morton, 1977). Thus, by measuring the F0 of a given vocalization, researchers can infer the state of arousal of a signaller. Moreover, F0 is a component of pitch, and is a main factor contributing to the perceived pitch of a vocalization. That is, receivers tend to perceive calls with higher F0s as higher pitched, and perceive calls with lower F0s as lower pitched (Taylor et al., 2016). From an ecological perspective, the acoustic structure of FACs has been shown to vary according to the type, quantity, and quality of food, with more highly preferred foods, such as fruit, showing higher mean frequencies (Kalan et al., 2015; Slocombe & Zuberbühler, 2005). Acoustic properties also appear to correspond with tree size. It has been shown that higher pitch calls are emitted for smaller trees, suggesting that higher pitch may be associated with more intense feeding competition. In fact, receivers tended to join feeding events wherein lower pitch calls were produced as opposed to higher pitch calls, thereby suggesting that receivers can infer food quantity from individual FACs (Kalan et al., 2015).

Chimpanzees are capable of acoustically modifying food calls in relation to social and ecological contexts. However, whether these vocalizations are intentionally modified or a reflection of internal emotional states is difficult to determine, especially in non-invasive studies on wild populations. Regardless, information pertaining to ecological contexts and emotional states can still be important for a receiver when making social decisions. For example, if a highly preferred food item elicits higher frequency calls, receivers may be alerted to a feeding event while also receiving reassurance that senders' intentions are not hostile or aggressive. However, whether FACs elicit appropriate responses from receivers, thereby fulfilling the second criterion for functional reference, remains debated. Additional research is needed to better understand the function(s) of these calls from both sender and receiver perspectives, while also looking at how acoustic properties vary according to social and ecological contexts.

Referentiality, Recruitment, Audience Effects, and Feeding Coordination in Chimpanzee FACs

Three key hypotheses have been proposed to better understand the function(s) of chimpanzee FACs and whether these vocalizations are referential to listeners: the "Recruitment hypothesis", the "Audience Effects hypothesis", and the "Feeding Coordination hypothesis". The recruitment hypothesis posits that a call should attract other group members while also conferring a fitness benefit onto the caller (Heinrich & Marzluff, 1991). The audience effects hypothesis refers to changes in signalling behaviour due to the presence of other individuals and posits that individuals direct calls toward particular group members (Zuberbühler, 2008). The feeding coordination hypothesis builds on these and suggests that FACs function to coordinate feeding behaviours and promote proximity between affiliative group members (Fedurek & Slocombe, 2013). These hypotheses are not mutually exclusive and research on both captive and wild chimpanzees has yielded mixed, and at times overlapping, support for these hypotheses. Nonetheless, each study furthers our understanding of how these calls function in, and across various, chimpanzee communities.

Functionally referential food calls have been suggested in captive and wild chimpanzees. In a study comparing food call structure between captive and wild groups, Slocombe & Zuberbühler (2006) showed that the FACs of chimpanzees in the Sonso community of the Budongo Forest in Uganda varied according to food preference. Similar results were obtained when calls were compared to those of captive chimpanzees. However, unlike the wild chimpanzees, captive individuals also exhibited acoustic variation in relation to different types of highly preferred foods. With an experimental playback study in captive chimpanzees, Slocombe & Zuberbühler (2005) found that food calls varied acoustically depending on the type of food (bread or apples). Upon playing recorded FACs, one individual also adjusted their foraging behaviour in accordance with the type of food being referenced in the call. Specifically, after hearing the ‘bread’ call, the individual began to search, and searched for longer, around the bread feeding “tree”. The authors concluded that acoustic differences in chimpanzee FACs are meaningful to listeners. However, there are limitations to this study. Only a single individual was found to extract information from the call to guide their foraging behaviour. This study was also carried out in a captive setting devoid of chimpanzees' natural foraging, and thus social, environment. With stable and predictable food sources in captivity, the costs and potential social benefits of food calling become less salient, thereby calling into question the motivation behind, and intentionality of, these calls. In studying chimpanzees in the Taï forest of Côte d'Ivoire, Kalan et al. (2015) found that FACs varied acoustically in accordance with not only the species of fruit, but also the size of the tree. The results suggest that FACs in wild chimpanzees may function referentially as they convey the type and amount of food available. Moreover, this study illustrated the value of natural foraging contexts in investigating functionally referential communication. In all, evidence for functionally referential food calling in captive and wild chimpanzees is somewhat limited, but intriguing.

Evidence from wild studies support both recruitment and audience effects in chimpanzee FACs. Kalan and Boesch (2015) found that Taï chimpanzee FACs functioned to recruit conspecifics to a food patch. Calls were significantly more likely to attract nearby, but out of sight, individuals to fruit-specific feeding events, thus supporting the recruitment hypothesis. Other studies have yielded somewhat limited evidence that chimpanzee FACs recruit group members to a feeding event, but this may be attributed to the way in which field data was collected. Kalan and Boesch's (2015) study is unique in that their analysis took into account group members who were nearby but out of sight. Conversely, other field studies did not explicitly test for recruitment of nearby individuals, as only individuals who were visually present were included in their analyses.

Fedurek and Slocombe's (2013) study on the Kanyawara community in Kibale National Park, Uganda found that male chimpanzees were more likely to emit FACs when affiliative group members were in visual proximity. This supports the hypothesis that food calls function to initiate cofeeding between socially significant individuals who are already present, thereby suggesting that chimpanzees take audience members into consideration. Audience effects have also been reported for Sonso chimpanzees. Slocombe et al. (2010) found that Sonso males were more likely to produce FACs when already feeding with other group members. Specifically, males were more likely to call in the presence of long-term grooming partners, thereby suggesting that the calls were not emitted to attract group members, but instead to nurture existing social bonds. Bouchard and Zuberbühler (2022) report that low-ranked Sonso males were more likely to call after high-ranked males arrived at a feeding event, also suggesting that FACs did not recruit group members. Rather, the authors interpret this as evidence for audience effects and that FACs serve to mediate potential feeding competition between low- and high-ranking males.

Considerable evidence suggests that audience effects pertain to male group members. Specifically, food calls appear to be targeted toward socially significant males. Kanyawara and Sonso males were more likely to food call when affiliative males were present (Fedurek & Slocombe, 2013; Slocombe et al., 2010). Similarly, Taï males were more likely to emit FACs when affiliative males were nearby (Kalan & Boesch, 2015). Moreover, Fedurek and Slocombe (2013) found that when Kanyawara males produced FACs, male party members fed together for longer durations. Male feeding partners were also more likely to remain until the end of the feeding event if the focal individual food-called. These results support the feeding coordination hypothesis as they suggest that FACs signal to individuals the initiation or prolongation of a feeding event, and ultimately coordinate feeding activity. While FACs seem to be dependent on male social relationships, rank and female sexual receptivity also appear to affect FAC production. Kalan and Boesch (2015) report that high-ranking Taï males were more likely to food call when estrous females were nearby and were often successful in attracting those females to the feeding event. It was also reported that calling males tended to copulate with those females either before, during, or after the feeding event, although this was not statistically tested.

Overall, FACs are highly dependent on social contexts. However, ecological factors such as food type and the size of the food patch also appear to influence FAC production. Kanyawara and Taï chimpanzees called more often for fruit (Fedurek & Slocombe, 2013; Kalan & Boesch, 2015), and Sonso chimpanzees called more when encountering larger feeding patches (Slocombe et al., 2010). Evidentially, there are mixed results concerning the function(s) of wild and captive chimpanzee FACs. However, the recruitment, audience effects, and feeding coordination hypotheses are not mutually exclusive. Together, they suggest that chimpanzees employ some degree of control over vocalizations, and that FACs might serve a variety of social function(s), indicating behavioural flexibility in the vocal domain. Still, systematic and detailed data from additional field sites are needed to better understand variability in food calling function(s) between communities, and to compare function(s) across populations.

Current Study

Objectives

This thesis investigates the social and ecological correlates, along with the acoustic structure of food-associated vocalizations in the Rekambo chimpanzee (*Pan troglodytes troglodytes*) community in Loango National Park, Gabon. Specifically, this study investigates if FACs function to attract conspecifics to a food patch, if callers direct FACs toward nearby group members, and if FACs function to prolong interindividual proximity while feeding. Regarding the form of FACs, this research looks at how the fundamental frequencies of food calls change over the course of a feeding event and how they vary in relation to the type of food being consumed, thereby examining if these calls function referentially.

This research specifically focuses on FACs emitted by Rekambo males for several reasons. As discussed, there is compelling evidence from numerous communities suggesting that chimpanzee FACs are socially motivated, and research has explored the potential social benefits associated with food-calling. If chimpanzees are indeed poised to gain social benefits from emitting FACs during certain feeding events, and males and females experience different social pressures (e.g., dispersal patterns, kin selection, and reproduction), it follows that there may be different selection pressures acting on male FACs than on female FACs (Lehmann & Boesch, 2008; Scott, 2013). For example, males may wish to call to other males to strengthen social bonds and alliances. Males may also call to solicit copulation from sexually receptive females. Alternatively, females, who primarily compete over food, may food call to reduce aggression from, or feeding competition with, more dominant female group members (Lehmann & Boesch, 2008). Of course, like males, newly emigrated females may also call to solicit copulation. Therefore, it may be that not only do male and female chimpanzees emit FACs for different social reasons, but they may also be food calling for different reasons depending on the sex of their audience members.

Furthermore, this research is restricted to males because there are a number of Rekambo females who are not yet fully habituated the presence of humans. Thus, collecting data on Rekambo females is considerably less efficient than collecting data on males. This was an important consideration given that there were also unforeseen logistical complications with the Ozouga Chimpanzee Project that severely limited the amount of focal data that could be collected for this thesis. For these reasons, coupled with an already relatively short data collection period, this study specifically examines FACs emitted by males of the Rekambo chimpanzee community. In light of the short study period, logistical issues, and the limited amount of focal data collected, this study can be seen as more of a pilot project which should be followed up with additional data collection and more in-depth analyses.

Research Questions, Hypotheses, and Predictions

Recruitment Hypothesis

Research Question 1: Do male chimpanzees (*Pan troglodytes troglodytes*) of the Rekambo community produce FACs to attract group members to a feeding event?

I hypothesize that FACs function to recruit group members to a feeding event. I predict that for feeding events wherein the focal individual food calls, other group members will be more likely to come and join that feeding event than when the focal does not food call, as has been demonstrated for Taï chimpanzees (Kalan & Boesch, 2015).

Audience Effects Hypothesis

Research Question 2: Do Rekambo males direct FACs toward group members who are nearby?

I hypothesize that focal individuals will direct FACs toward nearby, but out of sight, group members. I predict that upon arrival to the feeding event, the focal will be more likely to food call if there are more group members nearby, as has been shown in Taï chimpanzees (Kalan & Boesch, 2015).

Feeding Coordination Hypothesis

Research Question 3: Do Rekambo males produce FACs to prolong feeding durations with group members?

I hypothesize that FACs will function to prolong cofeeding duration. I predict that feeding events wherein the focal emits FACs on arrival will result in the focal feeding with at least one other group member for longer than when the focal does not food call, as has been demonstrated in Kanyawara chimpanzees (Fedurek & Slocombe, 2013).

Arousal Hypothesis

Research Question 4: How do fundamental frequencies of FACs vary in relation to the length of the feeding event?

Fundamental frequency (F0s) is an indicator of arousal (Morton, 1977). Therefore, I hypothesize that F0s of FACs will decrease as calling progresses throughout a feeding event, as initial excitement associated with food decreases over time spent feeding on it. I predict that food calls emitted earlier in a feeding event will have higher F0s than those emitted later on.

Functional Reference Hypothesis

Research Question 5: How do fundamental frequencies of FACs vary in relation to food type?

I hypothesize that for feeding events wherein FACs are emitted, the F0s of FACs will vary in relation to food type. In keeping with results from Taï (Kalan et al., 2015) and Sonso (Slocombe & Zuberbühler, 2005), I predict that FACs emitted for fruit will have higher F0s than FACs emitted for other food types.

Chapter 3: Methods

Study Species: Chimpanzees (*Pan troglodytes*)

Chimpanzees (*Pan troglodytes*) along with bonobos (*Pan paniscus*), are humans' closest living relatives. Humans and chimpanzees are estimated to have diverged seven to eight million years ago and share 98% of their DNA (Langergraber et al., 2012). Chimpanzees range across equatorial Africa and occupy a variety of different habitats from tropical forests to savannah woodlands. As a species, chimpanzees live in multimale-multifemale communities that average 35 members (Mitani & Watts, 2005), with the largest community described reaching over 200 individuals (Langergraber et al., 2017). Chimpanzees exhibit high degrees of fission-fusion dynamics wherein all community members are rarely together at the same time (Aureli et al., 2008). Instead, chimpanzees typically travel in smaller fluid subgroups with changing composition, sometimes on an hourly or daily basis, according to food availability and access to reproductive females (Lehmann & Boesch, 2004).

There are currently four recognized sub-species: the Western chimpanzee (*Pan troglodytes verus*), the Central chimpanzee, (*P. t. troglodytes*), the Nigeria-Cameroon chimpanzee (*P. t. ellioti*), and the Eastern chimpanzee (*P. t. schweinfurthii*). Across Africa, populations of all subspecies are declining. The International Union for Conservation of Nature (IUCN) Red List, which uses current research on population trends and threats to assess the likelihood of a species becoming extinct in the near future, classifies the Eastern, Central, and Nigeria-Cameroon subspecies as endangered, and the Western chimpanzee as critically endangered (IUCN, 2022). Declining populations are further exacerbated by slow life histories (i.e., late age of first reproduction, long gestation periods, and long interbirth intervals) and high rates of infant mortality (Purvis et al., 2000).

Central Chimpanzees (*Pan troglodytes troglodytes*)

The subspecies that is the subject of this thesis, Central chimpanzees (*Pan troglodytes troglodytes*), are found across the rainforests of Angola, Cameroon, the Central African Republic, Equatorial Guinea, Gabon, and the Republic of the Congo (IUCN, 2014). The most recent population estimates are 128,760 Central chimpanzees remaining in the wild, with the majority residing in only two countries: the Republic of the Congo (43%) and Gabon (34%) (Strindberg et al., 2018).

Under IUCN guidelines, Central chimpanzees are ‘endangered’, meaning their risk of extinction in the wild is very high. The greatest threats to Central chimpanzees include poaching, habitat degradation, disease, and climate change (IUCN, 2022). All subspecies are protected by national laws in habitat countries, as well as by international conventions. It is therefore illegal to capture, trade, or kill chimpanzees. However, chimpanzee meat is a culturally valuable commodity that is driving the decline of Central chimpanzee populations (Strindberg et al., 2018).

Habitat degradation and loss are major causes of declining Central chimpanzee population declines (IUCN, 2022). The impacts of extractive industries across Central Africa, such as mining (Spira et al., 2019), oil prospecting (Rabanal et al., 2010), logging (Morgan et al., 2018), and agriculture (Wich et al., 2014) contribute to chimpanzee habitat loss (Fotang et al., 2021; Morgan et al., 2018). Across Central Africa, selective logging targets old growth forests, and consequently removes trees suitable for chimpanzee nesting and feeding (Koops et al., 2012; Morgan et al., 2013). This, combined with industry noise, affects how chimpanzees move through, and disperse across, landscapes (Bonnin et al., 2020; Rabanal et al., 2010). This in turn can diminish behavioural diversity, including behaviours considered cultural (Kühl et al., 2019).

Great apes, including chimpanzees, are highly susceptible to diseases (Carne et al., 2014), and the IUCN (2022) lists disease, and particularly the Ebola virus, as one of the greatest threats to Central chimpanzees. The Ebola virus is highly infectious and fatal to both humans and great apes. Not only are the forests of Central Africa considered ‘hot spots’ for emerging infectious diseases (EIDs), including the Ebola virus (Reed et al., 2014), but the most lethal strains occur in central African countries (Leroy et al., 2004). Numerous Ebola outbreaks have been documented across Central Africa (Leroy et al., 2004; Muyembe-Tamfum et al., 2012; Reed et al., 2014). These outbreaks have coincided with increases in Central chimpanzees’ mortality and have significantly contributed to declining populations (Walsh et al., 2003). Infectious diseases are a serious threat to all great apes; however, those which are highly contagious and easily transmissible such as Ebola are particularly threatening to chimpanzees because of their gregarious nature and fluid social networks (Carne et al., 2014; Walsh et al., 2007).

Lastly, Central chimpanzees are vulnerable to the effects of climate change. Fluctuations in temperature and precipitation are said to already be affecting Africa’s tropical rainforests, including those in Central Africa (Lewis et al., 2013). These changes are predicted to negatively impact chimpanzee habitats, and especially fruit availability (Tutin & Fernandez, 1993). While Central chimpanzees are facing several independent threats, these threats are also interconnected and often exacerbate one another. For example, resource extraction intensifies the effects of poaching as large-bodied mammals, including chimpanzees, are often targeted to feed workers living and working in remote areas. Regions that were once remote and continuous forest are now easily accessible via logging roads, making it easier for poachers to meet bushmeat demands (Edwards et al., 2014; Laporte, 2007).

There are numerous long-term chimpanzee field-research sites. The majority are concentrated in East and West Africa, and therefore study the Eastern and Western subspecies (Gruber & Clay, 2016). This, combined with the threats outlined above make it all the more urgent to understand the behavioural diversity and complexity of the comparatively understudied Central chimpanzees. The Rekambo community of chimpanzees in Loango National Park, Gabon are one of the few long-term field projects situated in Centra Africa. Therefore, this particular population of habituated chimpanzees provides ample opportunity to investigate the behaviour and flexibility of the Central subspecies, which is crucial in designing and implementing effective conservation strategies.

The Ozouga Chimpanzee Project

Study Site

The Loango Ape Project began in 2005 with the aim of habituating and studying sympatric chimpanzees (*Pan troglodytes troglodytes*) and western lowland gorillas (*Gorilla gorilla gorilla*). However, since 2015 there have been two separately managed projects, each one focusing on one species of great ape. The Ozouga Chimpanzee Project (https://en.ozouga.org/) is now managed by Osnabrück University in Germany in collaboration with the 'Agence National pour la Protection de la Nature' (ANPN), the Gabonese government agency which closely oversees all research and eco-tourism taking place within the park (Boesch et al., 2007; Ozouga Chimpanzee Project field guidelines, 2022).

Loango National Park covers an area of 1,500 km^2 and is located along the southern coast of Gabon. Temperatures range between 18 and 32 °C, with a mean minimum of 22.7 °C and a mean maximum of 27.8 °C. May to September is the dry season, and October to April is the rainy season. There is, however, a short dry season from December to January (Head et al., 2011). The region borders the Atlantic Ocean and is a mosaic of rivers, swamps, mangroves, savannahs, coastal forest, and lagoon, as well as secondary and mature forests. Due to this mosaic of different habitat types, Loango National Park is ecologically distinct from other field sites where long-term chimpanzee research is conducted. Therefore, this project provides insight regarding variability in chimpanzee diet, sociality, and culture (Ozouga Chimpanzee Project field guidelines, 2022). In addition to chimpanzees and gorillas, forest elephants (*Loxodonta africana cyclotis*), red river hogs (*Potamochoerus porcus*; Figure 1), leopards (*Panthera pardus*), buffalo (*Syncerus caffer nanu*s; Figure 2), hippopotamus (*Hippopotamus amphibius*), as well as numerous species of monkeys, duikers, birds, reptiles, and insects inhabit Loango National Park. The research camp, called ‘Ozouga’ which is the local word for the fruit *Sacoglottis gabonensis*, is situated inside the park (2°04′S and 9°33′E) at the end of the savannah with forest to the east and the Atlantic Ocean 500 meters to the west (Figures 3 and 4).

Figure 1. A red-river hog (*Potamochoerus porcus*) feeding in Loango National Park.

Note: A red-river hog feeds amongst birds in the savannah behind the Ozouga research camp. Photo by Lindsey Warshawski.

Figure 2. A buffalo (*Syncerus caffer nanus*) feeding in Loango National Park.

Note: A buffalo feeds in the savannah surrounding the Ozouga research camp. Photo by Lindsey Warshawski.

Figure 3. Map of study area.

Note: The red star indicates the Ozouga research camp situated in Loango National Park, Gabon. Map created using Google Maps.

Figure 4. Aerial photo of the Ozouga research camp.

Note: Ozouga research camp situated at the end of the savannah, on the edge of the forest in Loango National Park, Gabon. Photo by the Ozouga Chimpanzee Project.

Loango Chimpanzees

Prior to the Rekambo community of chimpanzees being habituated to human presence, researchers used non-invasive monitoring techniques to examine various aspects of population sizes, densities, and genetics, as well as habitat use and dietary overlap between sympatric species. At the onset of the Ozouga Chimpanzee Project, DNA analysis of fecal samples distinguished at least two communities of chimpanzees in the study area (Boesch et al., 2007). Additional comprehensive analyses later yielded evidence for four (Head et al., 2013) to seven (Arandjelovic et al 2011) distinct chimpanzee communities in Loango, with some overlap in territories, and repeated instances of lethal intergroup violence (Arandjelovic et al. 2011; Boesch et al., 2007; Martínez-Íñigo et al., 2021a) characteristic of the species (Mitani et al., 2010). Densities of chimpanzees were estimated to be 1.72 individuals per km^2, whereas the densities for Loango's gorillas and elephants were estimated to be 1.2 per km^2 and 1.37 per km^2, respectively (Head et al., 2013). Research looking at the diets of these three species found high degrees of overlap, but with temporal and spatial variation. Elephants competitively excluded both species of great apes when food was more limited. However, chimpanzees only experienced exclusion by elephants specifically during periods of low fruit availability (Head et al., 2012).

Rekambo Chimpanzee Community

The Rekambo community of chimpanzees (https://en.ozouga.org/) was finally habituated to the presence of human researchers by 2017. Since then, direct observations of Rekambo individuals have provided a more comprehensive understanding of their home range and diet, as well as have revealed several novel behaviours that have not been observed at other field sites (Klein et al., 2021; Mascaro et al., 2022; Pika et al., 2019; Southern et al., 2021). Prior to habituation, non-invasive genetic monitoring estimated the Rekambo home range to be 45 km^2 (Arandjelovic et al., 2011), camera trap data supported a home range of 24.4 km^2, and preliminary direct observations estimated 36 km^2 (Head et al., 2013). However, after habituation, and using direct observational data, the Rekambo community home range is now estimated to be between 39.34 km^2 and 49.67 km^2, which is one of the largest home ranges for a chimpanzee community living outside of savannah-woodland habitat (Martínez-Íñigo et al., 2021b).

As a species, chimpanzees are largely frugivorous, but they also feed on a variety of plants and are known to hunt and consume the meat of other animals (Goodall, 1986). Rekambo chimpanzees feed on over 70 different kinds of stems, leaves, seeds, aril (seed coverings), and flowers (Loango Ape Diet Book, 2022). Rekambo individuals have also been observed hunting nine different mammal species, including monkeys and ungulates. The most frequently hunted species are red-capped mangabeys (*Cercocebus torquatus*) and putty-nosed monkeys (*Cercopithecus nictitans*), as well as moustached monkeys (*Cercopithecus cephus cephodes*). Less common prey includes crowned monkeys (*Cercopithecus pogonias nigripes*), as well as blue and yellow-backed duikers (*Cephalophus monticola defriesi; Cephalophus silvicultor*). Unsuccessful pursuits of bay duikers (*Cephalophus dorsalis castaneus*), red-river hogs (*Potamochoerus porcus*), and unidentified species of squirrels have also been observed. Rekambo individuals hunt species that have never been preyed upon by chimpanzees at other field sites (e.g., red-capped mangabeys and putty-nosed monkeys). Compared to other field sites, Rekambo chimpanzees hunt ungulates more frequently. Furthermore, Rekambo individuals show a hunting frequency of 2.65 hunts per month, which is high compared to other sites where red colobus monkeys (*Piliocolobus spp.*), a preferred prey species, are also absent (Klein et al., 2021).

Novel ways of food extraction and tool-use have also been reported in Rekambo chimpanzees. At other field sites, it has been suggested that chimpanzees prey on tortoises; however, the first direct observations of this behaviour come from the Rekambo community. Individuals have been observed capturing and consuming hinge-back tortoises (*Kinixys erosa*) (Figure 5). Notably, Rekambo chimpanzees employ percussive proto-tool technology to gain access to the meat. Individuals use a distinct smashing technique on a rock or branch (the proto-tool) to break through the carapace to then consume the meat inside, often willingly and peacefully sharing it with other group members (Pika et al., 2019).

Figure 5. Rekambo chimpanzees feeding on a tortoise (*Kinixys erosa*).

Note: Males Pandi (left) and Littlegrey (right) sharing a tortoise in a tree. Photo by Gael Willy Nwegnambie.

Rekambo chimpanzees have been directly observed exploiting underground nests of stingless bees (*Meliplebeia lendliana*). That the nests are located underground poses a unique challenge as they are difficult to detect. The nests, which contain the honey and the brood, are deep underground and the location is only discernable via a small waxy entrance that protrudes only a few millimetres above ground. While underground nests are exploited by other chimpanzee communities, the complex behaviour exhibited by Rekambo individuals to extract honey is exceptional, with three to five tool sets regularly employed to access a single food source. The range and flexibility of extraction repertoires employed by Rekambo chimpanzees exceeds the most complex tool use techniques described thus far in wild chimpanzees (Boesch et al., 2009; Estienne et al., 2017).

Most recently, the first observations of non-human primates applying insects to wounds have been reported for the Rekambo chimpanzee community. Rekambo individuals have been observed applying insects to not only their own wounds, but to the wounds of other group members. Insects are always applied to open wounds suggesting that this behaviour may be a form of medication. Moreover, that individuals apply insects to the wounds of other individuals suggests that this behaviour may qualify as prosocial (behaviours performed with the intention of benefiting others), the existence of which is currently debated in animals (Mascaro et al., 2022). What kind of insects are applied to wounds, and if these insects possess medicinal properties is currently being investigated. Evidentially, Rekambo chimpanzees have shed light on the species' feeding ecology and behavioural flexibility. Given the number of novel behaviours already observed in this relatively newly studied and recently habituated chimpanzee community, it is likely that future research will reveal further behavioural innovations.

Data Collection

Data collection took place from August to October 2022. At the beginning of the study period, the Rekambo community consisted of 40 individuals, including eight adult males, 14 adult females, three adolescent males and seven adolescent females, as well as a number of juveniles and infants. However, during the study period, five individuals disappeared. Two adolescent males including the alpha male's brother, and three adult females including two of higher rank who were relatively gregarious in nature, disappeared during the study period and have not been seen since (Table 1).

Table 1. Rekambo individuals at the beginning and end of the study period.

Name	Sex	Age Class
Arnold	M	Adult
Aroide	F	Adult
Assala	F	Adolescent
Bantou	M	Infant
Bella	F	Adult
Cesar *	M	Adolescent
Chenge	M	Adult
Chinois	M	Adult
Diboti *	F	Adolescent
Emmie	F	Adult
Ernest	M	Infant
Fanta	F	Adolescent
Freddy	M	Adult
Greta	F	Adolescent
Gump *	M	Adolescent
Iboga	M	Infant
Ida	F	Adult
Ikoulou	F	Adult
Invindo	F	Juvenile
Janil	F	Infant
Joy	F	Adult

Kira	F	Adolescent
Littlegrey	M	Adult
Madiba	F	Infant
Mimi	F	Adult
Moana	M	Adolescent
Monkey	F	Adult
Ngonde	M	Adult
Olive	F	Juvenile
Pai	F	Adult
Pandi	M	Adult
Pastis	F	Infant
Queliba	F	Adolescent
Roxy *	F	Adult
Sassandra	F	Infant
Spock	F	Adult
Suzee *	F	Adult
Thea	M	Adult
Wora	F	Adult
Zoe	F	Adolescent

Note: '' denotes members who disappeared during the study period. The total number of individuals at the beginning of the study period was 40, and by the end there were 35 individuals.*

Continuous non-invasive behavioural and vocalization data were collected using all-day focal sampling methods (Altmann, 1974). "Focal sampling" refers to when actions of, and interactions involving, the specified 'focal' individual, are documented for the duration of the sampling period. For each focal individual the sample period is the amount of time they are actually in view and their behaviours can be reliably documented (Altmann, 1974). For this research, only adult males were focalled, as some adult females of the Rekambo community are not fully habituated to humans and therefore cannot be reliably followed. Focal individuals were chosen based on who was first encountered when searching for the chimpanzees. When a party (i.e., more than one chimpanzee) was encountered, the individual with the least number of focal hours was selected as the focal.

When following chimpanzees, Ozouga Chimpanzee Project Forest and Heath protocols (2022) were strictly adhered to at all times. Chimpanzees were always followed from behind or to the side, and researchers never put themselves directly in the chimpanzees' path. A minimum distance of eight meters was kept between chimpanzees and researchers. Chimpanzees are highly susceptible to human viruses (Dunay et al., 2018), and lethal outbreaks have occurred in several chimpanzee communities (Kaur et al., 2008; Negrey et al., 2019; Patrono et al., 2018; Williams et al., 2008). Therefore, face masks were worn at all times when in the presence of chimpanzees (Figure 6). While Rekambo individuals are habituated to human presence, researchers remained as quiet as possible when in the presence of chimpanzees as to not disturb them.

Figure 6. The author collecting behavioural and vocal data.

Note: The author wearing a face mask and observing Rekambo chimpanzees as they rest on the forest floor. Photo by Gael Willy Nwegnambie.

Following chimpanzees in Loango is very different from other long-term chimpanzee field sites due to the abundance of forest elephants (*Loxodonta africana cyclotis*; Figure 7). At most sites, researchers typically leave camp before sunrise to arrive at the chimpanzees' nesting location before they awaken and begin their day. At these sites, researchers are able to 'nest' the chimpanzees. That is, they are able to stay with the chimpanzees until they make their nest for the night, and this in turn enables researchers to know exactly where the chimpanzees will be the next morning, and to arrive at the nesting site before the chimpanzees begin traveling for the day. However, Loango National Park has a high density of forest elephants (Morgan, 2007), and this affects all aspects of field protocols and safety measures (Ozouga Chimpanzee Project Forest Health Protocols, 2022). Due to the safety risks forest elephants present, researchers are not able to be in the forest before the sun rises or after it sets. Therefore, it is very rare to 'nest' chimpanzees at Loango, and the beginning of one's day is spent listening and searching for chimpanzees. Though, researchers generally have an idea of where to search first based on where the chimpanzees were left the day before. When in the forest, researchers are also always accompanied by at least one local Gabonese eco-guide who is trained to detect and safely maneuver around forest elephants.

Figure 7. A forest elephant (*Loxodonta africana cyclotis*) feeding in Loango National Park.

Note: A forest elephant feeds in the savannah surrounding the Ozouga research camp. Photo by Lindsey Warshawski.

Data were collected primarily during the dry season, with the very end of the period leading into the rainy season. (Head et al., 2011). The first ten forest days were spent learning to identify individual chimpanzees, how to follow them, and how to reliably collect data. After this training period, chimpanzees were focal followed for eight days, and a total of 79 observational hours were collected. Data were collected on six adult males, though one adult male (Thea) was removed from the final data set(s) due to only acquiring one focal day. Therefore, the final number of hours used in this analysis are 72 (Table 2). Data collection was carried out using

CyberTracker software (CyberTracker version 3.522; https://www.cybertracker.org/) on water-resistant smart phones (Cyrus CS45).

Table 2. Summary of observational hours, dominance ranks, and ages of adult males of the Rekambo chimpanzee community focal followed during the study period.

Males	Age	Rank	Number of observational hours
Pandi	21	1	12
Freddy	20	2	15
Chenge	24	3	26
Thea	19	4	7
Littlegrey	22	5	11
Ngonde	20	6	8
Total			79

Note: dominance ranks were calculated using elo-ratings and were provided by the Ozouga Chimpanzee Project (L. Southern, pers. comm.) and are from 2018-2020. There were no noticeable differences regarding rank during the study period which is monitored via pant grunts and submissive behaviours. Pandi was still the alpha male, Freddy was highly ranked, and Littlegrey and Ngonde were of low rank.

All FACs emitted by focals upon arrival (i.e. within one minute) to a feeding event were noted. Feeding events wherein chimpanzees fed on meat or insects were excluded from statistical analyses due to the small number of observations for these food types. This analysis focuses on vocalizations emitted upon arriving to a feeding event because as feeding progresses, social context (i.e., party composition) changes and this may affect subsequent calling behaviour as well as trigger chorusing, making it difficult to reliably document a caller's identity. Moreover, calls produced within the first minute, as opposed to later, are more likely to be associated with the initial social and ecological environment, as opposed to changing social dynamics that occur throughout a feeding event (Kalan & Boesch, 2015). Each feeding event received a unique ID.

Eco-guides identified the species of food being consumed, which was also noted. Feeding events are defined as the period from when the focal began gathering or eating food until they stopped feeding for more than two minutes or moved to a different food source or location (Kalan & Boesch, 2015). If the focal resumed feeding at the same location (within the two minutes of ceasing) it was considered a continuation of the initial feeding event (Kalan & Boesch, 2015). Pant hoots emitted by any individual within the first minute of the feeding event were noted. FACs and pant hoots emitted by the focal after arrival and those emitted by other (i.e., non-focal) individuals were noted *ad libitum*. Vocalizations were recorded with a Marantz Professional PMD661 recording device and a Sennheiser ME66/K6 directional microphone and windshield using a 44 kHz sampling frequency at 24 bits/s (Kalan & Boesch, 2015). FACs emitted by the focal during a feeding event were recorded whenever possible, and pant hoots were recorded for focal and non-focal individuals *ad libitum*.

Party composition was monitored continuously. IDs along with arrival and departure times were noted for individuals joining and leaving the focal's party. A party is defined as the group of individuals who were within visual distance of the focal, and thus the observer (Kalan & Boesch, 2015). FACs can travel and be heard outside of chimpanzees' immediate party. Therefore, this analysis takes into consideration nearby individuals who can reasonably be considered within earshot of a focal's FAC but did not arrive to the food patch with them. Thus, individual(s) who were observed to be in a focal's party within 30 minutes of arrival to the food patch are considered 'nearby' (Kalan & Boesch, 2015). For female party members, it was noted if a sexual swelling was present, and if the focal copulated with a female. State behavioural activities (i.e., resting, traveling, or eating) were continuously noted for focals.

Statistical Analysis

Behavioural Analysis

Three general linear mixed models (GLMMs) (Table 3) were fitted in R version 4.2.0 (R Core Team 2022). All behavioural GLMMs had a binomial error structure with a logit link function and were carried out using the function ‘glmer’ from the package ‘lme4’ (Bates et al. 2014). Random effects were included in all three models but only intercepts could be fitted. Random slopes could not be fitted due to the small sample size of this study and limited tolerance for model complexity. Independence of residuals was checked using diagnostic plotting (i.e., q-q- plot of residuals, and residuals plotted against fitted values). Model stability was assessed via a function (A. Kalan, pers. comm.) that removed levels of random effects one at a time from the dataset and then checked that the model coefficients did not vary substantially.

Multiple regressions are susceptible to collinearity. For the recruitment model, which had more than one predictor variable, collinearity between predictor variables was checked by examining variance inflation factors (VIFs) using the ‘vif’ function of the ‘car’ package. The vif value (1.62) was well below the acceptable threshold of 4 (Kalan & Boesch, 2015; Quinn & Keough, 2002). Also, for the recruitment model, a likelihood ratio test using the function ‘anova’ was used to carry out a full versus null model comparison. The full model corresponds to the alternative hypothesis wherein the predictor variable has an effect on the response variable, and included all the predictors (i.e., the response variable, test predictor(s), control predictor(s), and random intercept(s)). The null model corresponds to the null hypothesis wherein the predictor variable has no effect on the response variable and therefore excludes the predictor(s) of interest (i.e., the test predictor(s)). By comparing the full model to the null model, the overall significance of the test predictors for the GLMM is assessed. For the other two GLMMs there was only one test predictor, therefore a full versus null model comparison was not necessary.

Recruitment Model

The recruitment model tested the effect of the focal emitting FACs on recruiting group members to a feeding event. It specifically tested whether the arrival of other group members (the y/n response variable) was more likely when the focal produced food calls upon arriving to the feeding event (the y/n predictor variable). The effect of pant hoots (by any individual) upon arrival to the feeding event (y/n) was controlled for as these long-distance signals have been associated with announcing an individual's presence (Mitani et al., 1992), attracting group members to food sources (Clark & Wrangham, 1993), and generally facilitating fusion among affiliative group members (Fedurek et al., 2014). The type of food on which the focal fed was also controlled for as it has been reported that chimpanzees are more likely to call for certain kinds of foods, such as fruit (Fedurek & Slocombe, 2013; Kalan & Boesch, 2015). An attempt was made to control for food species for the same reason; however, the low number of repeated observations for each food species caused model instability, thus the variable was excluded. The duration of the feeding event was included as an offset term given that the longer a feeding event goes on for, the higher the probability there is for other individuals to join. For this reason, the continuous covariate, 'event duration', was log-transformed and set as an offset term (McCullagh & Nelder, 1989). The party size at the beginning of the feeding event was also controlled for, as this directly relates to the number of group members remaining that could possibly join a feeding event. This continuous covariate, 'party size', was z-transformed to a mean of 0 and standard deviation of 1 before running the model (Schielzeth, 2010). Focal ID was included as a random effect to account for variation due to repeated observations from the same individual. If not taken into consideration this can result in pseudoreplication which is a common statistical error in animal behaviour studies, and in particular, communication studies, as they often involve a large number of data points per individual. Because pseudoreplication results in artificial inflation of the data set, thus increasing the chances of type 1 error (rejecting the null hypothesis when it is actually true), the individual the data point was derived from was controlled for (Waller et al., 2013). Date was included as a random effect as data points taken closely together over a short period of time, such as in this study, are predicted to be correlated, thus susceptible to temporal autocorrelation (Mitchell et al., 2019). Only feedings events wherein the complete event was observed are included in this model. Eight feeding events were removed from the final dataset due to having to leave the feeding event before the focal finished eating. Therefore, the final sample size for the recruitment model is 58 (n=58) feeding events. The model equation is as follows:

arrivals y/n ~ FAC emitted y/n + pant hoot emitted y/n + feeding party size + food type + (1|focal_id) + (1|date) + +offset(log(event_mins)

Audience Effects Model

The audience effects model tested the effect of nearby group members on the focal producing FACs. It specifically tested whether the number of individuals presumed to be nearby (the predictor variable), and therefore in earshot of food calling (i.e., individuals who had been part of the focal's party within 30 minutes of the feeding event starting) affected the probability of the focal emitting food calls upon arriving to the feeding event (the y/n response variable). Similar to the recruitment model, and as discussed previously, focal ID and date were included as random effects to control for the effects of pseudoreplication and temporal autocorrelation, respectively. The type of food being consumed was also included as a random effect because including it as a control variable, as in the recruitment model, caused model instability. ‘Party size’ was initially included as a predictor variable; however, including more than one predictor in this model caused instability due to the small sample size. Therefore, the decision was made to only include the number of nearby individuals.

As in the recruitment model, only feeding events wherein the complete event was observed are included in this model. An additional six events were removed because the focal had not been reliably followed for at least 30 minutes prior to the feeding event beginning, making the number of ‘nearby’ individuals unknown for these events. Therefore, the final sample size for the audience effects model is 52 (n=52) feeding events. The model equation is as follows:

FAC emitted y/n ~ number of nearby individuals + (1|focal_id) + (1|date) + (1|food type)

Feeding Coordination Model

The feeding coordination model tested the effect of cofeeding duration on food call production. It specifically tested whether the focal producing food calls upon arrival to the feeding event (the y/n response variable) affected the amount of time (mins) the focal fed with at least one other individual (the predictor variable). As in the audience effects model, random effects included focal ID and date to address any potential effects of pseudoreplication and temporal autocorrelation. Food type was also included as a random effect because including it as a control variable caused model instability. The same data set was used as in the audience effects model and the final sample size is 52 (n=52) feeding events. The model equation is as follows:

FAC emitted y/n ~ number of minutes focal cofed + (1| focal ID) + (1| date) + (1| food type)

Table 3. Recruitment, Audience Effects, and Feeding Coordination models.

	Recruitment model	**Audience Effects model**	**Feeding Coordination model**
Response variable	- Other chimpanzee(s) arrived to feeding event	- Food call(s) produced by focal upon arrival to feeding event (y/n)	- Food call(s) produced by focal upon arrival to feeding event (y/n)
Test predictor(s)	- Food call(s) produced by focal upon arrival to feeding event (y/n)	- Number of nearby individuals (seen within 30 mins of feeding event onset)	- Duration of focal feeding with at least one other individual during feeding event (mins)
Control predictor(s)	- Pant hoot(s) produced by any chimpanzee upon arrival to feeding event (y/n) - Food type (fruit, aril, seeds, leaves, insects and other) - Party size at the onset of feeding event	N/A	N/A
Random intercept(s)	- Focal ID (5) - Date	- Focal ID (5) - Date - Food type (fruit, aril, seeds, leaves, and other)	- Focal ID (5) - Date - Food type (fruit, aril, seeds, leaves, and other)
Offset term	Feeding event duration (mins)	N/A	N/A
Total sample size	n= 58 (feeding events)	n= 52 (feeding events)	n= 52 (feeding events)

Note: Summary of three GLMMs for behavioural data with binomial error structure with a logit link function.

Acoustic Analysis

Acoustic Model

FAC recordings were selected for analysis based on the quality of the recording (i.e., absence of background noise), and extracted into individual calls using the digital audio editor freeware Audacity (Audacity version 3.3.2; https://www.audacityteam.org/). The fundamental frequency (F0) of individual calls were then measured using the speech analysis freeware Pratt (Pratt version 6.2.03; www.praat.org). F0s were measured via visual inspection of a spectrogram using the spectral slice tool while simultaneously listening to the call. The F0 for each call was measured three times, with slices taken from the start, middle, and end of the call. The average of these three measurements were then taken as the F0. Viewing range settings for spectrograms were set to 50 to 8,000 kHz and a 0.01s window length, following Kalan and Boesch (2018). Sixteen feeding events were observed wherein FACs were recorded. Four recordings were removed because caller identity could not be verified, and four more were removed due the recordings picking up substantial background noise. Thus, from eight feeding events, 190 individual food calls were extracted. Calls were numbered based on the order of which they were emitted during the feeding event, e.g., the first call emitted received the order number '1', the second call '2', and so on. Of these 190 calls, every second call was measured as this provides a representative sample of call variation while balancing effort. In the end, 15 calls could not be measured due to poor quality, and the final sample size of calls used in this analysis is 80 (n=80). Which call was measured (i.e., the first or the second, and every second call thereafter) was alternated so measured calls included all order numbers to ensure that the first call, which was predicted to be higher frequency, was not measured for every event.

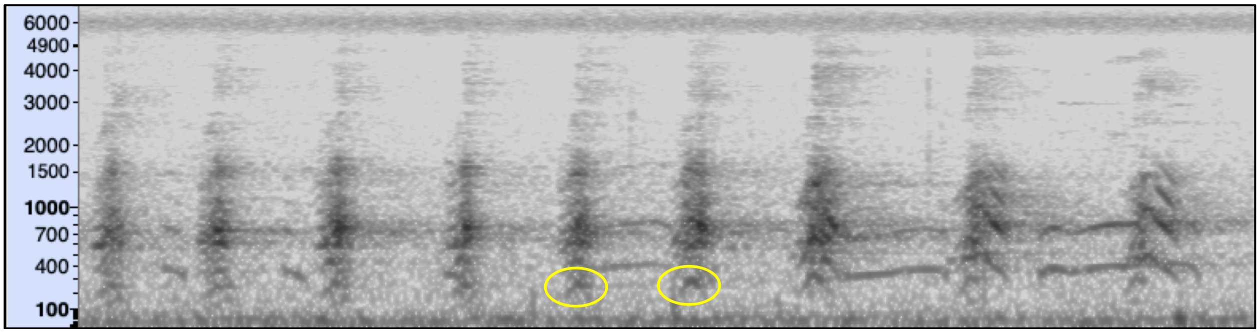

Figure 8. Spectrogram of Rekambo male Chenge's food call bout when feeding on *Sapium sp.* seeds.

Note: The fundamental frequency measured in hertz (Hz) is the lowest frequency and is circled in yellow. Grayscale depicts acoustic energy, with the darker colouring corresponding to more energy. Spectrogram made in Audacity.

A GLMM was fitted in R version 4.2.0 (R Core Team 2022) to test the effect(s) of food type and the order in which the call was produced throughout the feeding event on the fundamental frequency (F0) of the FAC. Random effects included focal ID to control for pseudoreplication, date and feeding event ID to address potential temporal autocorrelation, and the food species to control for any potential variation in F0 due to the particular species being fed on. The continuous response variable 'F0 of FAC' and covariate 'order FAC was emitted' were z-transformed to a mean of 0 and standard deviation of 1 before running the model (Schielzeth, 2010). This acoustics model had a gaussian error structure with identity link function and was carried out using the function 'lmer' from the package 'lme4' (Table 4). Independence of residuals, model stability, and vifs were checked via the same methods described for behavioural analyses. A likelihood ratio test of the function 'anova' was used to carry out a full versus null model comparison to determine the overall significance of the predictor variables. Single term deletions were carried out using the function 'drop1' to determine which predictor variable(s) were significant. The model equation is as follows:

F0 of FAC ~ food type + order FAC was emitted + (1|focal ID) + (1|date) + (1|food species) + (1|feeding event ID)

Table 4. Acoustic model.

	Acoustics model
Response variable	- Fundamental frequency (F0)
Test predictor(s)	- Food type (aril, fruit, and seeds) - Order call was emitted
Control predictor(s)	N/A
Random intercept(s)	- Focal ID (4) - Date - Feeding event ID - Food species (4)
Offset term	N/A
Total sample size	n = 80 (food calls)

Note: Summary of GLMM model for acoustic data with gaussian error structure with identity link function.

Ethics

Data collection for this thesis was exempt from the University of Victoria's formal ethics review due to the non-invasive and observational nature of this study. Data collection complied with the Ozouga Chimpanzee Project's forest health and safety protocols and project field guidelines.

Chapter 4: Results

Overview

During 79 focal hours, 66 feeding events were observed in which chimpanzees fed on aril (seed coverings) (15), flowers (1), fruit (22), insects (3), leaves (12), meat (3), and seeds (10) (Table 5). Focals emitted FACs within one minute of arrival to feeding events 26% of the time (n=17/66), and pant hoots within one minute of arrival 35% of the time (n=23/66). Focals produced FACs for all food types except insects (i.e., ants and wasps) and meat (i.e., tortoise). The majority of focal FACs were emitted for fruit (29%; n=5/17) and aril (41%; n=7/17). Similarly, the majority of focals' pant hoots when arriving to the feeding event were produced for fruit (39%; n=9/23) and aril (26%; n=6/23) (Table 6).

Table 5. Summary of food types and species consumed by Rekambo chimpanzees during the study period.

Food type	**Food species**	**Feeding events**	**Focal FAC on arrival**	**Focal pant hoot on arrival**
Aril (15)	*Pycnanthus angolensis*	13	7	6
	Staudtia gabonensis	2		
Flowers (1)	*Pandanus candelabrum*	1	1	
Fruit (22)	*Dacryodes normandii*	1	1	1
	Ficus sp.	2		1
	Nauclea didderichii	1		
	Poga oleosa	1		
	Sacoglottis gabonensis	1		
	Sapium sp.	1	1	
	Syzygium sp.	1		
	Tieghemella africana	13	2	6
	Vitex doniana	1	1	1
Insects (3)	ant (unknown species)	1		
	wasp (unknown species)	2		
Leaves (12)	*Dialium sp.*	4		
	Dichapetalum sp.	1	1	1
	Pandanus candelabrum	2		1
	Pseudospondias microcarpa longifolia	1		
	Sacoglottis gabonensis	1		
	unknown species	3		1
Meat (3)	*Kinixys erosa* (tortoise)	3		1
Seeds (10)	*Erythrophleum ivorense*	2	1	1
	Sapium sp.	8	2	3
Total number of feeding events		n = 66	n = 17	n = 23

Note: Also shown is the number of feeding events for each food species, along with the number of feeding events wherein focals emitted FACs and pant hoots upon arrival.

Table 6. Summary of feeding events.

	Feeding events observed	**Focal FAC on arrival**	**Focal Pant hoot on arrival**
Aril	15	7	6
Flowers	1	1	0
Fruit	22	5	9
Leaves	12	1	3
Other	6	0	1
Seeds	10	3	4
Total	n = 66	n = 17	n = 23

Note: The number of feedings events for each food type and the number of feeding events wherein focals emitted FACs and pant hoots upon arrival is also shown.

Recruitment Model

The full versus null comparison for the recruitment model showed that the arrival of other group members to a feeding event was not significantly influenced by FAC production (n = 58, $X^2 = 1.4$, df = 1, P = 0.24). The only variable showing a significant effect on the likelihood of other group members arriving to a feeding event was the party size (i.e., the number of individuals feeding) (estimate ±SE = -2.33 ± 0.96, CI -4.21 to -0.45, p = 0.02). With the negative estimate indicating a decrease in the probability of a focal food calling upon arrival when a larger feeding party was present. The remaining variables (pant hoots made on arrival and food type) showed no significant effect on group members joining a feeding event.

Audience Effects Model

Results of the audience effects model found that the number of nearby group members did not influence FAC production upon arrival to a feeding event (n = 52, estimate ± SE = -0.62 ± 0.82, CI -2.23 to 0.99, p= 0.33). As this model only had one predictor (number of nearby group members), no other possible effects influencing food calling upon arrival were investigated and there was no need to carry out a full versus null model comparison.

Feeding Coordination Model

Results of the feeding coordination model were significant (n = 52, estimate ± SE = 1.28 ± 0.71, CI -0.11 to 2.67, p = 0.02), and showed that producing food calls upon arrival significantly increased the duration in which the focal fed with at least one other individual. Figure 9 shows a positive relationship between cofeeding duration and the likelihood of the focal having food-called upon arrival to the feeding event. That is to say, focals were more likely to have emitted FACs upon arrival to feeding events where they subsequently cofed longer with other group members.

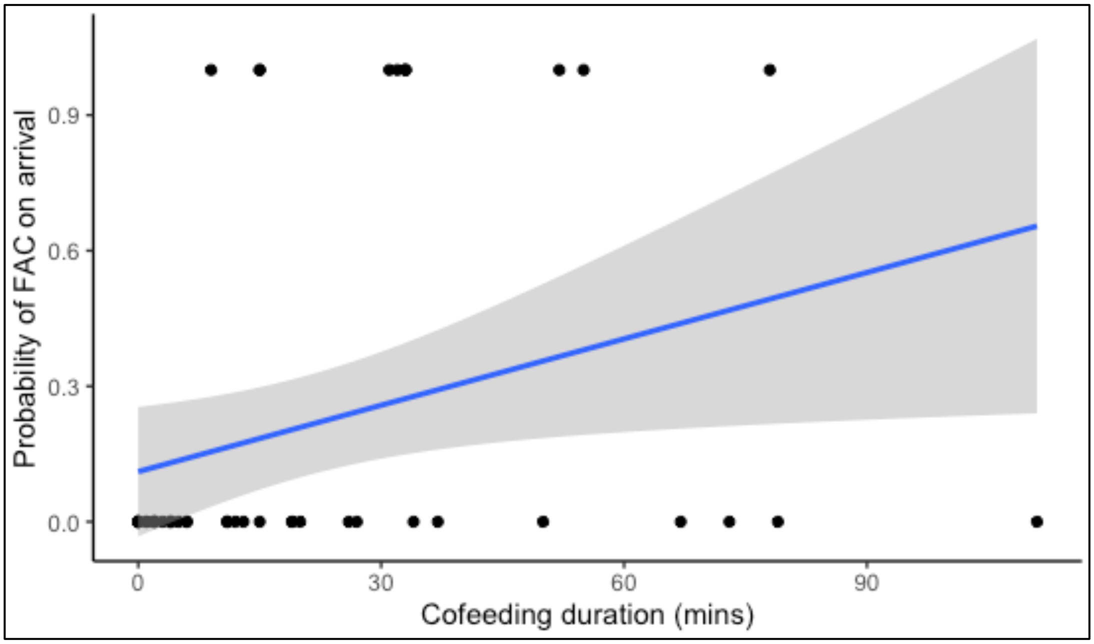

Figure 9. The effect of cofeeding duration on the probability that a focal produces an FAC.

Note: The blue line represents the model line, which shows a positive relationship between the duration in which the focal fed with at least one other group member and the probability of the focal producing a FAC upon arrival to the feeding event. The gray shaded area represents the 95% confidence interval, while the black dots represent feeding event observations (n=52).

Acoustics Model

Fundamental frequencies for a total of 80 calls from eight feeding events were analysed. Calls analysed were from four adult males (Chenge: n=13, Freddy: n=6, Littlegrey: n=45, and Ngonde: n=16). The majority of calls were emitted for aril (n=47/80), with the other calls being emitted for fruit (n=21/80), and seeds (n=12/80) (Table 7).

Table 7. Summary of FACs for acoustical analysis for each focal and food type.

Name	Food type	Number of calls analyzed
Chenge	Aril	7
	Seeds	6
Freddy	Seeds	6
Littlegrey	Aril	40
	Fruit	5
Ngonde	Fruit	16
Total		n = 80

For the acoustics model, the full versus null model comparison was significant (n = 80, $X^2 = 22.8$, df = 3, P = < .001). Results of the single term deletion showed that the significant predictor in this model was the order that the FAC was emitted throughout the feeding event. Specifically, the fundamental frequency of calls decreased as calling progressed throughout a feeding event, and calls emitted earlier in the feeding event tended to have higher fundamental frequencies than those emitted later on (Figure 10). Food type did not have a significant effect on the F0s of FACs. Though, calls for fruit exhibited average lower fundamental frequencies (mean = 540 Hz), compared to those emitted for aril (663 Hz) and seeds (632 Hz) (Table 8).

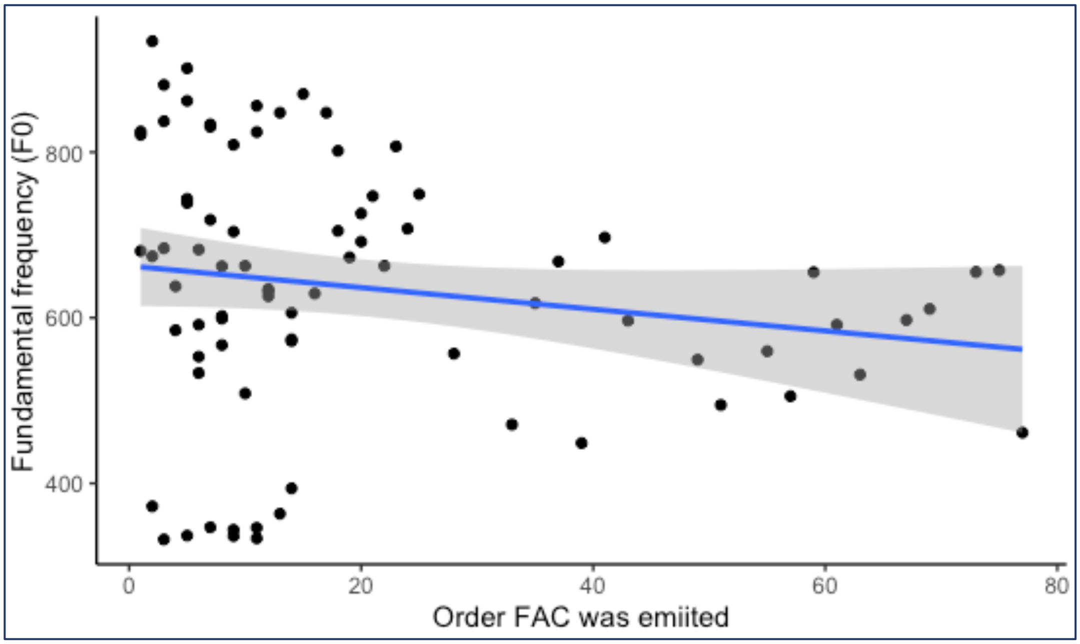

Figure 10. The effect of the order in which an FAC was emitted on F0.

Note: The blue line represents the model line, which shows a negative relationship between the order that the FAC was emitted during the feeding event and the fundamental frequency (F0) of the FAC. The gray shaded area represents the 95% confidence interval of the model estimate. The black dots are the F0s of FACs plotted against the order the FAC was emitted (n=80 food calls).

Table 8. Summary of the min, max, and mean fundamental frequencies (F0) for each food type with the number of calls analyzed.

	Min F0 (Hz)	**Max F0 (Hz)**	**Mean F0 (Hz)**	**Number of calls analyzed**
Aril	350	943	663	47
Fruit	302	1001	540	21
Seeds	276	973	632	12
Total				n = 80

Chapter 5: Discussion

Recruitment

Overall, this study found that Rekambo male FACs are influenced by social contexts. Results of the recruitment model showed that the likelihood of other group members arriving to a feeding event was not significantly influenced by the focal food calling upon arrival to that event. However, focals were less likely to call when they were already feeding in larger parties as opposed to smaller parties. This could be interpreted as less need or motivation to call when already feeding with many group members, thereby providing some indirect support for the hypothesis that FACs recruit conspecifics to a feeding event. While it was not statistically significant, the model did show a modestly positive relationship between food calls and group members arriving to a feeding event. The overall insignificance of the model may be attributed to the small sample size of this study therefore additional data could provide further clarification.

It may also be that focals are targeting their food calls toward specific individuals. This has been shown experimentally in Budongo forest chimpanzees who were more likely to food call when close social allies and higher ranked individuals were within close proximity (Schel et al., 2013). It is therefore possible that Rekambo chimpanzees may have been selectively food calling when socially significant group members were close by. However, a larger sample size (i.e., more feeding events) and more detailed data regarding interindividual relationships, such as grooming, proximity, and rank, would be needed to examine this. It is also possible that Rekambo males may have been more likely to attract others to fruit-specific feeding events, as has been reported in other communities, such as the South group of the Taï forest (Kalan & Boesch, 2015) and in Kanyawara chimpanzees (Fedurek & Slocombe 2013). Again, due to the already small sample size, it was not possible to carry out a fruit-only analysis to examine the effects of FACs on recruiting group members to food-specific feeding events.

Finally, while recruitment has been empirically demonstrated in Taï chimpanzees (Kalan & Boesch, 2015), in the Sonso community (Bouchard & Zuberbühler, 2022), and in captivity (O'Bryan, 2021), various studies looking at food calls in a number of chimpanzee communities have yielded different conclusions with regard to the social function(s) of these vocalizations (Slocombe, 2022). It is therefore possible that these vocalizations serve different function(s) across communities, and that Rekambo male FACs do not actually recruit group members. That Rekambo male food calls might serve function(s) other than recruitment may be due to the unique ecological conditions of this field site. Unlike other sites, there is no correlation between rainfall and fruit availability in Loango. The dry season, the primary period in which data were collected for this study, is a period of fruit abundance. This abundance is attributed to a high prevalence of two fruit species. *Vitex doniana* and *Staudita gabonensis* are available five to seven months, and four to five months, of the year, respectively. While both species were consumed during the study period, it seems they are rare or unimportant dietary components for other Central chimpanzees, namely those of the Mikongo forest of Lopé National Park in Gabon (Head et al., 2010). With such high quantities of fruit available throughout Loango, there may be fewer social benefits, and thus motivation, to advertise and subsequently recruit group members to a food source. Instead FACs might serve social functions when group members are already feeding together, such as reducing feeding competition between low- and high-ranked individuals as has been suggested for Sonso chimpanzees (Bouchard & Zuberbühler, 2022).

Audience Effects

Results of the audience effects model were not significant, as the number of nearby individuals had no effect on focals producing FACs when arriving to a feeding event. The model did show a modestly negative correlation between the number of nearby individuals and the focal food calling upon arrival. Thus, in this study, focals were somewhat less likely to call when group members were nearby. This aligns with the results of the recruitment model which showed that focals were less likely to call when feeding in larger parties than in smaller parties. If focals are less likely to call when groups members are nearby, it follows that they would be less likely to recruit others to a feeding event. In reporting this result it is important to keep in mind that this model only included ‘nearby’ individuals (i.e., those who had been seen with the focal at least 30 minutes prior to the feeding event) and did not include those who were nearby *and* visually present (i.e., party members) when the focal arrived at the feeding event, as in Kalan and Boesch’s (2015) study.

The number of individuals present, and therefore *who* these individuals were (e.g., kin, close social allies, or potential mates), was not included in this analysis due to the already small sample size which would cause model instability. It is therefore possible that more data (e.g., more feeding events with more details on present party members) may reveal that Rekambo males’ FACs depend on the composition of present *and* nearby group members, as has been shown in a number of other communities (Fedurek & Slocombe, 2013; Kalan & Boesch, 2015; Schel et al., 2013; Slocombe et al., 2010). In fact, the audience effects data show that Littlegrey, the fourth lowest ranking male in this study, was the focal for five (out of 52 feeding events) and produced FACs upon arrival for every event. These calls resulted in recruitment of nearby individuals for three events (i.e., 60% of the time). Moreover, for the five events wherein Littlegrey food-called, party members always consisted of at least one highly ranked male. While differences in calling behaviour in relation to rank could not be statistically modelled due to the small sample size of this study, this suggests that low-ranking males are responsible for a considerable portion of food calls, and that they might be more likely to call when higher-ranking males are nearby. This is in line with Bouchard and Zuberbühler's (2022) results for Budongo forest chimpanzees, wherein FACs were found to be directed toward higher ranking males, therefore serving to reduce aggression pertaining to feeding competition. Conversely, food calls by lower ranking males may also depend on the proximity of females, as in Kalan and Boesch's (2015) study wherein low ranked males called more often when females were nearby.

The presence of estrous females offers another intriguing avenue of research. Kalan and Boesch (2015) found that highly ranked males in the Taï forest were more likely to recruit estrous females to a food patch when they called upon arriving and were observed mating with those females either before or after recruitment. With a number of newly emigrated females (three in the last year alone) in the Rekambo community, it would be interesting to see if there is a relationship between FACs and sexually receptive females. Of course, it is also possible that Rekambo males are not targeting FACs toward estrous females, as has been reported in the Sonso (Slocombe et al., 2010) and Kanyawara (Fedurek & Slocombe, 2013) chimpanzee communities wherein they have instead been directed toward social male allies, which was also seen in Taï (Kalan and Boesch, 2015). Again, additional and more fine-scale data on nearby and present group members is needed to examine if Rekambo males direct FACs toward sexually receptive females or other socially significant group members. Until then, these results should be considered in light of the small sample size from which they are derived and should be taken with caution.

Feeding Coordination

In terms of feeding coordination, the positive correlation between food calling when arriving to a feeding event and the length of time the focal fed with at least one other individual, supports the hypothesis that FACs serve to prolong a feeding event. In species with large territories, fluid social dynamics, and strong inter-individual relationships, such as chimpanzees, vocal signals can coordinate behaviour and facilitate group movement. While FACs are not necessarily considered long-distance vocalizations, they can be heard outside of an individual's immediate party (Kalan et al., 2015). Thus, these signals can be used to communicate to both present and nearby individuals about a feeding event, and facilitate as well as prolong cofeeding with group members. These findings are in line with Fedurek and Slocombe's (2013) study on the Kanyawara community, which in addition to showing that FACs prolonged cofeeding, found that males were more likely to food call after they had been traveling as opposed to resting. Because group members are more likely to become separated during travel, it follows that the need to coordinate individuals' movement and behaviours should be stronger during and just after traveling compared to resting. Thus, the finding that FACs are more likely to be emitted after traveling further supports the hypothesis that FACs coordinate activities among group members. As was mentioned above regarding the audience effects model, more detailed data regarding *who* the focal was more likely to feed for longer with could help shed light on the social and adaptive function(s) of these vocalizations.

In regard to coordinating group behaviour, it was the impression in the field that many food calls were elicited at the beginning and end of the day. However, whether this is actually the case is difficult to determine given the unique characteristics of the Ozouga field site. The safety protocols regarding forest elephants outlined in the methods chapter (i.e., not being able to be in the forest before sunrise or after sunset) had implications for the data used in these analyses as several feeding events needed to be removed due to them being 'incomplete'. For a number of early morning feeding events, it was impossible to know if there were nearby individuals due to not being with the focal for a minimum of 30 minutes prior to the feeding event commencing. Similarly, for numerous late afternoon feeding events, it was unknown if group members arrived at a feeding event, due to the sun setting and having to leave the forest before the feeding event ended. For these reasons, 12 feeding events that occurred in the very early morning or at the very end of the day had to be removed from the final data sets. Of these 12 events, the focal food-called upon arrival for 5 feeding events (42%), and of those events wherein FACs were produced, 4 (80%) resulted in group members arriving, or being ‘recruited’. While these feeding events were not included in datasets of the models for the aforementioned reasons, it is worth considering given that there is research to suggest that call rates change over the course of the day. In particular, it has been reported that the highest call rates for chimpanzees occur in the mornings and in the evenings (Crunchant et al., 2021). Moreover, these times of day may be especially crucial from a social coordination perspective. Chimpanzees typically travel for food upon waking, and therefore an individual may want to recruit a particular group member to join them, which as previously pointed out, may in turn confer social benefits onto the signaller. In the evenings, vocalizations may coordinate nesting between affiliative individuals, which can have safety implications (e.g., safety in numbers during the night). While such investigations into the time of day of FACs may not be feasible for Loango chimpanzees, this is something that could be investigated at other long-term field sites where chimpanzees can be reliably followed from dawn to dusk.

Arousal

The negative relationship between the F0 of calls and the progression of calling throughout a feeding event supports the hypothesis that arousal decreases as a feeding event progresses. This aligns with research illustrating that the acoustic structure of vocalizations varies according to one's state of arousal (Fischer & Price, 2017). Higher fundamental frequencies in particular correlate with higher states of arousal, whereas lower fundamental frequencies correlate with lower states of arousal (Morton, 1977; Rendall et al., 2003). Therefore, the decrease in F0 can be interpreted as a decrease in arousal over the course of a feeding event. Reduced arousal may be attributed to ecological or social contexts. In an ecological context, arousal may relate to excitement, and the initial excitement of encountering food may decrease, or 'wear off' as individuals continue feeding.

Alternatively, changes in F0 while feeding may be attributed to social contexts of the feeding event, or even the status of long-term interindividual social relationships. Not only does F0 correlate to arousal, but higher frequency calls are indicative of submission or fear. Conversely, lower frequency calls indicate hostility (Morton, 1977). With this in mind, it is possible that higher frequency calls at the beginning of the feeding event may be uttered to signal submission to other party members, possibly to avoid any kind of feeding aggression or competition. In such a case, lower ranked individuals could be predicted to emit higher frequency calls than higher ranked individuals. Recall Littlegrey, the fourth lowest ranked male in this study who produced food calls in all of the feeding events in which he was focalled and recruited others to join in three out of five of those events. The average F0 of Littlegrey's FACs was 670 Hz, his average F0 for aril was 674 Hz, and 641 Hz for fruit. These frequencies are considerably higher than the other males' calls, which, when combined, showed an overall average frequency of 636 Hz, 590 Hz for aril, and 509 for fruit. While these data were not statistically modelled, the differences in F0s between Littlegrey and the other males are worth considering in light of the literature suggesting that high frequency calls correlate with fear and appeasement (Fedurek et al., 2021; Morton, 1977; Rendall et al., 2003). Since arrivals at feeding events are prone to aggressive outbreaks, which are often targeted toward subordinate group members (Ischer et al., 2020; Muller & Mitani, 2005), it follows that lower ranked individuals might attempt to minimize agonistic interactions via vocalizing. Future analyses could look at the acoustic parameters of FACs in relation to rank and the social contexts of feeding events (i.e., presence or absence of aggression) to further investigate how call structure varies according to social relationships. Such analyses would need to consider and control for age and sex given that F0 correlates to physiology. Specifically, adult males, who are the largest group members, produce higher frequency calls then physically smaller group members (e.g., adolescent males and females) (Kalan, 2019).

Functional Reference

Ecologically, food type did not have a significant effect on the F0s of FACs, suggesting that these vocalizations do not function referentially (i.e., refer to specific types of food). The model showed some variation between F0s for fruit and seeds, with fruit eliciting somewhat higher frequencies; however, these differences were not statistically significant. The lack of effect here may be attributed to the small sample size. More call samples with more food types would allow for more acoustic analyses. In particular, analyses on call duration and rate (Fischer & Price, 2017) or on peak frequency (Kalan et al., 2015) may elucidate additional acoustic variation in relation to food type.

Overall, these analyses are in line with results from other long-term chimpanzee field sites (Table 9). Rekambo chimpanzee FACs seem to serve a recruitment function, as has been shown in the Sonso and Taï communities, as well as in captivity. FACs produced by Rekambo chimpanzees also appear to coordinate feeding behaviours as seen in the Kanyawara community.

Table 9. Summary of the studies supporting audience effects, feeding coordination, functional reference, and recruitment across field sites.

Field Site	Audience Effects	Feeding Coordination	Functional Reference	Recruitment
Kanyawara	- Fedurek & Slocombe, 2013	- Fedurek & Slocombe, 2013		
Sonso	- Bouchard & Zuberbühler, 2022; - Schel et al., 2013; - Slocombe et al., 2010			- Bouchard & Zuberbühler, 2022
Rekambo		*current study*		*current study*
Taï	- Kalan & Boesch, 2015		- Kalan et al., 2015	- Kalan & Boesch, 2015
Captivity			- Slocombe & Zuberbühler, 2005; - Slocombe & Zuberbühler, 2006	- O'Bryan, 2021

Chapter 6: Conclusion

This research examined the social and ecological correlates of chimpanzee FACs. Overall, FACs appeared to be influenced by social context. Rekambo chimpanzees were more likely to feed for longer with at least one other group member after having food-called upon arrival to a feeding event, thereby supporting the Feeding Coordination hypothesis. In this sense, chimpanzee FACs can be said to function to coordinate group members and increase inter-individual proximity in foraging contexts. These findings corroborate results from other chimpanzee communities, namely Fedurek and Slocombe's (2013) study which found that Eastern male chimpanzee FACs functioned to prolong a feeding event. These analyses also showed some support for the Recruitment hypothesis. Rekambo chimpanzees were not significantly more likely to recruit group members when they food-called upon arrival. However, individuals were less likely to call when already feeding in larger parties. In all, whether Rekambo FACs serve additional social function(s) remains to be seen, and additional data are needed to provide a more robust analysis. Further investigation is also warranted given that food calls serve a variety of social functions across different communities (Bouchard & Zuberbühler, 2022; Fedurek & Slocombe, 2013; Kalan & Boesch, 2015; Slocombe et al., 2010).

Acoustic analyses did not support the hypothesis that food calls are functionally referential. However, given the tendency for fruit to elicit lower frequency calls, analyses with more data and additional acoustic properties, such as peak frequency or duration, may yield differences in calls emitted for different types of food or even food species. There was, however, support for the Arousal hypothesis, with the initial arousal of arriving to a feeding event appearing to influence FACs. Decrease in F0s over the course of a feeding event may be due to ecological reasons, with excitement decreasing as feeding progresses. Changes in F0s may also be due to social reasons, with individuals attempting to avoid aggression pertaining to feeding competition. Given the strong social bonds chimpanzees form with particular individuals, future studies combining variation in acoustic properties of food calls with audience members might show differences in arousal relating to the quality of inter-individual relationships.

This study furthers our knowledge of chimpanzee vocal communication under natural social and ecological conditions. At the population level, this research contributes to a better understanding of the behavioural diversity and complexity of the chimpanzees living in Loango National Park. This in turn lends itself to the growing literature supporting chimpanzee behavioural and cultural diversity in populations across Africa (Boesch et al., 2020; Kühl et al., 2019). Given the endangered status of chimpanzees, these findings also aid our understanding of population-level behavioural variation, which is paramount to tailoring conservation strategies in the wild (Kühl et al., 2019).

Evolutionarily, these analyses support existing literature that chimpanzees' signals are produced flexibly and intentionally in social foraging contexts. Changes in the F0s of FACs suggests that these vocalizations are acoustically variable, and therefore flexible. That food calls were not emitted for all feeding events, and that they appear to promote proximity between individuals suggests some degree of intentionality. In this sense, these results support the notion that some degree of social and communicative cognition is likely present in the LCA, thereby contributing to literature concerning the evolution of language (Bickerton, 2007; Zuberbühler, 2017).

References

1. Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3-4), 227–266. https://doi.org/10.1163/156853974X00534

2. Arandjelovic, M., Head, J., Rabanal, L. I., Schubert, G., Mettke, E., Boesch, C., Robbins, M. M., & Vigilant, L. (2011). Non-invasive genetic monitoring of wild Central chimpanzees. *PloS One*, *6*(3), e14761–e14761. https://doi.org/10.1371/journal.pone.0014761

3. Arcadi, A. C., Robert, D., & Boesch, C. (1998). Buttress drumming by wild chimpanzees: temporal patterning, phrase integration into loud calls, and preliminary evidence for individual distinctiveness. *Primates*, *39*(4), 505–518. https://doi.org/10.1007/BF02557572

4. Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Fiore, A. D., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., & Schaik, C. P. van. (2008). Fission-fusion dynamics: new research frameworks. *Current Anthropology*, *49*(4), 627–654. https://doi.org/10.1086/586708

5. Babiszewska, M., Schel, A. M., Wilke, C., & Slocombe, K. E. (2015). Social, contextual, and individual factors affecting the occurrence and acoustic structure of drumming bouts in wild chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*, 156(1), 125–134. https://doi.org/10.1002/ajpa.22634

6. Badihi, G., Graham, K. E., Fallon, B., Safryghin, A., Soldati, A., Zuberbuhler, K., & Hobaiter, C. (2023). Dialects in leaf-clipping and other leaf-modifying gestures between neighbouring communities of East African chimpanzees. *Scientific Reports*, *13*(1), 147–147. https://doi.org/10.1038/s41598-022-25814-x

7. Bates D, Maechler M, & Matrix LT (2014) lme4: linear mixed effects models using S4 classes. CRAN.R project, https://cran.r-project.org/web/packages/lme4/vignettes/lmer.pdf

8. Bickerton, D. (2007). Language evolution: A brief guide for linguists. *Lingua*, *117*(3), 510–526. https://doi.org/10.1016/j.lingua.2005.02.006

9. Boesch, C., Head, J., & Robbins, M. M. (2009). Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, *56*(6), 560–569. https://doi.org/10.1016/j.jhevol.2009.04.001

10. Boesch, C., Head, J., Tagg, N., Arandjelovic, M., Vigilant, L., & Robbins, M. M. (2007). Fatal chimpanzee attack in Loango National Park, Gabon. *International Journal of Primatology*, *28*(5), 1025–1034. https://doi.org/10.1007/s10764-007-9201-1

11. Boesch, C., Kalan, A. K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E. A., Barciela, A., Coupland, C., Egbe, V. E., Eno-Nku, M., Michael Fay, J., Fine, D., Adriana Hernandez-Aguilar, R., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G., … Kühl, H. S. (2020). Chimpanzee ethnography reveals unexpected cultural diversity. *Nature Human Behaviour*, *4*(9), 910–916. https://doi.org/10.1038/s41562-020-0890-1

12. Bonnin, N., Stewart, F. A., Wich, S. A., Pintea, L., Jantz, S. M., Dickson, R., Bellis, J., Chitayat, A., Ingram, R., Moore, R. J., & Piel, A. K. (2020). Modelling landscape connectivity change for chimpanzee conservation in Tanzania. *Biological Conservation*, *252*, 108816–. https://doi.org/10.1016/j.biocon.2020.108816

13. Bouchard, A., & Zuberbühler, K. (2022). Male chimpanzees communicate to mediate competition and cooperation during feeding. *Animal Behaviour*, 186, 41–55. https://doi.org/10.1016/j.anbehav.2022.01.009

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

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

16. Carne, C., Semple, S., Morrogh-Bernard, H., Zuberbühler, K., & Lehmann, J. (2014). The risk of disease to great apes: simulating disease spread in orangutan (*Pongo pygmaeus wurmbii*) and chimpanzee (*Pan troglodytes schweinfurthii*) association networks. *PloS One*, *9*(4), e95039–e95039. https://doi.org/10.1371/journal.pone.0095039

17. Cäsar, C., Byrne, R. W., Hoppitt, W., Young, R. J., & Zuberbühler, K. (2012). Evidence for semantic communication in titi monkey alarm calls. *Animal Behaviour*, *84*(2), 405–411. https://doi.org/10.1016/j.anbehav.2012.05.010

18. Chapman, C. A., & Lefebvre, L. (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour*, *39*(5), 891–896. https://doi.org/10.1016/S0003-3472(05)80953-4

19. Chapman, C. A., Wrangham, R. W., & Chapman, L. J. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, *36*(1), 59–70. https://doi.org/10.1007/BF00175729

20. Clark, A. P., & Wrangham, R. W. (1994). Chimpanzee arrival pant-hoots: do they signify food or status? *International Journal of Primatology*, *15*(2), 185–205. https://doi.org/10.1007/BF02735273

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

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

23. Coppinger, B., Cannistraci, R. A., Karaman, F., Kyle, S. C., Hobson, E. A., Freeberg, T. M., & Hay, J. F. (2017). Studying audience effects in animals: what we can learn from human

language research. *Animal Behaviour*, *124*, 161–165. https://doi.org/10.1016/j.anbehav.2016.12.020

24. Corballis, M. C. (2010). The gestural origins of language. *Wiley Interdisciplinary Reviews. Cognitive Science*, *1*(1), 2–7. https://doi.org/10.1002/wcs.2

25. Crockford, C., & Boesch, C. (2003). Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. *Animal Behaviour*, *66*(1), 115–125. https://doi.org/10.1006/anbe.2003.2166

26. Crockford, C., Herbinger, I., Vigilant, L., & Boesch, C. (2004). Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology*, *110*(3), 221–243. https://doi.org/10.1111/j.1439-0310.2004.00968.x

27. Crunchant, A.-S., Stewart, F. A., & Piel, A. K. (2021). Vocal communication in wild chimpanzees: a call rate study. *PeerJ (San Francisco, CA)*, *9*, e12326–e12326. https://doi.org/10.7717/peerj.12326

28. Cunningham, S., & Magrath, R. D. (2017). Functionally referential alarm calls in noisy miners communicate about predator behaviour. *Animal Behaviour*, *129*, 171–179. https://doi.org/10.1016/j.anbehav.2017.05.021

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

30. Dunay, E., Apakupakul, K., Leard, S., Palmer, J. L., & Deem, S. L. (2018). Pathogen transmission from humans to great apes is a growing threat to primate conservation. *EcoHealth*, *15*(1), 148–162. https://doi.org/10.1007/s10393-017-1306-1

31. Eckhardt, N., Polansky, L., & Boesch, C. (2015). Spatial cohesion of adult male chimpanzees (*Pan troglodytes verus*) in Taï National Park, Côte d'Ivoire. *American Journal of Primatology*, 77(2), 125–134. https://doi.org/10.1002/ajp.22316

32. Edwards, D. P., Sloan, S., Weng, L., Dirks, P., Sayer, J., & Laurance, W. F. (2014). Mining and the African environment. *Conservation Letters*, *7*(3), 302–311. https://doi.org/10.1111/conl.12076

33. Elgar, M. A. (1986). House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour*, *34*(1), 169–174. https://doi.org/10.1016/0003-3472(86)90020-5

34. Estienne, V., Stephens, C., & Boesch, C. (2017). Extraction of honey from underground bee nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon: techniques and individual differences. *American Journal of Primatology*, *79*(8), e22672–n/a. https://doi.org/10.1002/ajp.22672

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

36. Evans, C., & Marler, P. (1995). Language and animal communication: parallels and contrasts. In J. A-M. H. Roitblat (Ed.), *Comparative Approaches to Cognitive Science* (pp. 341-382). MIT Press.

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

38. Fedurek, P., Donnellan, E., & Slocombe, K. E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. *Behavioral Ecology and Sociobiology*, *68*(8), 1345–1355. https://doi.org/10.1007/s00265-014-1745-4

39. Fedurek, P., Slocombe, K. E., & Zuberbühler, K. (2015). Chimpanzees communicate to two different audiences during aggressive interactions. *Animal Behaviour*, *110*, 21–28. https://doi.org/10.1016/j.anbehav.2015.09.010

40. Fedurek, P., Tkaczynski, P. J., Hobaiter, C., Zuberbühler, K., Wittig, R. M., & Crockford, C. (2021). The function of chimpanzee greeting calls is modulated by their acoustic

variation. *Animal Behaviour*, *174*, 279–289. https://doi.org/10.1016/j.anbehav.2021.02.002

41. Fischer, J. (2021). Primate vocal communication and the evolution of speech. *Current Directions in Psychological Science: a Journal of the American Psychological Society*, *30*(1), 55–60. https://doi.org/10.1177/0963721420979580

42. Fischer, J., & Price, T. (2017). Meaning, intention, and inference in primate vocal communication. *Neuroscience and Biobehavioral Reviews*, *82*, 22–31. https://doi.org/10.1016/j.neubiorev.2016.10.014

43. Fitch, W. T. (2000). The evolution of speech: a comparative review. *Trends in Cognitive Sciences*, *4*(7), 258–267. https://doi.org/10.1016/S1364-6613(00)01494-7

44. Fotang, C., Bröring, U., Roos, C., Enoguanbhor, E. C., Abwe, E. E., Dutton, P., Schierack, P., Angwafo, T. E., & Birkhofer, K. (2021). Human activity and forest degradation threaten populations of the Nigeria–Cameroon chimpanzee (*Pan troglodytes ellioti*) in western Cameroon. *International Journal of Primatology*, *42*(1), 105–129. https://doi.org/10.1007/s10764-020-00191-2

45. Gardner, R. A., & Gardner, B. T. (1969). Teaching sign language to a chimpanzee. *Science (American Association for the Advancement of Science)*, *165*(3894), 664–672. https://doi.org/10.1126/science.165.3894.664

46. Goldin-Meadow, S., & Brentari, D. (2017). Gesture, sign, and language: the coming of age of sign language and gesture studies. *The Behavioral and Brain Sciences*, *40*, e46–e46. https://doi.org/10.1017/S0140525X15001247

47. Gomes, C. M., & Boesch, C. (2011). Reciprocity and trades in wild West African chimpanzees. *Behavioral Ecology and Sociobiology*, *65*(11), 2183–2196. https://doi.org/10.1007/s00265-011-1227-x

48. Goodall J. 1986. *The chimpanzees of Gombe: patterns of behavior*. Cambridge: Harvard University Press.

49. Gouzoules, S., Gouzoules, H., & Marler, P. (1984). Rhesus monkey (*Macaca mulatta*) screams: representational signaling in the recruitment of agonistic aid. *Animal Behaviour*, *32*(1), 182–193. https://doi.org/10.1016/S0003-3472(84)80336-X

50. Gruber, T., & Zuberbühler, K. (2013). Vocal recruitment for joint travel in wild chimpanzees. *PLoS ONE*, 8(9), e76073. https://doi.org/10.1371/journal.pone.0076073

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

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

53. Head, J. S., Boesch, C., Makaga, L., & Robbins, M. M. (2011). Sympatric chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: dietary composition, seasonality, and intersite comparisons. *International Journal of Primatology*, *32*(3), 755–775. https://doi.org/10.1007/s10764-011-9499-6

54. Head, J. S., Boesch, C., Robbins, M. M., Rabanal, L. I., Makaga, L., & Kühl, H. S. (2013). Effective sociodemographic population assessment of elusive species in ecology and conservation management. *Ecology and Evolution*, *3*(9), 2903–2916. https://doi.org/10.1002/ece3.670

55. Head, J. S., Robbins, M. M., Mundry, R., Makaga, L., & Boesch, C. (2012). Remote video-camera traps measure habitat use and competitive exclusion among sympatric chimpanzee, gorilla and elephant in Loango National Park, Gabon. *Journal of Tropical Ecology*, *28*(6), 571–583. https://doi.org/10.1017/S0266467412000612

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

57. Herb, B., Biron, S., & Kidd, M. (2003). Courtship by subordinate male Siamese fighting fish, *Betta splendens*: their response to eavesdropping and naive females. *Behaviour* 140, 71–78. https://doi.org/10.1163/156853903763999908

58. Hewes, G. (1973) Primate communication and the gestural origin of language. *Current Anthropology*, 14, 5-24. https://doi.org/10.1086/201401

59. Ischer, G., Zuberbühler, K., & Fedurek, P. (2020). The relationship between food calling and agonistic behaviour in wild chimpanzees. *Behavioural Processes*, *178*, 104182–104182. https://doi.org/10.1016/j.beproc.2020.104182

60. IUCN (2014). Regional action plan for the conservation of western lowland gorillas and central chimpanzees 2015–2025. Gland, Switzerland: IUCN SSC Primate Specialist Group. 54 pp.

61. IUCN. 2022. *The IUCN Red List of Threatened Species. Version 2022-2*. https://www.iucnredlist.org. Accessed July 11, 2023.

62. Janik, V. M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science (American Association for the Advancement of Science)*, *289*(5483), 1355–1357. https://doi.org/10.1126/science.289.5483.1355

63. Jarvis, E. D. (2019). Evolution of vocal learning and spoken language. *Science (American Association for the Advancement of Science)*, *366*(6461), 50–54. https://doi.org/10.1126/science.aax0287

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

65. Kalan, A. K. (2019). Evidence for sexual dimorphism in chimpanzee vocalizations: a comparison of male and female call production and acoustic parameters. In C. Boesch & R. Wittig (Eds.), *The Chimpanzees of the Taï Forest: 40 Years of Research* (pp. 410–421). Cambridge University Press.

66. Kalan, A. K., & Boesch, C. (2015). Audience effects in chimpanzee food calls and their potential for recruiting others. *Behavioral Ecology and Sociobiology*, *69*(10), 1701–1712. https://doi.org/10.1007/s00265-015-1982-1

67. Kalan, A. K., & Boesch, C. (2018). Re-emergence of the leaf clip gesture during an alpha takeover affects variation in male chimpanzee loud calls. *PeerJ* (San Francisco, CA), 6, e5079-e5079. https://doi.org/10.7717/peerj.5079

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

69. Kaur, T., Singh, J., Tong, S., Humphrey, C., Clevenger, D., Tan, W., Szekely, B., Wang, Y., Li, Y., Alex Muse, E., Kiyono, M., Hanamura, S., Inoue, E., Nakamura, M., Huffman, M. A., Jiang, B., & Nishida, T. (2008). Descriptive epidemiology of fatal respiratory outbreaks and detection of a human-related metapneumovirus in wild chimpanzees (*Pan troglodytes*) at Mahale Mountains National Park, Western Tanzania. *American Journal of Primatology*, *70*(8), 755–765. https://doi.org/10.1002/ajp.20565

70. Kiriazis, J., & Slobodchikoff, C. N. (2006). Perceptual specificity in the alarm calls of Gunnison's prairie dogs. *Behavioural Processes*, *73*(1), 29–35. https://doi.org/10.1016/j.beproc.2006.01.015

71. Kitzmann, C. D., & Caine, N. G. (2009). Marmoset (*Callithrix geoffroyi*) Food-Associated Calls are Functionally Referential. *Ethology*, *115*(5), 439–448. https://doi.org/10.1111/j.1439-0310.2009.01622.x

72. Klein, H., Bocksberger, G., Baas, P., Bunel, S., Théleste, E., Pika, S., & Deschner, T. (2021). Hunting of mammals by central chimpanzees (*Pan troglodytes troglodytes*) in the Loango National Park, Gabon. *Primates*, *62*(2), 267–278. https://doi.org/10.1007/s10329-020-00885-4

73. Koops, K., McGrew, W. C., de Vries, H., & Matsuzawa, T. (2012). Nest-building by chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: antipredation, thermoregulation, and antivector hypotheses. *International Journal of Primatology*, 33(2), 356–380. https://doi.org/10.1007/s10764-012- 9585-4

74. Krupenye, C., & Call, J. (2019). Theory of mind in animals: current and future directions. *Wiley Interdisciplinary Reviews. Cognitive Science*, *10*(6), e1503–n/a. https://doi.org/10.1002/wcs.1503

75. Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., Bocksberger, G., McElreath, M. B., Agbor, A., Angedakin, S., Ayimisin, E. A., Bailey, E., Barubiyo, D., Bessone, M., Brazzola, G., Chancellor, R., Cohen, H., Coupland, C., Danquah, E., … Kalan, A. K. (2019). Human impact erodes chimpanzee behavioral diversity. *Science*, *363*(6434), 1453–1455. https://doi.org/10.1126/science.aau4532

76. Langergraber, K. E., Prufer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E., Inoue-Muruyama, M., Mitani, J. C., Muller, M. N., Robbins, M. M., Schubert, G., Stoinski, T. S., Viola, B., Watts, D., Wittig, R. M., Wrangham, R. W., Zuberbuhler, K., Paabo, S., & Vigilant, L. (2012). Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences*, 109(39), 15716–15721. https://doi.org/10.1073/pnas.1211740109

77. Laporte, N. T., Stabach, J. A., Grosch, R., Lin, T. S., & Goetz, S. J. (2007). Expansion of industrial logging in Central Africa. *Science (American Association for the Advancement of Science)*, *316*(5830), 1451–1451. https://doi.org/10.1126/science.1141057

78. Last, C., & Muh, B. (2013). Effects of human presence on chimpanzee nest location in the Lebialem Moné forest landscape, south-west region, Cameroon. *Folia Primatologica*, 84(1), 51–63. https://doi.org/10. 1159/000346305.

79. le Roux, A., Cherry, M. I., & Manser, M. B. (2008). The audience effect in a facultatively social mammal, the yellow mongoose, Cynictis penicillata. *Animal Behaviour*, *75*(3), 943–949. https://doi.org/10.1016/j.anbehav.2007.07.014

80. Leaver, L. A., Hopewell, L., Caldwell, C., & Mallarky, L. (2007). Audience effects on food caching in grey squirrels (Sciurus carolinensis): evidence for pilferage avoidance strategies. *Animal Cognition*, *10*(1), 23–27. https://doi.org/10.1007/s10071-006-0026-7

81. Lehmann, J., & Boesch, C. (2004). To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology*, *56*(3), 207–216. https://doi.org/10.1007/s00265-004-0781-x

82. Lehmann, J., & Boesch, C. (2008). Sexual differences in chimpanzee sociality. *International Journal of Primatology*, *29*(1), 65–81. https://doi.org/10.1007/s10764-007-9230-9

83. Leroux, M., Schel, A. M., Wilke, C., Chandia, B., Zuberbühler, K., Slocombe, K. E., & Townsend, S. W. (2023). Call combinations and compositional processing in wild chimpanzees. *Nature Communications*, *14*(1), 2225–2225. https://doi.org/10.1038/s41467-023-37816-y

84. Leroy, E. M., Rouquet, P., Formenty, P., Souquière, S., Kilbourne, A., Froment, J.-M., Bermejo, M., Smit, S., Karesh, W., Swanepoel, R., Zaki, S. R., & Rollin, P. E. (2004). Multiple Ebola virus transmission events and rapid decline of Central African wildlife. *Science (American Association for the Advancement of Science)*, *303*(5656), 387–390. https://doi.org/10.1126/science.1092528

85. Lewis, S. L., Sonké, B., Sunderland, T., Begne, S. K., Lopez-Gonzalez, G., van der Heijden, G. M. F., Phillips, O. L., Affum-Baffoe, K., Baker, T. R., Banin, L., Bastin, J.-F., Beeckman, H., Boeckx, P., Bogaert, J., De Cannière, C., Chezeaux, E., Clark, C. J., Collins, M., Djagbletey, G., … Ewango, C. E. N. (2013). Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences*, *368*(1625), 20120295–20120295. https://doi.org/10.1098/rstb.2012.0295

86. Liebal, K., Waller, B. M., Burrows, A. M., & Slocombe, K. E. (2013). *Primate Communication: A Multimodal Approach*. Cambridge University Press. https://doi.org/10.1017/CBO9781139018111

87. Loango Ape Diet Book (2022).

88. Macedonia, J. M., & Evans, C. S. (1993). Essay on contemporary issues in ethology: variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, *93*(3), 177–197. https://doi.org/10.1111/j.1439-0310.1993.tb00988.x

89. Manser, M. B., Bell, M. B., & Fletcher, L. B. (2001). The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1484), 2485–2491. https://doi.org/10.1098/rspb.2001.1772

90. Marler, P. (1976). Social organization, communication and graded signals: The chimpanzee and the gorilla. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology.* Cambridge U Press.

91. Marler, P., & Hobbett, L. (1975). Individuality in a long-range vocalization of wild chimpanzees. *Zeitschrift für Tierpsychologie, 38*(1), 97–109. https://doi.org/10.1111/j.1439-0310.1975.tb01994.x

92. Martínez-Íñigo, L., Baas, P., Klein, H., Pika, S., & Deschner, T. (2021a). Intercommunity interactions and killings in central chimpanzees (*Pan troglodytes troglodytes*) from Loango National Park, Gabon. *Primates*, *62*(5), 709–722. https://doi.org/10.1007/s10329-021-00921-x

93. Martínez-Íñigo, L., Baas, P., Klein, H., Pika, S., & Deschner, T. (2021b). Home range size in central chimpanzees (*Pan troglodytes troglodytes*) from Loango National Park, Gabon. *Primates*, *62*(5), 723–734. https://doi.org/10.1007/s10329-021-00927-5

94. Mascaro, A., Southern, L. M., Deschner, T., & Pika, S. (2022). Application of insects to wounds of self and others by chimpanzees in the wild. *Current Biology*, *32*(3), R112–R113. https://doi.org/10.1016/j.cub.2021.12.045

95. McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman and Hall, London

96. McGrew, W. C., & Tutin, C. E. G. (1978). Evidence for a social custom in wild chimpanzees? *Man (London)*, *13*(2), 234–251. https://doi.org/10.2307/2800247

97. Messer, R.H., Gonzalez, G.D.S. (2019). Communication and social cognition. In: Shackelford, T., Weekes-Shackelford, V. (eds) Encyclopedia of Evolutionary Psychological Science. Springer, Cham. https://doi.org/10.1007/978-3-319-16999-6_3606-1

98. Miglietta, S., Bardino, G., Sotto-Mayor, A., Galli, A. S., Meulman, E., Breuer, T., Fuh, T., & Masi, S. (2021). Absence of specific individuals and high food abundance elicit food calls in wild western gorillas. *Behavioral Ecology and Sociobiology*, 75(6), 98. https://doi.org/10.1007/s00265-021-03027-y

99. Mitani, J. C., & Stuht, J. (1998). The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. *Primates*, 39(2), 171–182. https://doi.org/10.1007/BF02557729

100. Mitani, J. C., Hasegawa, T., Gros-Louis, J., Marler, P., & Byrne, R. (1992). Dialects in wild chimpanzees? *American Journal of Primatology*, *27*(4), 233–243. https://doi.org/10.1002/ajp.1350270402

101. Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, *20*(12), R507–R508. https://doi.org/10.1016/j.cub.2010.04.021

102. Morgan, B. J. (2007). Group size, density and biomass of large mammals in the Réserve de Faune du Petit Loango, Gabon. *African Journal of Ecology*, *45*(4), 508–518. https://doi.org/10.1111/j.1365-2028.2007.00761.x

103. Morgan, D., Mundry, R., Sanz, C., Ayina, C. E., Strindberg, S., Lonsdorf, E., & Kühl, H. S. (2018). African apes coexisting with logging: comparing chimpanzee (*Pan troglodytes*

troglodytes) and gorilla (*Gorilla gorilla gorilla*) resource needs and responses to forestry activities. *Biological Conservation*, *218*, 277–286. https://doi.org/10.1016/j.biocon.2017.10.026

104. Morgan, D., Sanz, C., Greer, D., Rayden, T., Maisels, F. and Williamson, E.A. 2013. *Great Apes and FSC: Implementing 'Ape Friendly' Practices in Central Africa's Logging Concessions*. IUCN/SSC Primate Specialist Group, Gland, Switzerland.

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

106. Muller, M. N., & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. In *Advances in the Study of Behavior* (Vol. 35, pp. 275–331). Elsevier Science & Technology. https://doi.org/10.1016/S0065-3454(05)35007-8

107. Muyembe-Tamfum, J. J., Mulangu, S., Masumu, J., Kayembe, J. M., Kemp, A., & Paweska, J. T. (2012). Ebola virus outbreaks in Africa: past and present. *Onderstepoort Journal of Veterinary Research*, *79*(2), 451–451. https://doi.org/10.4102/ojvr.v79i2.451

108. Negrey, J. D., Reddy, R. B., Scully, E. J., Phillips-Garcia, S., Owens, L. A., Langergraber, K. E., Mitani, J. C., Emery Thompson, M., Wrangham, R. W., Muller, M. N., Otali, E., Machanda, Z., Hyeroba, D., Grindle, K. A., Pappas, T. E., Palmenberg, A. C., Gern, J. E., & Goldberg, T. L. (2019). Simultaneous outbreaks of respiratory disease in wild chimpanzees caused by distinct viruses of human origin. *Emerging Microbes & Infections*, *8*(1), 139–149. https://doi.org/10.1080/22221751.2018.1563456

109. Nishida, T. (1980). The leaf-clipping display: A newly-discovered expressive gesture in wild chimpanzees. *Journal of Human Evolution*, *9*(2), 117–128. https://doi.org/10.1016/0047-2484(80)90068-8

110. Notman, H., & Rendall, D. (2005). Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour*, *70*(1), 177–190. https://doi.org/10.1016/j.anbehav.2004.08.024

111. O'Bryan, L. R., Lambeth, S. P., Schapiro, S. J., & Wilson, M. L. (2021). Playbacks of food-associated calls attract chimpanzees towards known food patches in a captive setting. *Primates*, *62*(6), 905–918. https://doi.org/10.1007/s10329-021-00936-4

112. Ozouga Chimpanzee Project Field Guidelines (2022).

113. Ozouga Chimpanzee Project Forest and Health Protocols (2022).

114. Patrono, L. V., Samuni, L., Corman, V. M., Nourifar, L., Röthemeier, C., Wittig, R. M., Drosten, C., Calvignac-Spencer, S., & Leendertz, F. H. (2018). Human coronavirus OC43 outbreak in wild chimpanzees, Côte d´Ivoire, 2016. *Emerging Microbes & Infections*, *7*(1), 1–4. https://doi.org/10.1038/s41426-018-0121-2

115. Pika, S., Klein, H., Bunel, S., Baas, P., Theleste, E., & Deschner, T. (2019). Wild chimpanzees (*Pan troglodytes troglodytes*) exploit tortoises (*Kinixys erosa*) via percussive technology. *Scientific Reports*, *9*(1), 7661–7661. https://doi.org/10.1038/s41598-019-43301-8

116. Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *The Behavioral and Brain Sciences*, *1*(4), 515–526. https://doi.org/10.1017/S0140525X00076512

117. Price, T., Wadewitz, P., Cheney, D., Seyfarth, R., Hammerschmidt, K., & Fischer, J. (2015). Vervets revisited: a quantitative analysis of alarm call structure and context specificity. *Scientific Reports*, *5*(1), 13220–13220. https://doi.org/10.1038/srep13220

118. Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society. B, Biological Sciences*, *267*(1456), 1947–1952. https://doi.org/10.1098/rspb.2000.1234

119. Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

120. Quintero, F., Touitou, S., Magris, M., & Zuberbühler, K. (2022). An audience effect in Sooty Mangabey alarm calling. *Frontiers in Psychology*, *13*, 816744–816744. https://doi.org/10.3389/fpsyg.2022.816744

121. Rabanal, L. I., Kuehl, H. S., Mundry, R., Robbins, M. M., & Boesch, C. (2010). Oil prospecting and its impact on large rainforest mammals in Loango National Park, Gabon. *Biological Conservation*, *143*(4), 1017–1024. https://doi.org/10.1016/j.biocon.2010.01.017

122. Reed, P. E., Mulangu, S., Cameron, K. N., Ondzie, A. U., Joly, D., Bermejo, M., Rouquet, P., Fabozzi, G., Bailey, M., Shen, Z., Keele, B. F., Hahn, B., Karesh, W. B., & Sullivan, N. J. (2014). A new approach for monitoring ebolavirus in wild great apes. *PLoS Neglected Tropical Diseases*, *8*(9), e3143–e3143. https://doi.org/10.1371/journal.pntd.0003143

123. Rendall, D. (2003). Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. *The Journal of the Acoustical Society of America*, *113*(6), 3390–3402. https://doi.org/10.1121/1.1568942

124. Rendall, D., Seyfarth, R. M., Cheney, D. L., & Owren, M. J. (1999). The meaning and function of grunt variants in baboons. *Animal Behaviour*, *57*(3), 583–592. https://doi.org/10.1006/anbe.1998.1031

125. Rumbaugh, D. M. (1977). *Language learning by a chimpanzee: the Lana project*. Academic Press. https://doi.org/10.1016/C2013-0-11427-4

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

127. Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

128. Schino, G., & Aureli, F. (2010). A few misunderstandings about reciprocal altruism. *Communicative & Integrative Biology*, *3*(6), 561–563. https://doi.org/10.4161/cib.3.6.12977

129. Schino, G., & Pellegrini, B. (2009). Grooming in mandrills and the time frame of reciprocal partner choice. *American Journal of Primatology*, *71*(10), 884–888. https://doi.org/10.1002/ajp.20719

130. Scott, N. M. (2013). Gesture use by chimpanzees (*Pan troglodytes*): differences between sexes in inter- and intra-sexual interactions. *American Journal of Primatology*, *75*(6), 555–567. https://doi.org/10.1002/ajp.22133

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

132. Slocombe, K. E., & Zuberbühler, K. (2005). Functionally referential communication in a chimpanzee. *Current Biology*, *15*(19), 1779–1784. https://doi.org/10.1016/j.cub.2005.08.068

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

134. Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., & Zuberbühler, K. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology*, *64*(12), 1959–1966. https://doi.org/10.1007/s00265-010-1006-0

135. Slocombe, K. E., Lahiff, N. J., Wilke, C., & Townsend, S. W. (2022). Chimpanzee vocal communication: what we know from the wild. *Current Opinion in Behavioral Sciences*, *46*, 101171–. https://doi.org/10.1016/j.cobeha.2022.101171

136. Southern, L. M., Deschner, T., & Pika, S. (2021). Lethal coalitionary attacks of chimpanzees (*Pan troglodytes troglodytes*) on gorillas (*Gorilla gorilla gorilla*) in the wild. *Scientific Reports*, *11*(1), 14673–14673. https://doi.org/10.1038/s41598-021-93829-x

137. Spira, C., Kirkby, A., Kujirakwinja, D., & Plumptre, A. J. (2019). The socio-economics of artisanal mining and bushmeat hunting around protected areas: Kahuzi–Biega National Park and Itombwe Nature Reserve, eastern Democratic Republic of Congo. *Oryx*, *53*(1), 136–144. https://doi.org/10.1017/S003060531600171X

138. Strindberg, S., Maisels, F., Williamson, E. A., Blake, S., Stokes, E. J., Aba'a, R., Abitsi, G., Agbor, A., Ambahe, R. D., Bakabana, P. C., Bechem, M., Berlemont, A., de Semboli, B. B., Boundja, P. R., Bout, N., Breuer, T., Campbell, G., De Wachter, P., Akou, M. E., … Fotso, R. (2018). Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. *Science Advances*, *4*(4), eaar2964–eaar2964. https://doi.org/10.1126/sciadv.aar2964

139. Suzuki, T. N. (2014). Communication about predator type by a bird using discrete, graded and combinatorial variation in alarm calls. *Animal Behaviour*, *87*, 59–65. https://doi.org/10.1016/j.anbehav.2013.10.009

140. Taylor, A., Charlton, B., & Reby, D. (2016). Vocal production by terrestrial mammals: source, filter, and function. In Suthers, R. A., Fitch, W. T., Fay, R. R., & Popper, A. N. (Eds.). (2016). *Vertebrate Sound Production and Acoustic Communication* (1st ed. 2016.). Springer International Publishing. https://doi.org/10.1007/978-3-319-27721-9

141. Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-Capped Chickadees encode information about predator size. *Science*, *308*(5730), 1934–1937. https://doi.org/10.1126/science.1108841

142. Townsend, S. W., & Manser, M. B. (2013). Functionally referential communication in mammals: the past, present and the future. *Ethology*, *119*(1), 1–11. https://doi.org/10.1111/eth.12015

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

144. Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*(1), 35–57. https://doi.org/10.1086/406755

145. Tutin, C. E. G., & Fernandez, M. (1993). Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé reserve, Gabon. *American Journal of Primatology*, *30*(3), 195–211. https://doi.org/10.1002/ajp.1350300305

146. Walsh, P. D., Abernethy, K. A., Bermejo, M., Beyers, R., De Wachter, P., Akou, M. E., Huijbregts, B., Mambounga, D. I., Toham, A. K., Kilbourn, A. M., Lahm, S. A., Latour, S., Maisels, F., Mbina, C., Mihindou, Y., Ndong Obiang, S., Effa, E. N., Starkey, M. P., Telfer, P., … Wilkie, D. S. (2003). Catastrophic ape decline in western equatorial Africa. *Nature (London)*, *422*(6932), 611–614. https://doi.org/10.1038/nature01566

147. Walsh, P. D., Breuer, T., Sanz, C., Morgan, D., & Doran-Sheehy, D. (2007). Potential for Ebola transmission between gorilla and chimpanzee social groups. *The American Naturalist*, *169*(5), 684–689. https://doi.org/10.1086/513494

148. White, D. J., King, A. P., Cole, A., & West, M. J. (2002). Opening the social gateway: early vocal and social sensitivities in Brown-Headed Cowbirds (*Molothrus ater*). *Ethology*, *108*(1), 23–37. https://doi.org/10.1046/j.1439-0310.2002.00755.x

149. Wich, S. A., & Sterck, E. H. M. (2003). Possible audience effect in Thomas Langurs (*Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology*, *60*(4), 155–159. https://doi.org/10.1002/ajp.10102

150. Wich, S. A., Garcia-Ulloa, J., Kühl, H. S., Humle, T., Lee, J. S. H., & Koh, L. P. (2014). Will oil palm's homecoming spell doom for Africa's great apes? *Current Biology*, *24*(14), 1659–1663. https://doi.org/10.1016/j.cub.2014.05.077

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

152. Williams, J. M., Lonsdorf, E. V., Wilson, M. L., Schumacher-Stankey, J., Goodall, J., & Pusey, A. E. (2008). Causes of death in the Kasekela chimpanzees of Gombe National Park, Tanzania. *American Journal of Primatology*, *70*(8), 766–777. https://doi.org/10.1002/ajp.20573

153. Wright, G. S., Chiu, C., Xian, W., Wilkinson, G. S., & Moss, C. F. (2014). Social calls predict foraging success in Big Brown Bats. *Current Biology*, *24*(8), 885–889. https://doi.org/10.1016/j.cub.2014.02.058

154. Zaccaroni, M., Binazzi, R., Massolo, A., & Dessì-Fulgheri, F. (2013). Audience effect on aerial alarm calls in the monogamous red-legged partridge. *Ethology, Ecology & Evolution*, *25*(4), 366–376. https://doi.org/10.1080/03949370.2013.798352

155. Zuberbühler, K. (2002). A syntactic rule in forest monkey communication. *Animal Behaviour*, *63*(2), 293–299. https://doi.org/10.1006/anbe.2001.1914

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

157. Zuberbühler, K. (2017). The primate roots of human language. In R. M. Quam, M. A. Ramsier, R. R. Fay, & A. N. Popper (Eds.), *Primate Hearing and Communication* (pp.

175–200). Springer International Publishing. https://doi.org/10.1007/978-3-319-59478-1_7

158. Zuberbühler, K., Noë, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour*, 53(3), 589–604. https://doi.org/10.1006/anbe.1996.0334