Communication in Chimpanzees: Vocalisations, Gestures and Joint Attention

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ABSTRACT

Studying the communicative system of chimpanzees, one of our closest living relatives, is a critical approach to gain insight into how the human language system may have evolved (Fitch, 2017). Current empirical data is constrained due to the customary use of single-site research samples and a focus on the communication of adult males. Moreover, there has been little investigation into the ontogeny of communication, and fair cross-species comparisons are currently lacking. I sought to redress these issues across three empirical chapters. Chapter 2 investigated a functionally referential food-associated call in five communities of wild chimpanzees, testing the social and ecological correlates of rough grunt production in adult males, females and non-adult individuals. Rough grunt production was found to vary according to community, sex, age, ecological and social factors. Chapter 3 then tested the claim for a natural referential gesture in chimpanzees, the 'exaggerated loud scratch' (Pika & Mitani, 2006). My data revealed that a referential function for this gesture was unique to the Ngogo community, and therefore not ubiquitous to the species. Finally, chapter 4 focused on whether engagement in joint attention events is uniquely human by experimentally presenting novel stimuli to dyads of humans (from the UK and Uganda), wild chimpanzees and Sulawesi crested macaques. All three species engaged in joint attention events, though humans were most likely to engage in them and demonstrated more of the component behaviours required for visually mediated joint attention to occur (e.g. communication). Collectively, my findings emphasise the importance of representative samples across age, sex and populations, in order to fully understand the behaviour of non-human species. Comparative methods are essential to understanding human language origins, but greater collaboration between research groups, disciplines and study sites will be critical to advance our knowledge of how our unique communication system evolved.

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AUTHOR'S DECLARATION

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

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CHAPTER 1: General introduction

The emergence of language marked a defining moment in human evolutionary history. As the most powerful communication system in the animal kingdom, it has been remarked to be a hallmark of the human species (Christiansen & Kirby, 2003) and supports other complex cognitive processes that are intrinsic to what makes us human. Given the multifaceted nature of language, analysing the component parts of this system has been critical in order to forge progress in our understanding of its origins and inner workings (Fitch, 2017). With modern advances we now understand more about how language components develop, and the brain mechanisms which underpin the production and reception of language (Friederici, 2017). In comparison however, the evolutionary origins of language remain relatively obscure.

Investigating the evolutionary origins of language with a comparative approach

For centuries, the question of how language evolved has been a subject of debate between scholars (e.g. Fiske, 1863), and it is still regarded by many as "the hardest problem in science"(Christiansen & Kirby, 2003, p.1). As spoken language leaves no artefacts or physical remains, tracing its origins requires cross-disciplinary research efforts with genetics, linguistics, computer modelling, psychology and paleo-anthropology all contributing valuable knowledge. One particularly powerful approach is to compare human behaviour to that of other species; focussing such a comparative approach on our closest living relatives in the primate family allows us to draw inferences about the capabilities of our extinct ancestors (Hauser, Chomsky, & Fitch, 2002). Living species are a rich source of data to test hypotheses regarding the evolution of specific language traits. Indeed, comparative evidence has been highly influential in the building of theoretical accounts of language origins, and particularly whether proto-language may have emerged in our hominid ancestors in the vocal or gestural domain (reviewed in: Fitch, 2010; Prieur, Barbu, Blois-Heulin, & Lemasson, 2020). Whether non-humans demonstrated key characteristics of language (e.g. syntax, intentional signal production) or rudimentary versions of them in their gestural or vocal communication formed an important basis for vocal and gestural theories of language origin. However, it has been highlighted more recently that gestural and vocal studies with primates typically adopted different methodological and theoretical approaches, which questioned the validity of many vocal-gestural comparisons (Slocombe, Waller, & Liebal, 2011). It is increasingly acknowledged that primate communication, like human language, is inherently multimodal, leading more scholars to argue for a multimodal origins of language (Fröhlich, Sievers, Townsend, Gruber, & van Schaik, 2019; Prieur et al., 2020).

Within the comparative approach, chimpanzees, as one of our closest living relatives, are particularly crucial evolutionary models for understanding human origins (Byrne, 2000; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Rosati, 2016; Tomasello, 2014). Identifying homologous traits in chimpanzee communication can provide insight into whether primitive versions of language characteristics were likely present in our last common ancestor 5-7 million years ago (Enard & Pääbo, 2004). Aside from homologies, identifying differences between our communication systems is equally important to ascertain when and why traits emerged in evolutionary history (Fitch, 2010; Penn, Holyoak, & Povinelli, 2008). The focus of this thesis will be to examine aspects of chimpanzee communication and social cognition to bridge gaps in the current literature, and facilitate our understanding of the evolution of language.

Using a comparative approach to study components of the language system

As language is unique to humans, studying the component parts of language is critical to gain insight into its origins (Fitch, 2017). However, currently no universally acknowledged list of language components exist (Fischer & Price, 2017). Typical linguistic approaches may consider components such as semanticity, phonology, syntax or auditory memory (Fishbein, Fritz, Idsardi, & Wilkinson, 2019; Fitch, 2010). Here I will consider how two of these traits have been studied using a comparative perspective: syntax and semanticity.

Syntax can be defined as the composition of communicative signals into meaning-based units according to specific rules, and has been considered a central component of the language system (Chomsky, 1957; Fitch, 2011). Some scholars argue that the complex computations required for syntax are absent in non-humans, with the mechanisms responsible for such cognition developing after our split from other primates (reviewed by Zuberbühler, 2019a). Artificial grammar studies, experiments that test subjects on sequences of stimuli that comply with (or breach) grammatical rules, are one popular methodology used to investigate the syntactic abilities of non-humans. These paradigms have historically found that while animal models can learn linear rules, they tend to fail to comprehend hierarchically organised grammar rules which characterise human language (e.g. Fitch & Hauser, 2004; Wilson, Smith, & Petkov, 2015). However, a more recent artificial grammar study has challenged this view, and revealed some similarities between marmoset, chimpanzee and human's ability to process 'non-adjacent dependencies' which requires tracking the relationships between signals over distances (Watson et al., 2021). For example, when reading the sentence "the man walking the dog fell over" we can understand that "fell over" was related to "the man" and not "the dog". This finding suggests that this type of computational processing may actually have ancestral origins as far back as 40 million years ago. However, as these studies often present stimuli absent of meaning they are not an accurate reflection of natural communication where syntax and semantics are interlinked (Zuberbühler, 2019b). When natural communication has been examined, it's been found that birdsong and non-human primate vocalisations show evidence of compositional syntax (reviewed in: Leroux & Townsend, 2020; Suzuki, Wheatcroft, & Griesser, 2019; Zuberbühler, 2019b). For example, black-fronted titi monkeys have two alarm calls: 'A-calls' are produced mostly to aerial threats and 'B-calls' are elicited by terrestrial threats and other disturbances. Sequences of A- and B-calls then denote both the type of threat and the location of the predator (e.g. an aerial predator on the ground; Cäsar, Zuberbühler, Young & Byrne, 2013). The combinatorial capacity of these monkeys is potentially unique too, as the signal meaning here is encoded by the proportion of calls rather than the order that the calls are produced in (Berthet et al., 2019). In these studies, the underlying mental processes happening here are often unaddressed, so currently only surface features of natural signals appear to hold syntactic qualities (Zuberbühler, 2019a). Despite this, the signal combinations produced by other animals can still be fruitfully compared to human syntax, and research on natural communication systems is required to provide the essential groundwork needed to elucidate the evolutionary origins of human syntactic abilities (Townsend, Engesser, Stoll, Zuberbühler, & Bickel, 2018).

Concerning semanticity, comparative work focuses on referential signals; a subset of semantic signals that convey information about events or objects in the environment. Seminal work with predator-specific vervet monkey alarm calls was the first to suggest that non-human vocalisations could convey information about the external world to listeners (Seyfarth, Cheney, & Marler, 1980; Struhsaker, 1967). These calls were then termed 'functionally referential' (Macedonia & Evans, 1993) since it is unknown what information listeners may comprehend from these calls (e.g. declarative "Leopard!" vs imperative "climb a tree"). Identification of functionally referential signals requires two key criteria to be met: (1) the signal is discrete and reliably produced in response to a specific event or object (context specificity); and (2) listeners need to respond to the signal in an adaptively appropriate manner (similar to the manner in which they would respond to directly perceiving the object or event referenced in the signal). While observational data on the context of signal production is sufficient to fulfil the first criteria, playback experiments are held as the gold standard to assess listener responses as they exclude other cues that may influence behaviour in response to naturally occurring calls (e.g. direct perception of the event; non-communicative reactions of others who have perceived the event). Vocalisations meeting these criteria have been recorded in a large variety of avian and mammalian species, primarily during predation contexts (see reviews: Gill & Bierema, 2013; Townsend & Manser, 2013). Functionally referential signals differ from human linguistic reference on a number of levels, leading some to question the utility of these signals for understanding language evolution (Wheeler & Fischer, 2012). Perhaps most notably, no assumptions or tests of the mechanisms driving the production of functionally referential signals are made, meaning that in contrast to humans, non-human signallers may therefore be inadvertently providing information to audience members they never intended to provide (Liebal, Waller, Burrows, & Slocombe, 2013). Alarm-calls in particular have been argued to be representative of emotional states rather than intentional efforts to communicate (Tomasello, 2008). Recent empirical tests of this claim have however shown that some alarm calls in chimpanzees meet key markers of intentional production (Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013), and functionally referential calls from non-alarm contexts have also been documented. For instance, chimpanzee rough grunts, which are produced in response to food, hold qualities that make them a particularly robust example of a functionally referential vocalisation (Townsend & Manser, 2013). Rough grunts occur almost exclusively during feeding contexts (Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013), and a playback study has confirmed that they elicit appropriate foraging behaviour from listeners (Slocombe & Zuberbühler, 2005). In addition, rough grunt production seems to be modulated by relatively complex audience effects (Fedurek & Slocombe, 2013; Kalan & Boesch, 2015; Slocombe et al., 2010) which is one marker of intentional usage (Townsend et al., 2017). Lately, some scholars have argued that amendments should be made on how functionally referential signals are defined, including that signallers should be actively (not automatically) indicating external objects or entities to their audience, and therefore that signals should be under voluntary control (Sievers & Gruber, 2016). This proposal aims to bridge the gaps between functional reference and human referential signals by offering more consideration to the psychological mechanisms involved in signal production. More research is needed to understand to what extent non-human signals can meet these new criteria, but at a minimum this concept as currently defined remains a useful tool to ascertain what signals refer to, despite not fully encompassing the cognitive processes underlying signaller and receiver behaviour (Townsend & Manser, 2013).

Besides functionally referential vocalisations, gestural signals have also been reported to hold referential qualities. Importantly, gestural signals tend to demonstrate the markers of intentionality that are rare in vocal behaviour (Byrne et al., 2017; Hobaiter & Byrne, 2014). In contrast to vocal studies, where the term ‘functional reference’ was applied to acknowledge that these calls were not a direct comparison to human reference (Macedonia & Evans, 1993), studies of reference in gestural signals began with direct comparisons to human pointing (Fröhlich, Sievers, Townsend, Gruber & van Schaik, 2019). The production of pointing gestures in non-humans have been extensively studied, with positive evidence for intentional referential pointing production being most prevalent in captive apes with human partners (reviewed in Krause, Udell, Leavens, & Skopos, 2018). Accounts of wild apes pointing with conspecifics exist, but are limited to anecdotal reports with only a handful of cases despite decades of continuous observation of wild populations (chimpanzees: Hobaiter, Byrne, & Leavens, 2014; bonobos: Veà & Sabater-Pi, 1998). Naturalistic occurrences of other deictic gestures have been documented (e.g. Genty & Zuberbühler, 2014), but are again rare. The chimpanzee 'exaggerated loud scratch' is the single natural gesture in chimpanzees that has been claimed to habitually function in a referential manner, by indicating the location on the signaller's body they wish to receive grooming (Pika & Mitani, 2006). These findings originate from a single community of chimpanzees, but as chimpanzees can show substantial community level differences in behaviour (Kalan et al., 2020; Whiten et al., 1999), claims for a ubiquitous referential gesture in this species requires a wider cross-site comparison to be conducted. However, since the gestures of great apes tend to exhibit more markers of intentionality and greater flexibility in production than vocalisations (Liebal et al., 2013), research effort into referential gestures may be more likely to uncover parallels in the underlying mechanisms between human and non-human referential signals.

Using a comparative approach to study aspects of social cognition

Studying language components such as reference with non-human primates can allow for inferences to be made about the communicative capacities of our common ancestors, but understanding the social cognition that underpins human communication has been argued to be crucial in order to ascertain why language is a uniquely human capacity (Scott-Phillips, 2014). Most human utterances are inherently ambiguous in meaning, and social cognition is fundamental for integrating contextual information and our understanding of others to ultimately understand the signaller's intended meaning. Several cognitive mechanisms are said to be responsible for underpinning the sophistication of human communication, but this section will focus on two aspects which can be fruitfully investigated within a comparative approach: the extent to which non-humans demonstrate intentionality in signal production, and an ability to engage in joint attention.

The act of purposefully sharing information, intentional signalling or 'Gricean' communication (Grice, 1957, 1982), has been expressed to be the "heart of the difference between human and animal communication" (Brinck, 2001, p. 259). In humans initial signs of intentional communication like pointing gestures are considered to be vital to linguistic development (Tomasello, Carpenter, Call, Behne, & Moll, 2005). In the comparative literature Dennett's (1983) intentionality framework has been applied to the production of non-human signals, and provides levels that gradually increased in metarepresentational complexity, from zero-order intention to fourth-order. The framework can be explained using alarm-call behaviour as an example; zero-order alarm calls would result from an autonomic arousal response that occurs when a signaller perceives a predator. First-order calls would result when the signaller intends to change the recipient's behaviour e.g. to recruit individuals and elicit group mobbing behaviour of a predator. Second-order calls would result from the signaller understanding the mental states of others, for instance by specifically targeting individuals who are ignorant of a predator's presence to change their mental state from ignorant to knowledgeable. Non-human vocalisations in particular, have traditionally been regarded as zero-order, emotionally driven responses (Tomasello, 2008), and thus identifying first-order communicative acts in non-humans has been a prominent research focus. Gestural researchers have led the way, initially adapting behavioural criteria established to test intentional gestural production in pre-linguistic human infants (Liebal et al., 2013). Across studies, great ape gestures have been shown to meet all the criteria for first order intentional production (Byrne et al., 2017; Cartmill & Byrne, 2007, 2010; Genty, Breuer, Hobaiter, & Byrne, 2009; Hobaiter & Byrne, 2011; Leavens, Hopkins, & Thomas, 2004; Leavens, Hostetter, Wesley, & Hopkins, 2004; Leavens, Russell, & Hopkins, 2005). However, progress here is hampered by a great variability in the number and type of behavioural criteria met before 'intentional' signal production is claimed in individual studies, as well as the questionable validity of some commonly used criteria (Ben Mocha & Burkart, 2021; Graham, Wilke, Lahiff, & Slocombe, 2020). An attempt to unify approaches and offer a framework for identifying first-order intentional signals across different species and modalities was proposed by Townsend et al. (2017). Under this framework first order intentional signals should be i) goal directed, ii) recipient directed and under volitional control, and finally iii) have an impact on recipient behaviour in a way that is conducive to the signal given. These criteria have been successfully applied to some chimpanzee alarm calls. For instance, Schel et al. (2013) showed that chimpanzee 'waa bark' and 'alarm huu' vocalisations (i) ceased when members of the audience noticed or moved away from a snake model, (ii) were rarely produced in the absence of an audience, and were directed at newly arriving or closely affiliated conspecifics. While (iii) recipient responses were not addressed directly by Schel et al. (2013), it has been reported elsewhere that chimpanzees respond to these alarm calls similarly to a natural encounter with a snake (Crockford, Wittig, & Zuberbühler, 2015). Though debates continue concerning the most robust evidence required to distinguish first-order from zero-order intentional signal production, there is mounting evidence that gestural and vocal signals can be produced with some degree of intentionality.

Although great apes do seem to produce signals to change behaviour in others (first-order intentional signal production), whether non-human communicative signals are mediated by a recipient's mental state (second-order intentional signal production) remains highly contentious. Extensive theory of mind research in our closest primate relatives has ascertained that they can understand the goals and intentions of others, and when competitive paradigms with conspecifics are implemented they understand the perceptions and knowledge of others as well (reviewed in Call & Tomasello, 2008). For example, when presented with two food options, subordinate chimpanzees preferentially choose the food that dominant individuals either do not witness the placement of or cannot see (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008). Recent research implementing eye-tracking technology and anticipatory looking paradigms has even suggested that great apes have an implicit understanding of others' false beliefs (Kano, Krupenye, Hirata, Tomonaga, & Call, 2019; Krupenye, Kano, Hirata, Call, & Tomasello, 2016). Although these studies demonstrate that great apes have an awareness of conspecific mental states, the degree to which such understanding of knowledge states influences their signal production requires separate investigation. One study on wild chimpanzees has reported that soft huu alarm calls are produced more often when listeners are ignorant or know less about a threat (Crockford, Wittig, Mundry, & Zuberbühler, 2012). However, lower level explanations for these findings have not been convincingly ruled out, and other researchers at the same field site found that the same call type was best characterised as being produced with zero-order intentionality (Schel et al., 2013). Given the theoretical importance of intentional signal production in shedding light on the evolution of language, a unified approach between modalities and research groups is essential to further our understanding.

Joint attention, when two or more individuals share attention about an object or event, is another social cognitive ability that is intrinsically connected to language. Joint attention skills have repeatedly been linked to language development in humans (e.g. Cochet & Byrne, 2016), and have been theorized to scaffold language acquisition and the development of other social cognition such as theory of mind abilities (Bettle & Rosati, 2021). The relationship between joint attention and later language skills in development has led to suggestions that from an evolutionary perspective, joint attention may have been a social precondition for language (Christiansen & Kirby, 2003), with the emergence of joint attention contributing to the uniqueness of the human socio-cognitive system. Thus, a clear understanding of joint attentional mechanisms is essential in forwarding our understanding of the origins of human communication. However, the lack of a universal definition for this concept and diverging operational criteria obstruct meaningful comparisons between studies (Gabouer & Bortfeld, 2021; Graham, Buryn-Weitzel, Lahiff, Wilke, & Slocombe, 2021), and particularly hampers cross-species work. For instance, joint attention events which are defined as 'gaze alternation between social partners and an object' often afford positive results in chimpanzees (e.g. Bard, Bakeman, Boysen, & Leavens, 2014; Pitman & Shumaker, 2009). Whereas stricter definitions that additionally require communicative signalling (to indicate an active sharing of attention; Carpenter & Liebal, 2011) fail to identify any evidence of these exchanges in chimpanzees (e.g. Tomonaga et al., 2004). An additional issue is that captive animals are often tested using unrealistic paradigms with human partners, and are then compared to human children tested with conspecifics. Carpenter, Tomasello and Savage-Rumbaugh (1995) for instance, presented chimpanzee and human infants with novel objects, and required repeated gaze alternation between the objects and the experimenters face to be considered as a joint attentional episode. However, such a paradigm assumes that chimpanzees would have the same motivation to share attention with a heterospecific partner as humans would with a conspecific partner, therefore the differences identified between species may be exaggerated. Since captive primates also have an elevated risk of impaired socio-cognitive development (Bard & Leavens, 2014), they are at an automatic disadvantage in studies like this compared to their human counterparts. In order to fairly assess the social cognitive abilities of non-human species, it's crucial to examine wild individuals tested in their natural environment with conspecifics. Currently, research on joint attention lacks these data, and I would argue the current species-level confounds in available data prevents valid assessments of whether this is a uniquely human ability.

Common limitations of comparative research on communication and social cognition

While a comparative approach is a powerful method to tackle questions regarding language origins (Hauser et al., 2002), various issues have allowed for gaps in our understanding to emerge. This section will now provide an overview of several common shortcomings within comparative communication and social cognition research; namely the use of single site studies, male-centric data, and a lack of direct comparability between species. Chimpanzees, as the focus of this thesis, will be used as the example animal model for this discussion.

Firstly, most published research on non-human primate communication and social cognition reports data from a single population of animals and then, either implicitly or explicitly, generalises those population-specific findings to the species as a whole. Many animals, however, show extensive within-species diversity, which may make the extrapolation of single population findings to the species problematic. Chimpanzees for instance show significant cultural variation between communities (Koops, Schöning, Isaji, & Hashimoto, 2015; Whiten et al., 1999), which can stem from the diverging environmental conditions experienced by groups (Koops, McGrew, & Matsuzawa, 2013). Chimpanzees have a wide geographic range across equatorial Africa, and occupy diverse habitats from savannah woodland to dense tropical rainforest. The subsequent variation in seasonality, climate and foraging opportunities leads to considerable population-level differences in behaviours that are adaptive to local conditions, such as tool-use propensity (Byrne, 2007; Kalan et al., 2020). When communities do exhibit the same behaviours, there can also be subtle differences in the execution of the behaviour, such as techniques used for termite-fishing (Boesch et al., 2020). The impact this has on communicative behaviour has been relatively unexplored, as most studies report data from single communities (Pika & Deschner, 2019). For example, investigations into the meaning of wild chimpanzee gestures are almost exclusively taken from the Sonso community (Byrne et al., 2017; Graham, Hobaiter, Ounsley, Furuichi, & Byrne, 2018; Hobaiter & Byrne, 2014; Roberts, Vick, & Buchanan-Smith, 2012, 2013). Whilst similarities between gestural repertoires and meanings within the great apes (Byrne & Cochet, 2017) have led to suggestions that gesture form and function may be innately constrained (Byrne et al., 2017), the possibility of population-specific variation in gesture meaning within species remains, and requires empirical investigation. Indeed, we can only have confidence that findings are generalisable to the species if they are replicated in multiple populations or a multiple-site approach is taken within a single study. Demonstrating absence or ubiquity of a communication facet in a species is crucial to understand continuities between human and non-human systems (Hauser et al., 2002), and is only truly possible with extensive cross-site comparisons.

The search for findings that are representative of a species not only requires data from multiple populations, but also findings that consider all age-sex classes. Considering the two sexes first, pervasive sex differences exist in many species (Janicke, Häderer, Lajeunesse, & Anthes, 2016), and the life histories of male and female chimpanzees differ considerably. Their fission-fusion communities are characterized by male dominance hierarchies, with males typically defending the groups territory (Goodall, 1986). Males and females show different foraging patterns (Bates & Byrne, 2009; Wrangham & Smuts, 1980), and show distinct sex differences in their sociality (Gilby & Wrangham, 2008) with females tending to be less gregarious and spending time primarily with their offspring (Murray, Mane, & Pusey, 2007; Thompson, Kahlenberg, Gilby, & Wrangham, 2007). Regarding communication, adult males are more vocal than adult females (Slocombe & Zuberbühler, 2010), which can make it difficult to explore the function of comparatively rare female vocalisations, such as pant hoots (Clark & Wrangham, 1993; Notman & Rendall, 2005). This has, however, resulted in exclusively male data concerning both pant hoot and rough grunt production being generalised to chimpanzees as a species. Some studies do focus specifically on female signalling behaviour (e.g. Laporte & Zuberbühler, 2010), or include female individuals but do not examine potential sex-differences in their behaviour (e.g. Kalan & Boesch, 2015; Schel et al., 2013). Not comparing male and female behaviour is also problematic as the fitness consequences of communication could also be vastly different for male and female individuals. For instance, male chimpanzee rough grunts have been hypothesised to function as a means to maintain proximity with affiliated individuals in the feeding patch (Fedurek & Slocombe, 2013), but the impact of advertising food sources on nutritional intake may be costlier for reproductive females than for adult males. Overall, a male-centric literature can promote assumptions that adult male behaviour alone is representative of the species, but we should not assume that the same social and ecological factors affect behaviour of males and females in the same way: we should test the idea explicitly with data.

As well as potential sex differences, it's equally important to consider whether behaviours may differ between age demographics. Despite the importance of an ontogenetic approach to understanding behaviour (Tinbergen, 1963), developmental studies in wild chimpanzees are rare. Their general life history is relatively well-documented (e.g. physical growth, age of weaning, age of independence), but data on behavioural and communicative development in wild populations is more limited

(Lonsdorf et al., 2014). Currently we know that infant chimpanzee communication shifts from a predominantly vocal, to a predominantly gestural means (Fröhlich, Wittig, & Pika, 2016), and that infants can show both flexibility and intentionality in their signal production (Dezecache, Zuberbühler, Davila-Ross, & Dahl, 2021; Fröhlich, Wittig, & Pika, 2019). Age-related changes also occur within modalities, as infant chimpanzees produce gestures more often than juvenile or sub-adults, whereas vocal production increases with age between juvenility to adulthood (Hobaiter, Byrne, & Zuberbühler, 2017). However the vast majority of data concerning the communication or social-cognitive systems of our closest primate relatives focuses on adult individuals (Liebal et al., 2013). Furthermore, many of the developmental studies that do exist have focused on captive-born individuals (e.g. Bard et al., 2014) who are not exposed to natural selection pressures, and may have impaired social-cognitive skills (Bard & Leavens, 2014; Leavens, Bard, & Hopkins, 2010). Ontogenetic data sourced from wild populations is crucial in order to assess the developmental trajectories of signal production and reception across modalities, as well as the underlying psychological mechanisms involved. Ultimately, such data will further our understanding of how and to what extent non-human communication systems differ from human language.

Finally, even with multi-site data and representative study populations, the ability to trace back behaviours in our evolutionary history will not be possible unless studies are conducted in a manner that facilitates meaningful cross-species comparisons. Species comparisons implementing directly comparable methods are rare, and when direct species comparisons are conducted, too often the paradigm designed for humans is simply given to the non-humans without consideration for its ecological validity. This commonly means that non-humans are expected to interact with a member of a different species, and their performance compared to that of humans interacting with a member of their own species. For example, when testing for altruistic helping behaviour Warneken and Tomasello (2006) required chimpanzees to understand the goals and intentions of their human caregivers. Although chimpanzees retrieved some objects that had fallen out of reach of the human caregiver they, perhaps unsurprisingly, did not help humans achieve goals related to stacking objects or putting objects in cupboards, leading to the conclusion that chimpanzees were less altruistic than 18-month old children. However, implementing a study design without consideration for the natural behaviour of the species can lead to underestimations of capacities. When faced with conspecifics with an ecologically relevant goal of obtaining out of reach food, chimpanzees helped others attain food, and were even willing to help others obtain out of reach tokens, the value of which was unknown to the helper (Melis et al., 2011). Underestimation of chimpanzee abilities using cross-species designs is also apparent in theory of mind research. Povinelli and Eddy (1996) for instance, when testing whether chimpanzees preferentially use begging gestures with attending vs not attending cooperative human experimenters, found that chimpanzees did not always differentiate between an experimenter who could perceive their gesture versus one who could not. These findings led the authors to deduce that chimpanzees fail to show any socio-cognitive understanding of what others can or cannot see. However as mentioned earlier, Hare, Call and Tomasello (2001) were able to show that chimpanzees can understand what other individuals see by implementing a competitive foraging paradigm between conspecifics. By adopting a methodology that was sensitive to species-typical behaviour, a more accurate interpretation of this primate's cognitive abilities could be made.

The current thesis

This thesis aimed to investigate the communication and joint attention abilities of chimpanzees with a view to generating representative data to contribute to our understanding of chimpanzee social-cognition and communication, and the evolutionary roots of human language. To address the limitations that have previously marred comparative research, this thesis includes data from six different chimpanzee communities and offers consideration to individuals from all demographic classes (i.e. males and females, from infancy to adulthood) in three empirical chapters. In this thesis I also include data from Sulawesi crested macaques and human infants as a comparison to chimpanzee social-cognitive skills. To do this I have created a robust species-appropriate paradigm that allows for direct between-species comparisons. Furthermore, both non-human species were represented by wild populations, and I included a diverse human sample from the UK and Uganda who were tested in their own homes. This allowed each species the fair opportunity to demonstrate these skills in their natural environments.

Chapter 2 will see an examination of the ecological and social correlates that modulate the production of food-associated calls in chimpanzees. As discussed earlier, chimpanzee 'rough grunts' have been suggested as a robust example of a functionally referential vocalisation produced during feeding (Townsend & Manser, 2013). The production of these calls in males appears to be modulated by several variables, including the size or quality of the food source (Brosnan & de Waal, 2001; Hauser & Wrangham, 1987; Slocombe et al., 2010) and the presence of important social partners (e.g. closely affiliated individuals or high ranking individuals; Slocombe et al., 2010; Schel et al., 2013). In males therefore, it's been theorized that the provision of information regarding the food source may act as a commodity between social partners, and that these calls may function to facilitate social bonding (Slocombe et al., 2010; Schel et al., 2013) or to coordinate feeding behaviour and retain proximity to affiliated individuals (Fedurek & Slocombe, 2013). However, the production of food-associated calling in chimpanzees has traditionally only been examined in adult male individuals, and therefore whether this function can be validly generalised to other demographic classes is unknown. The aim of this chapter was to redress this issue by investigating the production of rough grunts in adult males and females, and also by examining the ontogeny of this behaviour in young chimpanzees. Given the considerable diversity in habitat ecology and behaviour between chimpanzee communities (Kalan et al., 2020), this chapter included data from five wild populations to avoid a premature assumption that the function for this behaviour is uniform between populations.

Chapter 3 will reexamine the sole claim for a habitually used naturally occurring referential gesture in chimpanzees, the exaggerated loud scratch (Pika & Mitani, 2006). In the Ngogo community this gesture was suggested to be used by signallers to refer to the area on their body that they wished their partner to groom (Pika and Mitani, 2006). This claim is important as it suggests continuity between the referential abilities of humans and our closest primate relative. However, Pika & Mitani (2006) provide no interobserver reliability checks on their data and their sample was limited to male-male dyads and to a single community, therefore whether a referential function is ubiquitous to the species is unknown. In addition, several alternative functions for this gesture have been suggested in the literature, including to initiate grooming bouts (Goodall, 1986; Hobaiter & Byrne, 2014) or as a marker of social anxiety (Baker & Aureli, 1997; Botero, MacDonald, & Miller, 2013). My study therefore examined the referential function of this gesture in three communities alongside the already published data of Pika and Mitani (2006). Whether this gesture fulfilled an alternative function was then examined in detail in the Kanyawara community. This chapter examined data from males and females, with individuals aged from four years old with the goal to obtain a representative sample to investigate the function of this gesture during grooming interactions.

Finally, chapter 4 will then focus on joint attention, a social cognitive ability which has previously been claimed to be uniquely human based primarily upon the failure of non-humans to share attention with heterospecific partners (humans; Tomasello et al., 2005). To provide a fairer, more valid test of the ability to engage in joint attention events, I gave humans, chimpanzees and Sulawesi crested macaques the opportunity to share attention with group members about a novel, interesting stimulus in their natural environment. In the first study, I presented a moving laser light stimulus to 11-month old human infants and their mothers who lived in the UK and Uganda, wild chimpanzee dyads and wild crested macaque dyads. I coded videos of their interactions to ascertain if they engaged in any joint attention events with their partner about the laser. I also sought to assess what may be driving any species differences in engagement in joint attention, by examining each species' propensity to show components of joint attention behaviour (e.g. mutual gaze). In a second study I then presented the non-human primate groups with a range of other novel objects to further probe their motivation to share attention with others. The non-human groups were represented by multiple wild populations, and individuals of all ages were included in varied sex/age class dyads; this avoided premature assumptions of when this behaviour may emerge in the species, and which individuals may be more likely to share attention about an event (e.g. juveniles or adults). The goal of this chapter was to assess whether joint attention events are a uniquely human ability with a directly comparable dataset between species for the first time.

CHAPTER 2: Social and ecological correlates of food-associated calling in male, female and non-adult chimpanzees

ABSTRACT

Investigating non-human vocalisations that function in a referential manner, such as the rough grunt vocalisations of chimpanzees, remains an important avenue of research to address evolutionary questions concerning human language (Sievers & Gruber, 2016; Clay, Smith, & Blumstein, 2012; Townsend & Manser, 2013). While theories for the ultimate function of these calls have been suggested (e.g. Fedurek & Slocombe, 2013), current literature has been limited to a primarily adult-male perspective from single-site studies. However, without representative data from multiple communities and all demographic classes, the evolutionary history of these functionally referential food calls cannot be traced. This study explored the ecological and social correlates of adult male and female rough grunt behaviour in five wild communities of chimpanzees, as well as examining how calling patterns change over development. Male chimpanzees were more likely to produce rough grunts than females in most sites, but considerable community variation mediated the strength and direction of these sex differences. Adult male chimpanzees were more likely to call at larger and higher quality food patches, at feeding events with less females present, and if they had produced a pant hoot during their arrival. Given this, it is suggested that their calls may function to recruit females to a feeding site. Adult females did not show the same ecological or social correlates of calling as males, and the function of their calls remain obscure. Regarding young chimpanzees, it was found that rough grunt production slightly increased with age for male, but not female, individuals into late adolescence. A potential social learning or vocal contagion mechanism appeared to influence the likelihood of juvenile chimpanzees producing rough grunts, with juveniles significantly more likely to call if their mother also called. The findings from this study highlight how imperative it is to assess non-human animal communication in diverse samples in order to fully understand its possible functions.

INTRODUCTION

Many species produce vocalisations upon discovery of food, including avians (Bugnyar, Kijne, & Kotrschal, 2001; Evans & Marler, 1994; Suzuki, 2012), therapsids (Wilkinson & Wenrick Boughman, 1998), cetaceans (Deecke, Nykänen, Foote, & Janik, 2011; King & Janik, 2015) and primates (Hauser & Marler, 1993a; Kitzmann & Caine, 2009; Slocombe & Zuberbühler, 2005). This seemingly paradoxical behaviour tends to attract individuals to food sources which can result in a lower food intake for the initial signaller (Di Bitetti & Janson, 2001). Research has identified several putative benefits of food call production, which may balance the potential costs to the signaller, including reducing the risk of predation during feeding (Elgar, 1986), establishing resource ownership to prevent foraging competition during feeding (Gros-Louis, 2004), and reducing aggression between conspecifics (Hauser & Marler, 1993b; Ischer, Zuberbühler, & Fedurek, 2020). The fitness benefits of attracting conspecifics to a food source likely vary with species (Clay, Smith, & Blumstein, 2012). One useful tool for identifying why food calls are produced in a particular species is to examine the social and ecological correlates of food call production, in terms of the conditions that increase the likelihood of calls being produced, or that influence the structure of the calls produced. This allows an understanding of whether the calls are directed at a specific audience, and indicates the kind of information the calls may contain about the food source (intentionally or unintentionally) for listeners.

Food calling behaviour is highly diverse between species, with numerous ecological characteristics of the food source affecting vocal output, including the quantity, divisibility, type and accessibility of food (reviewed in Clay et al., 2012). For instance, red-bellied tamarins increase calling rates in response to higher quantities and quality of food (Caine, Addington, & Windfelder, 1995), whereas ravens show an increased calling rate in 'Haa' calls in response to specific food types (Bugnyar et al., 2001). Many species seem more likely to emit food calls or call at higher rates when encountering large or divisible food sources (Caine et al., 1995; Di Bitetti, 2005; Hauser & Wrangham, 1987), which mitigates the potential costs to the caller. The systematic variation in food call structure in response to characteristics of the food source also suggests these calls may provide information about the food patch to listeners. Indeed, in a handful of species for which playback experiments have been conducted, listeners have behaved as if food-associated calls referred to either a food source (Kitzmann & Caine, 2009) or a specific type of food source (e.g. high or low value food; Clay & Zuberbühler, 2011; Slocombe & Zuberbühler, 2005). This combination of context-specific production and listeners successfully extracting information from the calls qualifies these signals as functionally referential vocalisations (Macedonia & Evans, 1993), an important type of signal that may shed light on the evolutionary roots of referential signals in human language (see chapter 1).

It is not only ecological variables that influence call production, however. Social correlates of food call production have also been well-documented in a variety of species, indicating that these calls are directed to specific individuals or classes of individuals. For functionally referential food-associated calls this is an important step towards examining whether the calls are produced intentionally (Townsend et al., 2017), which in turn is critical for understanding the similarities and differences between human referential signals and functionally referential signals in non-humans. Audience effects, indicating that signals are directed at a specific class of individual such as kin or the opposite sex, are present in a wide variety of species. For example, common marmosets are more likely to emit vocalisations when family members are absent from the feeding site rather than present, suggesting these calls are used to attract family mates to feeding locations (Vitale, Zanzoni, Queyras, & Chiarotti, 2003). Male chickens call more often in the presence of females (Evans & Marler, 1994; Marler, Dufty, & Pickert, 1986), and pinyon jays alter calling behaviours when their mate is present (Dahlin, Balda, & Slobodchikoff, 2005). Some species show even more refined, tactical targeting of food calls, like brown capuchins who direct their calls to higher-ranking individuals (Pollick, Gouzoules, & De Waal, 2005).

Food calls have been particularly well studied in one of our closest living relatives, chimpanzees. Chimpanzees produce two food-associated calls, 'pant hoots' and 'rough grunts'. Pant hoots are long-distance calls that are individually distinctive (Fedurek, Zuberbühler, & Dahl, 2016). They are produced regularly in a feeding context, but also occur in other contexts (e.g. travelling, displaying), with limited evidence that distinct acoustic variants of the calls are produced in feeding contexts (Clark & Wrangham, 1993; Fedurek et al., 2016; Notman & Rendall, 2005). Within this context, pant hoots often precede rough grunt vocalisations and show combinatorial properties in a syntactic-like structure (Leroux et al., 2021). Signallers were more likely to produce these call combinations during feeding when it was a larger feeding patch, and when new individuals were joining their feeding party. Rough grunts, whether as part of a call combination or produced in isolation, are given almost exclusively in feeding contexts (Schel et al., 2013), and attract conspecifics to the food source (O'Bryan, Lambeth, Schapiro, & Wilson, 2020). Chimpanzee rough grunts are one of the few examples of a food-associated call considered to fulfil referential criteria (see chapter 1; Macedonia & Evans, 1993; Townsend & Manser, 2013), and have therefore often been the focus of research concerning food-associated vocalisations in chimpanzees. Within this call type, there is considerable acoustic variation that seems to vary systematically with ecological variables such as the value or type of food encountered (Kalan, Mundry, & Boesch, 2015; Slocombe & Zuberbühler, 2006), which subsequently results in appropriate foraging behaviour from listeners (Slocombe & Zuberbühler, 2005). Ecological variables also influence the likelihood of call production, with rough grunts produced more for higher quantities of food in captivity (Brosnan & de Waal, 2001; Hauser & Wrangham, 1987) and to larger food patches in the wild, at least when considering male callers (Slocombe et al., 2010).

In terms of the social correlates of food calling, male chimpanzee rough grunts seem to be directed towards specific individuals. In West Africa, high-ranking males from Taï National Park are more likely to produce calls when oestrus females are present (Kalan & Boesch, 2015), but in East Africa male calling was not mediated by oestrus female presence (Slocombe et al., 2010). Attracting mating females to a food patch has been linked to subsequent copulations in other species (Pizzari, 2003; Van Krunkelsven, Dupain, Van Elsacker, & Verheyen, 1996), suggesting direct reproductive benefits in recruiting these individuals to feeding patches. In East Africa, within the Sonso and Kanyawara communities, males are more likely to emit calls when important social partners are in the foraging party (Slocombe et al., 2010), or in close proximity (Fedurek & Slocombe, 2013). Additionally, in Kanyawara, Fedurek and Slocombe (2013) found males were more likely to call when males, but not females were in close proximity to the caller. Field experiments with the Sonso community likewise show that rough grunts are directed to males who are closely bonded to the signaller, but also to males who are higher-ranking than the signaller (Schel et al., 2013). These social correlates of rough grunt production have led to the suggestion that in Eastern male chimpanzees, food calling may function to facilitate social bonding (Schel et al., 2013; Slocombe et al., 2010). The provision of information about food sources may act as a commodity between close social partners, or rough grunts may facilitate social bonding indirectly by facilitating males to coordinate their feeding behaviour and retain proximity to important social partners (Fedurek & Slocombe, 2013). Indeed, research indicates that preferred partners of male chimpanzees remain in the feeding party for longer when the focal male produces rough grunts at the start of the feeding bout, suggesting that these calls prevent group fission and enable socially bonded individuals to remain together (Fedurek & Slocombe, 2013). Additionally, more rough grunts are produced following agonistic interactions (Ischer et al., 2020), a context where keeping bonded partners close is particularly important. These findings suggest that rough grunts may be used as social tools to mediate aggression, or as a strategy to keep important allies close. By providing useful information about food sources rough grunts allow receivers to maximise their foraging efficiency, and male signallers to benefit from increased opportunities to socially bond with important social partners.

While food calling behaviour appears well documented in male chimpanzees, the predominant approach of studying a single community, and the application of different methodologies within individual studies, makes it difficult to directly compare findings. Common variables including patch size, the operationalisation of bonded partners and the time interval examined for calling behaviour are often measured differently across studies. Using different methodologies has sometimes provided a triangulation of results (e.g. patch size affects calling behaviour at both Sonso and Taï south communities despite different ways of measuring patch size: Kalan et al., 2015; Slocombe et al., 2010). However, in other circumstances conflicting reports have occurred (e.g. food type (for example, ripe fruits or leaves) affects calling if only the initial stages of a feeding event is considered, but not if the entire feeding event is examined: Fedurek & Slocombe, 2013; Ischer et al., 2020). Existing research on single communities also reports a slight variation in calling rates across sites, with rough grunts produced in 56-57% of male arrival feeding events at Sonso (Ischer et al., 2020; Slocombe et al., 2010) and 45% of male arrivals at Kanyawara (Fedurek & Slocombe, 2013). In the Taï south community, male and female individuals are reported to call in 41%-60% of entire events (Kalan & Boesch, 2015; Kalan et al., 2015). The varying definitions of what constituted a feeding event and differences in the intervals examined could again explain the variance here. Alternatively, site differences in the literature may be due to genuine population-level variation in chimpanzee vocal behaviour. Chapter 1 provided an overview of how and why chimpanzee behaviour is likely to vary between sites, but aside from the substantial cultural differences already identified between communities (Kalan et al., 2020; Whiten et al., 1999), neighbouring sites within the same forest can also show heterogeneity in habitat ecology (Potts, Watts, & Wrangham, 2011) which could conceivably lead to differences in foraging related behaviour. However, in the absence of multi-community studies implementing identical methods, it is impossible to identify the cause of diverging findings between sites.

Chapter 1 considered the issue surrounding an empirical focus on adult males in the literature, and this issue highly constrains our knowledge of chimpanzee rough grunt production. In contrast to males, there is very little known about female calling behaviour. To elaborate on the discussion in chapter 1, a male-centric approach is problematic here as females are likely to have different ecological and social correlates affecting their behaviour; female reproductive success is directly linked to nutritional intake, whereas males' is dependent on mate availability, thus female foraging decisions can be different from those of males (Bates & Byrne, 2009). For male chimpanzees the potential social benefits of food calling appear to outweigh the costly behaviour of sharing food with individuals attracted to the food source by the calls (Fedurek & Slocombe, 2013; Ischer et al., 2020; Kalan & Boesch, 2015). However, for reproducing females the costs of attracting others to food patches, which may reduce their own nutritional intake, may represent a much larger cost; variance in female fitness has been found to be associated with their access to higher quality foraging (Thompson et al., 2007). Specifically, research has shown that females in neighbourhoods with superior access to food have shorter inter-birth intervals and lower infant mortality rates (Thompson et al., 2007). Not only are the costs to food calling likely to be higher for reproducing females than males, the benefits may also be different. While male chimpanzee rough grunts may function as a way to maintain social bonds (Slocombe et al., 2010), the social relationships of females are indisputably different to those of male chimpanzees. Females are the dispersing sex of the species and have different rank dynamics to males, making it difficult to determine their dominance hierarchies (Foerster et al., 2016; Pusey & Schroepfer-Walker, 2013). They exhibit low levels of intra-sex aggression (Wakefield, 2013) and only rarely form coalitions with other females (Newton-Fisher, 2006). Thus, the potential social bonding benefits of producing rough grunts may be much less important for females compared to males. Reproducing females may also direct their calls at an entirely different audience to males: their offspring. The use of vocalisations to advertise food sources to offspring has been noted in other species (Clarke, 2010; Miglietta et al., 2021; Radford & Ridley, 2006; Sherry, 1977), and young animals often rely on social interactions to learn essential information about locating and accessing safe food sources (Rapaport & Brown, 2008). Sharing critical information about food sources with offspring thus may be a primary motivation for adult females in order to ensure the fitness and survival of their young.

While studying both sexes can reveal more about the functions of food calling, to fully understand this behaviour we must also take an ontogenetic approach (Tinbergen, 1963). The development of chimpanzee vocalisations has rarely been studied, but it has been reported that grunts produced in response to food can occur before 12 months (Dezecache et al., 2021) but do not appear regularly until the second year of life (Laporte & Zuberbühler, 2011). Laporte and Zuberbuhler (2011) also showed that across contexts infants produced more grunts after another individual had also grunted, and that the prior vocalisation was most often produced by the mother. Concerning the latter findings, the authors believe these grunts were the precursors to the adult 'pant grunt', which are acoustically distinct to food-associated rough grunts (Slocombe & Zuberbühler, 2010). Therefore, it is unknown whether young chimpanzees mirror their mother's vocalisation patterns in a feeding context, nor when adult-like calling behaviour starts to emerge.

The current study aimed to redress the existing focus in the literature on adult males from single communities by examining rough grunt production across five chimpanzee communities (Kanyawara, Ngogo central, Ngogo west, Sonso and Taï south) in both male and female adults, and non-adult individuals. Specifically, I explored the ecological and social correlates of adult male and adult female rough grunt production, before then investigating how calling patterns change over development. Data was collected on whether or not individuals arriving at a food source called within 3 minutes of their arrival, and then I investigated factors that might predict whether an individual called or not.

First I investigated the effects of community and sex on the likelihood of adult chimpanzees producing rough grunts as they arrived at a feeding source. This enabled me to examine potential community variation in the propensity of individuals to call, using directly comparable methods for the first time. I expected that males, as the more vocal sex (Slocombe & Zuberbühler, 2010) would be more likely to produce rough grunts than females.

To identify ecological and social correlates of rough grunt production by adults I examined males and females separately, with the aim of replicating previous findings in males and exploring whether similar variables affected female calling. Focussing first on males, I investigated whether the ecological factors of food type, and patch size/quality affected their calling behaviour. I expected rough grunt production to be more likely with fruits than leaves (Fedurek & Slocombe, 2013), and to see a higher likelihood of male calling when an individual arrived at a larger and higher quality food patch, as found in previous studies (Kalan et al., 2015; Slocombe et al., 2010). Concerning social correlates, I expected first to see the broader audience effects already reported in the literature, with higher likelihoods of males calling when more male, and sometimes female, individuals were present (Kalan & Boesch, 2015). Next, I expected higher calling likelihood in the presence of specific individuals, namely important social partners or high-ranking individuals, in line with previous findings (Schel et al., 2013; Slocombe et al., 2010). As it appears to be proximate partners that mediate call production more so than their overall presence in the party (Fedurek & Slocombe, 2013), I distinguished between proximal partners and distal partners. I considered individuals arriving with the focal individual to be ‘proximate’, as these partners were on the ground with the focal individual and typically within 10 meters of them. Individuals were considered to be ‘distal’ from the focal individual when they were already present in the feeding tree as the focal individual arrived; these partners were typically over 10 meters from them and high in the canopy. These proximity effects were explored for both socially bonded and high-rank partners. Although the presence of oestrus females has been demonstrated to affect male calling in one site (Kalan & Boesch, 2015) the current study did not include this variable due to a lack of available data from each community. Next, as Leroux et al. (2021) recently identified that pant hoots and rough grunts are often produced as part of a call combination in the Sonso community, I wanted to investigate if this co-occurrence could be replicated in the current studies wider community sample. It was predicted that rough grunts would be more likely to occur following pant hoot vocalisations, as indicated in the findings of Leroux et al. (2021). Whilst the focal individual’s other vocal behaviour may influence rough grunt production, I also sought to explore, for the first time, whether the vocal behaviour of others also influences rough grunt production. Some chimpanzee feeding events, such as those involving large parties and abundant food, seem to result in high levels of excitement and en-masse calling behaviour (NL, personal observation). Affective contagion, when individuals share the emotional state of another, serves an important function in group-living animals, resulting in greater group cohesion and coordination, as well as strengthening social bonds (Briefer, 2018). Part of replicating the emotional expression of another involves replicating their vocal behaviour, which in chimpanzees has been reported to occur in the play context. Laugh-elicited laughter helped to maintain play bouts between individuals and seemed to promote positive interactions (Davila-Ross, Allcock, Thomas, & Bard, 2011). In a feeding context, vocal contagion may facilitate group cohesion during feeding, and promote positive interactions; with rough grunts having previously been recorded after agonistic events, potentially to facilitate restoration of peaceful co-feeding (Ischer et al., 2020). If vocal contagion was occurring, I expected that focal individuals would be more likely to call if pant hoots or rough grunts had been produced by others prior to the focal individual’s arrival at the food source.

Given the paucity of data surrounding female food calling behaviour, here I decided to explore the same ecological correlates that are known to affect the vocal production of males. This included food type and patch size/quality, where I anticipated similar calling patterns as described for male chimpanzees. For social correlates, I expected females would be more likely to call when other females were nearby, as previously reported (Kalan & Boesch, 2015). The presence of males did not affect female calling in the same study, however the community reported here had very few adult males at the time

(N=3), and therefore I was interested to see if this result could be replicated in groups with considerably more adult males in the community. In contrast to the males, the presence of important social partners and high-ranking individuals had not yet been investigated in relation to female food calling, therefore these factors were included here as exploratory variables. As female chimpanzees rarely produce pant hoots in a feeding context in comparison to males (Clark & Wrangham, 1993, 1994) I did not include variables relating to pant hoot production. However, vocal contagion (whether other individuals had produced rough grunts or pant hoots prior to a focal individual's arrival) was included here again as an exploratory hypothesis for food calling behaviour.

As existing literature contains little data on the vocal behaviour of young chimpanzees, my investigation into the development of food-associated calling was largely exploratory. In line with findings regarding chimpanzee 'social grunts' (Laporte & Zuberbühler, 2011), I expected that as individuals aged from infancy to sub-adulthood, they would produce more rough grunts. I included sex as a variable here, as if adult males and females show different calling patterns, it's possible this emerges early in development. I then wanted to examine the potential for the social learning of food call behaviour, since this has been suggested as a mechanism for the development of other grunt vocalisations (Laporte & Zuberbühler, 2011). To do this, I examined whether young chimpanzees were more likely to produce rough grunts after their mother had also vocalised. It was predicted that juvenile chimpanzees would be more likely to produce rough grunts if their mothers had produced a rough grunt. I expected this to be more common in younger, dependent individuals, and that this may change as individuals became older (as found with 'social grunts'; Laporte & Zuberbuhler, 2011).

METHODS

Study sites and subjects

Data were collected from five chimpanzee communities: Kanyawara, Ngogo central, Ngogo west, Sonso and Taï south (see Appendix 1 for a summary of data contributions). The Kanyawara and Ngogo communities are located in Kibale National Park, western Uganda. Kibale is a semideciduous forest with mixed terrain including grasslands, papyrus swamps and secondary forests. The Kanyawara group's territory is bordered by agriculture and occupied villages (Wrangham, Chapman, Clark-Arcadi, & Isabirye-Basuta, 1996), and both Ngogo groups are situated approximately 10km away towards the centre of the forest. Detailed descriptions of Kibale forest are provided by Chapman and Lambert (2000) and Struhsaker (1997). The Sonso community is located in the Budongo forest in the western Rift Valley in Uganda. The Budongo Forest Reserve is also a semideciduous tropical forest, and possesses similar mixed forests to Kibale (Plumptre & Reynolds, 1994). Our final community was located in Taï National Park, Côte d'Ivoire in west Africa. This area consists of evergreen, lowland forests that are described in detail in Boesch and Boesch-Achermann (2000).

Data at Kanyawara, Ngogo central and Ngogo west were collected between September 2018-March 2020 by NL, with assistance provided by CW, JW, MH, JM or EA throughout the study duration. These chimpanzees are well habituated, having been studied since 1987 and 1995 respectively (Muller & Wrangham, 2014; Wrangham, Clark, & Isabirye-Basuta, 1992). At the Ngogo sites there was significant social turmoil affecting the structure of the community; once a cohesive group identified as the largest known population, the current study period took place immediately after a community fission (Sandel & Watts, 2021). I considered this group as two communities as peaceful encounters between the central and western individuals had ceased by the end of 2017 (Sandel & Watts, 2021).

Data from the Sonso group were collected by AS across four study periods between 2010-2012. Sonso has been the subject of continuous study since 1991 (Newton-Fisher, 1997). Finally, data were collected from July 2011- May 2012 by AK from the south group in Taï National Park, which has been habituated since 1999 (Mielke, Crockford, & Wittig, 2019). The demographic of these groups were diverse, ranging from 19 to 133 community members; Table 1 provides a description of the community demography at the commencement of study.

I defined adult males as individuals who were 15 years old or over. Adult females were defined as those of the same age or older than the youngest mother recorded at the site (Ngogo west = 14, all other sites = 13 years), or females who had immigrated into the community. Offspring were defined as dependent offspring if they were aged 10 or younger. To examine the development of rough grunt production I distinguished between infants (0-3 years), juvenile chimpanzees (4-10 years) and sub-adults (11-14 years for males; 11-13 or 14 for female individuals depending on the age of the youngest mother recorded at the site (see definition for adult females).

Table 1. Demographic description of each study site examined for rough grunt production at the commencement of study.

	Kanyawara	**Ngogo central**	**Ngogo west**	**Sonso**	**Taï south**
Sub species	*P. troglodytes schweinfurthii*	*P. troglodytes schweinfurthii*	*P. troglodytes schweinfurthii*	*P. troglodytes schweinfurthii*	*P.troglodytes verus*
N community members	54	119	74	75	19
N adult males	11	26	7	9	3
N adult females	23	41	23	24	4

Ethical note

This study complied with the ASAB/ABS guidelines for the use of animals in research; ethical approval for data collection in Kanyawara and Ngogo communities was granted by the Biology Animal Welfare Ethical Review Board (University of York), and in Sonso was granted by the Psychology Ethics committee. The Ugandan Wildlife Authority and the Ugandan National Council for Science and Technology granted permission to collect data in Uganda. In Taï National Park data were collected with the relevant permissions from Ivorian authorities in accordance with national laws and animal care regulations of Côte d'Ivoire and Germany. Ethical approval was granted by the Max Planck Institute for Evolutionary Anthropology, and complied with the ethical standards of the Primatology department's guidelines for non-invasive research.

Data collection

Data collected on all *P. troglodytes schweinfurthii* groups (see Table 1) involved all-occurrence recordings of feeding events where the researcher's focal animal was present. Researchers conducting full-day focal animal follows (Altmann, 1974) would start to record a feeding event upon their arrival to a feeding location with their focal animal (adult female mothers at the Kanyawara and Ngogo communities; adult and sub-adult males at Sonso). Any individuals who preceded them to the location that were still actively feeding were marked as being already present. Thereafter, any individual who started feeding at the location was considered as an arrival.

Timestamps of all individual's feeding start times and feeding end times (defined as the time they became engaged in a non-feeding behaviour) were recorded. For animals already present the time of the researcher's arrival was given as their start feeding time, and were therefore an underestimate of their true feeding duration. All rough grunts and pant hoots produced by individuals in the feeding patch were noted, in terms of the minute in which the vocalisations were produced and the identity of the caller. If the caller could not be identified with certainty the vocalisation was recorded with an unknown ID. If individuals resumed feeding at the same location (without leaving the tree) this was recorded as a separate bout to their initial feeding period, but not considered as a new arrival. Each event was given a unique ID, and ecological characteristics (species and part eaten) were noted.

For the Taï south community continuous behavioural and vocal data was collected from focal individuals (adult females) during dawn to dusk follows (average duration: 8.88 ± 2.9 h per day). A feeding event began when the focal individual started to eat or collect food, and all subsequent feeding bouts were recorded until the focal individual ceased to feed in that same patch. Timestamps were recorded of any subsequent arriving individuals, as well as the pant hoots or rough grunts of any individuals present with the focal, but their feeding durations were not recorded. Identical ecological properties were noted as for the other sites, and a unique ID again assigned to each feeding event.

While focal animals determined which feeding events researchers were present for, other individuals recorded as arriving at the feeding event (and who subsequently fed at the location) also contributed data to my models. Therefore, hereafter in this study ‘focal’ refers to an individual who arrived (and fed) at a food source, regardless of whether they were the subject originally being followed by the researchers.

At all sites feeding data was not collected on meat, insects and terrestrial herbaceous vegetation due to the difficulty in determining what constitutes a feeding patch in these cases.

Measures extracted

Rough grunt production on arrival at a food source

The main variable of interest was whether or not a chimpanzee produced rough grunts as they arrived at a food source. In order to calculate this, I had to define a standardised arrival period. For comparability between sites, I defined an individual's arrival time in the analysis as the 1 minute prior to their first feeding bout start time. Therefore, only individuals who were recorded as feeding were included in the analysis. An individual’s overall ‘arrival period’ was then defined as their arrival time and the subsequent 3-minute interval. Whether the individual called in their arrival period was extracted (yes/no). When individuals were not observed to call in their arrival period, and a call occurred during the arrival period that could not be assigned to an animal, I excluded these arrival events from analysis due to the resulting uncertainty in whether or not the arriving individual may have called.

Food patch size/quality and type of food

Patch size and quality was assessed by calculating ‘chimp minutes’ (the cumulative duration of the first feeding bout for all individuals present; Slocombe et al., 2010). As individuals were often already present or remained at the feeding site after researcher departure, this measure was often an underestimate of patch size/quality. At Taï south total feeding duration was only available for the focal animal, so for ‘chimp minutes’ here I multiplied focal feeding duration by the number of individuals present at the feeding event to achieve an estimate of patch size/quality. I constrained the analyses to the most common food types that were well represented in all sites: fruit and leaves. I also only considered feeding events from known tree species.

Dominance rank calculations

Rank data were only available for members of the Kanyawara and Sonso communities, and within the Sonso community data were only available on male individuals. Therefore, I was unable to explore focal rank effects for female individuals in this study. At Kanyawara dominance ranks were determined using the established Elo rating method (Albers & De Vries, 2001) with the methods of Muller et al. (2021), which recorded the directionality of pant grunts and the outcomes of aggressive interactions (win/lose) from January 1993 through to December 2019. Individuals enter the hierarchy on the date of their first subordinate interaction after turning 9 years old, therefore all adult males (N = 12) had rank scores available. For each individual an average ordinal rank was calculated for each 3-month period, with 1 being the highest ranking. At Sonso ranks were determined using the directionality of pant grunts only, as data on agonistic encounters were unavailable. Here I did not have outcomes from chronologically ordered interactions available that are normally used to calculate Elo scores, instead only the total number of pant grunt exchanges between dyads in a 3-month period were reported. To then simulate the Elo method I converted this data into a list of independent interactions between dyads, and generated 100 datasets where the order of pant grunt interactions within these 3-month periods were randomised. All adult males (N = 11) again had rank scores available, and for each individual an average ordinal rank was calculated for each 3-month period, with 1 being the highest ranking.

I extracted the rank of the arriving male at a feeding event by identifying the 3-month period in which the feeding event had occurred, and extracting the male's 3-month averaged ordinal rank score for that period. To investigate how the presence of high-ranking individuals affected calling behaviour of arriving individuals, I checked whether any of the most dominant individuals in the community (the top quartile of rank positions during the 3-month period in which the feeding event had occurred; 4 individuals at Kanyawara, 3 at Sonso) were present at the feeding event, to produce a binary measure (high-ranking males present/absent).

Composite friendship index (CFI)

Data required for the identification of important social partners were only available at Sonso and Kanyawara. At Sonso between 2009-2012 AS conducted focal follows on common community members to collect data on their social relationships; specifically, all occurrence focal grooming and aggressive interactions, in addition to 15 minute behavioural scans on nearest neighbours and party compositions. At Kanyawara similar data was available from the long-term data set collected by local field assistants, and was extracted for the period of data collection.

All focal individuals had to be subject to a minimum of 12 hours of focal observation during the whole study period to calculate a measurement of affiliation or a 'composite friendship index'. This index was calculated for each arriving individual and all other adult members of that community. I used the same index as published in Schel et al. (2013), which uses party level association, nearest neighbour association and grooming frequency to calculate friendship scores (see Appendix 2 for formulae used). To capture a complex social construct such as friendship many primate studies include multiple measures to capture both spatial and temporal association patterns (e.g. Gilby & Wrangham, 2008; Silk, Altmann, & Alberts, 2006; Thompson & Cords, 2018). Here, a composite index was appropriate rather than using these independent measures separately as each measure was significantly correlated with the other measures (Spearman's rho tests for correlation; party level association x nearest neighbour association: *r* = .299, *p*<.001; nearest neighbour association x grooming frequency: *r* = .392, *p*<.001; grooming frequency x party level association: *r* = .455, *p*<.001).

For each arriving individual I calculated their friendship scores with all adult community members and converted these scores into standardised z-scores. I then identified the standardised friendship scores that the arriving individual had with each member of the feeding party (already present and arriving with the focal). A positive z score of 1.5 or above was considered to indicate that the arriving focal individual had a close social bond with that member of the feeding party. This then enabled me to create a binary variable of whether the arriving individual had any important social partners present or not.

Statistical models

Model 1: Community and sex effects on rough grunt production

I wanted to establish whether adult males were more likely to produce rough grunts than adult females when arriving at a food source, and whether there were any community differences in propensity to produce rough grunts. I included focal age as a control predictor, as previous research has linked ageing with alterations in feeding behaviour (Thompson et al., 2020). I included random effects of focal ID, feeding event ID and tree species.

The sample analysed comprised a total of 2754 arrivals, from 119 individuals, 130 tree species and 1305 feeding events.

Model 2: Ecological effects on adult male food calling behaviour

To investigate if I could replicate findings surrounding the effects of ecological correlates on male calling behaviour, I examined the effect of food type (fruits or leaves) and patch size/quality ('chimp minutes') on whether an individual produced a rough grunt during their arrival period.

I again controlled for focal age, and also included the total number of adult individuals present (party size) as a control predictor. Party size has not previously been reported to predict calling behaviour (Kalan & Boesch, 2015; Kalan et al., 2015; Slocombe et al., 2010), but this measure served as a valuable proxy of general arousal which is often assumed to drive vocal behaviour in non-human primates (Tomasello, 2008). It might be expected that larger groups result in higher arousal (and thus more calling) so party size was included as a control predictor. Community was included as a control predictor too, as it was suspected that differences may exist between chimpanzee groups following diverging results reported from single-community studies. I included random effects of focal ID and tree species in the final model.

Ngogo west was excluded for contributing too few cases to this model (N = 2). Furthermore, 'event ID' could not be included as a random effect here as the N arrivals each event contributed often equalled 1. It was therefore difficult to estimate the effect of this variable and it contributed to considerable instability in the model. I corrected for this by only including one individual per feeding event in the model and removing feeding event ID from the final model. Where events had multiple individuals contributing data, I selected the individual who had the least amount of data available overall in the model. If individuals in the event contributed equally to the model then I assigned values to their rows using a random number generator, and selected the highest value row.

The sample analysed comprised a total of 627 arrivals, from 39 individuals and 85 tree species.

Model 3: Effects of social environment and vocal behaviour on adult male food calling

The second adult male model explored social correlates, and whether vocal behaviour affected their calling during their arrival period. Social variables included the total number of adult males and females present, the presence/absence of important social partners (arriving with the focal; already present) and of high-ranking individuals (arriving with the focal; already present). I also explored the concept of vocal contagion by examining whether other individuals' vocalisations affected rough grunt production. For this I established whether any non-focal individuals had produced a pant hoot or a rough grunt during the focal individual's arrival period (both yes/no). The final test predictor here examined whether the focal animal's production of a pant hoot in the 3 minutes prior to their arrival period (yes/no) predicted rough grunt production.

Focal rank was not of primary interest here, but was included as a control variable since previous research has found that high-ranking males call less to females in the vicinity than low-ranking individuals (Kalan & Boesch, 2015). Other control variables included focal age and community (see models 1 and 2 for justification) and patch size/quality (chimp minutes) as an ecological control. I included random effects of focal ID, feeding event and tree species.

The final model included a total sample of 694 arrivals, 20 individuals, 38 species and 297 events.

Model 4: Ecological effects on adult female food calling behaviour

To investigate whether ecological correlates affected female food calling behaviour, I examined the same test variables present in the male model (model 2). Thus I looked at the effect of food type (fruits or leaves) and patch size/quality ('chimp minutes') on whether a focal individual produced a rough grunt during their arrival period.

The control predictors and random effects here again replicated model 2 (control: community, focal age and number of adult individuals present at the feeding event; random: focal ID and tree species). However, I also included an additional control predictor for whether the female had dependent offspring (yes/no). I included this as I considered that nursing females may be particularly sensitive to the nutritional quality of the food patch.

This model experienced the same problem as model 2 regarding the random effect 'feeding event ID'. I removed this random effect and instead only included one focal individual per feeding event in the model using the same selection process as detailed for model 2.

The sample analysed comprised a total of 649 arrivals, from 86 individuals and 87 tree species.

Model 5: Effects of social environment and vocal behaviour on adult female food calling

Here I again wanted to enable direct comparisons with male calling behaviour, thus this model replicated model 3 aside from the exclusion of one test predictor; focal pant hoot production was not included here as females rarely produce pant hoots in a feeding context (Clark & Wrangham, 1993, 1994).

Control variables included focal age and community. Although the male social model included food patch size/quality (chimp minutes) as a control predictor, as no ecological variables were significant predictors of female calling it was not included in this model. Also unlike the male model, focal rank was not included as a control predictor due to a lack of available female rank data from all communities. I included random effects of focal ID, feeding event and tree species.

The final model included a total sample of 304 arrivals, 33 individuals, 31 species and 193 events.

Model 6: Effects of sex and age on young chimpanzee food calling

For studying the vocalisations of young chimpanzees I was concerned that vocalisations of infants may have been too soft and potentially inaudible to be reliably recorded by observers (who were a minimum of 7m away). At 4 years, chimpanzees typically move independently from their mother (i.e. are not in ventral or dorsal body contact), have started weaning and typically begin to show more adult-like foraging behaviours (Lonsdorf, Stanton, Wellens, & Murray, 2021; Smith et al., 2013). Consequently, I was more confident that all rough grunts produced by juvenile chimpanzees would have been reliably heard and recorded. For my statistical model on the development of rough grunt production then I excluded infants, but included both juveniles and sub-adult individuals. Orphaned individuals were also excluded from the model, as it's unknown if their atypical life history affects their foraging or communicative behaviour.

Data on infant (0-3 years) rough grunt production is reported descriptively with the caveat that some vocalisations may have been missed by observers. Data on infants was only available at Kanyawara, Ngogo central and Ngogo west. The sample comprised a total of 73 arrivals, from 22 individuals (14 male).

For my GLMM examining the food calling behaviour of young chimpanzees (juveniles and sub-adults; see ‘study sites and subjects’ section for age definitions) I first wanted to establish whether their call production was affected by their sex, and whether this changed over development as they aged. I examined the interaction between sex and focal age on whether an individual produced a rough grunt during their arrival period.

For control predictors I included patch size/quality (chimp minutes) as an ecological control, and the total number of adult individuals on arrival (see model 2 for justification). This model experienced the same problem as model’s 2 and 4 regarding the random effect ‘event ID’. This was again controlled for by only including one focal individual per feeding event in the model using the same selection process as detailed for model 2. Random effects on this model included focal ID, tree species and community (I had sufficient data from all five communities to include this as a random effect in this model).

The sample analysed comprised a total of 428 arrivals, from 57 individuals, 79 tree species and 5 communities.

Model 7: Effect of mother vocalisations on the food calling of dependent offspring

For the examination of social learning (producing rough grunts according to their mother’s vocalisation patterns) it was felt that this was only relevant in younger chimpanzees (4-10 years) who were dependent offspring, and therefore likely to be arriving with their mothers to feeding events. Orphaned juveniles were necessarily excluded from this model which required data on the behaviour of a mother.

This model tested whether the mother had rough grunted during or in the 3 minutes after the focal individual’s arrival (yes/no). Focal sex, age and community were included as control variables. Here again the random effect ‘event ID’ had to be removed, and only one focal individual per feeding event was included in the model using the same selection process as detailed for model 2. As mothers could have multiple offspring I included mother ID as a random effect, alongside focal ID and tree species.

The sample analysed comprised a total of 122 arrivals, from 23 individuals, 22 mothers, and 35 tree species.

Statistical analysis

To assess whether these variables predict food-associated calling behaviour, Generalized Linear Mixed Models (GLMM; Baayen, 2008) were used for all analyses, with binomial error distributions and logit link function.

Continuous predictor variables were always scaled by z-transforming to a mean of zero and standard deviation of one, to allow for easier interpretation of the model coefficients (Schielzeth, 2010) and model convergence. To control for repeated observations of the same individuals, and from the same feeding events, focal ID and event ID were included as random effects in all models. Tree species was also included as a random effect on all models as chimpanzees may value the available crop from trees differently dependent on species, which may lead to a different outcome for the likelihood of producing calls.

In order to keep type 1 error rates at a level of 0.05 all theoretically identifiable random slopes should be included in each model (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009). Estimates of the correlations between the random intercepts and slopes were also included except when these appeared unidentifiable, as indicated by absolute correlation parameters being essentially one (Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017). In this case these correlations were dropped from the model.

Model stability was estimated by dropping the levels of the random effects one at a time from the data, and comparing the estimates derived for models fitted to these subsets with those obtained for the full data set (Nieuwenhuis, Te Grotenhuis, & Pelzer, 2012). There were at least two fixed effects included in each model, so I assessed collinearity between these. This was done using Variance Inflation Factors (VIF; Field, 2005) based on a standard linear model which did not include the interaction or random effects.

To ascertain the effect of the test predictor and to avoid cryptic multiple testing, full-null model comparisons were carried out with the null model lacking the test predictor, but otherwise being identical to the full model in terms of the random effects structure. The effect of individual fixed effects was tested by comparing the full model with the reduced model lacking them, one at a time (Barr et al., 2013). For the full-null model comparison, as well as the full-reduced model comparisons, a likelihood ratio test was used (Dobson, 2002); R function drop1 with argument ‘test’ set to “Chisq”.

Models were implemented in R (version 4.0.2; R Core Team 2020) using the function glmer of the package lme4 (version 1.1-21; Bates, Mächler, Bolker, & Walker, 2015). Model stability was assessed using a function kindly provided by Roger Mundry. Confidence intervals of the model estimates were obtained using a parametric bootstrap (function bootMer of the package lme4, N=1,000 bootstraps).

RESULTS

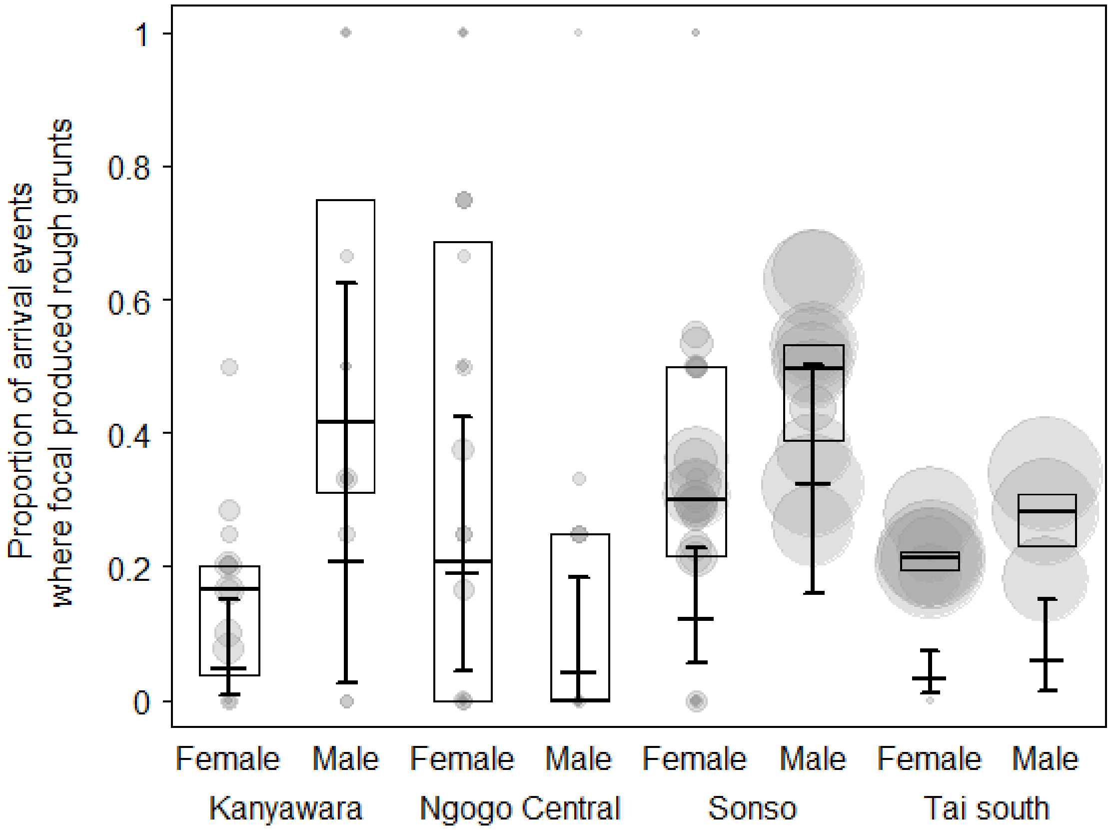
Here I report the main findings for each of the research questions and models; further model results including estimates, standard errors and confidence intervals can be found in Appendix 3.

Model 1: Community and sex effects on rough grunt production

Descriptively overall, adult males produced rough grunts in 41% of arrivals compared to 26% of arrivals in adult females. The likelihood of producing rough grunts on arrival also varied with community, with individuals (males and females combined) calling in 22% of events at Kanyawara, 24% at Taï south, 30% at Ngogo central and 43% of events at Sonso. With this model I examined whether an interaction between sex and community existed, and found that the interaction was significant from the full-null model comparison; likelihood ratio test χ^2=30.054, df=3, *p*<.001. Although overall adult males were more likely to produce rough grunts than females, the direction and magnitude of sex differences varied with community (Figure 1). The control predictor of focal age was not significant (χ^2=0.094, df=1, *p*=.759).

In order to further interrogate the significant interaction between sex and community identified in the model, I first ran post-hoc comparisons on sex within each community. These post-hoc tests revealed that males at Sonso were significantly more likely to rough grunt than females during their arrival (Est=1.247, SE=0.406, z=3.069, *p*=.002). Two trends were also identified; the first that males tended to be more likely to rough grunt during arrival than females at Kanyawara (Est=1.644, SE=0.876, z=1.876, *p*=.061), and a second that females tended to be more likely to rough grunt at Ngogo central than males (Est=-1.715, SE=0.936, z=-1.833, *p*=.067). No trends or significant differences between the sexes at Taï south were found (Est=0.611, SE=0.568, z=1.075, *p*=.282).

Figure 1. The proportion of arrival events where the focal produced rough grunts, for females and males from the four communities.



Note: Boxes depict median and quartiles for the raw data. Horizontal lines with error bars depict estimates from the fitted model and their 95% confidence interval (when all other categorical variables were manually dummy coded and then centred, and continuous variables were at their average). The area of the points is proportionate to the number of focal observations (range: 1-178).

Next, I ran post-hoc comparisons on community within adult males and adult females separately. Table 2 shows the pairwise comparisons for each community; males at Sonso were significantly more likely to produce arrival rough grunts than males at Ngogo central, and females from Ngogo central and Sonso were significantly more likely to produce calls than females at Taï south.

Table 2. A summary of post-hoc comparisons exploring community level differences in rough grunt production within adult males and adult females.

Focal sex	Community (A)	Community (B)	Estimate	SE	Z	*p*
Adult male	Kanyawara	Ngogo central	-1.828	1.133	-1.614	.107
		Sonso	0.613	0.906	0.677	.498
		Taï south	1.449	0.976	-1.484	.138
	Ngogo central	**Sonso**	**2.441**	**0.929**	**2.627**	**.009**
		Taï south	0.379	01.009	0.376	.707
	Sonso	**Taï south**	**-2.062**	**0.597**	**-3.454**	**.001**
Adult female	Kanyawara	Ngogo central	1.531	0.795	1,926	.054
		Sonso	1.010	0.682	1.481	.139
		Taï south	-0.415	0.736	-0.564	.572
	Ngogo central	Sonso	-0.521	0.617	-0.844	.399
		Taï south	**-1.946**	**0.709**	**-2.746**	**.006**
	Sonso	**Taï south**	**-1.426**	**-0.536**	**-2.661**	**.008**

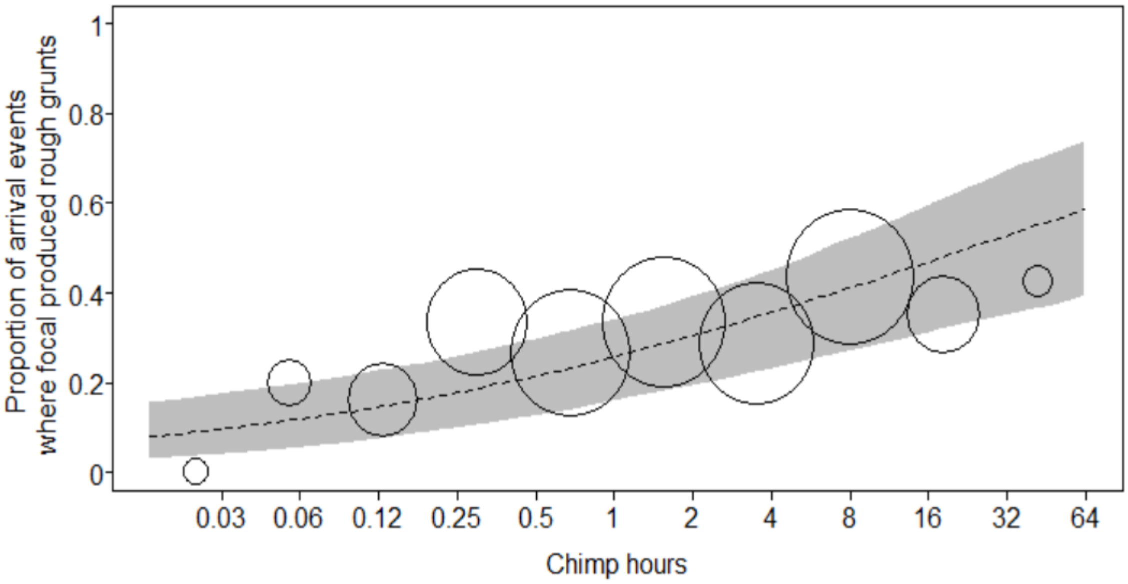
Note: Figures given in bold indicates significant pairwise comparisons (*p*<.05)

Model 2: Ecological effects on adult male food calling behaviour

Here I found that the full-null model comparison was significant indicating that the variables in this model explained a significant amount of variation in calling behaviour; likelihood ratio test χ^2=18.155, df=2, *p*<.001. Examination of the model coefficients revealed that 'chimp minutes', but not food type, significantly predicted calling. Arriving individuals at feeding events with higher chimp minutes (indicating larger patch size and/or higher quality) were more likely to produce rough grunts (χ^2=18.131, df=1, *p*<.001; Figure 2). However, the production of rough grunts was similar regardless of whether the focal animals were feeding on fruits or leaves (χ^2=0.336, df=1, *p*=.562).

In line with model 1 significant effects were found for the control predictor community (χ^2=10.949, df=3, *p*=.012). Unexpectedly, the control predictor for the number of adult individuals present at the feeding event was also significant (χ^2=4.421, df=1, *p*=.039), and indicated that individuals were less likely to rough grunt when more adult individuals were present with the focal individual at the feeding event. My final control predictor for focal age was not significant (χ^2=0.089, df=1, *p*=.766).

Figure 2. The proportion of arrival events where the arriving focal male produced rough grunts for increasing chimp minutes



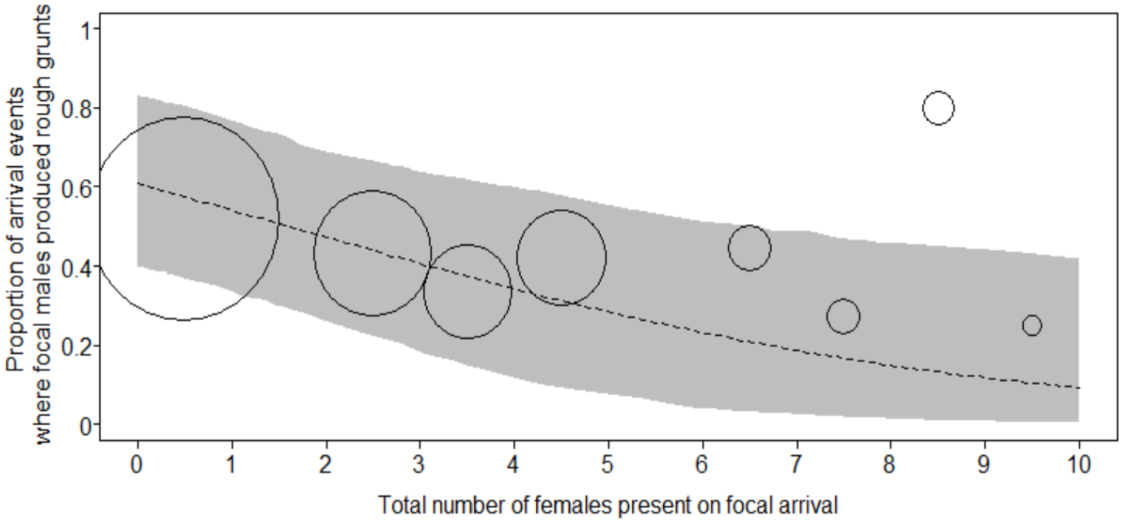
Note: 'Chimp minutes' here is shown in chimp hours. The area of the points is proportionate to the number of observations (range: 5-124). The dashed line shows the fitted model and the grey shaded area the 95% confidence interval (when part eaten and community are both manually dummy coded and then centred, and with age and number of adults present values being at their average).

Model 3: Effects of social environment and vocal behaviour on adult male food calling

I found that the full-null model comparison was significant; likelihood ratio test χ^2=42.91, df=9, *p*<.001. Examination of the model coefficients revealed first that the total number of adult females present was significant, with male focal individuals being less likely to rough grunt when more adult females were at the feeding event (χ^2=5.577, df=1, *p*=.018; Figure 3). Conversely, the total number of adult males present did not affect male calling behaviour (χ^2=1.965, df=1, *p*=.161). The coefficients also showed that if focal individuals had produced a pant hoot during their arrival period, there was a higher likelihood for the focal to also produce a rough grunt during arrival (χ^2=24.904, df=1, *p*<.001; Figure 4).

I found no evidence that the presence of important social partners who were already present (χ^2=0.249, df=1, *p*=.618) or arriving with the focal (χ^2=0.558, df=1, *p*=.455) affected male calling. Similarly, the presence of high-ranking individuals that were already present (χ^2=0.360, df=1, *p*=.549) or arriving with the focal (χ^2=0.942, df=1, *p*=.332) did not affect the likelihood for males to produce rough grunts during their arrival. I also failed to identify any evidence for vocal contagion, with no indication that male individuals were more likely to rough grunt when other individuals had produced pant hoots (χ^2=0.104, df=1, *p*=.747) or rough grunts (χ^2=0.003, df=1, *p*=.957) just prior to their arrival.

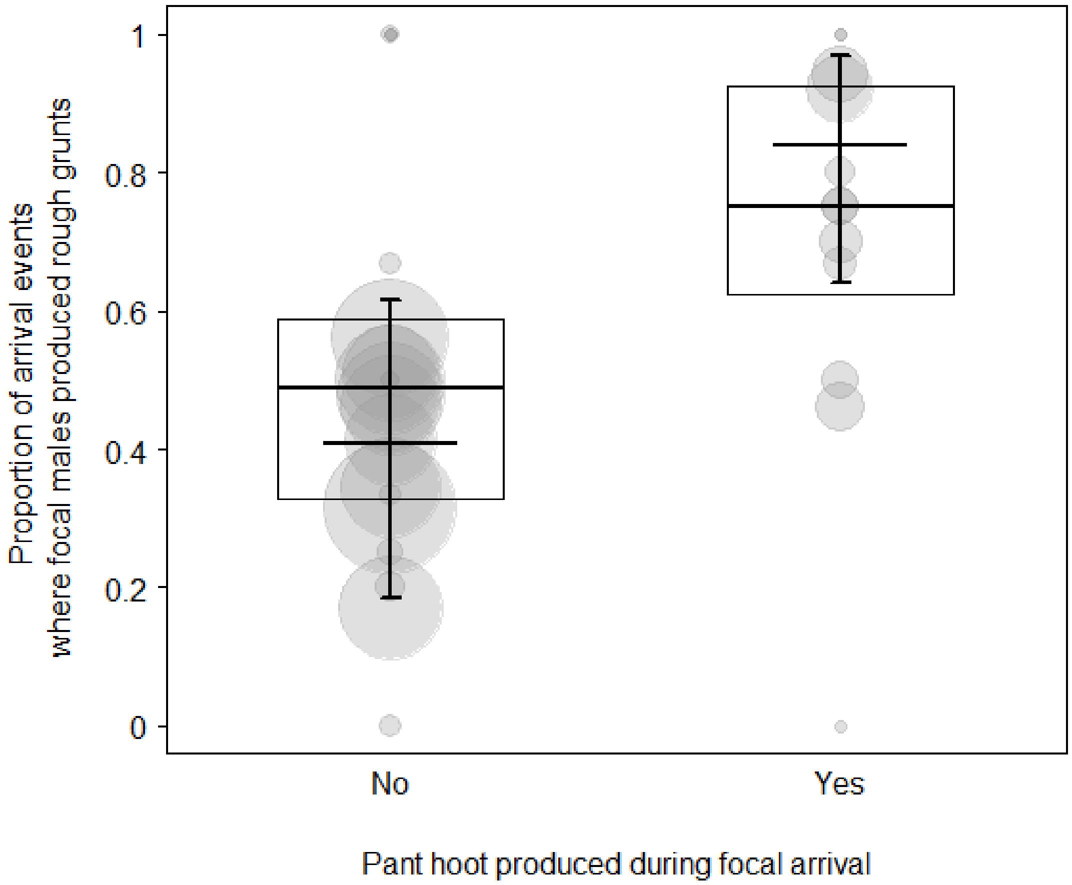
Figure 3. The proportion of observations with a rough grunt, by the number of females present when the male focal individual arrives at the feeding event.



Note: The area of the points is proportionate to the number of observations (range: 4-358). The dashed line shows the fitted model and the grey shaded area the 95% confidence interval (when all other categorical variables were manually dummy coded and then centred, and continuous variables were at their average).

There were significant effects for the control predictors focal rank (χ^2=4.470, df=1, *p*=.030) and 'chimp minutes' (χ^2=9.531, df=1, *p*=.002). The former revealed that lower-ranking individuals had a higher likelihood to produce rough grunts during their arrival to food patches than higher-ranking individuals, and the latter replicated my results from model 2. The control predictor for focal age was not significant (χ^2=3.803, df=1, *p*=.051), and in line with model 1 the likelihood of calling was not different for those from the Sonso and Kanyawara communities (χ^2=2.237, df=1, *p*=.135).

Figure 4. The probability for the male focal individual to rough grunt, when they did or did not pant hoot.



Note: Boxes depict median and quartiles for the raw data. Horizontal lines with error bars depict estimates from the fitted model and their 95% confidence interval (when all other categorical variables were manually dummy coded and then centred, and continuous variables were at their average). The area of the points is proportionate to the number of focal observations (range: 1-95).

Model 4: Ecological effects on adult female food calling behaviour

In contrast to the adult male ecological model the full-null model comparison for the female ecological model was not significant; likelihood ratio test χ^2=3.903, df=2, *p*=.142. This indicates that taken together the part being eaten (fruits or leaves) and the abundance and/or quality of the food patch (indicated by chimp minutes) did not predict a significant amount of variation in female calling behaviour. However, it is perhaps noteworthy that there was a trend for events where grunts were given being associated with higher chimp minutes than events without grunts (χ^2=2.826, df=1, *p*=.093) which is the same pattern as seen in the male chimpanzees.

In line with model 1 the control predictor community did have a significant effect on female rough grunt production (χ^2=9.807, df=4, *p*=.044). The other control predictors of age (χ^2=0.016, df=1, *p*=.901), the total number of adult individuals present (χ^2=.030, df=1, *p*=.862), and whether the female was a mother of dependent offspring (χ^2=1.593, df=1, *p*=.207) did not significantly predict adult female rough grunt production.

Model 5: Effects of social environment and vocal behaviour on adult female food calling

Here again, in contrast to the adult male model, the full-null model comparison was not significant for females; likelihood ratio test χ^2=12.33, df=8, *p*=.137. Most coefficients were individually non-significant, but there were two exceptions to this; namely the presence of important social partners arriving with the focal individual (χ^2=4.755, df=1, *p*=.029), and whether other individuals had produced a rough grunt during the focal individual's arrival (χ^2=4.568, df=1, *p*=.033). For the former adult females were more likely to rough grunt if they were arriving with an important social partner. For the latter females were more likely to rough grunt if other individuals were also producing rough grunts at the feeding patch. However, these findings should be interpreted with caution given that the full-null model was non-significant, and therefore I cannot rule out that these variables were significant by chance.

The control predictor for focal age was not significant (χ^2=0.044, df=1, *p*=.835), and again the likelihood of calling was not different for those from the Sonso and Kanyawara communities in line with model 1 (χ^2=0.635, df=1, *p*=.426).

Model 6: Effects of sex and age on young chimpanzee food calling

Here I examined rough grunts produced by infant chimpanzees aged from 9-months to 47-months old at Kanyawara, Ngogo central and Ngogo west. Table 3 reveals the number of individuals from each sex and age group that I collected data from.

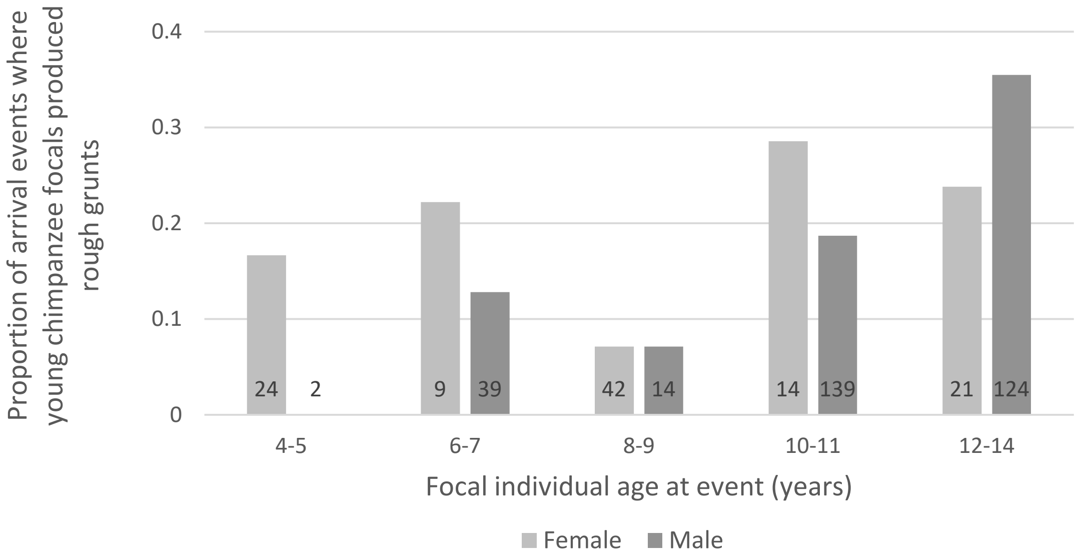
Table 3. The number of events and number of recorded rough grunts for infants by age (months) and sex.

	0-11 months		**12-23 months**		**24-35 months**		**36-47 months**	
	Female	*Male*	*Female*	*Male*	*Female*	*Male*	*Female*	*Male*
N events	2	4	6	15	3	7	1	35
N rough grunts	0	1	0	0	1	1	0	0

During this age range I identified only 3 rough grunts produced during the focal individual's arrival period. The youngest infant was an 11-month old male from Ngogo central. A second female individual from the same community was aged 2 years 4 months, and the final male infant was from Ngogo west, also aged 2 years and 4 months. In all 3 cases the infants were travelling in a party restricted to kin (mothers, siblings), and in all cases the mother had also vocalised during their arrival to the feeding event. Of the remaining events where the focal infant did not produce a rough grunt (N=70) another individual had vocalised in 9 events, in 6 of which the signaller was the mother.

When considering the effect of sex and age on the likelihood of young chimpanzees (juveniles, sub-adults; see 'study sites and subjects' section for age descriptions) producing rough grunts on arrival at a food source in all five communities, the full-null model comparison was not significant; likelihood ratio test χ^2=7.268, df=3, *p*=.064. However, the coefficients did reveal a trend for the interaction between focal sex and focal age (χ^2=3.622, df=1, *p*=.057; Figure 5). Here, it appears that male individuals were marginally more likely to rough grunt with increasing age, particularly as they approach adulthood, whereas female rough grunt production remained relatively stable across development. Again, this finding is tentative given the non-significant full-null model comparison.

Figure 5. The proportion of non-adult observations with a rough grunt, by focal age (years).



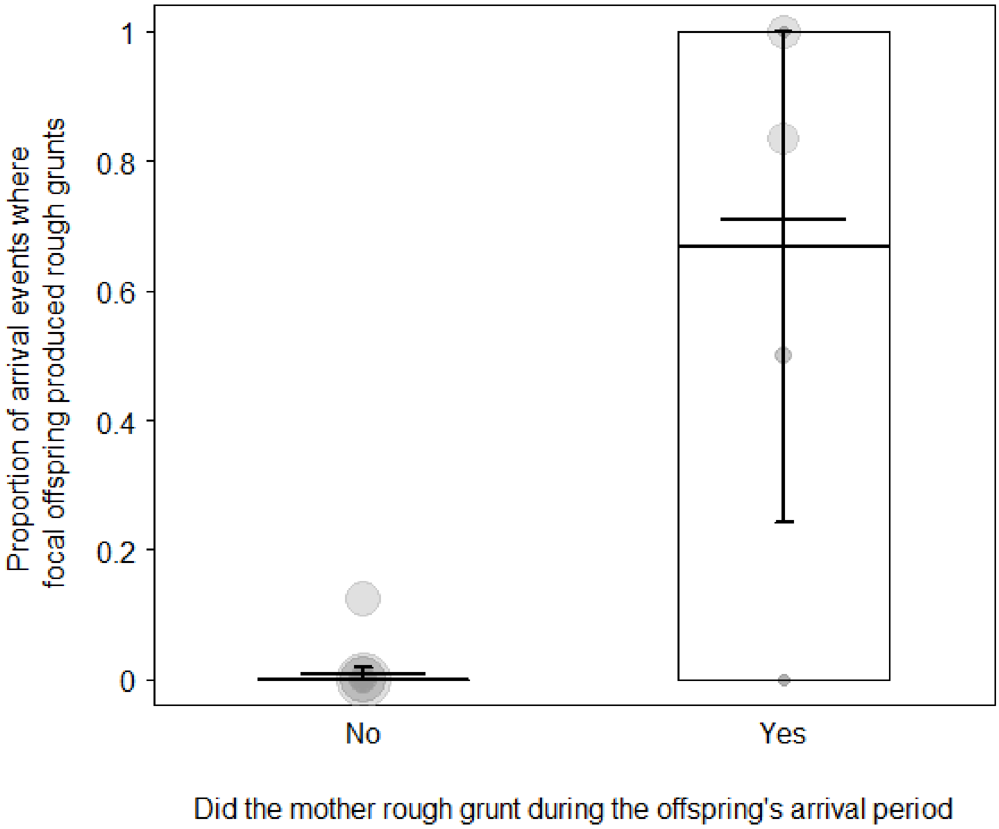
Note: Numbers in bars show the number of observations.

The control predictors for chimp minutes (χ^2=<.001, df=1, *p*=.975), and the total number of adults on arrival (χ^2=0.504, df=1, *p*=.478) were not significant.

Model 7: Effects of mother vocalisations on the food calling of offspring

Finally, I examined whether the vocalisations of mothers to dependent juvenile chimpanzees (aged 4-10 years) affected the juvenile's likelihood to produce rough grunts during their arrival. The full-null model comparison was found to be significant; likelihood ratio test χ^2=61.176, df=1, *p*<.001. Examination of the model coefficients revealed that when mothers rough grunted during or immediately after their juvenile offspring's arrival, the juvenile offspring was significantly more likely to also have rough grunted (χ^2=61.176, df=1, *p*<.001; Figure 6). None of the control variables of focal age (χ^2=1.472, df=1, *p*=.225), focal sex (χ^2=1.128, df=1, *p*=.288) or community (χ^2=5.383, df=2, *p*=.068) were significant. The model coefficients did however indicate signs of complete separation for the test predictor 'mother rough grunts during and/or after focal arrival'. From inspecting the data, it appears this is due to there only being one case where there was a rough grunt from offspring when the mother did not rough grunt during or immediately after their arrival. Ideally there would be more variation in the response for all levels of the fixed effects, but in this case there is a strong separation in the responses. Nevertheless, when looking at the confidence intervals for this variable zero is not crossed. This suggests that I can be confident that this test predictor is significant, and that offspring are indeed more likely to rough grunt during their arrival when their mother also rough grunted, though I cannot be certain of the magnitude of this effect.

Figure 6. The probability for dependent offspring to rough grunt on arrival at a food source as a function of whether the mother produced rough grunts in the arrival period.



Note: Boxes depict median and quartiles for the raw data. Horizontal lines with error bars depict estimates from the fitted model and their 95% confidence interval (when all other categorical variables were manually dummy coded and then centred, and continuous variables were at their average). The area of the points is proportionate to the number of focal individual (offspring) observations (range: 1-18).

DISCUSSION

In this study wild chimpanzees have shown considerable variation in the likelihood of producing rough grunts when arriving to feeding sources. First, I found that both sex and community membership affects rough grunt production. The following paragraphs will consider a comparison of communities within sexes, but here I will elaborate on the significant interaction between sex and community which revealed that, in line with my predictions, adult males were more likely to rough grunt on arrival at a food source than adult females in the majority of communities. This finding could reflect the higher overall vocal production in males compared to females (Slocombe & Zuberbühler, 2010), and/or could indicate that this type of call may function differently in adult male and female chimpanzees. However, post-hoc tests revealed that males were only significantly more likely to rough grunt than females in the Sonso community, though there was a trend in this direction at Kanyawara too. Instead, I unexpectedly found a trend that males were less likely than females to call on arrival to a food source at Ngogo central, and identified no sex differences in calling behaviour at Taï south. Higher male than female calling rates at Sonso and Kanyawara supports the hypothesis that males may gain more fitness benefits from advertising valuable food resources than females. Male fitness is constrained by access to reproductive females (Wrangham, 1976), and my data found that male calls were produced more often when less females were present (see following paragraphs for further discussion of this possible recruitment function). Therefore, elevated male calling at these sites likely reflects an adaptive strategy to increase access to reproductive females. In contrast, food is the key determiner for female fitness, with high access to good quality food resulting in lower inter-birth intervals and greater offspring survival rates (Thompson et al., 2007). Thus, the costs of attracting others to a valuable food source, which may compromise individual intake, are higher for females than males, and in line with this at Kanyawara and Sonso females called less often than males. The patterns of calling observed at Kanyawara and Sonso seem to reflect the fitness strategies expected of each sex. Kanyawara females appeared especially reluctant to call. These females have also been regarded as relatively antisocial, since their interactions with other females appear to result by chance of having an overlapping 'neighbourhood' with another female, rather than actively associating with them (Gilby & Wrangham, 2008). Their solitary habits may result from fruit resources being particularly scarce at this site (Potts et al., 2011), which can result in lower reproductive rates (Thompson et al., 2007; Wrangham et al., 1996). Foraging alone then, and suppressing vocalisations which may advertise food, may be particularly crucial for female fitness at Kanyawara. To assess this hypothesis, more detailed analysis of the food availability (i.e. phenology data with density mapping of tree species that chimpanzees feed from) would be required.

Regarding Ngogo central, it is unclear whether the unexpected finding, that females tended to be more likely to call than males, is driven by atypical calling behaviour in the males or females of this community. Notably, researchers conducted full day focal follows of females with infants at Ngogo, and therefore the male data may not be representative: I may have oversampled specific males who tend to associate with females with young infants. It is therefore possible that my sampling was biased towards certain males, or certain circumstances which are associated with lower calling rates. To rectify this, it will be important to conduct focal follows on both males and females, aiming for most males and most females from the community to contribute data. On the other hand, females in this community may have driven this pattern of results by being unusually vocal. Ngogo central was the largest community in my dataset, and the large population size has been suggested to have altered the social dynamics of the females in this community. Specifically, females here tend to form 'cliques' of 3-4 females who have strong affiliative bonds, and low aggression rates between them (Wakefield, 2008, 2013). Unlike other East African groups where females sometimes form 'neighbourhoods', the formation of these cliques are independent from ranging patterns, with separate cliques using overlapping ranges (Wakefield, 2008). Forming these close female-female bonds may be adaptive to reduce aggression from feeding competition in an unusually large community, but importantly studies with other primates have demonstrated that stronger female bonds can result in lower infant mortality rates, suggesting that sociality enhances female fitness (Silk, Alberts & Altmann, 2003; Silk, Altmann & Alberts, 2006). To investigate whether females call to maintain proximity to female group members, it would be useful to examine whether females at Ngogo central retain other females in the party (particularly from their 'clique') by producing rough grunts during feeding events.

In the Taï south community, both male and female individuals seem relatively unlikely to produce rough grunts during their arrival to feeding events. West African chimpanzees have higher levels of predation pressure which make calling costlier, and may force individuals at Taï south to forage in larger social groups rather than foraging in isolation (Boesch, 1991). Moreover, at the time of study this group was observed to fusion rarely (Kalan, personal observation), and research suggests that with decreased community size, party sizes and male-female associations increase (Lehmann & Boesch, 2004). Given this, advertising food sources at Taï south may be redundant if small population sizes and high predation pressures mean that individuals tend to be grouped together. To test whether this is the case, the likelihood of calling in feeding events when the community was all present could be compared to those where some group members were absent, with the expectation that the likelihood of calling should be greater when some individuals are absent and can be recruited to the feeding party.

By using comparable methods across sites for the first time I was able to assess the validity behind apparent community level differences in the likelihood that individuals produced rough grunts during arrival. To do so, I assessed community differences within each sex. Surprisingly, I found no statistical support that males at Kanyawara and Sonso show differences in their likelihood to rough grunt upon arrival to a food source, as indicated in previous studies (Fedurek & Slocombe, 2013; Slocombe et al., 2010). But I did identify that adult males at Sonso were more likely to call than males at Taï south and Ngogo central. Future research needs to investigate whether feeding ecology, cultural differences in calling behaviour or the function of rough grunting may be driving this population-level variation in vocal behaviour. For instance, out of the four communities included in model 1, Kanyawara and Sonso have the most similar demographics in terms of the total number of community members and number of adult males. Therefore, if social functions are driving this behaviour, individuals at these sites are likely to have more similar numbers of affiliated or dominant individuals to target with their calls. Ngogo central on the other hand was the largest community in our sample (i.e. 44 more members than Sonso, with 17 more adult males), and the habitat ecology for this community is also renowned for its abundance of fruit resources, which may explain the unusual population density at this site (Watts, Potts, Lwanga, & Mitani, 2012). It's possible then that at Ngogo central, where food resources are abundant, the provisioning of information about food sources is less of a commodity between individuals. Therefore, perhaps unlike Sonso (Schel et al., 2013; Slocombe et al., 2010) rough grunting during feeding behaviour is less important to social relationships for male chimpanzees at Ngogo central. Instead, perhaps other cooperative behaviours displayed frequently in this community (e.g. hunting and boundary patrols; Langergraber, Watts, Vigilant, & Mitani, 2017; Mitani & Watts, 1999; Watts & Mitani, 2002) fulfil these functions. Regarding adult females, females at both Sonso and Ngogo central were significantly more likely to rough grunt than females at Taï south. It is possible that by restricting the data set to feeding events on fruit and leaves to ensure cross-site comparability I may have inadvertently eliminated food types with high nutritional value (e.g. nuts) from certain sites, such as Taï south, that may elicit high levels of calling. Although fruit and leaves made up the majority of feeding events in all the study communities the relative value of these types of foods may vary across communities, and may influence calling behaviour. While future research is needed to elucidate the factors driving this variation between communities, with my approach it is clear that these differences in calling behaviour result from genuine population-level differences rather than artefacts of varying data collection procedures.

When testing social and ecological correlates of male rough grunt production I replicated some findings from the literature, but not all. In terms of ecological factors I replicated previous findings that male chimpanzee rough grunts are given more in response to larger, and higher quality food patches (Kalan et al., 2015; Slocombe et al., 2010) with rough grunts being more likely to occur in events with higher 'chimp minutes'. I did not however find that their responses changed with regard to food type. While these results support those of Ischer et al. (2020), who also examined calling to fruit and leaves in the Sonso community, they contrast with previous findings from the Kanyawara and Taï south communities (Fedurek & Slocombe, 2013; Kalan & Boesch, 2015). It may be that my measure for this ecological correlate was not precise enough, as I distinguished only between fruits and leaves, whereas previous studies that did identify an effect of food type included more refined categories regarding fruit ripeness (ripe, unripe) and leaf age (young, mature).

In terms of social factors influencing male rough grunt production in the Sonso and Kanyawara communities I replicated some findings from the literature, but not the majority. In line with previous findings from the Taï community, I found that males are less likely to call when more females were in the party (Kalan & Boesch, 2015) indicating that females already in the feeding party are not the targets of these calls. The current study was unable to investigate whether the oestrus status of present females would have altered their vocal behaviour, but these results indicate that if rough grunts are produced to recruit others to the food source adult females may nevertheless be a target for social recruitment. Regardless of current oestrus status, it's possible that maintaining association with potential mating partners is important for future reproductive opportunities. If the function of male calling behaviour is to attract females to food sources, the tendency for males at Ngogo central to call less often (i.e. than Sonso males) may suggest they are already relatively successful at maintaining access to mating partners, given that there are similar sex-ratios in the two communities. The cost-effectiveness of calling would then be lessened, as advertising valuable food sources may then only increase competition if other males hear the calls and approach. It would be important in future to determine whether female recruitment to feeding trees does increase the reproductive success of males at Sonso, and then to examine whether males at Ngogo central maintain greater proximity to females in contexts outside of feeding behaviour. In line with Fedurek and Slocombe (2013), I found that the number of males in the party did not influence calling. This indicates that the previous finding from the Taï south community, that males were likely to call when more males were in the party (Kalan & Boesch, 2015), may be an artefact of the very small number of adult males (N=3) in the community at the time of study.

In line with the findings of Leroux et al. (2021), I also found that arriving males from Kanyawara and Sonso were more likely to rough grunt if they had also produced a pant hoot during their arrival period. However, it is important to note that while rough grunts occurred in a significant proportion of arrivals where pant hoots also occurred (78/103), there were many cases of rough grunts being produced in the absence of pant hoots during arrival (246/591). Unlike the Leroux et al. (2021) study, I did not have the fine-grained temporal information on call production required to see how many of these instances where both call types were produced were true call combinations (inter-call duration of up to 2 seconds; Leroux et al., 2021). Furthermore, in the absence of data from playback experiments we cannot ascertain the meaning of these call combinations to listeners. Combined calls can express alternative meanings to the single calls they are composed of (Zuberbühler, 2018), and thus pant-hoot/food call combinations may hold separate functions to rough grunts alone. Therefore, in future it would be important to distinguish whether rough grunts occur as part of a call combination or independently. Finally, in line with Kalan and Boesch's (2015) findings from the Taï south community, I found that the control predictor for focal rank had a significant effect on male calling behaviour, with low-ranking individuals being more likely to call than high-ranking individuals. Low-ranking individuals may have more to gain socially in advertising food sources; perhaps by increasing affiliation with valuable social partners, increasing mating opportunities or attracting close allies to food sources.

Unexpectedly, there were a number of other social correlates of male rough grunt production identified in previous studies that I did not find any support for in my data set from the Sonso and Kanyawara communities. There was no evidence that calling was more likely in the presence of certain types of individual. More specifically, I found no evidence that the presence of important social partners increases the likelihood of rough grunts during arrival, whereas previous studies found this to be an important social correlate of calling (Fedurek & Slocombe, 2013; Schel et al., 2013; Slocombe et al., 2010). Methodological differences with these previous studies may account for this discrepancy. First, while the current study calculated a composite friendship index using party level associations, nearest neighbour associations and grooming frequency (as published in Schel et al., 2013), other studies either did not examine grooming behaviour (Fedurek & Slocombe, 2013) or exclusively used grooming interactions (Slocombe et al., 2010) to determine the relative strength of social bonds. Measuring social bonds is complex, and it’s possible that slight changes in the applied measures resulted in each study investigating different relationship strengths. Future research could productively examine whether rough grunt production is mediated by the presence of social partners with whom the potential caller has different degrees of association or friendship. This would avoid arbitrary determinations of which values represent closely bonded partners, and aid our understanding of which individuals are being targeted with these calls. While I did adopt the same methods as Schel et al. (2013) for my measure of social bonds, critically these authors examined the calling behaviour of already present individuals, and in regard to their relationship with an arriving individual. A signaller’s motivation to produce calls may vary; calls produced during feeding may act as an invitation or encouragement for socially bonded recipients to join the signaller, but arrival calling may not be directed at this audience.

Methodological inconsistencies may also explain why I failed to replicate the previous finding that rough grunt production was more likely in the presence of high-ranking individuals (Schel et al., 2013). Instead of examining the magnitude of rank differences between signallers and social partners as Schel et al. (2013) did, I looked at whether the highest-ranking individuals in the community were present at the feeding event. While rank difference may be a more intricate measure, one of the primary goals of this project was to produce directly comparable findings with adult female chimpanzees, where exact rank calculations were not possible. Furthermore, as the highest ranking males pose the most aggression risk in a community (Muller & Mitani, 2005) any potential benefits of targeting these individuals, such as increasing tolerance or affiliation with valuable partners (Ischer et al., 2020; Schel et al., 2013), should still have been captured with my measure. Currently, it appears that neither of these are the primary function of adult male rough grunts during their arrival to feeding events.

Novel findings from my investigation of male rough grunt production include several indications that rough grunt production is not simply a product of high arousal. First, a control predictor in model 2 for the total number of adult individuals in the feeding party (where it was assumed that large parties would be more arousing than smaller parties) was unexpectedly significant. In contrast to previous studies that found no effect for party size on the likelihood of calling (Kalan & Boesch, 2015; Kalan et al., 2015; Slocombe et al., 2010), I found that males were significantly less likely to call in larger adult parties. However, as this was not a test predictor (and therefore multiple-testing was not controlled for) future studies need to explore this further. Second, I found no evidence of emotional or vocal contagion: males were not more likely to call when conspecifics had also produced rough grunts in the 3 minutes prior to their arrival, nor when conspecifics had already produced pant hoots in this period. This absence of affective contagion suggests that rough grunts are not merely a manifestation of excitement or arousal stemming from group vocal behaviour, and suggests an alternative motivation for food-associated calling.

A diverse array of functions have been suggested in the literature for rough grunt production in adult male chimpanzees; the most prominent theories are to attract foragers (particularly valuable social partners) as a form of social recruitment (O'Bryan et al., 2020; Schel et al., 2013), and to coordinate feeding behaviour with close allies (Fedurek & Slocombe, 2013) both of which may increase opportunities for social bonding, or as a social tool to restore tolerance following aggression (Ischer et al., 2020). I did not have the necessary data to test between these competing ideas, but given the important community-level differences I have identified it's possible that these calls hold different functions between sites; particularly as the demographics between communities are so diverse. At Kanyawara and Sonso at least, where social correlates were examined, my data does not support the social bonding theory as males were not more likely to call for important social partners or high-ranking individuals. Here the social recruitment of females to the feeding source seems more likely; perhaps to increase future reproductive opportunities by maintaining proximity with these individuals. In future, cross-site studies where the necessary data to test between these different functions is collected in a directly comparable fashion would allow us to better understand which functions are fulfilled by male rough grunt production, or whether functions vary according to the ecology and social dynamics of the community.

Collecting directly comparable data on males and females allowed me to test for the first time if female rough grunt production is sensitive to the same ecological and social correlates as males, or whether calling in females may fulfil different functions given the likely differences in costs and benefits to the behaviour in the two sexes. I found that in contrast to the males, ecological factors did not explain a significant amount of variation in the likelihood of rough grunt production in females. Whilst there was a trend for females to be more likely to call in response to larger, or higher quality patches (as I established for adult males), this finding was tentative given the overall non-significant outcome of the model. As the measure of chimp minutes is a composite index, representative of both food abundance and quality, it's possible that for females advertising high quality food sources is still too costly. Perhaps if I was able to separate these measures I would have found that females are willing to call for abundant, lower quality food sources. Though future research could usefully investigate this possibility further it seems clear that female calling is less sensitive than male calling to the value of the food source. This could be a result of females considering the wider social context in combination with the ecological context to a greater extent than males. For example, when foraging with kin it may be important to call to high quality food sources to maximise nutritional benefits of offspring, but not if there are males nearby who could be attracted to the source and displace the caller, or reduce foraging efficiency with agonistic interactions and displays. I did not have sufficient sample sizes to examine the interactions between most of my predictor variables, but this could certainly add important insights in future research. Despite increased nutritional demands faced by reproducing females (Thompson et al., 2007), the control predictor of having dependent offpring did not influence the likelihood of female calling. I was unable to explore this as a test predictor due to a small sample of females without dependent offspring being available. With a more balanced sample in future, it would be interesting to explore interactions between reproductive status and other predictor variables. This could ascertain if, despite appearing to be equally likely to call, the factors that promote calling are different for females with and without dependent offspring.

In contrast to the males, when taken together social variables were unable to account for a significant amount of variation in whether females from the Sonso and Kanyawara communities called during their arrival at a food source. Significant coefficients within the overall non-significant model highlight interesting areas for future investigation. These include calling seeming more likely when arriving with important social partners. In my data adult females had fewer social partners than adult males, and sometimes this was limited exclusively to their older offspring. Thus examining the presence of kin for females may be a more relevant variable to explore in future. My model also indicated that females were more likely to call if other individuals had produced rough grunts during their arrival. This may suggest that females are more susceptible to vocal contagion than males, with higher arousal from group vocalising causing their own calling to increase. However, given the non-significant overall model future research would need to confirm this effect. The non-significant overall model and remaining non-significant coefficients highlight some interesting contrasts with previous findings from the Taï south community in Cote d'Ivoire. Females in my sample were not more likely to vocalise when other females were arriving with them or already present, contrary to prior research (Kalan & Boesch, 2015). Given the elevated predation risks from leopards

(Boesch, 1991), and higher rates of female-female competition over food at Taï compared to East African communities (Mielke et al., 2019; Wittig & Boesch, 2003), females in this community may have more incentive to call to other females; perhaps to promote group feeding to avoid predation, or as a tactic to counteract female-female food related aggression by claiming resources. However, given the overall non-significant model limited confidence in this finding is warranted, and this idea needs to be further explored. As with the adult males I found no change in rough grunt production for adult females in relation to the total number of males in the party, or if high-ranking individuals were in the party. Although Ischer et al. (2020) theorise that rough grunting may be used as a social tool to restore peaceful co-feeding following aggression, my findings suggests that females do not produce rough grunts on arrival as a preventative measure against aggression from males in general or high-ranking males, who are most likely to display frequent and high levels of aggression towards females (Muller, 2002; Muller & Mitani, 2005). Thus I found no evidence for females using grunts on arrival at a food source to promote tolerance.

Given the non-significant models examining factors influencing call production, it is clear that adult female call production is not sensitive to the same social and ecological factors as males from the same communities. However, it does remain unclear what the function of female rough grunting is. Overall, adult females appear more reluctant to advertise food sources than adult males, with a lower likelihood to produce rough grunts even when food is abundant. Social recruitment and promotion of tolerance when feeding appear unlikely to be the primary functions of calling, as I found no evidence that group composition affected the likelihood to call. Currently, an exclusive female function of targeting dependent offspring also seems unlikely, but further testing of interactions between predictor variables with large data sets, and a more balanced representation of females with different reproductive statuses is needed. Future exploration of different factors, such as the presence of kin or particularly aggressive males in the feeding party, would be a valuable next step to help identify possible functions for female arrival rough grunting.

My data has also provided important insights into the development of rough grunt production. Although I identified very few instances of rough grunting in infants (3/73), I did document the occurrence of rough grunting during the first year of life as previously suggested for this call type (Dezecache et al., 2021). It's possible that my study has underestimated infant grunting; it seems likely that soft vocalisations could have been inaudible to observers, particularly if other chimpanzees were also vocalising during their arrival period, and that these were missed during data collection. It was notable that mothers were silent in all but 6/73 arrivals, but in half of these six cases the infant also grunted. In line with this pattern in infancy, there was a potential social learning effect in the juvenile chimpanzee sample (4-10 years). Descriptively, in 18/25 instances when mothers produced rough grunts during or immediately after their arrival at a food source, juvenile chimpanzees also produced rough grunts. This mirrors previous findings focussed on the production of social grunts in young chimpanzees (Laporte & Zuberbühler, 2011), and supports the idea that infants mirror the vocalisation patterns of their mothers during early development prior to learning appropriate contextual or social specificity in which to produce calls. However, it is important to note that more temporally detailed data is needed to confirm that juvenile calling is being triggered by their mother's calls: in the absence of data showing that the mother reliably calls first, the juvenile and mother may simply be responding to the same ecological or social features of the feeding event, and thus both producing calls. It would also be important for future research to investigate whether juveniles are sensitive to the calling of other individuals present at a feeding event, and if so whether they are more likely to mirror kin (e.g. older siblings), same sex-adults or dominant individuals, and whether the relative importance of the mother as a potential vocal model decreases with age.

Model 6 also identified an interesting trend suggesting some age and sex variation in rough grunt production in young chimpanzees (from juvenility to sub-adulthood). In line with findings regarding chimpanzee 'social grunts' (Laporte & Zuberbühler, 2011), it was found that the likelihood of producing rough grunts increased slightly as age increased. This developmental trajectory was clearest in male individuals, and particularly in the later years leading up to adulthood. Descriptively, male rough grunting became much more likely to occur between the ages of 8 and 14 years. During this period testosterone increases sharply, and males begin to become socially independent from their mothers (Thompson, Muller, Machanda, Otali, & Wrangham, 2020). Perhaps the resulting increase in socialisation around non-kin adults and attempting to affiliate with non-kin leads to changes in their calling behaviour. The smaller sample of female young chimpanzees seemed to show relative stability in the likelihood of rough grunt production. This data set indicates therefore that the adult sex differences in propensity to produce rough grunts during arrival at a food source start to emerge in late adolescence. However, further investigation with a larger more balanced data set is needed to better understand the developmental trajectory of rough grunt production in females.

The current work has highlighted the critical need to widen the demographic groups studied when examining the vocal behaviour of chimpanzees. Firstly, my results suggest that including data from multiple sites is imperative as genuine population-level differences exist in rough grunt behaviour; potentially due to the vastly different habitats or feeding ecology that chimpanzees across Africa experience (Boesch et al., 2020; Potts et al., 2011). Cross-site comparisons are equally important when considering social factors, as here I included five different communities with vastly different demographics (ranging from a population of 19-119) which may affect the number of bonded partners or high-ranking individuals. Unfortunately, here I was only able to examine two of the more similarly sized communities for social correlates, but it would be an important future step to take. A cross-site approach is becoming more evident in other areas of chimpanzee vocal behaviour (Fedurek et al., 2021), but efforts need to continue to make this a consistent consideration when investigating chimpanzee behaviour.

My findings also emphasise the need to move away from male-centric approaches, with multiple sex-differences identified in the likelihood to produce rough grunts. From my investigation of ecological and social correlates it was clear that females were not producing rough grunts in a comparable manner to males. Therefore, findings should not be extrapolated from male individuals and considered to be representative of 'chimpanzees' as a species. These sex differences may also emerge during development, particularly during late adolescence, therefore a representative male/female sample is necessary even in an ontogenetic approach. My analysis with juveniles also identified for the first time a potentially important role of social learning, regarding when these individuals should produce rough grunts. Understanding how vocal behaviour changes during development could provide valuable insight into the function of these vocalisations, and needs to continue to be studied in order to fully understand this behaviour.

To further expand our knowledge of food-associated calling in chimpanzees, it would be valuable for future studies to investigate rough grunts that are also produced later on during feeding bouts. I focused my analysis on calling during arrival, but the function of calls produced during the feeding bout may depend on the immediate context. For instance, these calls could be produced in response to aggression (Ischer et al., 2020), to claim ownership over a patch of food to reduce competition (Gros-Louis, 2004), or in response to seeing or hearing individuals arriving in the vicinity of the food patch to invite them to join (Schel et al. 2013). Data from whole feeding bouts could therefore reveal flexible functions for this vocalisation. The implementation of more intricate acoustic analysis may also be essential to truly understand the meaning of these calls, as characteristics such as pitch have been found to alter in regard to ecological qualities of the feeding event (Kalan et al., 2015; Slocombe & Zuberbühler, 2006). Although captive playback experiments have indicated that listeners are sensitive to this acoustic variation, and seem able to make inferences regarding the quality or value of the food found by the caller (Slocombe & Zuberbühler, 2005), the degree to which acoustic variants of rough grunts influence decisions about whether to join a feeding tree in the wild or not requires investigation.

To conclude, this study has identified that adult male chimpanzees are more likely to produce rough grunts during arrival to feeding sources than females in most sites. However important community differences exist that affect the likelihood of calling, and mediate the extent and direction of these sex differences. By examining the ecological variables across four wild communities I was able to replicate that male chimpanzees are more likely to call for food patches that are larger and/or of higher quality. In contrast, ecological variables did not account for a significant amount of the variation in female calling across five sites. When examining social variables in two communities, in male chimpanzees I identified a negative relationship between the number of females in the party and arrival calling, and established that rough grunts were more likely to occur if the focal individual also produced pant hoot vocalisations. In females, social variables did not account for a significant amount of variation in their calling behaviour. Given these findings, the function of these calls in adult females is unclear. In male chimpanzees I did not find support for a social bonding function of these calls (i.e. to maintain male social bonds), so it’s possible that social recruitment (particularly of female individuals) may be a more likely function of arrival rough grunts. Concerning infants, rough grunt production was rare but increased with age, particularly in late adolescence in males, indicating that sex-differences in the propensity to grunt emerges before adulthood. Social learning, or potentially vocal contagion, may play an important role in the decision for young chimpanzees to produce these calls. Critically these findings have demonstrated that conducting cross-site comparisons, and including individuals from both sexes and across all ages is vital; the exclusion of any of these demographics, or single-site studies, will not provide a full picture regarding the function of a behaviour.

CHAPTER 3: Is a referential gesture ubiquitous to wild chimpanzees? An exploration of alternative functions for the exaggerated loud scratch gesture

ABSTRACT

A fundamental aspect of human communication is our ability to refer to external objects and events through both words and gestures (such as pointing), yet the evolutionary origins of such signals remain obscure. Wild apes rarely or never point, but it has been claimed that male chimpanzees from the Ngogo community habitually use a loud, exaggerated scratch gesture to refer to specific body locations they wish to be groomed (Pika & Mitani, 2006). This study influentially suggested continuity between referential abilities in humans and our closest living relatives, making it an important finding to try and replicate in other chimpanzee communities. Here, I compared whether exaggerated loud scratch (ELS) gestures are used in a referential manner across four wild communities (Ngogo, Kanyawara, Sonso, and Waibira) of eastern chimpanzees. This data revealed that scratchers were significantly more likely to receive grooming in the scratched location at Ngogo compared to the other three sites. In Kanyawara, Sonso and Waibira this response occurred at low rates, and signallers did not seem to pursue this goal suggesting the ELS gesture does not function referentially at these sites. Further exploration into alternative functions of this gesture with the Kanyawara community showed that, in this community, it functions to initiate grooming bouts and to reengage partners during grooming pauses. Individuals who produced the signal to initiate grooming were more likely to subsequently offer grooming to the recipient. In contrast, during grooming bouts, when groomers produced an ELS they were more likely to receive grooming than without an ELS. When they did not receive grooming, they showed goal-directed behaviours in the pursuit of this goal. This study demonstrates that chimpanzees do not ubiquitously use the ELS in a referential manner, but that they can use this gesture in a highly flexible fashion, with signal function being dependent on the intricate details of the social contexts in which they are produced. The subtle group-specific differences in the usage of this signal identified here may be indicative of cultural diversity in the function or meaning of gestural signals in chimpanzees.

INTRODUCTION

Referential signals, which direct the attention of recipients to particular aspects of the environment, are an important type of semantic signal where the mapping between signal and meaning is easier to identify than for signals denoting more abstract concepts (Liebal & Oña, 2018; Townsend & Manser, 2013). In children referential pointing gestures tend to emerge before words, and proficiency in early pointing has been considered an important milestone in language development (Bates, 1979; Butterworth, 2003; Kita, 2003; Liszkowski, Brown, Callaghan, Takada, & de Vos, 2012), with many studies supporting a close link between early pointing and later language abilities (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Colonnesi, Stams, Koster, & Noom, 2010). From the onset of speech production children start to use word-point combinations (Esteve-Gibert & Prieto, 2014) which precede two-word utterances for external objects (Goldin-Meadow & Butcher, 2003). As speech develops referential words can then denote a wide range of objects, events, ideas, and concepts (Pika, 2012; Sperber & Wilson, 1986). Referential communication is therefore a cornerstone of early language acquisition, and it is critical to understand the evolutionary origins of this aspect of language.

To study referential communication in non-human species research initially focused on functionally referential vocalisations, which have been identified in a wide variety of taxa (Gill & Bierema, 2013; Townsend & Manser, 2013). However, as chapter 1 detailed, how far traditional definitions of functionally referential calls can truly show continuity with human reference has been debated (Wheeler & Fischer, 2012). However, the cognitive mechanisms underlying the production and reception of gestural signals are believed to show more aspects of continuity with human communication; critically, non-human gestural signals appear to be produced intentionally (Byrne et al., 2017; Hobaiter & Byrne, 2014). Deictic gesturing (a type of reference where the meaning is dependent on the context in which it is used) appears to be relatively widespread in non-human species within captive environments. For example, several species have succeeded in pointing to out of reach foods for human experimenters, including domestic horses (Malavasi & Huber, 2016), dolphins (Xitco, Gory, & Kuczaj, 2004), and non-human primates (e.g. tonkean macaques: Canteloup, Bovet, & Meunier, 2015; orangutans*:* Call & Tomasello, 1994; chimpanzees: Leavens, Russell, & Hopkins, 2005; Tomasello, George, Kruger, Farra, & Evans, 1985; Tomasello, Gust, & Frost, 1989; bonobos: Zimmermann, Zemke, Call, & Gómez, 2009). However, although these studies demonstrate that these species are capable of producing deictic gestures with human partners, they do not reflect their propensity to produce such gestures during natural interactions. As outlined in chapter 1, accounts of naturally-occurring pointing gestures with conspecifics are rare (chimpanzees: Hobaiter, Byrne, & Leavens, 2014; bonobos: Veà & Sabater-Pi, 1998), but reports for other spontaneous referential communication has been claimed in some other taxa. For instance, ravens 'offer' or 'show' partners objects (Pika & Bugnyar, 2011). Another avian species, Australian magpies, have been reported to use a 'pointing' gesture towards model eagles to inform other group members of its presence (Kaplan, 2011). In this case it is difficult to separate the individual simply orienting towards the referent, from the richer interpretation that a gesture is produced which provides information to conspecifics. Perhaps surprisingly, some of the most compelling evidence for natural referential gesturing from a non-primate subject comes from two coral reef fish species; both groupers and coral trout use a 'headstand' signal to indicate the location of hidden prey to potential interspecies hunting partners (moray eel and octopus; Vail, Manica, & Bshary, 2013). Although there were limited events where this gesture was exhibited, it produced reliable responses in the recipients and had a clear external referent available. These data on referential gestures in species more distantly related to humans are vital for assessing the selective pressures that made such signalling an adaptive strategy. However, when trying to trace when in the human lineage's referential abilities first emerged, it is important to refocus attention on primates.

In non-human primates, only a few naturally occurring referential gestures directed at conspecifics have been described. For instance, bonobo females produce a 'foot pointing' gesture that appears to refer to their own sexual swelling, and which results in genital-genital rubbing in 85% of cases with the intended recipient (Douglas & Moscovice, 2015). However, it is difficult to ascertain whether the claimed referential function of the signal is understood by recipients, or whether they simply interpret it as a gestural request for action. There may be more similarity between these foot 'points' or leg swing gestures and other widespread 'present genitals' postures females and males perform to solicit copulations, than referential points. Another sexual solicitation bonobo gesture, 'beckoning', has been claimed to be spatially referential by indicating a desired location for mating behaviour (Genty & Zuberbühler, 2014). However, in this case the behaviour was rarely observed and the gestures lacked a consistent form. In chimpanzees there has been only one study claiming habitual use of a referential gesture, the exaggerated loud scratch (ELS), which was briefly described in chapter 1. An ELS gesture (also termed 'big loud scratch'; Hobaiter & Byrne, 2011b) is commonly reported across chimpanzee communities (Goodall, 1986; Hobaiter & Byrne, 2011b), and is utilized both to initiate joint travel (Hobaiter & Byrne, 2014; also observed in orangutans: Fröhlich, Lee, Setia, Schuppli, & van Schaik, 2019) and to solicit grooming (Hobaiter & Byrne, 2014; Pika & Mitani, 2006; also observed in bonobos: Graham, Hobaiter, Ounsley, Furuichi, & Byrne, 2018). In one community it was claimed to function as a deictic referential gesture during grooming by indicating a specific body part that the signaller would like their partner to groom, and thus termed the 'directed scratch' (Pika & Mitani, 2006). Presenting body parts to the groomer to fulfil the same function during grooming has been reported in other communities of chimpanzees (Hobaiter & Byrne, 2014) and in wild bonnet macaques (Gupta & Sinha, 2016).

The chimpanzee ELS gesture, or 'directed scratch', appears to provide some of the most convincing evidence for a customary and frequently used gesture functioning to direct the attention of recipients in a referential manner (Pika & Mitani, 2006). Pika and Mitani (2006) found that in 64% of cases when a groomee produced a directed scratch, they successfully received grooming in the scratched area. However, there are a number of limitations to this study: First, only a small number of the grooming bouts were filmed, so whether subsequent grooming matched the scratched area was largely coded in real time, and no inter-observer reliability on this crucial measure was available. Second, Pika and Mitani (2006) did not test whether the signaller's goal was to elicit grooming in a specific location to understand if these signals are intentionally produced: rates of persistence or elaboration in the cases where the putative goal was not met are required to examine this. Third, they restricted their analysis to those scratches that could be seen by the recipient, presupposing a visual component and excluding all other examples of this audible gesture. Finally, their finding was based on adult male-male dyads from a single community of chimpanzees only, while investigations of the potentially referential use of this gesture in other dyads (e.g., between female-male, female-female), and members of other chimpanzee communities remain missing.

Whilst Pika and Mitani (2006) offered one function for the chimpanzee ELS gesture in a grooming context, it is also important to consider other possible functions for this gesture that have been suggested in the literature. Firstly, Goodall (1986) suggested that ELSs are used to initiate grooming bouts. This interpretation was supported by Hobaiter and Byrne (2014), who similarly reported that this gesture appeared to be a means to initiate grooming. They found that signallers desisted signalling when grooming started in 82% of cases (indicating an 'apparently satisfactory outcome'), but specifically scratches appeared to primarily denote 'groom me'. Secondly, research across several species suggests that scratching can be an indicator of social anxiety. Cases of self-scratching are more common during times of social stress, including after aggressive encounters (pigs: Norscia, Collarini, & Cordoni, 2021; barbary and long-tailed macaques: Aureli, 1997), during mating seasons when competition is high (ring-tailed lemurs: Sclafani, Norscia, Antonacci, & Palagi, 2012) and when subordinates groom dominant individuals (e.g. barbary macaques: Kaburu, MacLarnon, Majolo, Qarro, & Semple, 2012). In chimpanzees, anxiety-induced scratching has been discussed for both captive and wild individuals (Baker & Aureli, 1997; Botero et al., 2013). Thus, within the grooming context where individuals are in vulnerable and proximate positions it is conceivable that the ELS, particularly in subordinate individuals, could be conflated with signs of social anxiety.

The aim of this study was to test competing accounts for the function of the ELS during grooming in chimpanzees. Specifically, I examined dyadic interactions to first investigate whether (i) the ELS functioned as a referential gesture to denote the area the signaller wished to receive grooming in, as reported by Pika and Mitani (2006). For this I examined data from three chimpanzee communities (Kanyawara, Sonso, and Waibira) alongside the published data from the Ngogo community (Pika & Mitani, 2006). If the signaller received grooming within 5cm of the scratched area, within 10s of the scratch ending, I considered this as support for a referential function for the ELS. To test whether the goal of the signaller was to elicit grooming in the scratched area, I used established criteria for goal-directed intentional signal production: the signaller should persist, elaborate, or terminate the interaction more often when their putative goal is not met (they do not receive grooming in the scratched area), compared to when it is met (grooming received in the scratched area; Townsend et al., 2017). In order to explore alternative functions for the ELS gesture, I examined the video data from Kanyawara in more detail to test the following functions: whether (ii) the ELS is used to initiate grooming bouts, as reported by Goodall (1986) and Hobaiter and Byrne (2014). If this hypothesis is true, I expected a higher rate of ELSs in the 20s prior to grooming initiation than during the grooming bout. In line with Hobaiter and Byrne's (2014) suggestion that the ELS means 'groom me', I predicted that the signaller was more likely to then receive grooming rather than give grooming at the start of the bout. Once a grooming bout had commenced, I wanted to (iii) explore the possibility that ELSs are used to re-initiate grooming when grooming stops, predicting that the rate of ELSs will be higher in a grooming pause than the rest of the grooming bout. Following this, I wanted to explore whether (iv) the ELS could function to request grooming (Hobaiter & Byrne, 2014) not only before initiation but also during grooming bouts. It was predicted that groomers will be more likely to receive a favourable grooming role switch (receive grooming) in the 10s following an ELS than during the rest of the grooming bout. Here again, I was able to examine cases of persistence, elaboration, or grooming termination to ascertain whether receiving grooming was the goal of the signaller. Finally, I wanted to investigate whether (v) the ELS is a sign of social anxiety, and here I expected individuals to produce more ELSs when grooming with higher-ranking than lower-ranking partners, and with less-affiliated than highly-affiliated partners.

METHODS

Study sites and subjects

Video and observational data were collected from three wild chimpanzee communities: Kanyawara, Sonso and Waibira. These data were then compared to the previously published data (analysed material) available from the Ngogo community (see Appendix 1). A detailed overview of the location, habitat ecology and site descriptions for Kanyawara, Sonso and Ngogo have been outlined in chapter 2. The final community, Waibira, is located in the Budongo forest in the western Rift Valley in Uganda. This group has been observed since 2011, and some individuals were still undergoing habituation at the time of study.

Video data were collected at Kanyawara in four study periods (February - May 2013, June 2014 - March 2015; July 2016 – September 2016; January 2018 - October 2018) by CW and NL. This group comprised approximately 57 individuals in 2013 (Muller & Wrangham, 2014) during the first study period, and approximately 61 individuals in 2018 (personal observation) during the final study period. Specifically, data were collected from 22 male and 21 female chimpanzees, and their ages ranged between 4 and 50 years at the time of observation.

Video data from the Sonso and Waibira communities were collected by CH between 2011-2016 for Sonso and 2014-2020 for Waibira. The Sonso community had an approximate group size of 69 individuals at the time of study (Hobaiter, Samuni, Mullins, Akankwasa, & Zuberbühler, 2017), and data were collected on 18 females and 16 males aged from 17-34 years. The Waibira community, accounting for those partially habituated to human presence, had between 100-120 individuals (Hobaiter et al., 2017). From this group I had data on 12 females and 28 males ranging between the ages of 22-41 years.

For the Ngogo community the published dataset was provided to the current study in the form of an excel sheet detailing the basic data that underpinned analyses in the previously published paper. No video data were provided for Ngogo. These data originated from vocal commentary of grooming interactions which were collected in the period February - March 2005 by SP. These data were therefore collected prior to the community fission in 2017 (Sandel & Watts, 2021) unlike the data presented in chapter 2. Thus at the time of study Ngogo was the largest known community consisting of approximately 145 chimpanzees. Data were collected on 25 adult male individuals, with ages ranging between 19 and 47 years at the time of observation.

Ethical note

This study complied with the ASAB/ABS guidelines for the use of animals in research. Ethical approval for data collection in Kanyawara was granted by the Biology AWERB Ethics Committee (University of York), and the Institutional Animal Care and Use Committee of Harvard University, Tufts University and the University of New Mexico. Ethical approval for data collection in Budongo was granted by the Animal Welfare and Ethics Committee of the University of St Andrews. The Ugandan Wildlife Authority and the Ugandan National Council for Science and Technology granted permission to collect data in Uganda.

Equipment

Observational video data were collected with a Panasonic HDC-SD40/60/90 and Panasonic HC-VX980 model camcorder at Kanyawara, with a Sennheiser MKE 400 external microphone attached. At Sonso and Waibira video data were collected with a Panasonic HDC-SD60 or similar model. At Ngogo real-time commentary on grooming interactions was dictated into a digital recorder, Audioline VR-500. Kanyawara videos were coded using Noldus Observer XT 10/12/14 event logging software for observational data (http://www.noldus.com/animal-behavior-research).

Data collection

For the hypothesis on the function of the ELS as a referential gesture a cross-site analysis was performed including all four communities. All other hypotheses were addressed with data from the Kanyawara community only, as this is where systematic video data were collected.

At Kanyawara in the first two study periods focal adult chimpanzees were video recorded for samples of ca. 15 minutes duration, which often included grooming bouts, but not always the initiation and termination of the bouts. In the last two study periods grooming bouts were video recorded with every effort made to capture the whole bout from initiation to termination. Wherever possible, data from both individuals in the dyad were used in the analysis. Overall 775 dyadic grooming bouts containing 585 ELSs (including those in the 20s prior to grooming) were collected, with a total of 2,944 minutes of dyadic grooming from 239 unique dyads.

For Sonso and Waibira data collection involved focal behaviour sampling (Altmann, 1974) with all social interactions with the potential for gestural communication recorded. While recording was not continuous, a three-second pre-record function allowed the capture of the start of the onset of any interaction at which the camera was directed. Wherever possible this included recording of the signaller, potential recipients, and any subsequent behavioural responses. A running record of the frequency with which particular individuals were observed was maintained and used to select who to film where multiple targets were available. For Sonso 947 dyadic grooming bouts were identified and checked for groomee ELSs, resulting in 68 groomee ELSs from 34 unique dyads; for Waibira 578 bouts were identified and checked, resulting in 45 groomee ELSs from 32 unique dyads.

Data from the Ngogo community were provided to the current study in the form of analysed material which was published in Pika & Mitani (2006). For the collection of the raw data (by SP), instances of scratching during male-male grooming bouts were dictated ad libitum on a digital voice recorder. The groomer ID, groomee ID, and any scratches given and their frequency were recorded, as well as the partner's response to the signaller's scratch: whether 1) the partner stopped grooming the spot he was grooming and changed to grooming the scratched location, or 2) the partner continued grooming the same location he had been grooming before the scratch (see Pika & Mitani, 2006, and Pika & Mitani, 2008 for further details). Overall 249 dyadic grooming bouts were observed, containing 186 groomee ELSs from 79 unique male-male dyads.

Video coding

Kanyawara videos were coded with Observer XT software to extract continuous details about (1) whether there was dyadic grooming or not, (2) grooming roles, (3) grooming role switches, (4) whether individuals were actively grooming or in a pause, (5) ELS gestures by either individual, (6) 'present groom' gestures ("body is moved to deliberately expose an area to the recipient's attention"; Hobaiter & Byrne, 2011b) by either individual, and (7) arm-raise gestures ("raise arm and/or hand vertically in the air"; Hobaiter & Byrne, 2011b) by either individual.

Definitions

Exaggerated Loud Scratch (ELS)

Pika & Mitani (2006) defined this signal as 'a relatively loud and exaggerated scratching movement on a part of his (own) body, which could be seen by his grooming partner'. This is in line with Hobaiter & Byrne's (2011b, termed Big Loud Scratch) definition of a 'loud exaggerated scratching movement on the signaller's own body', and here scratches were accompanied by behaviour that suggested intentional signalling (response waiting, audience checking, persistence). The current study did not require scratches to be intentionally produced by the signaller to enter any analyses as this was absent in Pika and Mitani's (2006) definitions. Thus, it is unknown whether ELSs from the Ngogo community in this chapter met these markers or not. While I did not require scratches to be intentional in order to have a comparable dataset, I do examine some indicators of intentional production (e.g. persistence) which is detailed in the statistical models section.

In order to reliably operationalise these definitions, I looked for scratches in the video data that were: (1) exaggerated in terms of involving the movement of the entire arm, not just the fingers or wrist, (2) were big in terms of covering an area of at least 15cm, (3) involved at least two scratches at the same location, (4) were not part of self-grooming, so did not involve the individual inspecting or grooming the scratched location. But, as this gesture contains a strong audible component, (5) I did not restrict analysis to ELSs produced within the recipient's visual line of sight.

Dyadic grooming bout

Two individuals grooming with one another; this could be uni-directional or bi-directional. Bouts started as soon as one (or both) individual(s) started grooming the other, and there were no other individuals involved in the bout. Bouts were terminated when either individual started grooming a third individual, or when the dyad had ceased grooming for 60s. If, for instance chimp A and chimp B groomed from 01:10-02:30, then 03:35-06:00, then these time periods would be considered two separate grooming bouts.

'Groomee' ELS

This category refers to cases where the signaller was the recipient of grooming before, during and/or after the ELS signal.

Initiation, sequence and response ELS

Kanyawara, Sonso and Waibira ELS gestures were video coded as either (1) 'initiation' gestures, meaning neither the signaller nor the partner gave an ELS gesture in the 10s prior, (2) ‘sequence’ gestures, meaning the signaller had already given another ELS in the 10s prior, or (3) ‘response’ gestures, meaning the signaller’s partner had already given another ELS in the 10s prior (sequence took priority over response). Some analyses included only ‘initiation’ ELSs, whereas others included all ELS types (see model outlines).

Extracting data to test the referential gesture hypothesis

To investigate this hypothesis, I used data from all four communities. Once all groomee ELSs had been identified in the videos from Kanyawara, Sonso, and Waibira, it was manually recorded: (1) whether the partner groomed within 5cm of the scratched area within 10s after the end of the ELS, (2) whether the scratcher produced a ‘present groom’ gesture that overlapped with the ELS, (3) whether the signaller scratched the same area again within 10s (persistence), (4) whether the signaller gave a ‘present groom’ gesture, presenting the same area as the scratched spot within 10s (elaboration), and (5) whether the signaller terminated the grooming bout within 10s. Cases were excluded in which: (1) the ELS covered the same spot that was already being groomed, (2) the signaller gave a ‘present groom’ gesture that had some temporal overlap with their ELS, and (3) the grooming behaviour in the 10s following the ELS was not adequately visible. Ngogo data provided to the current study were limited to an excel sheet which detailed (i) the grooming bout number, (ii) whether the grooming bout included a ‘groomee’ ELS or not (yes/no), and (iii) the identity of the two grooming individuals. When grooming bouts did include groomee ELSs it was also noted (iv) which individual produced the scratch, and (v) whether the scratched location was subsequently groomed by the partner (yes/no).

Inter-coder reliability

Inter-coder reliability was only possible for Kanyawara, Sonso and Waibira where video data were available. CW and NL performed all the Observer XT video coding on the Kanyawara videos. To assess inter-coder reliability CW and NL both coded the same 40 dyadic grooming bouts, from the total 775 bouts. In sum, 205 minutes of dyadic grooming were coded for inter-coder reliability of the total 2,944 minutes coded (6.96%). Cohen’s kappa was calculated for all seven grooming behaviours outlined in the ‘video coding’ section further above, using the Reliability Analysis function in Observer XT. The kappa value over all collapsed grooming behaviours for frequency/sequence (tolerance window = 1s) was 0.86, and for duration/sequence 0.96, both indicating excellent levels of coder agreement (Fleiss, 1981).

CW and KS coded all groomee ELS events for the referential gesture hypothesis, using the data sets collected at Kanyawara, Sonso and Waibira. To assess inter-coder reliability, CW and KS both coded the same 20 of the total 230 groomee ELS events (8.70%). Cohen’s kappa was calculated for all five behaviours outlined in the section above; the overall kappa value obtained was 0.90, indicating excellent levels of coder agreement (Fleiss, 1981).

Measures extracted

Dominance rank calculations

The dominance rank difference between the target individual and the partner was included in all statistical models (generally as a control predictor), thus ranks had to be calculated for the communities. In the cross-site comparison of the referential function of the ELS, the published Ngogo dataset used the directionality of pant-grunts and aggressive interactions between February - July 2005 among group males to rank them into low-, mid- and high-ranking categories (Pika & Mitani, 2008). To provide comparable rank groupings from the other sites, Elo rankings were first calculated based on the methods of Muller et al. (2021) using long term data on directionality of pant grunts for males aged 15 years or older (as described in chapter 2). Sub-adult males were all given an Elo score that was one ordinal rank lower than the lowest-ranking adult male. To be comparable to the Ngogo dataset here I then divided ranked males into three equally sized groups (high, mid and low ranking) for each month. If there was one 'leftover' individual (e.g. ten males divided by three), then there was an extra individual put in the low-ranking category. If there were two 'leftover' individuals (e.g. eleven divided by three) then there was one extra individual put in the low- and one extra individual in the mid-ranking categories.

In the tests of alternative functions of the ELS conducted with data from the Kanyawara community, I used an average ordinal rank for each month, including females, with 1 being the highest ranking. Individuals who had not yet entered the adult dominance hierarchy were given a rank of n+1, where n=the Elo rating of the lowest ranking individual for any given month. For instance, if in a given month there were 20 adults in the dominance hierarchy with ranks 1-20, then all non-adults were given a rank of 21.

Composite Association Index (CAI)

This is an alternative measure of affiliation or friendship to the one used in chapter 2. Here, CAI was only determined and used for the Kanyawara community as the necessary data were not available for the other communities for the years matching the ELS data collection. CAI entered into statistical models as a control predictor for all models except the cross-site model, where this data was not available for all four communities. This index (based on Gilby & Wrangham, 2008) includes party level association, nearest neighbour association and five-metre association. This differs from the composite friendship index (CFI) calculated in chapter 2 (see Appendix 2 for formulae and calculations used) in terms of five-metre proximity being used instead of grooming frequency (which was used in chapter 2 because five-metre proximity was not available for Sonso). Since the study periods at Kanyawara were spread out over several years and had varying durations, CAI for all dyads was determined for every 3-4 month period. As already demonstrated in chapter 2, the individual measures that contribute to the composite tend to be significantly correlated. To check this was still the case with this specific dataset, I examined a single time period which CAI was calculated for. Here I identified significant correlations between a majority of measures (Spearman's rho tests for correlation; party level association x nearest neighbour association: r = .081, p = 0.73; nearest neighbour association x five-metre proximity: r = .317, p<.001; five-metre proximity x party level association: r = .189, p<.001).

Statistical models

Model 1: Referential function

To establish whether ELSs refer to the location where the signaller wishes to receive grooming in male-male dyads, I tested the effect of 'community' (Kanyawara, Sonso, Waibira, Ngogo) on the probability of a target individual's (here groomee signaller) ELS eliciting grooming from the partner within 5cm of the scratched location (Yes/No), within 10s of the end of the scratch. For this model both initiation and response ELSs were examined. Sequence ELSs were excluded here as if they were produced in the same location on their body this constituted an instance of persistence (see below). Then, if sequence ELSs were produced in a new location this would indicate a new goal of the signaller (according to the referential hypothesis).

Although the effect of community was the main focus, I also wanted to control for the rank class of the target individual and a potential interaction with rank class difference (between target individual and partner; categorised as lower, same or higher) with community. Previous research suggests these may influence whether or not the scratched area is groomed (Pika & Mitani, 2006). Thus, I included target individual rank class (high, medium, low), and the interaction between community and rank class difference (partner being higher, same or lower rank class than the target individual) in the model. Table 4 provides an outline of the model composition.

While this model only examined male-male dyads in order to be comparable to the Ngogo dataset, I descriptively examined all dyads (male-male, male-female and female-female together) in the remaining communities to examine a referential function of this gesture.

I was also interested in examining whether the signaller would actively pursue the goal of receiving grooming in the scratched location by showing persistence, elaboration and/or termination of the grooming bout. This was possible for Kanyawara, Sonso and Waibira, where videos were available for all groomee ELSs. I did not run a statistical model on this data as the data were very unbalanced across the behavioural categories, but present descriptive statistics in the results.

Model 2a: Grooming initiation

This model examined whether ELSs are given to initiate dyadic grooming. I investigated the effect of ‘period’ (20s before dyadic grooming, during dyadic grooming) on the number of ELSs given (count) by the target individual. I included both individuals in the dyad as target individuals, as long as they had the full 20s period before dyadic grooming available. For instance, if the dyadic grooming bout involved chimp A and chimp B, and both were visible for the full 20s before grooming commenced, then I recorded the number of ELSs produced by chimp A as the target individual, with chimp B as the partner, as well as the number of ELSs produced by chimp B as the target individual, with chimp A as the partner. For this model all types of ELSs were included (initiation, response and sequence).

Although the effect of ‘period’ was the main focus, I also wanted to control for interactions with rank difference and CAI. Here my exploratory hypothesis was that conspecifics may be more receptive to gestures (here, with the goal to initiate grooming) of high-ranking individuals than lower-ranking individuals, and similarly that individuals may be more receptive to signals from close social partners. For the latter, it’s previously been found that individuals who spend more time in proximity together are more likely to respond to gestural signals, possibly to better enable the coordination of joint activities (Roberts & Roberts, 2019). Thus, I included the interaction between period and rank difference, and period and CAI in the model (Table 4).

Model 2b: Grooming initiation; grooming role

A further aim of research question two was to determine whether producing an ELS immediately prior to a grooming bout commencing was associated with a higher likelihood to become the groomee at grooming initiation.

Although the main focus was the effect of the target individual producing an ELS (Yes/No) on the probability for the target individual to subsequently become the groomer or groomee, I also wanted to control for a potential interaction with Elo rank difference (henceforth rank difference; see justification in model 2a). Thus I included the interaction between ELS and rank difference as the fixed effect (see Table 4). Again, data were included from both individuals in the dyad (i.e. both were entered as the target individual once), as long as they had the full 20s period before dyadic grooming available. For this model all types of ELSs were included (initiation, response and sequence).

Model 3: Grooming re-initiation when in pause

To address the third research question; whether ELSs are given to re-initiate grooming when there is a pause in grooming, I tested the effect of ‘period’ (during pause, during active grooming) on the number of ELSs (count) produced by the target individual. A pause was defined as a break in active grooming between a given dyad of 3 to 60s duration.

Although my main interest was the effect of ‘period’ on ELS count, I also wanted to control for potential interactions with rank difference and CAI (see justification in model 2a). Thus I included the interactions between period and rank difference, and period and CAI, as fixed effects (see Table 4). Both individuals from the dyad were included as target individuals in this analysis. For this model all types of ELSs were included (initiation, response and sequence).

Model 4a: Requesting a favourable grooming switch

To address the fourth research question; whether ELSs are given by groomers to elicit grooming from the partner, I tested the effect of ‘period’ (10s after groomer ELS, remainder of duration as groomer) on ‘favourable switch’ count, for the target individual. A ‘favourable switch’ was a grooming direction switch where the target individual (here the groomer signaller) then received grooming (either becoming the groomee, or engaging in mutual grooming).

Although the main focus was the effect of ‘period’ I also wanted to control for potential interactions with rank difference and CAI. I hypothesised that high-ranking individuals may be more likely to be subject to favourable grooming switches, as dominant individuals have been recorded to be more likely to receive than give grooming effort in some communities (Kaburu & Newton-Fisher, 2015). As with model 2a, regarding CAI I theorized that individuals may be more receptive to signals from close social partners, and here more willing to give grooming to friends than less affiliated individuals. Thus I included the interactions between period and rank difference, and period and CAI, as fixed effects (see Table 4).

Both individuals from the dyad were included as target individuals in this analysis, as long as they produced at least one ELS while in the role of the groomer. This model only considered initiation ELSs. Sequence ELSs were not included here as they were considered as cases of persistence (see model 4b). I also excluded response ELSs as I considered that for this function they may serve as ‘counter requests’, and therefore I could not predict who might ‘win’ such negotiations.

Model 4b: Requesting a favourable grooming switch; goal-directed behaviour

A further aim of research question four was to test the effect of whether or not the goal of a favourable switch was met (Yes/No) on the probability for the target individual (here the groomer signaller) to persist, elaborate or terminate grooming (Yes/No). Here persistence was defined as another ELS in any body area, and elaboration was defined as a ‘present groom’ or ‘arm raise’ gesture.

Although the main focus was the effect of the goal being met (or not), I also wanted to control for rank difference and CAI. Here I considered that rank and CAI may have affected the responsivity of the partner (with high-rank signallers and closely bonded signallers potentially having more instances where their goal was met), and therefore the necessity of the signaller to produce further signals may be affected. Thus I included these three fixed effects in the model (see Table 4). Both individuals from the dyad were included as target individuals in this analysis, as long as they produced at least one ELS while in the role of the groomer. This model only considered initiation ELSs (see model 4a for details surrounding the exclusion of sequence and response ELSs).

Model 5: Social anxiety

To address the fifth research question; whether individuals produce more ELSs when grooming with a higher-ranking or less affiliated partner, suggesting ELSs might be a sign of social anxiety, I tested the effects of rank difference and CAI on the number of ELSs produced by the target individual during the dyadic grooming bout.

Although the main focus was on the effects of rank difference and CAI, I also wanted to control for a potential interaction between the two. Here I reasoned that individuals may have a large rank difference, but still be closely bonded which may counteract any anxiety induced by dominant individuals. Thus I included this interaction as a fixed effect (see Table 4). Both individuals from the dyad were included as target individuals in this analysis. For this model all types of ELSs were included (initiation, response and sequence).

Table 4. Details of the statistical models constructed to test research questions regarding the function of the exaggerated loud scratch (ELS) gesture.

Research questions	Response	Test predictors	Control predictors	Random intercepts	Random slopes	N
Model 1: Referential function. Does the ELS refer to the location the signaller wishes to receive grooming in, for male-male dyads?	Binomial model: Was the target individual (here signaller) groomed within 5cm of the scratched location (Yes/No)	Community*Rank class difference[b]	Rank class difference, Signaller rank class	Target ID, Partner ID, Dyad ID, Bout ID	None identifiable	279 observations, 38 Target IDs, 50 Partner IDs, 89 Dyad IDs, 179 Bout IDs
Model 2a: Grooming initiation[a]. Are ELSs given to initiate dyadic grooming?	Poisson model: Number of ELSs given by the target individual	Period[c]*Rank difference, Period[c]*CAI; Offset by log-transformed period duration	Rank difference, CAI	Target ID, Partner ID, Dyad ID, Bout ID	CAI, Period, Rank difference, Period*Rank difference and Period*CAI within Target ID and Partner ID. Period and Rank difference within Bout ID and Dyad ID	639 observations, 38 Target IDs, 38 Partner IDs, 102 Dyad IDs, 161 Bout IDs
Model 2b: Grooming initiation; grooming role[a]. In the 20s prior to grooming, is the production of an ELS associated with initial grooming role (groomer or groomee)?	Binomial model: Grooming role of target individual when grooming commences (Groomer/Groomee)	Target individual ELS (yes/no)*Rank difference	Rank difference	Target ID, Partner ID, Dyad ID, Bout ID	Rank difference within Target ID and Partner ID	214 observations (104 where individual became groomer), 33 Targets IDs, 35 Partner IDs, 85 Dyad IDs, 126 Bout IDs

Research questions	Response	Test predictors	Control predictors	Random intercepts	Random slopes	N
Model 3: Grooming re-initiation when in pause[a]. Are ELS given to re-initiate grooming when there is a pause in grooming?	Poisson model: Number of ELSs given by target individual	Period[d]*Rank difference, Period[d]*CAI; Offset by log-transformed period duration	Rank difference, CAI	Target ID, Partner ID, Dyad ID, Bout ID	Period, CAI, Rank difference, Period*CAI, Period*Rank difference within Target ID and Partner ID, Period and Rank difference within Dyad ID and Bout ID	1860 observations, 48 Target IDs, 48 Partner IDs, 173 Dyad IDs, 465 Bout IDs
Model 4a: Requesting a favourable grooming switch[a]. Do groomers give ELS to elicit grooming from the partner?	Poisson model: Number of favourable switches elicited by the target individual (here groomer)	Period[e]*Rank difference, Period[e]*CAI; Offset by log-transformed period duration	Rank difference, CAI	Target ID, Partner ID, Dyad ID, Bout ID	Period, CAI, Rank difference, Period*CAI within Target ID, Period, CAI, Rank difference, Period*CAI, Period*Rank difference within Partner ID	364 observations,40 Target IDs, 37 Partner IDs, 107 Dyad IDs, 163 Bout IDs
Model 4b: Requesting a favourable grooming switch; goal-directed behaviour[a]. Do groomers persist, elaborate or terminate grooming when the putative goal of eliciting grooming from the partner is not met?	Binomial model: Goal-directed behaviour by the target individual (here groomer; Yes/No)	Goal met – was there a favourable grooming switch for the target individual (Yes/No)	Rank difference, CAI	Target ID, Partner ID, Dyad ID, Bout ID	Rank difference and CAI within Target ID and Partner ID	299 observations, 40 Target IDs, 37 Partner IDs, 106 Dyad IDs, 162 Bout IDs

Research questions	Response	Test predictors	Control predictors	Random intercepts	Random slopes	N
Model 5: Social anxiety[a]. Does an individual produce more ELSs when grooming with a higher-ranking or less affiliated partner?	Poisson model: Number of ELSs given by target individual	Rank difference* CAI; offset by log-transformed observation duration	N/A	Target ID, Partner ID, Dyad ID, Bout ID	Rank difference*CAI within Target ID and Partner ID	1500 observations, 49 Target IDs, 49 Partner IDs, 227 Dyad IDs, 750 Bout IDs

[a] The indicated models were conducted solely with the Kanyawara community

[b] The test predictor 'rank class difference' constituted three levels: lower, same and higher

[c] Here the test predictor 'period' had two levels: the 20s before grooming start, and during the grooming bout.

[d] Here the test predictor 'period' had two levels: during a grooming pause, and during active grooming.

[e] Here the test predictor 'period' had two levels: the 10s after an exaggerated loud scratch, and the remaining duration of the signaller's time as a groomer in the bout

Statistical analysis

Generalized Linear Mixed Models (GLMM; Baayen, 2008) with binomial error distributions and logit link function or Poisson error distributions with log link function (McCullagh & Nelder, 1989) were used for all analyses.

Quantitative predictor variables were always scaled by z-transforming to a mean of zero and standard deviation of one, to allow for easier interpretation of the model coefficients (Schielzeth, 2010) and to ease model convergence.

For all Poisson models where I was interested in the count of a particular behaviour during two different periods, which varied considerably in observation effort, I included the (log-transformed) observation time as an offset term in the models (McCullagh & Nelder, 1989). To control for repeated observations of the same individuals and dyads grooming, target ID, partner ID and dyad ID were included as random intercepts. Additionally, in the cases where there were multiple observations from the same dyadic grooming bout, bout ID was also included as a random intercept. To avoid underestimation of standard errors and keep type 1 error rates at 0.05, all theoretically identifiable random slopes were included in each model (Barr et al., 2013; Schielzeth & Forstmeier, 2009). Estimates of the correlations between the random intercepts and slopes were also included. However if a 'singular fit' message suggested some of the random effects terms to be unidentifiable, as indicated by absolute correlation parameters being essentially one (Matuschek et al., 2017), then these correlations were dropped from the model. In all cases where these were dropped, the correlations did not contribute much to the explanatory value of the model (assessed by the difference in log-likelihood; the effects of dropping these are reported in the supplementary material).

Model stability was estimated by dropping the levels of the random effects one at a time from the data and comparing the estimates derived for models fitted to these subsets with those obtained for the full data set (Nieuwenhuis et al., 2012). When there were two or more fixed effects, I assessed collinearity using Variance Inflation Factors (VIF; Field, 2005) based on a standard linear model, which did not include interactions (if any were present in the model), nor random effects. Dispersion was also assessed for all non-binomial models. None of the models showed concerning values for VIF or dispersion.

To ascertain the effect of the test predictors and to avoid cryptic multiple testing (Forstmeier & Schielzeth, 2011), full-null model comparisons were carried out, with the null model lacking the test predictors in the fixed effects part, but otherwise being identical to the full model in terms of the random and fixed effects structure. The effect of individual fixed effects was tested by comparing the full model with reduced models lacking them, one at a time (Barr et al., 2013). For the full-null model comparison, as well as the full-reduced model comparisons, a likelihood ratio test was used (Dobson, 2002; R function drop1 with argument 'test' set to "Chisq"). When the full-null model comparison was significant, I then examined whether any of the included interactions between fixed effects were found to be significant (when relevant). If interactions were non-significant, a reduced model was subsequently fitted excluding the interaction.

Models were implemented in R (version 4.0.2; R Core Team 2020); using the function glmer of the package lme4 (version 1.1-21; Bates, Mächler, Bolker, & Walker, 2015). VIF were determined using the function vif of the package car (Fox & Weisberg, 2018). Model stability was assessed using a function written by Roger Mundry. Confidence intervals of the model estimates were obtained using parametric bootstraps (function bootMer of the package lme4, N=1,000 bootstraps).

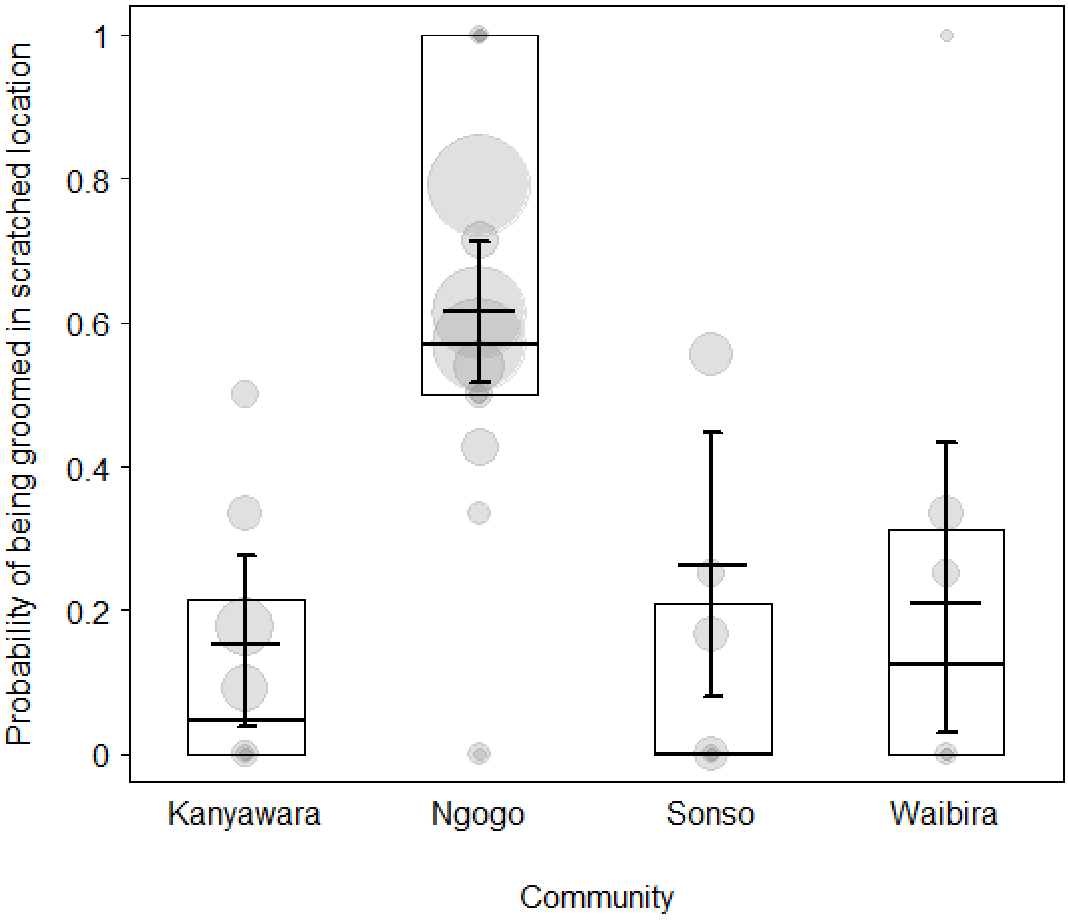
RESULTS

Here I report the main findings for each of the research questions and models; further model results including estimates, standard errors and confidence intervals can be found in Appendix 4.

Model 1: Referential function

The full model fitted the data better than the null model; likelihood ratio test χ^2=29.249, df=9, *p*<.001. However, as the community*rank class difference interaction was found not to be significant a reduced model was fitted excluding this interaction, but including community, focal rank class and rank class difference as main effects. The reduced model showed a significant effect of community (χ^2=22.624, df=3, *p*<.001). The fixed effect 'community' was releveled to explore where the significant differences lay between the communities. My results indicated that Ngogo males were reported to groom the scratched location significantly more often than I observed at Kanyawara, Sonso or Waibira (Figure 7). There were no significant differences between the other three communities.

Figure 7. Probability of a groomee exaggerated loud scratch eliciting grooming from the partner within 5cm of the scratched location, for male-male dyads, for each community.

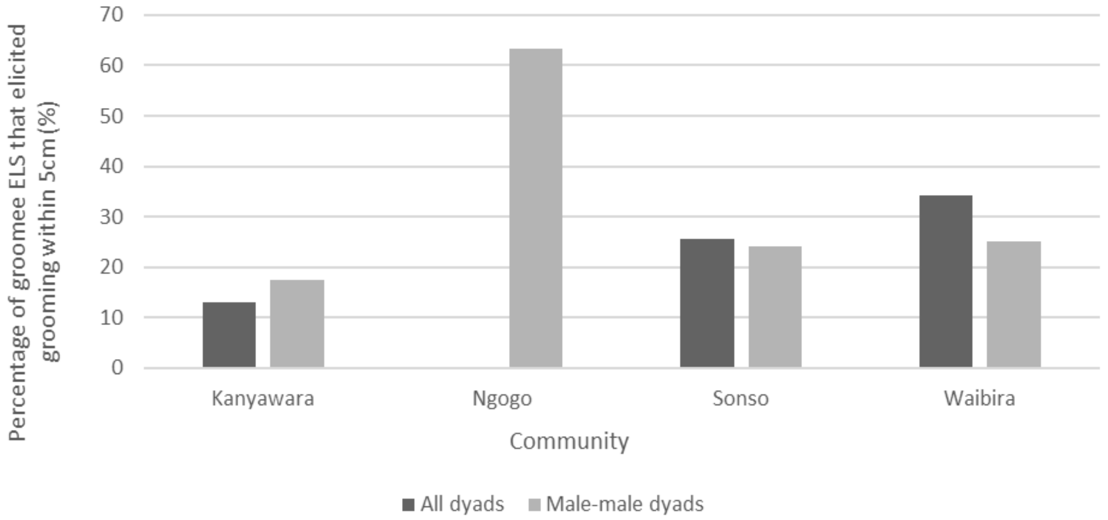


Note: Boxes depict median and quartiles for the raw data. Horizontal lines with error bars depict estimates from the fitted model and their 95% confidence interval (when rank class difference and signaller rank class are both manually dummy coded and then centred). The area of the points is proportionate to the number of signaller observations (range: 1-52).

For Kanyawara, Sonso and Waibira I also had data on dyads including females (female-female and female-male). When including all dyads, the percentage of groomee ELSs to receive grooming within 5cm of the scratched location within 10s remained low, when either considering all dyads or only male-male dyads (Figure 8).

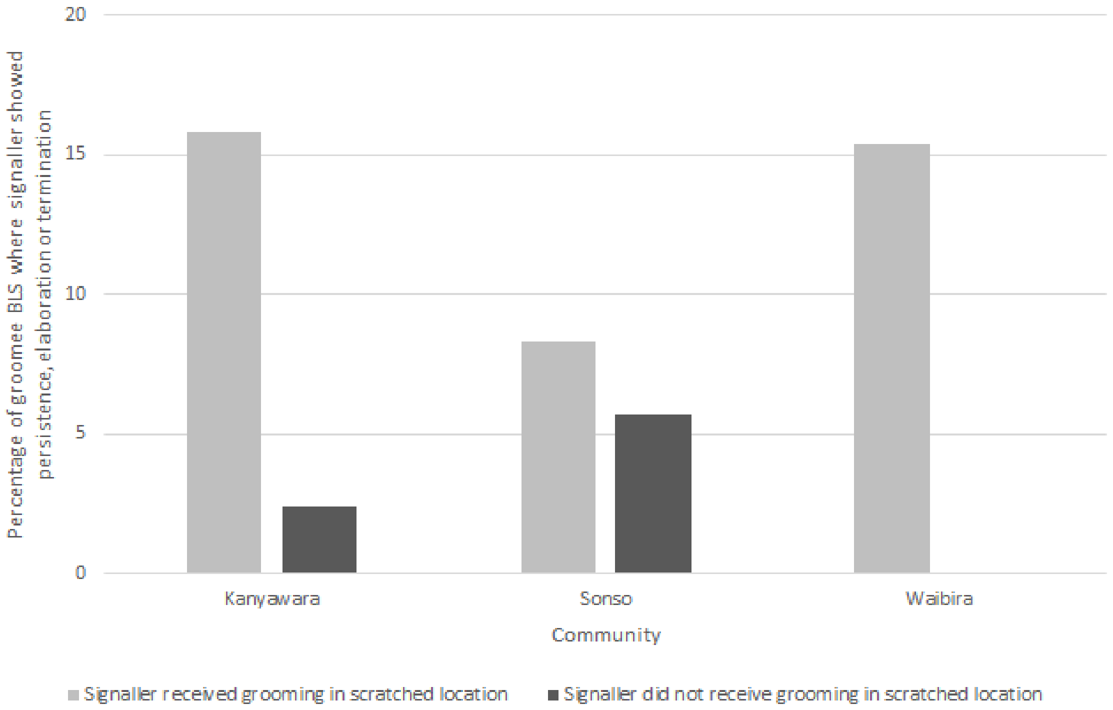
Furthermore, for these three communities it was possible to explore the behaviours of the signaller when the partner did not groom within 5cm of the scratched location. Instances of these markers of goal-directed behaviour were relatively rare, but Figure 9 shows that chimpanzees were more likely in all three communities to persist, elaborate or terminate the interaction when they received grooming in the scratched area, compared to when they did not.

Figure 8. The percentage of groomee exaggerated loud scratches that elicited grooming within 5cm, within 10s after the end of the exaggerated loud scratch.



Note: Shown for Kanyawara (N=145 groomee exaggerated loud scratches for all dyads, N=46 for male-male dyads), Ngogo (no data for all dyads, N=188 male-male), Sonso (N=47 all dyads, N=29 male-male), Waibira (N=38 all dyads, N=16 male-male).

Figure 9. Percentage of groomee exaggerated loud scratches from all dyads where the signaller showed persistence (an exaggerated loud scratch in the same location), elaboration (a present groom of the same location) and/or termination of the grooming interaction in the 10s following the exaggerated loud scratch, when the partner groomed the scratched location and when they did not.



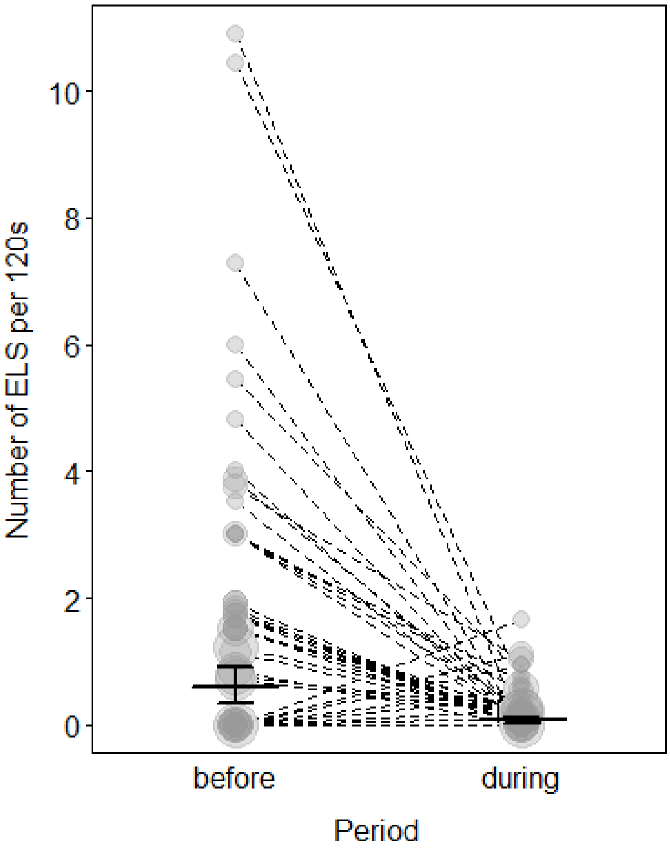
Note: Shown for the three communities where video data were available: Kanyawara (N=145 groomee), Sonso (N=47), Waibira (N=38).

Model 2a: Grooming initiation

The full model fitted the data better than the null model; likelihood ratio test χ^2=21.405, df=3, *p*<.001. As the period*rank difference and period*CAI interactions were found not to be significant a reduced model was then fitted excluding these interactions, but including period, rank difference and CAI as main effects.

The reduced model showed a significant effect of period (χ^2=26.834, df=1, *p*<.001) which revealed that the number of ELSs produced by the target individual was higher in the 20s period before the start of dyadic grooming, as compared to the number during the remainder of the grooming bout (see Figure 10).

Figure 10. Number of exaggerated loud scratches (ELSs) given in the 20s before a dyadic grooming bout, and during the bout, for each dyad.



Note: Horizontal lines with error bars depict the fitted model (where number of exaggerated loud scratches was offset by log-transformed period duration) and its 95% confidence interval, for a duration of 120s. The area of the points is proportionate to the number of observations for each dyad for that period (range: 1-6).

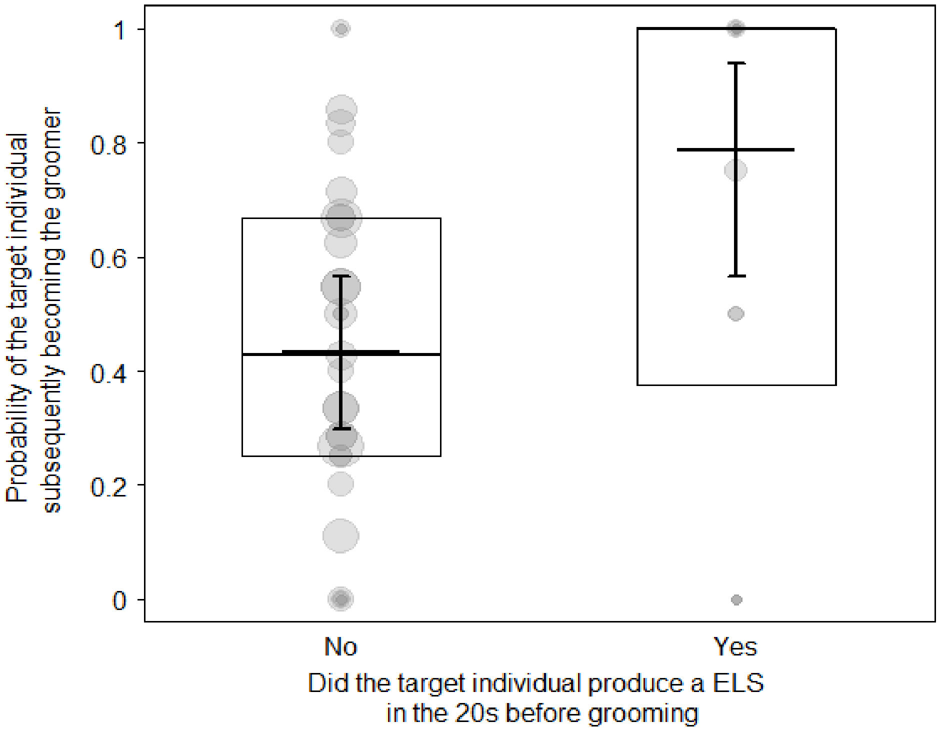
Model 2b: Grooming initiation; grooming role

To investigate whether an individual's grooming role at the commencement of grooming was influenced by whether or not they produced an ELS in the 20s prior to grooming, I examined this in the cases where an individual was visible for the full 20s before grooming started. I then recorded whether they produced an ELS in this period or not, and whether they became the groomer or groomee when grooming started.

Overall the full model fitted the data better than the null model; likelihood ratio test χ^2=7.839, df=2 p=.019. The ELS*rank difference interaction was found not to be significant, so a reduced model was fitted excluding this interaction but including ELS (Yes/No) and rank difference as main effects.

The reduced model showed a significant effect of ELS (χ^2=7.632, df=1, p=.006), as well as rank difference (which was included as a control variable; χ^2=11.525, df=1, p<.001) on subsequent grooming role. Individuals were significantly more likely to become the groomer (rather than groomee) when they gave an ELS in the 20s before dyadic grooming started (Figure 11). When the partner was dominant individuals were more likely to become the groomer (65/92 cases) than when the partner was subordinate (28/99 cases). Thus, when ELSs were produced prior to grooming commencement higher-ranking individuals were more likely to be groomed than to groom another. This excludes cases where both individuals had the same ordinal rank e.g. both were sub-adults.

Figure 11. Probability of the target individual becoming the groomer, when they did or did not give an exaggerated loud scratch in the 20s before the start of a dyadic grooming bout.



Note: Boxes depict median and quartiles for the raw data. Horizontal lines with error bars depict the fitted model and its 95% confidence interval (with average rank difference to the partner). The area of the points is proportionate to the number of observations of individuals (range: 1-15).

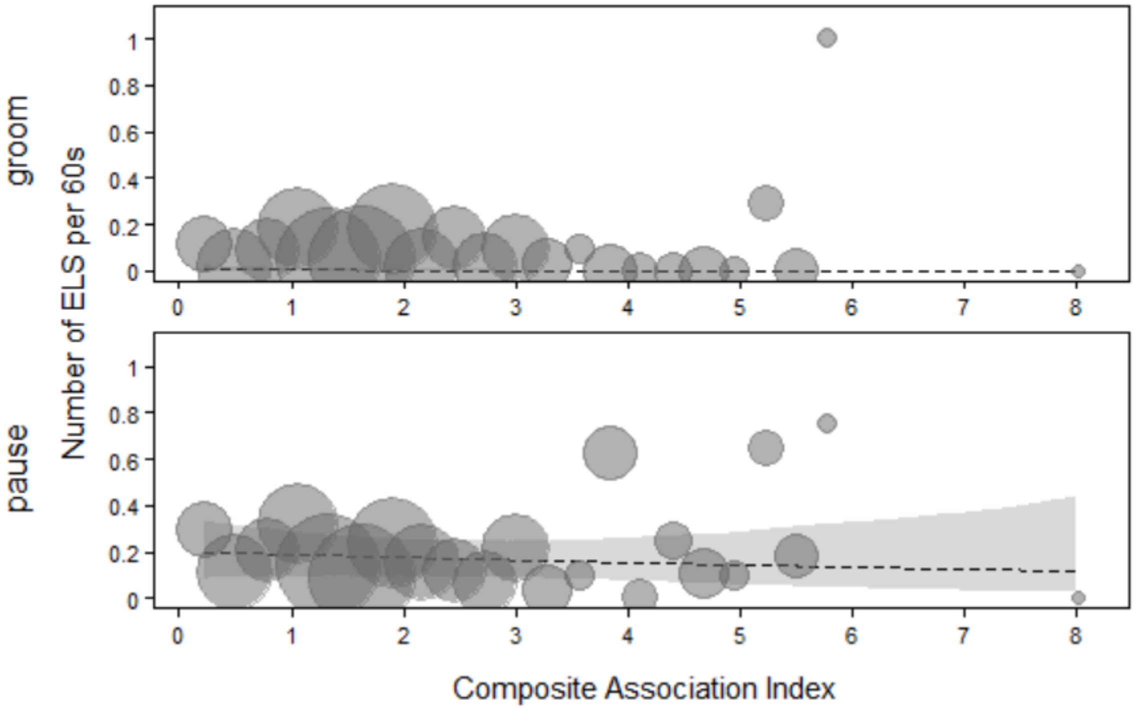
Model 3: Grooming re-initiation when in pause

To explore whether the ELS might also play a role in re-initiating grooming I analysed the number of ELSs produced in pauses, as compared to during active grooming.

The full model fitted the data better than the null model; likelihood ratio test χ^2=70.779, df=3, *p*<.001. As the period*rank difference interaction was then found not to be significant a reduced model was fitted excluding this interaction, but including period, CAI, and rank difference as main effects, as well as the period*CAI interaction.

The reduced model showed a significant effect of period*CAI (χ^2=4.365, df=1, *p*=.037). The count of ELSs was higher in pauses than during active grooming, but while CAI did not seem to affect ELS count during active grooming, there was a slight increase in ELS count for less affiliated individuals during pauses (Figure 12).

Figure 12. Number of exaggerated loud scratches produced during pauses and active grooming as a function of Composite Association Index between the dyad partners.



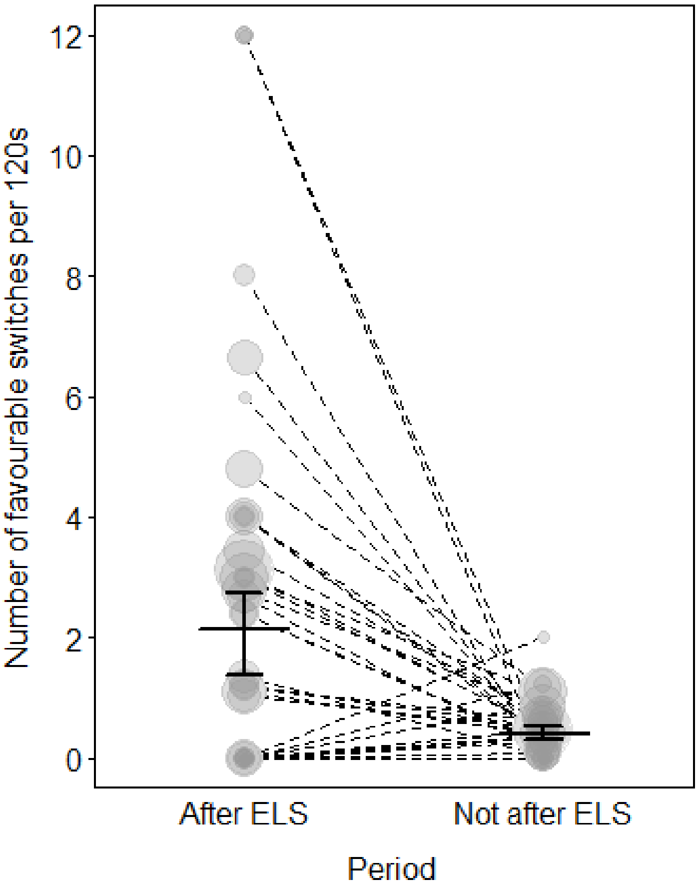
Note: The upper plot shows this during active grooming, the lower plot shows this when in a pause. The area of the points is proportionate to the number of observations (range: 2-126). The dashed line shows the fitted model and the shaded areas its 95% confidence interval (conditional on rank difference values being at their average), and for a duration of 60s.

Model 4a: Requesting a favourable grooming switch

Here I examined whether the groomer might use an ELS to elicit grooming from the partner (i.e. to elicit a 'favourable switch'). The full model fitted the data better than the null model; likelihood ratio test χ^2=32.877, df=3, *p*<.001. The period*rank difference and the period*CAI interactions were found not to be significant so a reduced model was fitted excluding the interactions, but including period, CAI and rank difference as main effects.

The reduced model showed a significant effect of period (χ^2=32.390, df=1, *p*<.001). The count of favourable switches was significantly higher in the 10s following an ELS, as compared to the count during the remainder of the grooming bout (see Figure 13).

Figure 13. The number of 'favourable switches' where the groomer received grooming from their partner, following an exaggerated loud scratch (after ELS), and during the rest of the dyadic grooming bout (not after ELS).



Note: Horizontal lines with error bars depict the fitted model and its 95% confidence interval (when rank difference and CAI are at their average), and for a duration of 120s. The area of the points is proportionate to the number of observations for each groomer for that period (range: 1-20).

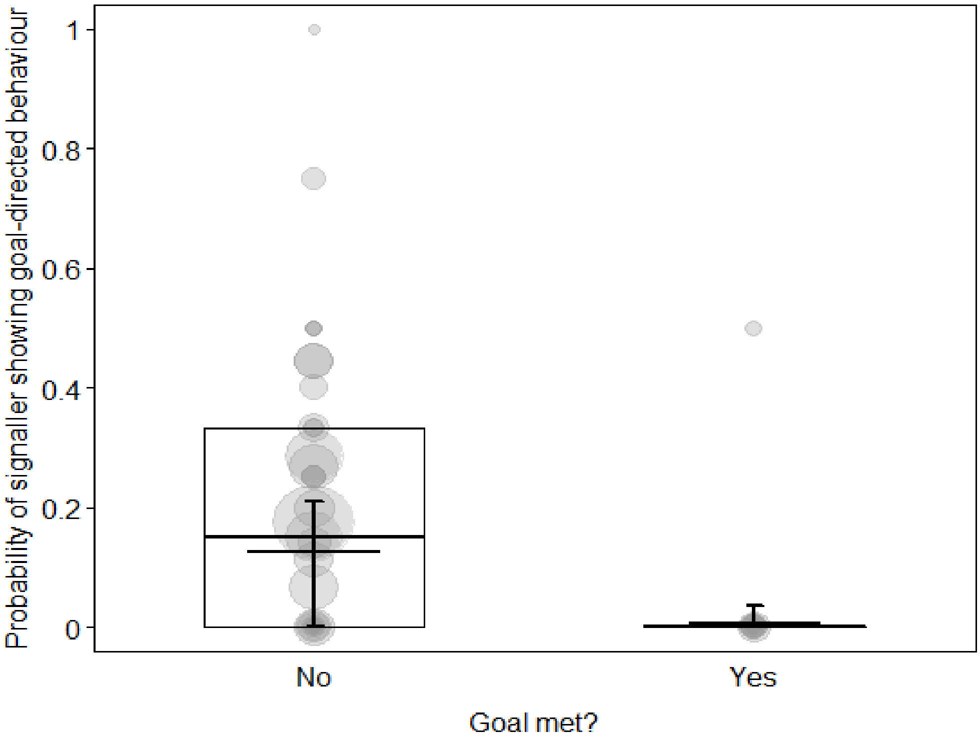
Model 4b: Requesting a favourable grooming switch; goal-directed behaviour

To ascertain whether the groomer actively pursued the goal of eliciting grooming from the partner (a 'favourable' switch), I explored the effect of whether or not the groomer received grooming in the 10s after they produced an ELS gesture (Yes/No) on whether or not they showed goal-directed behaviours: persistence, elaboration and/or termination of grooming.

Overall the full model fitted the data better than the null model; likelihood ratio test χ^2=15.156, df=1, *p*<.001. When the signaller produced an ELS but their 'goal' of eliciting a favourable grooming switch was not met, they were significantly more likely to show persistence, elaboration and/or termination of the grooming interaction (Figure 14). The control variables rank difference and CAI were not found to have a significant impact on whether or not the signaller showed goal-directed behaviours.

This model was not very stable in terms of the fixed effect of interest ('goal met') meaning it was hard to estimate the effect of this variable conclusively, and the result should be considered with caution. Nevertheless, descriptively when the goal of receiving a favourable grooming switch was not met following an ELS, the individual then showed goal-directed behaviour in 49/240 cases (20.42%). Conversely, when a favourable switch was achieved the individual showed goal-directed behaviour in only 1/59 cases (1.69%).

Figure 14. Probability of the exaggerated loud scratch signaller showing goal-directed behaviour (persistence: producing another exaggerated loud scratch; elaboration: producing a present groom gesture; termination of grooming) when the goal of eliciting a 'favourable' grooming switch was or was not met.



Note: Boxes depict median and quartiles. Horizontal lines with error bars depict the fitted model and its 95% confidence interval (with average CAI and rank difference to the partner). The area of the points is proportionate to the number of signaller observations (range: 1-40).

Model 5: Social anxiety

Finally, to establish whether ELSs are a stress response when grooming with a more dominant and/or less affiliated partner, I explored the effect of rank difference and CAI (and their interaction) with the partner on the number of ELSs an individual produced during grooming.

The full model did not fit the data better than the null model; likelihood ratio test χ^2=1.340, df=1, *p*=.247. However, as the rank difference*CAI interaction was only included in order to rule this out, and my main interest was in the two main effects, a reduced model was then fitted excluding the interaction and only including rank difference and CAI as main effects. This also showed no significant effects of either rank difference (χ^2=0.617, df=1, *p*=.432), or CAI (χ^2=0.191, df=1, *p*=.662). This suggests that the number of ELSs an individual produced in a dyadic grooming bout was not significantly influenced by the rank difference or the social bond between signaller and partner.

DISCUSSION

My exploration of the function of the ELS signal in a grooming context failed to replicate the previous finding from Ngogo of this signal functioning in a referential manner in three other communities. I found that signallers in male-male dyads at Ngogo were reported to groom the scratched location significantly more often than what was observed for the three remaining sites. In Sonso, Waibira, and Kanyawara the likelihood of receiving grooming in the scratched area was too low to consider this a putative function for this signal in these communities, both when considering male-male dyads and all dyads including females. Furthermore, signallers rarely behaved in a manner consistent with pursuing this putative goal; markers of goal-directed behaviour (persistence, elaboration and termination of the grooming interaction) that are expected in the face of not achieving the desired goal of a signal were conversely more frequently observed when the goal of obtaining grooming in the scratched location was met, than when it was not met. At Kanyawara, Sonso and Waibira individuals may instead use ‘present groom’ signals to indicate to their partner where they wish to be groomed, as has been identified in the Sonso community before (Hobaiter & Byrne, 2014). Similarly, bonnet macaques have also been documented to use present groom gestures for this function (Gupta & Sinha, 2016). Together, these data show that the ELS was only effective at directing partners to a desired grooming location in the Ngogo community, and therefore that the habitual use of a referential gesture in chimpanzees is not ubiquitous in this species. This has ramifications for our understanding of the evolution of referential signals, and highlights the need to continue to look for gestures that may fulfil a referential function in naturalistic conspecific interactions.

There are several reasons why the current exploration for the ELS as a referential gesture may have failed to replicate Pika and Mitani's (2006) original findings in three other chimpanzee communities. One possibility is that methodological inconsistencies between Pika and Mitani (2006) and the present study led to this discrepancy. Firstly, for Kanyawara, Sonso, and Waibira my sample sizes were much smaller for male-male dyads compared to the Ngogo sample. This resulted from there being fewer adult males in these communities, but also fewer grooming bouts available from exclusively male dyads. However, whilst lower sample sizes may have resulted in less precise estimates for the three new communities, they should not have resulted in systematically lower estimates. I also failed to replicate the Ngogo results when analysing a larger dataset including females in dyads, with low instances of 'matches' between scratched and subsequent grooming locations remaining (13% at Kanyawara, 26% at Sonso, and 34% at Waibira). While data on intentional goal-directed use of this signal is absent for Ngogo, my descriptive results indicated that individuals from the other communities did not seem to be pursuing the goal of their partner grooming the scratched location. Thus, although my samples are smaller, given the smaller number of males at these sites compared to Ngogo I still had representative samples of behaviour from the available males. Therefore, it seems unlikely that more data from these three sites would have altered the pattern observed. Secondly, scratches from Kanyawara, Sonso and Waibira were assessed from video data using strict criteria for what constituted an ELS and a 'match' of grooming to that area, whereas the original dataset was limited to real-time coding observations from one observer. The limited nature of the data provided to the current study from Ngogo also prevented a more detailed examination of the grooming behaviour that occurred e.g. which locations had been scratched, and other signals produced by the scratcher (for instance, persistence scratches). Instead, only binomial values (yes/no) for whether the scratched location was groomed were available. While I collaborated with the authors to ensure I was defining ELSs in a comparable manner at Kanyawara, Sonso and Waibira, retrospective memories and assertions about how data were collected in real time can be unreliable. Therefore, in the absence of video data (where previously coded behaviours can be later verified) it is difficult to establish whether my definitions exactly matched those used in Ngogo, or to validate that the Ngogo data consistently met the same criteria. It is important that video data coded by multiple observers with inter-observer reliability are collected in future from the Ngogo chimpanzees to verify the referential function of this gesture at this site, though whether this function will have been retained in each Ngogo community following the community fission (Sandel & Watts, 2021) is uncertain.

Another possible explanation for the lack of replication of the referential function of the ELS gesture outside Ngogo is that the 'directed scratch' may be culturally-specific to the Ngogo community. While extensive overlap in the form and broad function of the gestural repertoire of different great ape species has led some to suggest that the available repertoires of great ape gesture types are innately specified (Byrne et al., 2017; Graham et al., 2018), it is also the case that they are flexibly deployed across different meanings (Hobaiter & Byrne, 2014). Moreover the social and ontogenetic environment may shape the use of some gestures (Hobaiter & Byrne, 2011a; Kalan & Boesch, 2018; Pika & Deschner, 2019), and some attention getting gestures (e.g. knuckle knock; branch slap) have been reported to be absent in some communities and habitually used in others (Whiten et al., 1999). Equally, cultural variation in the use of discrete call types has been shown across wild orangutan populations, with different calls used in the same behavioural context across sites and some calls being habitually produced in some sites and not in others (Wich et al., 2012). Although group-specific variation in the presence of a gestural signal has been suggested in wild chimpanzees, variation in meaning or function of gestures has not been explored previously in different groups of the same species (Pika & Deschner 2019). More cross-site comparisons are required to determine whether cultural differences in gesture usage may be more widespread in the chimpanzee repertoire (Pika & Deschner, 2019); particularly given that all research on gesture meaning in chimpanzees, aside from Pika and Mitani (2006), has focussed exclusively on the Sonso community (Graham et al., 2018; Hobaiter & Byrne, 2014, 2017; Roberts et al., 2012, 2013). The data from my study also highlight another potential community-level difference in fine-grained meaning, with ELSs being used to initiate grooming at both Sonso and Kanyawara. However while scratchers in Sonso subsequently receive grooming in the majority of cases ('groom me'; Hobaiter & Byrne, 2014), the majority of scratchers in Kanyawara subsequently provide grooming to their partner ('let me groom you'). A potentially cultural distinction in gesture meaning in chimpanzees would represent an exciting continuity with human symbolic gestural usage (i.e. gestures that convey meanings based on conventions). Although a vast majority of non-symbolic gestures are shared between chimpanzees and human infants (Kersken, Gómez, Liszkowski, Soldati, & Hobaiter, 2019), a diversity in the meaning of human-unique symbolic communicative signals is relatively common. For instance, to many European citizens a "thumbs up" would be interpreted as an agreement or perhaps "good luck", but in some cultures (e.g. in Iran) this serves as a derogatory gesture (Archer, 1997; Najarzadegan, 2016). Similarly, whilst nodding or shaking one's head to denote agreement or disagreement is common in many cultures, the meanings are reversed in Bulgaria (Andonova & Taylor, 2012). Though the current data presents an exciting prospect for the future of ape gestural research, first replicated video data and evidence of goal-directed behaviour from the signaller's perspective is needed from Ngogo to confirm this cultural specificity in meaning.

While my data did not support a referential function for the ELS outside of Ngogo, further investigation of alternative functions in the Kanyawara community did reveal an important role for this gesture in aiding cooperative interactions. In line with Goodall (1986) and Hobaiter and Byrne (2014) I found support for the ELS being used to initiate grooming, both prior to a bout beginning and to re-initiate grooming when it had paused. Here, the ELS allows individuals to communicate a desire to start grooming behaviour which is vital to maintaining social bonds, social tolerance and for reinstating relationships following aggression (Dunbar, 1991, 2010; Terry, 1970). Advertising a willingness to cooperate can result in various fitness benefits in the animal kingdom. For example, Arabian babblers use an ‘object presentation’ signal to initiate secretive copulations (Ben Mocha, Mundry, & Pika, 2019) which can avoid conflict with conspecifics and ensure opportunities to mate. Similarly, male chimpanzees limit their solicitation signals to short-distance audible gestures only when engaging in consortship behaviour, where being overheard by other males has significant costs (Hobaiter & Byrne, 2012). Another benefit can be to increase hunting success, for instance groupers use ‘head shakes’ to engage moray eels in cooperative hunting behaviour, and this results in groupers being almost five times more likely to capture prey (Bshary, Hohner, Ait-el-Djoudi, & Fricke, 2006). Recruitment calls are an effective signal for cooperation in a few contexts, such as in suricates to initiate group mobbing behaviour of predators (Manser, 2001; Manser, Bell, & Fletcher, 2001) or in spotted hyaenas to recruit clanmates for cooperative territory defence (Gersick, Cheney, Schneider, Seyfarth, & Holekamp, 2015). Being able to effectively engage conspecifics (or even heterospecifics) in cooperative acts thus has several advantages to an individual, and my findings suggest a pivotal usage of the ELS by chimpanzees in instigating and re-engaging partners in one such cooperative behaviour.

At Kanyawara I further explored variation in the use of the ELS across the grooming bout. Here the ELS gesture appeared to facilitate grooming direction switches. Groomers that produced ELSs often elicited a favourable grooming switch, and demonstrated higher levels of persistence, elaboration or termination of the grooming bout if the goal of receiving grooming from the partner was not met compared to when it was. At Kanyawara, the ELS signal may therefore play an important role in negotiating the dynamics of a grooming bout by allowing groomers to indicate when reciprocation of this valuable service should be delivered. It is interesting that whilst a groomer ELS during a grooming bout seems to indicate a request to receive grooming, an ELS produced before the initiation of a grooming bout seems to indicate a willingness to groom the potential partner, with signallers more likely to become groomers, than groomees. This indicates potential for flexibility in the ‘meaning’ of the signal depending on the specific behavioural context the signal is produced in (before or during a bout; produced by the groomer or groomee) in this community. If this is the case receivers would likely have to combine the signal with contextual cues in order to respond in these two differential ways. Future research would need to confirm that when producing an ELS prior to a grooming bout the signaller’s goal was to offer grooming to a partner. If this is confirmed, this flexibility in meaning from the signaller’s perspective would demonstrate the importance of context for correctly interpreting signal meaning

(Graham, Furuichi, & Byrne, in Press; Wheeler & Fischer, 2012). The integration of context with signals to access the speaker's meaning is fundamental to language (Scott-Phillips, 2015). For instance, stating "Michael's on fire!" after his fifth goal in a football game would presumably garner very different responses than if he had just escaped a burning building. Using the behavioural context to interpret whether the appropriate response to an ELS signal is to offer grooming or be willing to receive it has the potential to show commonalities with this aspect of pragmatics in language.

I found promising evidence for two different communicative functions for the ELS in the Kanyawara community (initiate or reinitiate grooming and request reciprocation of grooming), and in contrast found no support for scratching being an indication of anxiety. The number of ELSs produced was neither influenced by the rank difference between partners, nor by the social bond between the signaller and partner. Since chimpanzees have been noted to scratch during times of social stress (Baker & Aureli, 1997; Botero et al., 2013) perhaps ELS gestures differ in form to anxiety induced scratches. Alternatively, maybe the particular interactions that I focused on were not in fact a source of anxiety for individuals. It has been suggested that grooming may actually be an anxiety-reducing context, with scratch-rates diminishing regardless of the strength of association between partners in some cases (e.g., japanese macaques: Ueno, Yamada, & Nakamichi, 2015). This then reiterates the idea that grooming in chimpanzees can serve to reinforce relationships following instances of aggression (Terry, 1970). It is possible that outside of this context, or indeed during specific aspects of grooming (perhaps during grooming of vulnerable areas or with more grooming partners), scratching may remain a marker of anxiety.

The importance of the current work is not limited to identifying the function of the ELS, but also in emphasising the necessity of both replication and collaboration during data collection. Research on non-human primates is prone to multiple methodological criticisms, such as small sample sizes, pseudoreplication and difficulties in directly comparing findings across studies (Slocombe et al., 2011; Waller, Warmelink, Liebal, Micheletta, & Slocombe, 2013). The importance of validating previous findings is therefore particularly paramount in a literature vulnerable to false positive results. Often, replication has been seen as devoid of innovation in scientific fields (Nosek, Spies, & Motyl, 2012), but here I have demonstrated that replication can reveal interesting new avenues of research. The exciting possibility of a community-specific variation in gesture use could suggest that new approaches, spanning several groups of individuals, when examining signal function and meaning may reveal important insights into the flexibility of communication systems. Indeed, it will be important in the future to test the proposed functions of the ELS signal I found in the Kanyawara community in other communities. Collaboration across researchers working with different groups may be vital to ensuring such cross-site comparisons are feasible.

In conclusion, this research identified that a referential function for the exaggerated loud scratch gesture appears limited to the Ngogo community. The likelihood of recipients of groomee ELSs responding by grooming the scratched area was significantly lower in Kanyawara, Sonso and Waibira compared to Ngogo. In addition, there was no evidence that signallers in these three communities pursued the goal of obtaining grooming in the scratched location. Taken together, these results indicate that the habitual use of a referential signal in conspecific grooming interactions is not ubiquitous in chimpanzees, which has implications for our understanding of the evolution of referential signals. My findings also raise the possibility of group-level variation in signal function and meaning within chimpanzees, but methodological differences need to be excluded before this can be confirmed. Focussing on the Kanyawara community, I found support that the ELS fulfils two functions in this group of chimpanzees: firstly, to initiate grooming bouts and to re-initiate grooming during pauses or interruptions to grooming, and secondly for the groomer to request reciprocation of grooming from their partner during a bout. The ELS plays an important role in this community of chimpanzees in initiating and negotiating the dynamics of these crucial cooperative dyadic interactions.

CHAPTER 4: Are joint attention events uniquely human? A comparative study with Humans (*homo sapiens*), Chimpanzees (*Pan troglodytes schweinfurthii)* and Sulawesi Crested Macaques (*Macaca nigra)*

ABSTRACT

Joint attention has been attributed with underpinning the uniqueness of the human cognitive system (Tomasello et al., 2005), yet the basis for such claims have been built upon a paucity of reliable evidence from non-human species. To rigorously test the assertion that engagement in joint attention events is uniquely human, directly comparable data from non-human species is required. Two studies were conducted here to test whether humans, wild chimpanzees and wild Sulawesi crested macaques partake in visually-mediated joint attention events. I examined three levels of joint attentional engagement, with increasingly stringent operational definitions aimed at providing increasingly strong evidence that the interaction partners were attending to the stimulus together in a joint manner. In study 1 a moving laser light was presented as a novel stimulus to dyads in their natural environment. It was found that dyads from all species engaged in the first two levels of joint attention events, with only humans and macaques demonstrating the highest level of shared attention events. Examination of the first 50 seconds of the laser trial revealed that humans showed more of the component behaviours required to fulfil my definitions of joint attention events; humans looked more at the face of their partner and produced more communicative signals compared to chimpanzees and macaques. Humans also engaged with the laser for longer than the non-human species, indicating they may have been more interested in this stimulus. In study 2, physical novel objects were presented to encourage increased engagement from the non-human groups. Here, at least one chimpanzee and macaque dyad demonstrated each level of joint attention event, including shared attention events where both individuals look to the object then each other while producing communicative signals. This research challenges previous assumptions that engagement in joint attention events is uniquely human: chimpanzees, and for the first time a monkey species, have shown they are capable of engaging in joint attention events.

INTRODUCTION

Joint attention occurs when individuals share attention about an object or event, and has been suggested to represent the “small difference that made a big difference” in human cognition (Tomasello, Carpenter, Call, Behne, & Moll, 2005, p.16). The motivation and skills to share attention with others is argued to be central for the emergence of ‘we intentionality’ and successful joint action and cooperation (Tomasello et al., 2005). In human development, the ability to engage in joint attention typically emerges between 9-12 months of age and is a vital milestone (Bakeman & Adamson, 1984; Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Mundy et al., 2007; Moore & Dunham, 1995). As discussed in chapter 1, joint attention skills are intimately connected to language abilities; an infant's joint attention skills can significantly predict later language abilities (Cochet & Byrne, 2016; Mundy & Gomes, 1998; Salo, Rowe, & Reeb-Sutherland, 2018), with joint attention scaffolding linguistic interactions to facilitate speech acquisition (Adamson, Bakeman, Suma, & Robins, 2019; Tomasello & Farrar, 1986). These close links between early joint attention skills and language acquisition have resulted in suggestions that joint attention may have been the social pre-adaptation that enabled the emergence of language during human evolution (Christiansen & Kirby, 2003). It has been argued that only humans engage in joint attention events (Tomasello et al., 2005), but to rigorously test this claim and to understand the evolutionary history of our joint attention abilities comparative data from other primate species is required.

As chapter 1 briefly addressed, competing terms and definitions for joint attention have made it difficult to compare findings, and ultimately disrupted the ability to determine which species show a capacity for joint attention (Graham et al., 2021). First an individual's joint attention skills are often labelled as 'joint attention', but a suite of skills exist which underpin the ability of dyad partners to engage in joint attention events: Responding to joint attention (R-JA) skills include successfully following the gaze direction or a pointing gesture of a social partner to a common attentional focus, whereas producing points or showing objects to guide another's attention are examples of initiating joint attention (I-JA) skills (Mundy & Newell, 2007). Joint attention events then are facilitated by R-JA and I-JA skills of the interaction partners, but these skills in isolation without the motivation to share attention are not sufficient for joint attention events to occur. Making clear distinctions between this triad of joint attention abilities is important, as non-humans could show R-JA or I-JA skills, but not necessarily engage in joint attention events (Mundy & Newell, 2007). Second, when focussing on joint attention events a myriad of terms are used in the literature to describe a dyad sharing attention, including 'joint visual attention', 'coordinated joint attention', 'triadic attention' and 'shared attention'(Gabouer & Bortfeld, 2021). Critically, operational definitions of these diverse terms also vary, from 'looking to where another individual is looking' (Butterworth, 1995) also termed parallel attention (Gaffan, Martins, Healy, & Murray, 2010), to a dyad demonstrating a mutual awareness and 'knowing together' that they are attending to the same thing (Tomasello, 1995). It seems vital to adopt a definition of joint attention events that establishes the jointness of the interaction (Carpenter & Liebal, 2011), and is less likely to be a product of individualistic, selfish or competitive motivations that may also promote the monitoring of a group member and their focus of attention (Graham et al., 2021). One way to establish jointness is to look for communicative signals (facial expressions, gestures and vocalisations) produced by the dyad, as this involves individuals actively sharing that they are engaged in the interaction (Carpenter & Liebal, 2011). In humans, it was suggested that such jointness may also be captured by the quality of look given by interaction partners without other overt communicative signals (Hobson & Hobson, 2007). However, a recent study has shown that ‘sharing looks’, which were argued to show jointness, cannot be reliably distinguished from checking or orienting looks by 3rd party observers (Graham et al., 2021), indicating that overt communicative signals are the best markers of jointness within a joint attention event. While I argue that it is important to adopt a definition of joint attention that requires evidence of jointness, previous comparative work has rarely done so. Such divergent terms and definitions in the literature mean that the complexity of behaviour that non-humans are required to show changes between studies, and leads to conflicting accounts as to whether joint attention events were demonstrated.

Despite the challenges created by divergent terminology and definitions, comparative research is vital to draw inferences about the evolutionary origins of this ability in humans (Hauser et al., 2002). We can, for instance, study species from independent clades to assess the convergent evolution of joint attention skills, and understand the social and environmental constraints that may have contributed to the emergence of these abilities. For instance, Ben Mocha, Mundry and Pika (2019) hypothesised that cooperative breeding, and increased pro-social characteristics, may have given rise to joint attention capacities in Arabian babblers. They report that during the production of two communicative signals, the ‘babbler walk’ and ‘object presentation’, signallers gaze alternate between their direction of movement and the targeted recipient to solicit the conspecific to follow them in joint travel. However, whilst the Arabian babblers studied here showed strong evidence of intentional communication within dyadic interactions, the absence of an external entity for the babblers to share attention about means this is incomparable to joint attention events shown in prelinguistic children. Other social species do show some joint attention abilities, for instance dolphins are able to follow their trainer’s points and gaze (R-JA), as well as being able to indicate objects to experimenters (I-JA; Pack & Herman, 2006). While studying taxa that are distantly related to humans can challenge arguments that a behaviour is uniquely human (Tomasello et al., 2005), data on our extant primate relatives is needed to estimate what the abilities of our more recent extinct ancestors may have been. As established in chapter 1, chimpanzees are a particularly powerful model that can provide insight into the socio-cognitive capabilities that our last common ancestor may have possessed approximately 5-7 million years ago (Enard & Pääbo, 2004).

Our primate relatives do exhibit a number of joint attention skills, with many studies reporting a proficiency in R-JA skills in particular. Being able to follow the gaze of a social partner is well-demonstrated across primate taxa, including the great apes (Bräuer, Call, & Tomasello, 2005; Tomasello, Call, & Hare, 1998), old world monkeys (Emery, Lorincz, Perrett, Oram, & Baker, 1997; Scerif, Gomez, & Byrne, 2004), new world monkeys (Amici, Aureli, Visalberghi, & Call, 2009) and lemur species (Ruiz, Gómez, Roeder, & Byrne, 2009). Chimpanzees show quite sophisticated gaze following abilities; they follow both eye and head direction to follow gaze around barriers, and check back to partners when no object of interest is in the indicated location (reviewed in Call & Tomasello, 2008). In the wild gaze following has been suggested to be a valuable cue for ignorant group members to locate threats (Crockford, Wittig, & Zuberbühler, 2017). However, bonobos may be even more sensitive to gaze cues than chimpanzees. For instance, Kano and Call (2014) presented short videos of conspecific models to each great ape species, where the models cued the location of targets. Eye tracking devices revealed that bonobo participants followed the gaze of conspecifics at a higher rate than chimpanzees, but human children remained more advanced than all the great apes in this skill. In contrast to gaze or head direction, following human pointing gestures to target objects seems to be more challenging for non-human primates, with most studies reporting chance performance on object choice paradigms where a human points to the baited container (reviewed in Miklósi & Soproni, 2006). Although some studies with ‘enculturated’ chimpanzees and bonobos (Lyn, Russell, & Hopkins, 2010) or modified spatial set-ups (Mulcahy & Call, 2009) do show evidence of point-following, it does not seem as robust as gaze or head direction following.

Concerning the I-JA abilities of non-human primates, the great apes have been shown to use gaze alternation between objects and human or conspecific social partners (Bard, Bakeman, Boysen, & Leavens, 2014; Carpenter, Tomasello, & Savage-Rumbaugh, 1995; Pitman & Shumaker, 2009). However the animals’ rearing environment seems to impact their usage of gaze alternation, with encultured chimpanzees and bonobos using gaze alternation more than mother-raised individuals, and doing so at similar levels to 18-month old human infants (Carpenter et al., 1995). Whilst this is the case, wild chimpanzees also gaze alternate between social partners and potential threats, and do so from a young age (Dezecache, Crockford, & Zuberbühler, 2019; Schel, Townsend, et al., 2013). Although an encultured rearing environment may encourage this behaviour, it is still present in the species without human interference, although whether this is an intentional strategy to direct the attention of another to an object or event remains unclear. Gaze alternation may also arise from an individual having two competing loci of attention they need to monitor (e.g. a potentially dangerous snake and conspecifics who they want to stay in spatial proximity to). Clearer evidence for directing the attention of another to an external object or event comes from captive great apes, who have been regularly documented to use attention directing gestures with human caregivers to request out of reach food (e.g. Cartmill & Byrne, 2007). In such scenarios, chimpanzees spontaneously produce whole hand or index finger points, which show evidence of being referential and intentionally produced (Leavens & Hopkins, 1998; Leavens, Russell, et al., 2005). However, just as great ape gestures to conspecifics seem to be imperative requests for action (Cartmill & Byrne, 2010; Graham et al., 2018; Hobaiter & Byrne, 2014, 2017), the pointing of captive apes also seems to be driven by desire for an object or to request an action is performed with an object, not a desire to simply share attention or information (Bullinger, Zimmermann, Kaminski, & Tomasello, 2011; Halina, Liebal, & Tomasello, 2018). As chapter 1 mentioned, anecdotal reports of pointing in wild bonobos (Veà & Sabater-Pi, 1998) and chimpanzees (Hobaiter et al., 2014) exist, but are exceedingly rare given the combined observation time of these species across study sites. Thus, chimpanzees and bonobos seem able to direct the attention of others to external objects and events through gaze alternation and gestures, but whether the motivation underlying the production of these signals is to share attention is less clear.

While non-human primates show the capacity, and are sometimes quite adept, at both R-JA and I-JA skills, whether any non-human primates use these skills to engage in joint attention events remains unresolved. Although multiple papers claim to show joint attention events in other primates, the applied definitions often focus on triadic attention i.e. gaze alternation between social partners and an object (e.g. Bard et al., 2014; Carpenter et al., 1995; Pitman & Shumaker, 2009). Though triadic attention has many of the necessary components of a joint attention event, the absence of any communicative behaviour makes it difficult to establish the jointness of the interaction: there are many reasons why an individual may look back and forth between an object and partner without the sharing of attention (Carpenter & Call, 2013). Whilst alternating gaze is a good example of checking the recipient’s attention, this could be done for competitive or selfish reasons, and in isolation it may not show the sharing of attention (Tomasello, 1995). To achieve this a stricter definition which requires communicative signalling is required. But as chapter 1 described, research that specifies these more stringent requirements for jointness in the triadic interaction fails to identify any evidence of these exchanges in non-human primates. For instance, Tomonaga et al (2004) found that mother-infant chimpanzee dyads produced no communicative interactions during their exposure to an animated novel object. This was despite the stimulus eliciting responses from the dyad which intuitively seem ideal for fostering joint attention; initially resulting in fearful responses and later leading to object manipulation by both partners. However, this study was limited to only 3 mother-infant dyads, so if joint attention events are rare in non-humans it’s possible the behaviour was missed with such a small sample size. Other studies have asked chimpanzees to interact with human caregivers, rather than with conspecifics (e.g. Bard et al., 2014; Carpenter et al., 1995). Chapter 1 discussed how chimpanzees in such paradigms may experience lower motivation to share attention with an heterospecific partner, but these cross-species interactions can also require chimpanzees to understand human communicative signals, so it is perhaps unsurprising that apes fail to share attention in these settings. However, related research shows that chimpanzee dyads exposed to novel objects tend to engage independently from each other, and show no evidence of having a shared goal between partners (Bard & Vauclair, 1984; Tomasello et al., 2005; Tomonaga et al., 2004). This suggests that non-human apes may lack a motivation to share experiences with conspecifics about objects, and aligns with the common assertion that non-human apes do not produce communicative signals (e.g. points) for the purposes of sharing attention (Carpenter & Call, 2013; Carpenter et al., 1998).

The lack of evidence to date of chimpanzees engaging in truly 'joint' joint attention events is perhaps surprising given that chimpanzees do display component behaviours that are necessary to meet the criteria, i.e. attention to objects or events, mutual gaze and communication. Chimpanzees engage with objects particularly when young, and do show evidence of involving social partners in object exploration through social referencing (Bard, 2017; Russell, Bard, & Adamson, 1997). For the occurrence of mutual gaze, research indicates that the visual attention of chimpanzees is drawn to social features and faces of conspecifics (Tomonaga & Imura, 2009; Kano, Shepherd, Hirata, & Call, 2018), and that they engage in mutual gaze contact with social partners from infancy (Bard et al., 2005). Chimpanzees also have a rich communication system; their communicative signals show evidence of intentionality (Byrne et al., 2017; Hobaiter & Byrne, 2011; Hopkins, Taglialatela, & Leavens, 2011; Leavens & Hopkins, 1998; Schel et al., 2013), flexible usage across contexts (e.g. Hobaiter & Byrne, 2014), and referentiality (e.g. Slocombe & Zuberbühler, 2005).

Given that chimpanzees show the component behaviours needed to engage in joint attention events, it may be that previous efforts have not tested this species in the optimal conditions for joint attention events to arise. As already highlighted most studies of joint attention (R-JA, I-JA and joint attention events) in great apes focus on human-chimpanzee interactions, whereas human children are never asked to interact with and share attention with a different species. Most non-human primate research on joint attention also stems from 'BIZARRE' (Barren, Institutional, Zoo, and other Rare Rearing Environments; Leavens, Bard, & Hopkins, 2010) ape samples (e.g. Bard et al., 2014; Carpenter et al., 1995; Tomonaga et al., 2004). BIZARRE apes are often separated from their biological mothers and nursery reared, and being reared in these conditions creates an elevated risk of impaired socio-cognitive development (Bard & Leavens, 2014). In addition, BIZARRE apes are often directly compared to WEIRD (Western, Educated, Industrial, Rich and Democratic; Henrich, Heine, & Norenzayan, 2010) human children raised amongst their family. Differences between these groups may not result from species differences, but from the vastly different developmental experiences the participants have had (Bard & Leavens, 2014). Within humans, sole focus on WEIRD populations is itself problematic, as research suggests that cultural ecology (e.g. familial education and religion) can alter the manifestation of joint attention skills in childhood (Gavrilov, Rotem, Ofek, & Geva, 2012); thus WEIRD samples may not be representative of species-typical behaviour (Bard & Leavens, 2008). There are some circumstances where BIZARRE apes can show joint attention skills more frequently than wild populations. For instance, pointing is rare in wild chimpanzees but commonplace in artificial rearing environments. In captivity physical barriers prevent individuals from reaching objects alone, and attentive human partners are responsive to such gestural requests (Leavens, 2021; Leavens, Hopkins, & Bard, 2005). Though this can be the case, BIZARRE apes ultimately fail to enlighten us about the natural behaviour of this species, or their motivation to share attention with conspecifics.

To summarise, currently there is insufficient relevant evidence to evaluate the extent to which engagement in joint attention events is uniquely human. Previous non-human animal research has often adopted overly simplistic definitions of joint attention events, and positive findings involving the monitoring of others in relation to an object may be the result of selfish rather than sharing motivations. Moreover, prior studies have often applied these definitions to BIZARRE apes from unusual rearing environments and WEIRD humans, who may constitute unrepresentative samples. Lastly, most studies have focussed on cross-species human-ape interactions, rather than conspecific interactions. To address these limitations, I tested human, chimpanzee and Sulawesi crested macaque dyads with a directly comparable paradigm in their natural environments. I adopted operational definitions of joint attention events that require partners to make mutual awareness of attending to the same thing manifest through communication (Siposova and Carpenter, 2019). I also looked for simpler forms of potential joint attention events to allow a more fine-grained distinction of where species differences may emerge. In all species I therefore assessed whether they exhibit three different levels of joint attention. First I identified (i) triadic attention events, where both individuals looked to the stimulus and then looked to each other, resulting in mutual face direction. The second level was (ii) triadic attention with communication events, where both individuals looked to the stimulus and then looked to each other, resulting in mutual face direction. During mutual face direction at least one individual was required to have produced a communicative signal. Finally, I searched for (iii) shared attention events, where both individuals looked to the stimulus and then looked to each other, resulting in mutual face direction. During mutual face direction, both individuals were required to have produced a communicative signal.

I sought to create a paradigm which optimised conditions for natural interactions between conspecifics, therefore I actively avoided the use of BIZARRE non-human primate samples (Leavens et al., 2010) and instead collected data from wild populations. Chimpanzees represented one of my non-human groups; as one of our closest living relatives they are an ideal model to question statements regarding the recent evolutionary history of human traits. The second non-human species was Sulawesi crested macaques; an old-world monkey species which allows us to delve deeper into the evolutionary history of joint attention behaviours. This is a valuable addition to my study as while previous literature has investigated the presence of R-JA and I-JA skills in monkey species, to my knowledge the current study will be the first to examine joint attention events in this primate group. Sulawesi crested macaques were chosen as promising candidates for demonstrating joint attention: they are highly communicative, socially tolerant and do not find eye-gaze threatening (Micheletta, Engelhardt, Matthews, Agil, & Waller, 2013); all traits which may foster joint attention abilities. I examined both non-human groups across their lifespan in order to allow for the possibility that these skills emerge later in non-human species, and therefore to avoid premature claims that they lack a capacity for joint attention (Bard & Leavens, 2014). Finally, my human group was also examined in their home environments, and here I avoided the exclusive recruitment of an unrepresentative WEIRD sample (Henrich et al., 2010). By doing so I avoided the assumption that human joint attention developmental trajectories are universal, and have a wider representation of human joint attention skills as a species (Bard & Leavens, 2014). This diverse human sample included mother-infant dyads living in the UK and Uganda, and were tested when infants were 11 months old. This age point was selected as it is after the ‘9 month revolution’ when joint attention skills typically begin to emerge (Tomasello et al., 2005), but prior to pointing and language skills (which begin to surface from 12 months old; Colonnesi, Stams, Koster, & Noom, 2010) where obvious differences with non-humans are already apparent.

STUDY 1: Testing for joint attention events with a laser light stimulus

In study 1 I presented a dyad with a moving light of a laser pointer as a novel, interesting stimulus that the dyad may have wished to share attention about. In line with my operational definitions previously outlined for triadic attention events, triadic attention with communication events, and shared attention events, I measured individual’s head direction to the stimulus and to conspecifics, as well as any communicative signals elicited from the dyad (facial expressions, gestures, vocalisations). I used head direction instead of gaze for comparative purposes, as eye gaze measurement in chimpanzees (who rarely have white sclera) is extremely difficult without eye-tracking devices. Although eye-gaze is not always congruent with head direction (Bethell, Vick, & Bard, 2007) this method ensured fair estimates across species. I also examined the dyads overall engagement with the laser to ascertain if each species showed equal interest in the novel stimulus. Using these methods, I examined whether each species demonstrated the behavioural sequences necessary for each level of joint attention events. For all levels, given the well-documented emergence of joint attention events in human infants from 9 months of age (Bakeman & Adamson, 1984; Carpenter et al., 1998; Mundy et al., 2007), it was expected that humans would participate in more joint attention events than the non-human groups. However, whether joint attention events would be identified in any non-human dyads remained the crucial question. If no joint attention events were identified in the non-human dyads this would represent a qualitative species difference and indicate that joint attention events are a uniquely human ability. If joint attention events were identified in non-human dyads this would indicate that non-humans have the capacity to engage in joint attention events, and this is not a uniquely human ability. In case of clear species differences, I sought to examine components of joint attention (e.g. looking at partner, mutual face direction, engagement with stimulus) to see what may be driving such differences.

STUDY 1 METHODS

Study sites and subjects

I collected data from 3 species, chimpanzees, Sulawesi crested macaques and humans, in dyadic pairs (Focal A, Focal B; see Appendix 1 for a summary of data contributions). In humans the experiment was conducted once with mothers and their infants when the infants were approximately 11 months old. For the non-human groups, I aimed to present the stimulus to infant-mother dyads, but as our knowledge of the developmental trajectory of joint attention in non-human primates is limited, I also aimed to test as many unique dyads (including other related individuals and unrelated individuals) as possible. Some individuals participated in multiple trials: individual chimpanzees participated in 1-2 trials and individual macaques participated in 1-3 trials.

Chimpanzees, Pan troglodytes schweinfurthii

Chimpanzee participants were from three wild communities, Kanyawara, Ngogo central and Ngogo west, which all reside within Kibale National Park, western Uganda (see chapter 2 for descriptions of the study site at these communities).

Data were collected by NL and CW, with the help of research assistants EA, JW and MH, between January 2018 and March 2020. All individuals in the community were targeted preferably in dyads, but if all other experimental conditions were met then others were also allowed to be present during the interaction. However, only the 2 primary interactants with the stimulus were later coded (Focal A and Focal B). In total, 81 experiments were conducted. For a successful trial I required both target individuals to engage with the stimulus. Both target individuals engaged with the stimulus in 33 of these experiments, resulting in a final sample of 32 unique dyads comprising 58 individuals (see Table 5 for summary).

Table 5. Demographic distribution of chimpanzee participants that had successful laser trials completed.

Community	Focal A	Age class	Sex	Focal B	Age class	Sex	Dyad relatedness (maternal kin only)
Kanyawara	UT	Infant	F	TR	Juvenile	F	Non-kin
	OMG	Infant	M	OL	Juvenile	F	Nephew/Aunt
	BE	Infant	F	BZ	Adult	F	Offspring/Mother
	NPT	Infant	F	NP	Adult	F	Offspring/Mother
	OMG	Infant	M	OM	Adult	F	Offspring/Mother
	OTR	Infant	M	OT	Adult	F	Offspring/Mother
	TZ*	Infant	M	TG*	Adult	F	Offspring/Mother
	WJ	Infant	M	WA	Adult	F	Offspring/Mother
	WO	Infant	F	WL	Adult	F	Offspring/Mother
	BT	Juvenile	M	UN	Sub-adult	M	Non-kin
	WC	Sub-adult	M	WL	Adult	F	Offspring/Mother
	NP	Adult	F	JU	Adult	F	Non-kin
	TT	Adult	M	OG	Adult	M	Non-kin
Ngogo central	KB	Infant	F	JL	Adult	F	Offspring/Mother
	ZN	Juvenile	M	SL	Juvenile	M	Non-kin
	FK	Juvenile	F	CB	Sub-adult	M	Siblings
	FD	Juvenile	F	AR	Adult	F	Offspring/Mother
	CD	Juvenile	M	HK	Adult	M	Non-kin
	HZ	Juvenile	M	BK	Adult	M	Non-kin
	PW	Sub-adult	M	CN	Juvenile	M	Non-kin
	FI	Adult	F	SH	Juvenile	M	Non-kin
	GR	Adult	M	CN	Juvenile	M	Non-kin
	HD	Adult	M	FL	Sub-adult	M	Non-kin
	CT	Adult	M	CP	Adult	M	Non-kin
	EV	Adult	M	PP	Adult	M	Non-kin
	JS	Adult	M	BF	Adult	M	Non-kin
	MK	Adult	M	GR	Adult	M	Non-kin
	MT	Adult	M	MG	Adult	M	Unknown
Ngogo west	SJ	Infant	M	VG	Infant	F	Non-kin
	LI	Infant	M	NN	Juvenile	F	Siblings
	EJ	Juvenile	F	HO	Juvenile	M	Non-kin
	BU	Adult	M	HO	Juvenile	M	Siblings

Note: Age classes were classified as follows: infancy 0-4 years, juvenile 5-10 years, sub-adult male 11-14 years, sub-adult female 11-13 years, adult male 15+ years, adult female 13 or 14 + years (dependent on breeding age, based upon Thompson, Muller, Machanda, Otali, & Wrangham, 2020)**.** Individuals with an asterisk (*) were involved in two experiments as part of the same dyad.

Sulawesi crested macaques, Macaca nigra

Sulawesi crested macaques were studied at the Macaca Nigra Project, Tangkoko, North Sulawesi, Indonesia. Data collection was focused on the PB1b group, which is the "research only" group, but additional data was collected from R1, which was a mixed research and tourism group. PB1b mainly ranged in primary growth forest with some secondary growth areas where wildfires have passed through. R1’s range included some primary growth, but large areas of secondary growth and some agricultural land near Batu putih village. The macaques were all habituated to research observation at 5-metres, but tourists regularly approached R1 more closely. All adult females and males in PB1b and R1 groups were individually known by the Macaca Nigra Project, and in addition the researchers could identify all infants in these groups, but juveniles and most sub-adults were not individually known.

Data were collected by AP from March 2018 to September 2019, KG from March 2018 to October 2018 and January 2019 to March 2019, and CW and KS in June and July 2019. All individuals in the PB1b group were targeted preferably in dyads, but if all other experimental conditions were met then others were also allowed to be present during the interaction, but again I only coded the two primary interactants. Sometimes the identities of macaque individuals were unknown (e.g. juveniles and sub-adults) or could not be confirmed from the video or before they left the experimental area in real time (adults, infants). Any unknown individuals of the same age class later joining the trial were treated as separate individuals and assigned unique ID codes. A total of 95 experiments were conducted. Both target individuals engaged with the stimulus in 36 experiments, resulting in a final sample of 31 unique dyads comprising 48 individuals (see Table 6 for summary). Only 1 dyad from the R1 group contributed data, as tourism guides were discovered to regularly expose this group to similar laser stimuli, so no further experiments were conducted on this group once this became known.

Table 6. Demographic distribution of macaque participants that had successful laser trials completed

Community	Focal A	Age Class	Sex	Focal B	Age Class	Sex	Dyad relatedness
PB1b	FP6B	Infant	F	BA3B	Infant	M	Non-kin
	XP4B	Infant	M	KA1B	Infant	F	Non-kin
	FP6B	Infant	F	UnkJuv04	Juvenile	U	Unknown
	FP6B	Infant	F	UnkMJuv02	Juvenile	M	Unknown
	JA1B	Infant	M	UnkFJuv04	Juvenile	F	Unknown
	KA1B	Infant	F	UnkFJuv05	Juvenile	F	Unknown
	KP6B	Infant	F	UnkJuv07	Juvenile	U	Unknown
	QP4B	Infant	M	MJuvUnk04	Juvenile	M	Unknown
	UP3B	Infant	M	UnkJuv04	Juvenile	U	Unknown
	AA3B	Infant	F	AA	Adult	F	Offspring/Mother
	BA3B*	Infant	M	BA*	Adult	F	Offspring/Mother
	CA2B*	Infant	M	CA*	Adult	F	Offspring/Mother
	CP5B*	Infant	M	CP*	Adult	F	Offspring/Mother
	DP5B	Infant	F	DP	Adult	F	Offspring/Mother
	JA1B*	Infant	M	JA*	Adult	F	Offspring/Mother
	KA1B	Infant	F	KA	Adult	F	Offspring/Mother
	KP7B	Infant	F	KP	Adult	F	Offspring/Mother
	NP5B	Infant	M	NP	Adult	F	Offspring/Mother
	UP3B	Infant	M	UP	Adult	F	Offspring/Mother
	KP6B	Infant	F	FP	Adult	F	Non-kin
	YP5B*	Infant	M	MA*	Adult	F	Non-kin
	CP5B	Juvenile	M	UnkFJuv02	Juvenile	F	Unknown
	KP6B	Juvenile	F	UnkJuv06	Juvenile	U	Unknown
	UnkFJuv06	Juvenile	F	UnkMJuv03	Juvenile	M	Unknown
	UnkMJuv05	Juvenile	M	UnkMJuv06	Juvenile	M	Unknown
	XP4B	Juvenile	M	UnkMJuv07	Juvenile	M	Unknown
	YP5B	Juvenile	M	UnkFJuv07	Juvenile	F	Unknown
	GA1B	Juvenile	F	GA	Adult	F	Offspring/Mother
	CP	Adult	F	UnkJuv02	Juvenile	U	Unknown
	JU	Adult	F	UnkFAdu01	Adult	F	Unknown
R1	UnkJuv09	Juvenile	U	UnkMJuv04	Juvenile	M	Unknown

Note: For age classifications, infancy was defined as individuals from 0-11 months prior to weaning. For older individuals their birthdates were unknown. Therefore, age classes were defined based upon body size, reproductive status and whether the individual had immigrated to the group. Individuals with an asterisk (*) were involved in two experiments as part of the same dyad. Individuals where their sex was marked as 'u' is indicative that their sex was not identifiable from the video recordings.

Humans, Homo sapiens

To assess engagement in joint attention events in this group, I exclusively tested mother-infant dyads (referred to as Focal A and Focal B for consistency with other groups). Participants were recruited from both the UK and Uganda to provide a culturally diverse and representative sample. The early life environments of the two groups differ on several dimensions, including the number of caregivers the infants experience, the amount of social play the infants engage in, and the proximity and body contact between the mother and infant (Holden et al., in review).

Participants in Uganda were mothers and infants living in the Nyabyeya parish, Masindi district. Local research assistants encouraged pregnant mothers to register the birth of their babies to ensure accurate birth dates. Recruitment for the longitudinal research project, of which this experiment was part, took place at local information meetings regarding the research, which were advertised during village and church meetings and through word of mouth. Mothers were invited to join the study if the mother's main language was Alur, Lugbara or Swahili, where translators were available for experimental instructions. I assessed the joint attention abilities of 12 dyads (5 female) who were approximately 11 months old (range: 10 months 24 days - 11 months 15 days). Ten infants had a sibling at the time of study (number of siblings: range = 1-7, mean = 3.8), with the remaining children having no documented siblings. Experiments were conducted by researchers from the University of York together with Ugandan research assistants from December 2018 to July 2019.

Participants in the UK were mother-infant dyads living in and around the city of York. Mothers were recruited at local children's centres, infant classes and through social media (Facebook) and word of mouth; also as part of a longitudinal research project. Mothers were invited to join the study if they were native English speakers. I assessed the joint attention abilities of 12 dyads (6 female) who were approximately 11 months old (range: 10 months 17 days - 11 months 1 day). Seven infants had a single sibling at the time of study, with the remaining children having no documented siblings. Experiments were conducted by researchers from the University of York from August 2018 to August 2019.

Ethical note

This study complied with the ASAB guidelines for the use of animals in research, and ethical approval was granted by the Animal Welfare and Ethical Review Body (Dept of Biology, University of York). To work with the chimpanzees, permission was granted by the Ugandan Wildlife Authority, the Ugandan National Council for Science and

Technology, and the President’s Office. For work with the crested macaques at Tangkoko, permission was obtained from the Indonesian State Ministry of Research and Technology (RISTEK), the Directorate General of Forest Protection and Nature Conservation (PHKA), and the Department for the Conservation of Natural Resources (BKSDA), North Sulawesi.

The human work was approved by the Dept of Psychology Ethics committee at the University of York, with the research with Ugandan samples also gaining approval from the Ugandan National Council for Science and Technology, and the Ugandan Virus Research Institute Regional Ethics Committee. Mothers in the human groups gave overall written consent when signing up for their and their infant’s participation in the longitudinal research. Written consent for this specific task was obtained on the day the task was carried out.

Equipment

The task involved the erratically moving light from a laser pen (wavelength: 532nm; output power 1Mw (class 3); colours: red, green and blue). The task was filmed using two Panasonic HC-VX980 camcorders, with Sennheiser MKE 400 microphones attached. Videos were later coded using Noldus Observer XT 14 event logging software (http://www.noldus.com/animal-behavior-research).

Procedure

An experimental task where researchers presented a laser light stimulus to participants was conducted. The stimulus was presented on the ground, or other available surface, in front of focal individuals A and B so that both individuals could perceive the stimulus. Projecting the laser on to the participants’ bodies was avoided. The laser light was moved erratically, but not too quickly to allow individuals to track its movement. Two cameras, one focused on each focal individual, were used to film the entire interaction in all species groups. Researchers aimed to turn the stimulus off 2-3 times during a trial for a period of 3-5s each, as the disappearance and reappearance of the laser would often recapture the interest of focal individuals. The laser was also turned off if non-focal individuals entered the experimental area and disrupted their dyadic engagement with the laser (e.g. by engaging a focal animal in play), or if the arriving individuals were later targets for the experiment. Researchers aimed to present the stimulus for 180s, although overall trial time could be longer if other individuals interrupted during the experiment (resulting in researchers turning the stimulus off), or if focal individuals momentarily became engaged in behaviours that would not enable them to attend to the stimulus (e.g. playing, or grooming in the non-human groups). Trials in all groups were terminated when focal individuals had been exposed to the stimulus for approximately 180s. Trials were terminated prematurely if focal individuals left the experimental area, if non-focal animals remained in the experimental area and prevented stimulus presentation, or if a focal individual engaged in a context that was incompatible with laser engagement for an extended period of time. In these cases, a second trial was attempted at a later time which could be in a new location, and/or on a different day. Trials were also terminated immediately if either individual expressed distress or fear in response to the stimulus. In these cases, the stimulus was not presented to these individuals again.

In human trials, mothers were given information prior to the trial that was necessary for them to provide informed consent. Mothers were verbally told by researchers that a laser light would be shone in front of them and their child for about 3 minutes, and were asked to react to the laser as they normally would to a new exciting object (e.g. a beautiful butterfly flying into the room). In Uganda, a local research assistant provided this information verbally to the mothers in a language the mother was fluent in. If a mother in Uganda was unfamiliar with laser lights, then they were briefly shown the light out of sight of the child.

In all trials researchers commentated any identifiable individuals who entered the experimental area or interacted with the stimulus. The location of the stimulus and whether it was off or on was also commentated, as well as any audible vocalisations in the non-human groups.

Video coding

Videos were coded with Noldus Observer XT software in order to extract continuous details about behaviours from both focal individuals A and B during specified experimental periods (see Table 7). I first coded the presence of the stimulus to ascertain the amount of exposure focal individuals could have been subjected to. For focal individuals A and B I then coded face direction, instances of mutual face direction, communication (facial expressions, vocalisations and gestures) and laser engagement.

Table 7. Coding scheme for experimental periods, stimulus presence and behaviours of interest produced by focal individuals A and B during laser experiments.
Note: Categories that were coded separately for focal A and B are distinguished by an asterisk (*). Face direction was the singular category which had different coding rules between solo experimental periods (where social looking included looks to other individual's bodies) and social experimental periods (where social looking was limited to other individual's faces). Therefore, only the rules for coding during the social experimental period are detailed here.

Behaviour category	Behaviour	Description
Experimental period	Not coded	The stimulus had not been presented, the stimulus had been off for 30 seconds, or both Focal A and B had started an activity that prevented laser engagement (e.g. playing, mutual grooming). For the latter, 'not coded' was activated 10 seconds after the laser turned off, or 10 seconds after the last focal individual disengaged.

	Solo experimental	The period where only one individual had reacted to the stimulus in a manner that indicated they were aware of its presence. Behaviours that were considered indicative of this included startling, freezing, tracking the stimulus, repetitive looks to the laser or any physical engagement (e.g. hitting or swatting the stimulus). The individual must have shown such laser-oriented behaviours for a minimum of 3 seconds for this behaviour to be activated from the start of their engagement.
	Social experimental	The period where both individuals had reacted to the stimulus in a manner that indicated they were aware of its presence. The same behaviours were considered indicative of this as outlined for the 'solo experimental' period. Both individuals must have shown such laser-oriented behaviours for a minimum of 3 seconds each, and "social experimental" was then activated when the second individual had started to engage.
Stimulus presence	Stimulus not present	The stimulus had not been presented, or was off for 10 seconds or more.
	Stimulus present	The laser was on, or cases where the laser was off or out of sight for less than 1 second.
	Stimulus off	The laser was turned off for over 1 second, and less than 10 seconds.
	Stimulus out of sight	When video commentary indicated that the stimulus was still present, but was not visible on camera. This must have been the case for at least 1 second.
Face direction* during social experimental periods	Face not visible	When the individuals face/head was not visible for over 3 seconds. In all groups if the focal individual's ears were visible, then head direction was still considered as available.
	Facing stimulus	The individual's face was pointing towards the stimulus, or the location where the stimulus was last present when turned off. The latter was only coded when the stimulus had been off for under 10 seconds. All instances were coded.
	Facing partner	The individual's face was pointing towards their partners face (not body). All instances were coded.
	Facing other individual	The individual's face was pointing towards another individual's (not the partner's) face (not body). All instances were coded.
	Facing experimenter	The individual's face was pointing towards the experimenter or looking directly at the camera (often

		being held by the experimenter). All instances were coded.
	Facing elsewhere	The individual's face was pointing towards an object/location that was not the stimulus, another individual's face or the experimenter. All instances were coded, unless the individual was facing either the stimulus or partner before AND after the "elsewhere" interval, in which case this was only coded if it was 1 second in duration or over.
Mutual face direction	No mutual face looks	Focal A and focal B were not simultaneously looking at each other's faces.
	Mutual face direction	Focal A and focal B were simultaneously looking at each other's faces. All instances were coded.
Facial expressions*	No expression	The individual was not producing a facial expression. If an individual stopped producing an expression for less than 3 seconds, this was not coded (i.e. 'facial expression' remained activated).
	Facial expression	The individual was producing a facial expression (see Appendix 5 for a list of expressions coded in each species). All instances were coded.
	Facial expressions unavailable	This was selected when it was uncertain whether the individual was producing a facial expression, as the view of their face was blocked or their back was turned. This was only coded if it occurred for over 3 seconds, unless the individual was looking at their partner's face (then all instances were coded).
Vocalisations*	No vocalisation	The individual was not producing a vocalisation. If an individual stopped producing a vocalisation for less than 3 seconds, this was not coded (i.e. "vocalisation" remained activated).
	Vocalisation	Any volitional, audible signal that came out of the individual's mouth (coughs for instance, were not coded). Here I distinguished between the following: (1) vocal only bout (the individual produces an audible signal that does not include speech); (2) vocal and language bout (the individual produces an audible signal (e.g. a gasp) and speech; humans only) and (3) language only bout (the individual produces speech; human only) In the non-human groups, I did not distinguish between the type of calls being produced, but included any audible vocal signal (excluding yawns and coughs). For the chimpanzees for instance, this included whimpers,

		screams, grunts, pant-grunts, barks, hoos, pant-hoots and waa-barks. All instances were coded.
	Vocalisations unavailable	This was selected when it was uncertain whether the individual was producing a vocalisation, for instance if there was no audio available or there was a noisy environment which may have masked a vocal signal. This was only coded if it occurred for over 3 seconds.
	Vocalisation uncertain producer	This was selected if a vocalisation occurred that may have been produced by focal A or B, but the signaller identity was unknown. This behaviour was only relevant for the macaque sample.
Gestures*	No gesture	The individual was not producing a gesture. If an individual stopped producing a gesture for less than 3 seconds, this was not coded (i.e. "gesture" remained activated).
	Gesture	The individual was producing a gesture (see Appendix 6 for a list of gestures coded in each species). All instances were coded.
	Gestures unavailable	This was selected when it was uncertain whether the individual was producing a gesture, for instance if the view of their body was blocked or not visible. This was only coded if it occurred for over 3 seconds.
Stimulus engagement*	No engagement	The individual was not engaged with the stimulus.
	Quiet engagement	Included: (1) watching (facing the stimulus from over 20cm away); (2) inspecting (facing the stimulus from under 20cm away); (3) close manual engagement and touching (tracing the laser movement within 10cm of the stimulus, without necessarily touching the substrate); (4) pointing with hand towards stimulus (hand must be over 10cm away from the stimulus on the substrate); (5) pointing with index finger towards the stimulus (hand must be over 10cm away from the stimulus on the substrate); and (6) other quiet engagement (any unspecified behaviour). These behaviours could occur when the laser was present, or within 10 seconds of the laser being turned off. If the individual switched between types of quiet engagement (1-5), then the behaviours were coded hierarchically i.e. a higher item (e.g. 4) could interrupt a lower item (e.g. 2) no matter its duration. A lower item must have lasted for a minimum of 3 seconds to have interrupted a higher items coding. (e.g. 'watching' must

		have lasted for 3 seconds to interrupt ‘pointing with index finger’). Item (6) entered the hierarchy based on the coders perception of how salient the behaviour was in relation to the already categorised behaviours. E.g. the focal animal looking at their own hand after attempting to grab the laser was considered equivalent to ‘inspecting’ in the hierarchy. If less than 1 second of quiet engagement occurred before audible engagement, then this was not coded (the entire period was instead considered as ‘audible engagement’). Quiet engagement must have occurred for a minimum of 3 seconds to have interrupted a period of audible engagement.
	Audible engagement	Included: (1) hitting the stimulus (movement from the elbow or shoulder, which included slapping, banging or drumming with any body part within 5cm of the stimulus); (2) hitting the stimulus with an object (using another object to hit the stimulus); and (3) other audible engagement (any unspecified behaviour). These behaviours could occur when the laser was present, or within 10 seconds of the laser being turned off. If the individual switched between types of audible engagement (1-3), then the behaviours were coded hierarchically i.e. a higher item (e.g. 3) could interrupt a lower item (e.g. 1) no matter its duration. A lower item must have lasted for a minimum of 3 seconds to interrupt a higher items coding. (e.g. ‘hitting’ must have lasted for 3 seconds to interrupt ‘hitting with an object’). Item (3) entered the hierarchy based on the coders perception of how salient the behaviour was in relation to the already categorised behaviours. E.g. a focal animal charging/displaying towards the stimulus was considered as equivalent to ‘hitting with an object’ in the hierarchy. If less than 1 second of quiet engagement occurred before audible engagement, then this was not coded (the entire period was instead considered as ‘audible engagement’). All cases of audible engagement were coded (no minimum duration).
	Unclear engagement	This was selected when it was uncertain if the individual was actively engaged with the stimulus, e.g. in cases where the stimulus was not visible.

Extraction of measures

Joint attention events

When partners looked at each other's faces I wanted to ascertain how likely a joint attention event of some type was to occur. Using the Behaviour Analysis tool in Observer XT, I first extracted all instances of mutual face direction during 'social experimental' intervals. To then assess whether the species demonstrated each level of joint attention, I extracted the following behaviours from the focal individuals: whether one or both individuals looked to the stimulus in the 3s prior to the onset of mutual face direction; and whether one or both individuals was producing a communicative signal during the mutual face direction behaviour (where onset may have occurred prior to mutual face direction, but not after).

Species differences in independent joint attention behaviours

I also wanted to examine the likelihood for each species to exhibit independent behavioural components of joint attention events, or whether aspects of the experiment itself may explain species differences in the occurrence of joint attention events. Specifically, for each species I examined: (1) the amount of laser exposure they received; (2) their attention to conspecifics; (3) the occurrence of mutual face direction; (4) their communication; and (5) their engagement with the stimulus.

While experimenters aimed to expose individuals to the laser for up to 180s, both non-human groups experienced notably more interruptions or early terminations than the human group, which resulted in diminished trial length for chimpanzees and macaques. In order to control for this, I only examined these components in a controlled 50s interval (henceforth 'control interval') to fairly assess the occurrence of behaviours between groups. Control intervals were required to have both individuals in the dyad in unobstructed view, in close proximity and did not include sustained periods (>10s) where the laser was turned off. These intervals were not required to be consecutive 50s, and could be terminated and resumed to meet these conditions. With these criteria 11 chimpanzee and 23 macaque social experimental periods were excluded for not having a 50s control interval available. Furthermore, since one member of the dyad often engaged prior to the second individual joining ('solo experimental' periods) a further restriction was the amount of time the first individual was engaged alone with the stimulus. Individuals engaged for a long period alone may have lost interest before the second individual also engaged. I therefore capped the prior solo experimental period of engagement to 30s. This resulted in a further 6 chimpanzee, 4 macaque and 1 human social period being excluded. Finally, to avoid pseudoreplication I removed 2 dyads (1 chimpanzee and 1 macaque) where either focal A or focal B were part of multiple experiments, and retained the mother-infant dyads for greater comparability to the human group.

Inter-coder reliability

To assess inter-coder reliability, each behavioural category was coded in a subset of videos by NL and independent research assistants blind to my hypotheses. Cohen's kappa scores were calculated for all categories detailed above using the Reliability Analysis function in Observer XT.

30% of the total number of trials conducted were assessed for Inter-coder reliability (N trials = 57; at least 25% of the total experiments conducted in each species). As face direction was coded differently between solo and social experimental periods, here I include the assessed inter-coder reliability specifically for social experimental periods. I obtained the mean kappa scores of 0.75 for frequency/sequence and 0.86 for duration/sequence (with a 1s tolerance window) for this behaviour. For all remaining behaviours I achieved a mean frequency/sequence score of 0.82 and a mean duration/sequence score of 0.89, indicating an excellent level of inter-coder agreement and that videos had been coded reliably

Statistical models

Model 1: Triadic attention events

Here I examined whether both individuals had looked to the stimulus prior to mutual face direction occurring. For the GLMM model, I examined the effect of species on the occurrence of triadic attention events (binary: yes/no). I excluded 5 human mutual face direction instances as it was 'uncertain' whether one of the focal individuals had looked to the laser prior to mutual face direction occurring. This resulted in an analysed sample of 109 mutual face direction events, with 41 focal A individuals and 44 focal B individuals

Model 2: Triadic attention with communication events

For this level I required that both individuals had looked to the stimulus prior to mutual face direction occurring, as well as at least one of these individuals communicating during mutual face direction. The GLMM model examined the effect of species on the occurrence of at least one individual communicating during triadic attention (binary: yes/no). This model required the same exclusions as model 1 (N = 5), as well as a further 8 chimpanzee, 12 macaque and 2 human mutual face direction instances, where it was uncertain if at least one individual had communicated during the interval. This resulted in an analysed sample of 87 mutual face direction events, 32 focal A individuals and 35 focal B individuals

Model 3: Sharing attention events

For this level I required that both individuals had looked to the stimulus prior to mutual face direction occurring, as well as both of these individuals communicating during the interval that they were engaged in mutual face direction. The GLMM model examined the effect of species on the occurrence of both individuals communicating during triadic attention (binary: yes/no). This model required the same exclusions as models 1 and 2 (N = 27), as well as a further 3 chimpanzee, 1 macaque and 8 human instances, where it was uncertain if both individuals had communicated during mutual face direction. This resulted in an analysed sample of 75 mutual face direction events, 28 focal A individuals and 30 focal B individuals.

Statistical analysis

Joint attention events

To assess whether engagement in joint attention events are predicted by species, Generalized Linear Mixed Models (GLMM; Baayen, 2008) were used for all analyses, with binomial error distributions and logit link function.

To control for repeated observations of the same focal individuals, focal A ID and focal B ID were included as random intercept effects. In order to keep type 1 error rates at a level of 0.05 all theoretically identifiable random slopes should be included in each model (Barr et al., 2013; Schielzeth & Forstmeier, 2009). However as there were no identifiable random slopes for either model this was not necessary.

Model stability was estimated by dropping the levels of the random effects one at a time from the data and comparing the estimates derived for models fitted to these subsets with those obtained for the full data set (Nieuwenhuis et al., 2012).

To ascertain the effect of the test predictor, full-null model comparisons were carried out with the null model lacking the test predictor, but otherwise being identical to the full model in terms of the random effects structure. For the full-null model comparison a likelihood ratio test was used (Dobson, 2002); R function drop1 with argument 'test' set to "Chisq".

Models were implemented in R (version 4.0.2; R Core Team 2020) using the function glmer of the package lme4 (version 1.1-21; Bates, Mächler, Bolker, & Walker, 2015). Model stability was assessed using a function kindly provided by Roger Mundry. Confidence intervals of the model estimates were obtained using a parametric bootstrap (function bootMer of the package lme4, N=1,000 bootstraps).

As each model centred on the occurrence of mutual face direction events, all models started with an initial sample of 114 mutual face direction cases, 42 focal A individuals and 45 focal B individuals. In each case, I compared the full model comprising species with a null model limited to only the random effects: Focal A and Focal B.

Species differences in independent joint attention behaviours

Following the necessary exclusions required for control intervals to be comparable between species, an analysed sample of 44 control intervals, with 44 focal A individuals and 44 focal B individuals remained. To statistically test for species differences in the duration and number of these behaviours, I applied non-parametric Kruskall-Wallis tests, due to the varying sample sizes available in each of our groups (N: chimpanzees = 15, macaques = 6, humans = 23). Following any significant results, I then applied Mann

Whitney U tests with a bonferroni adjusted alpha level (*p* = .016) to conduct three pairwise comparisons between all groups. These tests were implemented using IBM SPSS Statistics 26 software.

STUDY 1 - RESULTS

Joint attention events

Occurrence of mutual face direction

During social experimental intervals, I identified a total of 114 mutual face direction events across all species, specifically 16 instances in chimpanzees, 22 in macaques and 76 humans (Table 8). As the duration (s) of social experimental periods varied across species (chimpanzees mean = 109, SD = 78; macaques mean = 93, SD = 65; humans mean = 194, SD = 31), I was not interested in the absolute frequency of these mutual face direction events, but rather what happened when a dyad engaged in mutual face direction.

Table 8. For the laser experiment: description of the number of dyads that engaged in mutual face direction, the number of mutual face direction events displayed by the dyad, and the mean duration of mutual face direction per species.

	N dyads engaged in mutual face direction	**Range of mutual face direction instances across dyads**	**Mean duration of mutual face direction (s)**	**Standard deviation of mutual face direction (s)**
Chimpanzees (N = 33)	11	0-3	1.5	0.68
Crested macaques (N =36)	16	0-3	1.0	1.16
Humans (N = 24)	21	0-14	1.5	0.73

Note: N denotes the number of dyads per species that engaged in social experimental periods in total.

Model 1: Triadic attention events

Following exclusions detailed in the data analysis section, 109 mutual face direction events were examined here, and in 43 cases both individuals had looked to the laser stimulus in the 3s prior to display triadic attention (chimpanzees = 2/16, macaque = 7/22, human = 34/71). The GLMM showed a significant effect of species (χ^2=7.696, df=2, *p* =.021), with humans significantly more likely to engage in triadic attention than chimpanzees (Est=2.127, SE=0.954, z= 2.229, *p*=.026) but not macaques (Est=-0.833, SE=0.657, z=-1.268, *p*=.205), and chimpanzees and macaques also showing a similar likelihood to display triadic attention when engaging in mutual face direction (Est=1.294, SE=1.002, z= 1.291, *p*=.197; Figure 15).

Model 2: Triadic attention with communication events

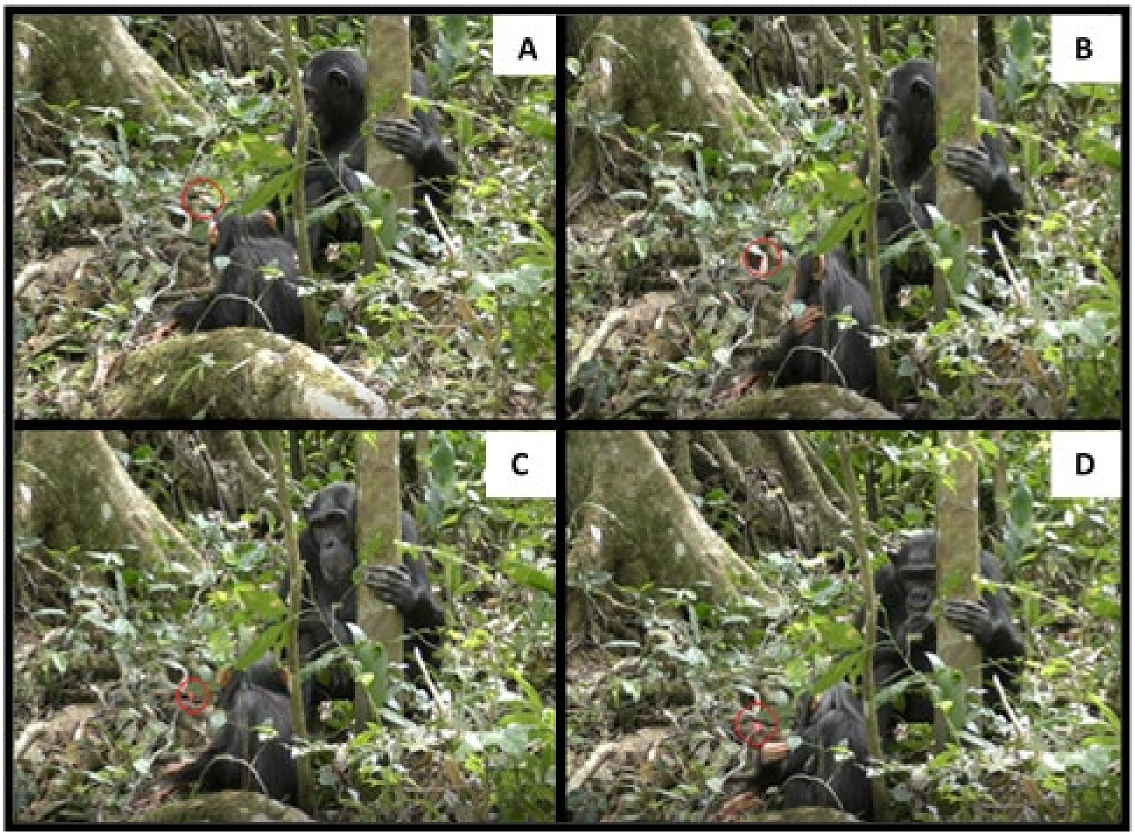
For the 87 mutual face direction instances where triadic attention and the communication of at least one partner was also available, at least one individual communicated in 36 cases (N: chimpanzees = 1/8, macaques = 2/10, humans = 33/69). The GLMM model showed an overall significant effect of species (χ^2=6.091, df=2, *P*=.048), however model stability was poor and pairwise comparisons were therefore not examined. While the instability of the model means this finding should be treated with caution, Figure 15 illustrates the similarity of species performance between triadic attention and triadic attention with communication events.

In terms of the types of communicative signals exhibited, the chimpanzees only produced one gesture, whereas the macaques produced a gesture, vocalisation and facial expressions (N = 2). In the human dyads, the infants produced a communicative signal in 15/33 cases (N facial expressions = 9, gestures = 4, vocalisations = 6) whereas the mothers communicated in 32/33 cases (N facial expressions = 24, gestures = 17, vocalisations = 27). As these cases are the first known documentation of non-humans displaying this behaviour, I briefly discuss an instance demonstrated in the chimpanzee and macaque groups.

The chimpanzee dyad that demonstrated triadic attention with communication from one partner comprised of a mother, OM, and her 26-month old male infant, OMG. In this instance, both individuals were resting on the ground in the 10s prior to laser presentation. Once the laser was presented, the dyad engaged in mutual face direction after 84s, but it was uncertain whether one of them had communicated. Forty-two seconds later, OMG and OM engaged in a second mutual face direction event. At this point OMG had been engaged with the stimulus for 127s, and OM for 111s. During the 10s prior to mutual face direction, both individuals were looking to the stimulus, and OM was also audibly engaged by hitting the stimulus repeatedly and then smelling her hand after each ‘strike’ of the laser. In the 3s prior to mutual face direction, OM stopped audible engagement and both individuals displayed only brief looks to the laser (see Figure 16A). Both individuals then briefly looked ‘elsewhere’ (but in different directions), during which time OMG started to gesture (scratches; Figure16B) before engaging in mutual face direction (Figure 16C), with the gesture bout continuing over the mutual face direction period.

One macaque dyad that also demonstrated triadic attention with communication comprised of a mother, DP, and her 7-month old female infant, DP5B. Here both individuals were foraging on the ground in the 10s prior to laser presentation. DP5B started to engage with the laser 76s prior to mutual face direction, whilst DP was engaged with the laser for only 1.5s beforehand. In the 10s prior to mutual face direction, both individuals were foraging, and the laser was not present initially. In the 3s prior, the laser was turned on and both individuals paused from foraging to watch the stimulus (see Figure 17A). DP started a vocalisation bout in this time. DP5B, who was approximately 0.5 metres in front of her mother at the time, then turned around which resulted in brief mutual face contact (0.5s; Figure 17B) during which DP was still vocalising. DP5B then jumped onto her mother before DP moved away from the stimulus.

Figure 16. Still images from the triadic attention and communication instance between a chimpanzee mother-infant dyad, OM and OMG.



Note: The red circle highlights the position of the laser in each frame. (A) illustrates both dyads looking towards the laser stimulus; (B) captures the beginning of OMG producing a scratching gesture, before (C) which shows the mutual face direction instance. (D) then shows the second scratching gesture produced by OMG immediately after the mutual face direction period.

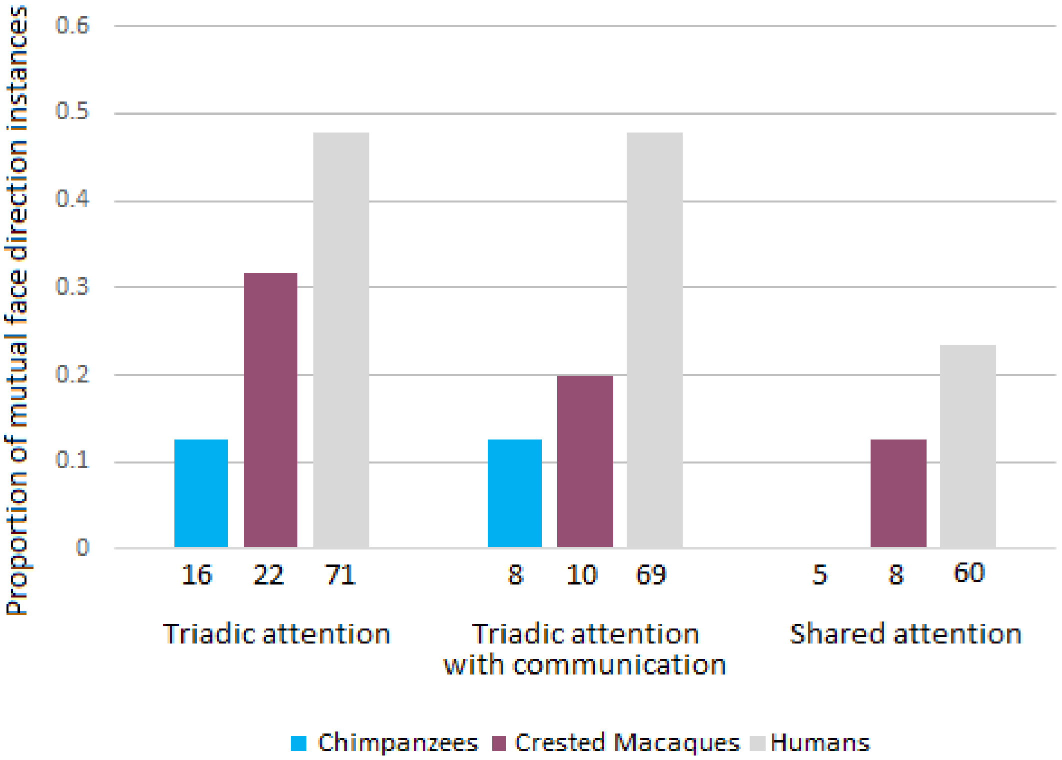
Figure 17. Still images from the triadic attention with communication instance between a crested macaque mother-infant dyad, DP and DP5B.

Note: The red circle highlights the position of the laser in each frame whilst the blue box indicates the dyad. (A) shows both individual's attending to the laser stimulus, which was promptly followed by mutual face direction event depicted in (B).

Model 3: Shared attention events

For the 73 mutual face direction instances where triadic attention and the communication of both individuals was available, I found that both individuals communicated during mutual face direction in 15 instances (N: chimpanzees = 0/5, macaques = 1/8, humans = 14/60). Due to the limited variance of the response variable in this model, a GLMM model was untenable and therefore not completed. Figure 15 shows the likelihood that dyads of each species demonstrated shared attention events. For the types of communicative signals exhibited, both macaque individuals in the dyad produced a facial expression. In the human dyads, the infants produced facial expressions in 9 cases, gestured in 2, and vocalised in 6 cases. The mothers produced facial expressions in 10 cases, gestured in 8, and vocalised in 13 cases.

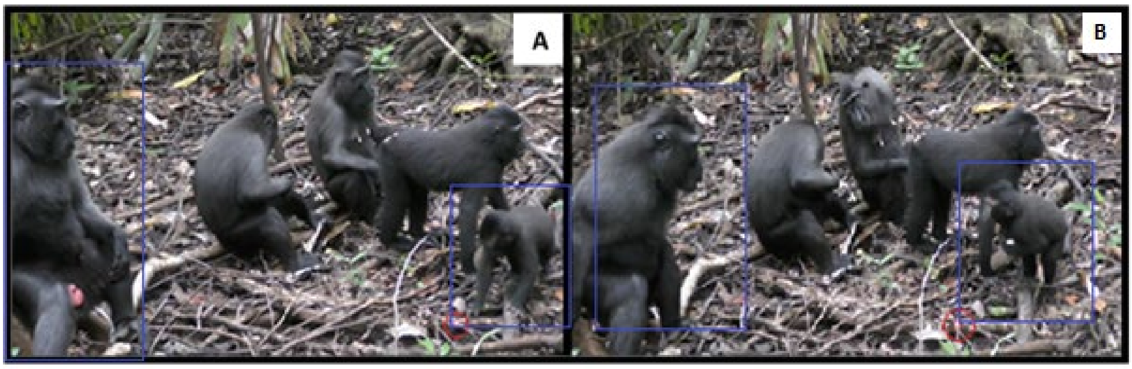
Figure 15. For the laser experiment: descriptive analysis revealing the proportion of mutual face direction instances that demonstrated each level of joint attention events in chimpanzees, crested macaques and humans.



Note: Numbers below bars indicate the N available cases that were assessed for each species on each level of joint attention.

Here, the single macaque case took place between a 6-month old male infant, JA1B, and an unrelated adult male, FM. Initially JA1B was foraging near his mother prior to laser exposure, and FM was not in view. JA1B was engaged with the laser alone for 46s, after which the laser was not presented for 170s due to equipment failure and the focal individual travelling. When the laser next appeared, JA1B had moved toward FM, and FM immediately engaged by watching. Prior to the mutual face direction period, JA1B had been engaged for a total of 146s, and FM was engaged for 100s beforehand. In the 10s prior to the event, JA1B was quietly engaged with the stimulus by trying to touch it with an unknown juvenile. FM was watching their interaction with the laser before starting to lipsmack (facial expression), but appeared to be looking at an individual off camera. In the 3s prior, JA1B was interacting with the laser alone approximately 1.5 metres in front of FM, and FM was watching the laser before starting to lipsmack again (Figure 18A). FM then leaned toward JA1B whilst lipsmacking and the infant responded by looking to FM's face (resulting in mutual face direction; figure 18B) and lipsmacking. JA1B walked towards FM (within 1 metre) and both occasionally looked toward or interacted with the laser.

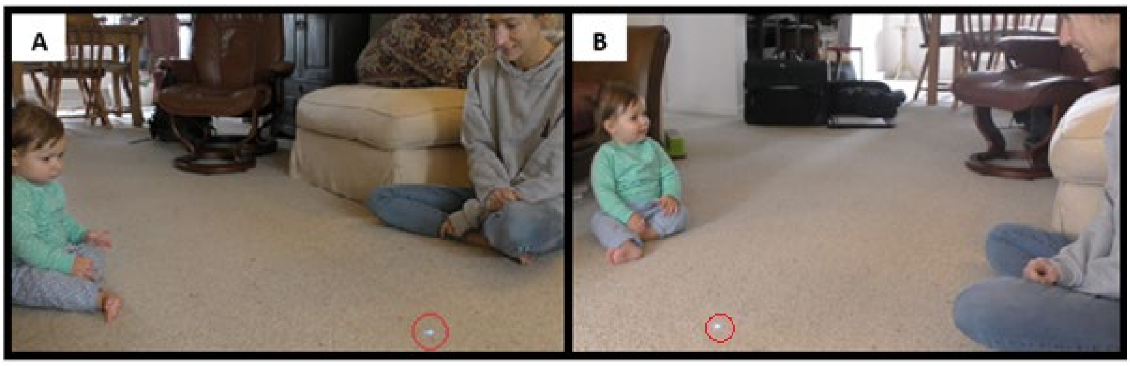
Figure 18. Still images from the joint attention event between a crested macaque adult male, FM (left), and unrelated male infant, JA1B (right).



Note: The red circle highlights the position of the laser in each frame whilst the blue boxes indicate each member of the dyad. (A) shows both macaques facing the laser stimulus, which was followed by a mutual face direction event shown in (B).

For comparison, I also present two examples of shared attention events from my human group. An example from the UK group was between infant UK05 and their mother. Both individuals had been engaged with the stimulus for 39s prior to the event, and this was their second instance of mutual face direction. In the 30s prior to the event, the mother pointed to the stimulus a number of times and was asking the infant “what is that?” and “where’s it coming from?”. In the 3s before the event, the mother asked the infant “can you catch it?” while they both watched the laser (Figure19A). The mother then looked to the infant’s face while smiling, and the infant looked to her and also smiled whilst engaging in mutual face direction (Figure 19B). The mother then looked almost immediately back to the laser and again asks “can you catch it?” and the infant starts to move towards the laser.

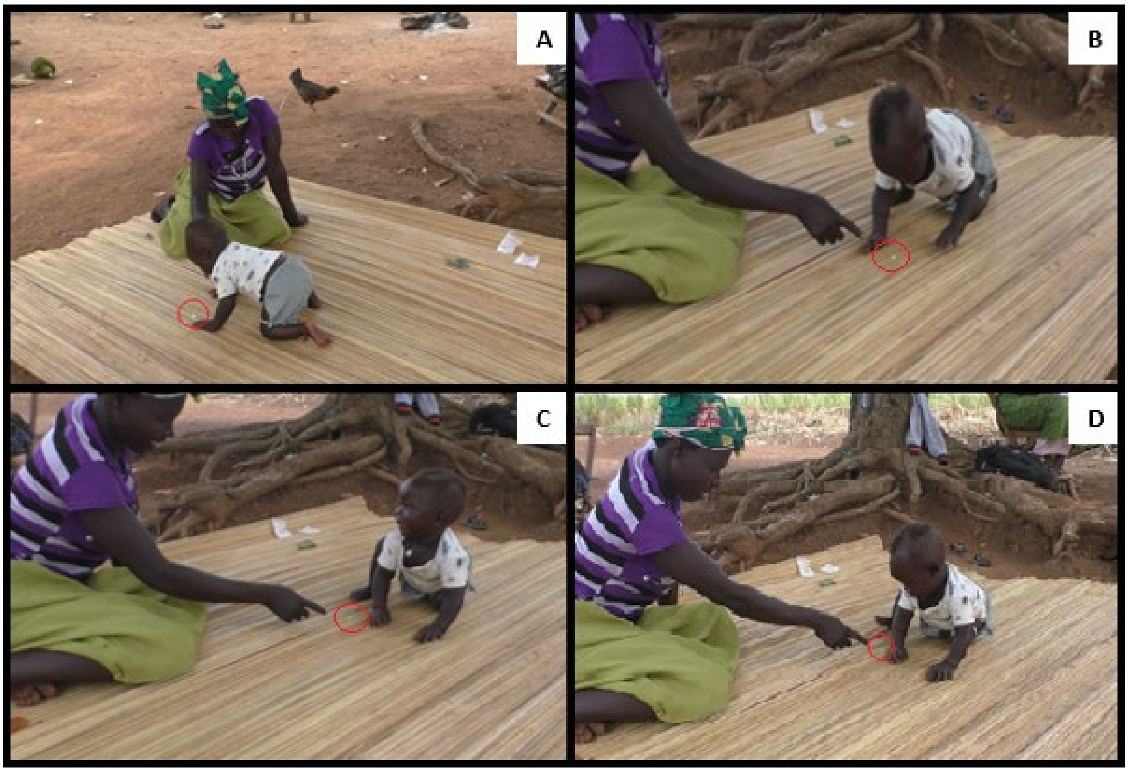
Figure 19. Still images from a joint attention event between an 11 month old infant, UK05 and their mother.



Note: The red circle highlights the position of the laser in each frame. (A) shows both individuals looking towards the laser stimuli, followed by (B) where the individuals are engaged in mutual face direction.

In an example from the Ugandan group, infant UG55 and their mother had been engaged with the stimulus together for approximately 45s. Prior to the shared attention event, the mother and infant had not engaged in any other mutual face direction instances. In the 30s prior to this event, the mother repeatedly pointed to the stimulus whilst the infant was trying to touch the laser; crawling towards the laser and following its movement on the mat. In the 3s prior, the infant had moved within 1m of their mother, and was still trying to touch the stimulus as she pointed (Figure 20AB). The infant then looked towards the mother's face, and this resulted in mutual face direction during which both the infant and mother were smiling (Figure 20C). The mother continued to point during this time, and the infant then looked back to the stimulus to resume his close manual engagement (Figure 20D)

Figure 20. Still images from a joint attention event between an 11 month old infant, UG55 and their mother.



Note: The red circle highlights the position of the laser in each frame. (A) shows both members of the dyad facing the laser stimulus; In (B) the mother produces a pointing gesture, which is followed by a mutual face direction event in(C). (D) shows the infant re-attending to the stimulus while the mother continued to point.

In summary, I identified (i) triadic attention events, (ii) triadic attention with communication events, and (iii) shared attention events in non-human species. Once both individuals had engaged in mutual face direction, triadic attention events were relatively rare in chimpanzees (0.13) but not significantly different from the proportion of mutual face direction events that became triadic attention events in macaques (0.32).

A significantly higher proportion of mutual face direction events became triadic attention events in humans (0.48) compared to the chimpanzees, but not the macaques. These patterns became more stark as I looked at triadic attention with communication from one and two partners, with shared attention events (communication from both partners) only being identified in humans and a single macaque dyad. While triadic attention with communication was rarely witnessed, or shared attention in the non-human groups (or not at all for chimpanzees concerning the latter), these results indicate that even with a relatively small sample size a non-human species is capable of demonstrating this capacity.

Species differences in independent joint attention behaviours

I then wanted to investigate what might be driving these clear species differences; particularly why humans are more likely to engage in joint attention events than non-humans, and why chimpanzees appear to not show evidence of shared attention events as defined with the most stringent criterion. The following section explores behaviours in the 50 second control intervals to shed light on why these differences may have arisen, with 44 intervals examined in total (chimpanzees = 15, crested macaques = 6, humans = 23).

Laser exposure

I first wanted to ensure that each species received equal exposure to the stimulus, and therefore had equal opportunity to show behaviours in response to the laser during these control intervals. No significant differences were found in the duration that the stimulus was present between species (H(2)=3.934, *p* = .140) indicating that each group received equal exposure to the stimulus during the control intervals (Table 9).

Table 9. Descriptive statistics detailing the median and interquartile ranges of the duration of laser exposure for each species.

	Chimpanzees		**Crested macaques**		**Humans**	
Measure	*Mdn*	*IQR*	*Mdn*	*IQR*	*Mdn*	*IQR*
Laser Exposure	40.00	6.56	32.90	20.73	43.38	20.28

Attention to conspecifics

Here I examined whether humans engaged in more joint attention events because they are looking at the faces of other individuals more often than chimpanzees or macaques, thus enabling more opportunities for mutual face direction to occur. First, I summed the number and duration of looks to ‘partner’ and ‘other’ in all species from both focal A and B in order to gauge differences between attention to conspecific faces. As experimenters are also conspecifics to the human group, looks to the experimenters were also considered for this group only. As the number of individuals in proximity to the focal dyad was not consistent across individuals or species, creating variable opportunities for attending to conspecific faces, I also explored how often the focal animals spent looking specifically at their partner's face.

(i) Number of looks to conspecifics

I found significant differences between species in the number of looks towards the faces of conspecifics (H(2)=14.86, *p*=.001; Table 10). Mann Whitney U tests revealed that chimpanzees and macaques looked at the faces of conspecifics a comparable amount (U=58.50, z=1.06, *p*=.302). Whereas humans looked at the faces of other individuals significantly more than both chimpanzees (U=288.00, z=3.46, *p*<.001) and macaques (U=115.50, z=2.51, *p*=.009).

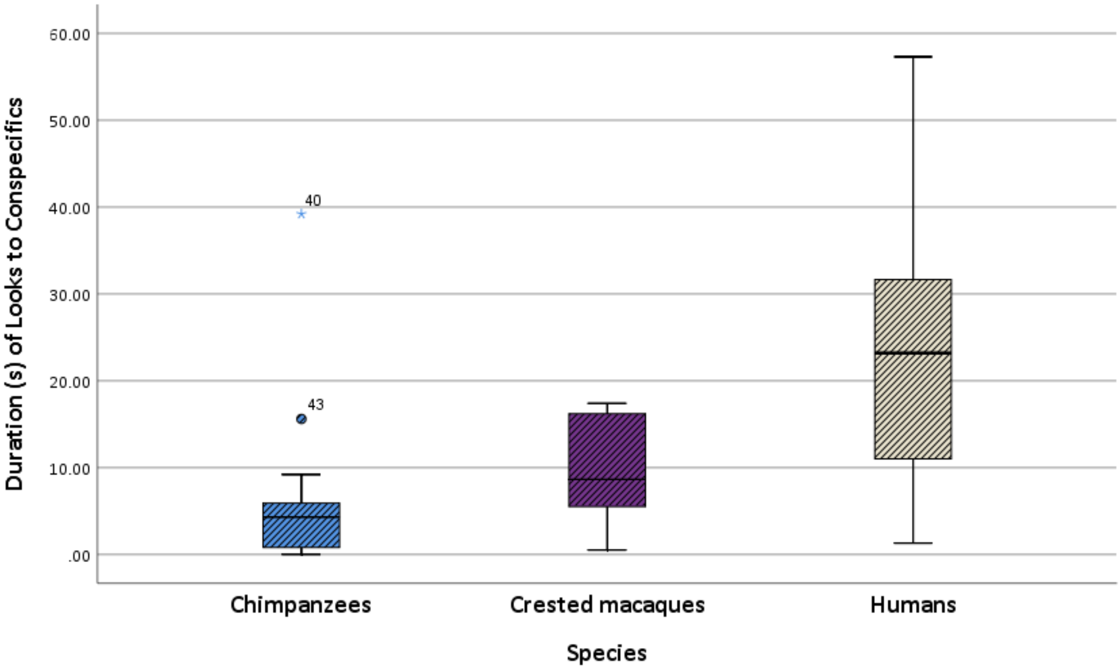
Table 10. Descriptive statistics detailing the median and interquartile ranges for the number of looks towards conspecifics and partners for each species.

	Chimpanzees		**Crested macaques**		**Humans**	
Measure	*Mdn*	*IQR*	*Mdn*	*IQR*	*Mdn*	*IQR*
Looks to conspecifics	2.00	5.00	4.00	3.00	8.00	7.00
Looks to partner	1.00	5.00	2.00	2.25	7.00	4.00

(ii) Duration of looks to conspecifics

I also found significant differences between species in the duration that individuals spent looking at the faces of conspecifics (H(2)=13.36, *p*=.001; Figure 21). Post hoc comparisons revealed that chimpanzees and macaques spent a comparable amount of time looking at conspecific faces (U=64.00, z=1.49, *p*=.154), but humans spent longer looking at conspecific faces than chimpanzees (U=283.50, z=3.32, *p*<.001). However, the duration that humans and macaques looked at the faces of conspecifics did not differ significantly with a bonferroni adjusted alpha level (U=109.50, z=2.18, *p*=.026).

Figure 21. Box plots detailing the duration (seconds) that dyads spent looking towards conspecifics in chimpanzees, crested macaques and humans.



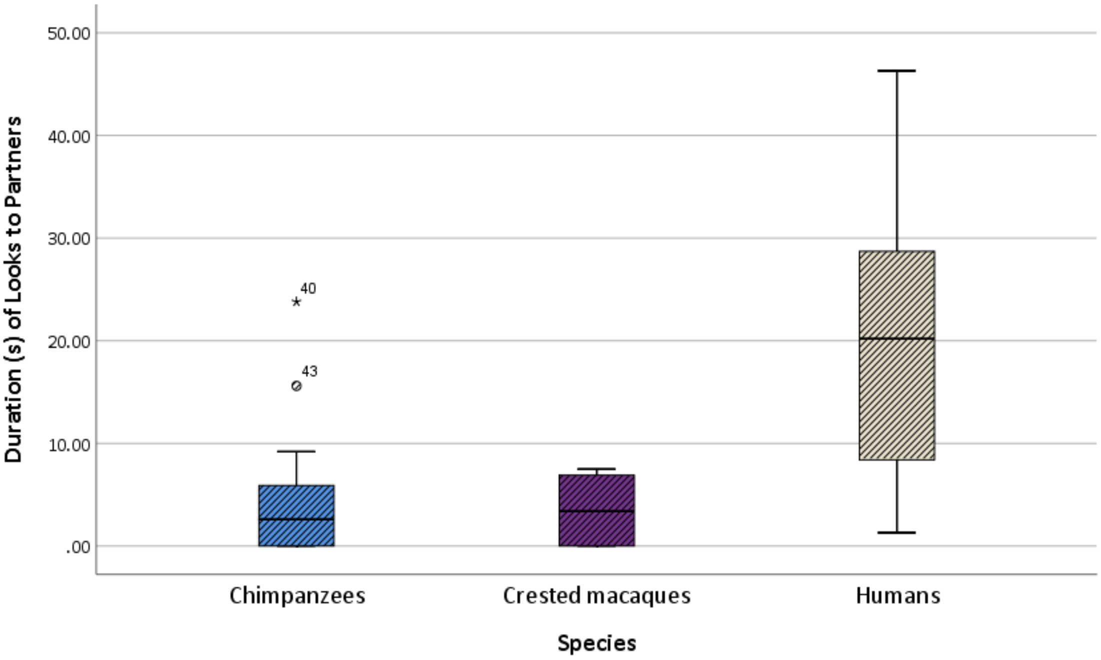
(iii) Number of looks to partner

I found significant differences between species in the number of looks focal individuals made towards the faces of their partner (H(2)=17.16, *p*<.001), which is revealed descriptively in Table 10. Mann Whitney U tests revealed that chimpanzees and macaques looked at their partner's face a comparable amount (U=40.50, z=-0.36, *p*=.733). Whereas humans looked at the faces of their partner significantly more than both chimpanzees (U=290.50, z=3.54, *p*<.001) and macaques (U=125.50, z=3.05, *p* =.001).

(iv) Duration of looks to partner

There were also significant differences in the duration that individuals spent looking at their partner (H(2)=17.02, *p*<.001; Figure 22). Post hoc comparisons revealed that chimpanzees and macaques spent a comparable amount of time looking at their partner's face (U=46.00, z=0.08, *p*=1.000), but humans spent longer looking at their partner's face than chimpanzees (U=295.50, z=3.68, *p*<.001) and macaques (U =121.00, z=2.80, *p*=.003).

Figure 22. Box plots detailing the duration (seconds) that dyads spent looking towards their partners in chimpanzees, crested macaques and humans.



Mutual face direction periods

Having determined that humans generally look to conspecifics and partners faces more often than chimpanzees and macaques (with the exception of the duration spent looking at conspecifics for the latter), I then wanted to ascertain whether this heightened attention to social stimuli in humans led to more mutual face direction periods in human dyads than non-humans in the control interval. Unexpectedly, no significant differences were found in the number of mutual face direction periods between species (H(2)=3.09, *p*=.213; Table 11), nor in the duration of these mutual face direction periods between species (H(2) = 1.79, *p* = .409; Table 11).

Table 11. Descriptive statistics detailing the median and interquartile ranges for the number and duration (seconds) of mutual face direction periods between dyads for each species.

	Chimpanzees		**Crested macaques**		**Humans**	
Measure	*Mdn*	*IQR*	*Mdn*	*IQR*	*Mdn*	*IQR*
Number of mutual face direction instances	0.00	0.00	0.00	1.00	0.00	1.00
Duration (s) of mutual face direction instances	0.00	0.00	0.00	1.27	0.00	1.30

Communication

As triadic attention was more common than the other levels of joint attention events in all species, it may be that differences between humans and non-humans occurred due to the communication component of my operational definitions of joint attention events. Here I explore the number of communicative signals and duration of communication that dyads displayed during their control intervals.

(i) Number of Communicative Signals

I found significant differences in the number of communicative signals dyads produced between species (H(2)=32.82, *p*<.001; Table 12). The pairwise comparisons found no significant differences between chimpanzees and macaques (U=41.50, z=-0.33, *p*=.791), but did find that humans produced significantly more communicative signals than chimpanzees (U=343.00, z=5.15, *p*<.001), and macaques (U=138.00, z=3.73, *p*<.001).

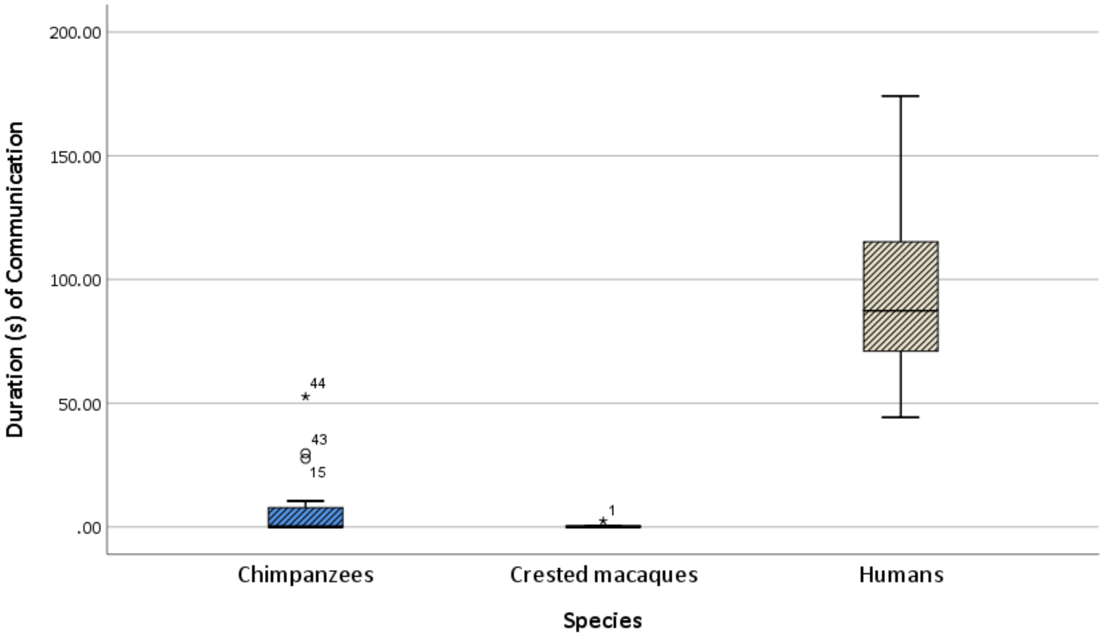
Table 12. Descriptive statistics detailing the median and interquartile ranges for the number of communicative signals that dyads produced for each species.

	Chimpanzees		**Crested macaques**		**Humans**	
Measure	*Mdn*	*IQR*	*Mdn*	*IQR*	*Mdn*	*IQR*
Number of communicative signals	0.00	3.00	0.00	1.25	13.00	6.00

(ii) Duration of Communication

Significant differences were also found for the duration of communication from a dyad between species (H(2)=32.76, *p*<.001; Figure 23). Mann Whitney U tests revealed no significant differences for communication duration between chimpanzees and macaques (U=40.00, z= -0.46, *p*=.733), but did show that humans communicated for significantly longer periods than chimpanzees (U=343.00, z=5.14, *p*<.001) and macaques (U=138.00, z=3.72, *p*<.001).

Figure 23. Box plots detailing the duration (seconds) that dyads spent communicating in chimpanzees, crested macaques and humans.



Stimulus engagement

Finally, I wanted to explore whether the human dyads expressed more interest in the stimulus than the non-human groups, which may have increased their desire to share attention about the laser with a partner. This section therefore included how much the dyad attended to the stimulus (sum of each focal individuals looking time towards the laser, coded by head direction), as well as the dyads number and duration of engagement events and the type of engagement they displayed (using engagement coding).

(i) Attention to stimulus

First, I examined how often each group was looking to the laser stimulus during the control interval. I found no difference in the number of looks dyads made towards the stimulus between species (H(2)=3.09, *p*=.213; Table 13). I did however find significant differences in the duration that dyads were facing the stimulus between species (H(2)=22.58, *p*<.001; Table 13). Mann Whitney U tests revealed no significant differences for the duration of looking to the stimulus between chimpanzees and macaques (U=19.00, z= -2.02, *p*=.045), but did show that humans looked at the stimulus for significantly longer than chimpanzees (U=300.00, z=3.81, *p*<.001) and macaques (U=135.00, z=3.55, *p*<.001).

(ii) Number of Engagement events

Significant differences were then found in the number of engagement events dyads participated in between species (H(2)=8.07, *p*=.018; Table 13). Post hoc comparisons indicated that there were no significant differences between chimpanzees and macaques (U=28.50, z=-1.29, *p*=.205) or between chimpanzees and humans (U=239.00, z=1.99, *p*=.048), but did find that humans had significantly more engagement events than macaques (U=113.50, z=2.40, *p*=.014).

Table 13. Descriptive statistics detailing the median and interquartile ranges for the number and duration (s) of looks to the stimulus a dyad made, as well as the number of engagement events dyads engaged in for each species.

	Chimpanzees		**Crested macaques**		**Humans**	
Measure	*Mdn*	*IQR*	*Mdn*	*IQR*	*Mdn*	*IQR*
Number of looks to stimulus	11.00	5.00	6.50	9.75	11.00	6.00
Duration (s) of looks to stimulus	36.70	26.60	23.60	26.30	70.50	23.70
Number of engagement events with the stimulus	10.00	5.00	7.00	7.50	13.00	7.00

(iii) Duration of Engagement

The duration of dyad engagement with the stimulus also significantly differed between species (H(2)=23.42, *p*<.001; Figure 24). Post hoc tests revealed no significant differences for engagement duration between chimpanzees and macaques (U=20.00, z=-1.95, *p*=.055), but did show that humans engaged for significantly longer with the laser than both chimpanzees (U=305.00, z=3.96, *p*<.001) and macaques (U=135.00, z=3.55, *p*<.001).

(iv) Type of Engagement

I then wanted to examine how each group engaged with the stimulus by examining the behaviour modifiers I coded for each engagement type (quiet and audible). Descriptively, Table 14 gives a breakdown of the N engagement types exhibited from dyads during their control interval. Humans show the most audible engagement and displayed the most engagement types, although notably this is mostly due to the inclusion of pointing which non-human primates very rarely demonstrate in the wild. Given this, inferential statistical comparisons were not appropriate here.

Figure 24. Box plots detailing the duration (seconds) that dyads spent engaged with the stimulus in chimpanzees, crested macaques and humans.

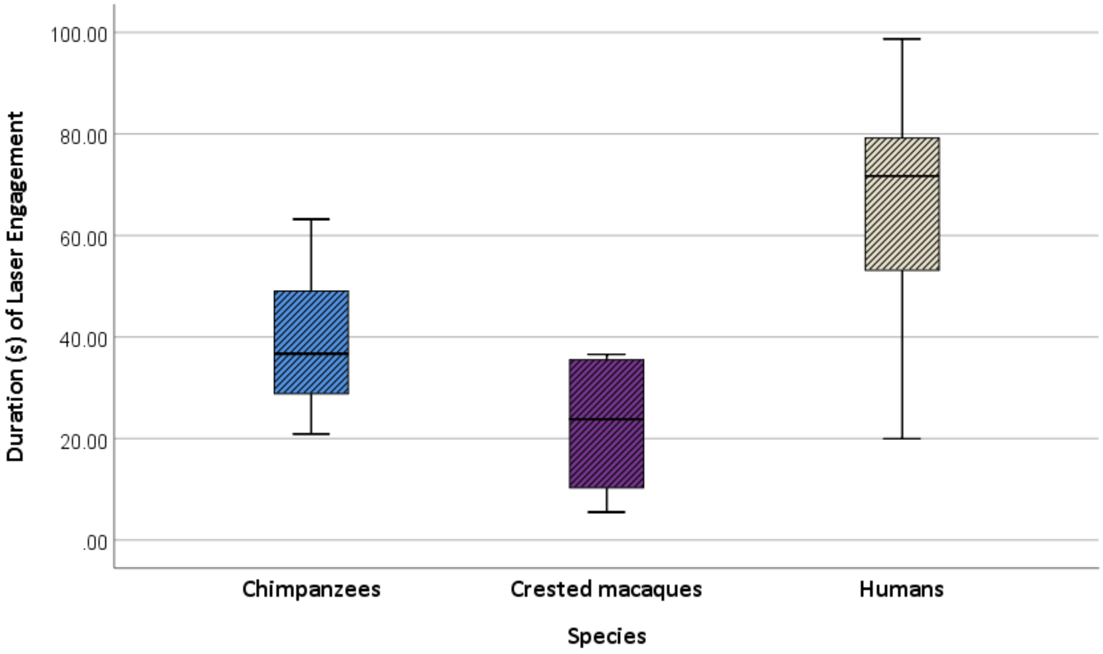


Table 14. The total number of individuals that displayed each engagement type during the 50s control period (engagement types that did not occur during this time are not included).

	Chimpanzees		**Macaques**		**Humans**	
	Focal A	Focal B	Focal A	Focal B	Focal A	Focal B
Quiet engagement						
Watching	15	15	6	6	23	23
Close manual engagement	4	2	3	0	15	10
Inspecting	0	0	3	0	1	0
Pointing (with index finger)	0	0	0	0	5	19
Pointing (with whole hand)	0	0	0	0	3	0
Other quiet engagement	0	0	0	0	2	0
Audible engagement						
Hitting	1	2	0	0	5	4
Other audible engagement	0	0	0	0	1	1

STUDY 1 - DISCUSSION

The current investigation of joint attention events supported my first prediction that human dyads would excel at demonstrating each level of joint attention, but more strikingly, for the first time I have shown that a non-human primate can (albeit rarely) demonstrate each level of joint attention, including shared attention events. When mutual face direction occurred, human dyads were significantly more likely than chimpanzees to engage in a triadic attention event, but both chimpanzees and macaques did engage in this level of joint attention. Both of the non-human groups also showed the next level of joint attention, by engaging in triadic attention with communication events. Interestingly, macaques but not chimpanzees were able to show the highest level of joint attention, shared attention events, where both partners communicated during mutual face-direction.

These findings emphasise the value of adopting a directly transferable experimental task to test for joint attention events across species. Previous research on this subject was diverse but incomparable, and ultimately impeded the ability to assess the capacity of different animals to show joint attention events (Graham et al., 2021). In applying the same definitions and operationalisation of joint attention to chimpanzees, crested macaques and humans, I have been able to provide evidence that these events are not uniquely human. Furthermore, by systematically distinguishing between different levels of joint attention events which applied increasingly stringent operational definitions, I have been able to explore to what extent each species met criteria for joint attention engagement. These levels acknowledged that joint attention is not a single process, and creates a scale of jointness that is critical in order to clearly understand which socio-cognitive aspects are present or absent in populations (Siposova & Carpenter, 2019).

When exploring what may be driving the species differences identified in the likelihood of engaging in a joint attention event, it was found that human dyads showed higher frequencies or longer durations of most of the component behaviours than chimpanzees or macaques. This supported my second hypothesis. In terms of component behaviours required to meet my operational definitions of joint attention events, individuals needed to look at the laser, look at the face of their partner and to produce communicative signals. While I found no significant differences in the number of looks each species made towards the stimulus, it was found that humans attended to the stimulus for significantly longer than both of the non-human groups.

In terms of visual attention to conspecific faces, humans looked to the faces of conspecifics more often than chimpanzees and macaques, and for longer than chimpanzees, but surprisingly not macaques. However, when narrowed down to looks towards a single partner, human dyads exhibited both more instances and longer durations of looking than both non-human species. It may be that the elevated duration of looking to conspecifics in macaques reflects their social environment where multiple individuals are often proximate most of the time. The increase in social partners may thus have led to more opportunities to look to their faces, and therefore explains why this effect disappeared when I limited the tests to attention towards a single partner.

After identifying species differences in the amount and duration that each group attended to conspecific faces, it was surprising that no overall differences in the number or duration of mutual face direction events was found between species during the control intervals. The number of mutual face direction events in the first 50 seconds of joint laser engagement was low in all groups. One potential explanation here is that, during the initial stages of an experiment, individuals are independently invested in exploring the stimulus alone before wanting to check the partner's attention or share attention with them. This could then explain the low levels of triadic attention in the non-human primates overall, as chimpanzee average trial length was almost half that of human trials (109s versus 194s respectively), and macaque trial periods were less than half the time of humans (93s).

Finally, as predicted humans showed significantly higher frequencies and longer durations of communicative events than the two non-human groups. Future research should investigate whether these species differences in the production of communicative signals is specific to this experimental set up, or represent more general patterns of species differences in communicativeness. Overall, I identified important species differences in most of the component behaviours required by my operational definitions of joint attention events, which likely contributed to the elevated proportion of mutual face direction events that became joint attention events in humans compared to the two non-human primate species. It is however, important to consider that other factors may also have contributed to this species difference.

Even if equal opportunity for engagement with the laser across species could have been provided, there may still be species differences in how interesting they found the moving laser stimulus, which may have impacted their motivation to share attention about it. This could indicate that the stimulus was less interesting to the chimpanzees and macaques. I also found that humans engaged for significantly longer than both non-human groups, and that the type of engagement was quite different between human and non-human species. Humans engaged more with the stimulus in a tactile manner (e.g. touching and hitting its location) compared to the non-human groups, who only watched the laser in the majority of cases. Again, it may be that the non-human trials were too short to enable the animals to overcome any neophobic response or wariness of the novel stimulus, or that this type of stimulus was not interesting enough to approach and interact with. Another potential explanation for the species differences in laser engagement is that the non-human groups may have already been exposed to laser stimuli in the past. For the macaques, while further experiments were terminated with the tourism group R1 once it was discovered that tourist guides were showing the macaques lasers, I could not rule out that PB1b, the primary research group, had already been presented laser stimuli by tourism guides prior to the researcher's arrival. I encountered a similar possibility for the chimpanzees, as photogrammetry measures for body size had already taken place at both Kanyawara and in the Ngogo communities. These measures involve using parallel lasers mounted on a camera which are beamed onto the bodies of participants in order to ascertain the distance between targeted body areas. Given these issues, I wanted to test whether non-humans could share attention with a stimulus that was more likely to be genuinely novel, and also one that they could handle and hold and may therefore be more engaged with.

STUDY 2: Testing for joint attention events with novel object stimuli

One of the fundamental reasons that the non-human primate groups may have shown less joint attention to the laser stimulus compared to humans is that they spent significantly less time engaging with it compared to humans; potentially showing a comparative lack of interest in it. This could have been because they were previously exposed to a laser (so it was less novel for these groups), they were more neophobic of it or because they were unable to pick up and handle the object. A second experiment was therefore conducted with new stimuli in the non-human primate groups. As the human group in study 1 did exhibit all levels of joint attention events in response to the laser they were not examined any further here.

In this second study, the experiment conducted involved exposing the dyad to a novel physical object which they could interact with both visually and in a tactile manner. Previous research which exposed wild baboons and geladas to novel objects found that both species showed some interest in the stimuli, with 30% of baboon participants physically handling the objects, but also that younger individuals in both species showed more exploration than the adult individuals (Bergman & Kitchen, 2008). In captive chimpanzees, infants have been found to demonstrate social referencing (checking looks to their caregiver) when encountering novel objects (Russell et al., 1997), and in the wild infant chimpanzees will preferentially explore items manipulated by their mothers (Lamon, Neumann, & Zuberbühler, 2018). With this in mind, small family groups were the primary targets that researchers aimed to expose to the novel objects, or younger individuals, in the hopes of increasing their likelihood to engage with the stimulus. It was also hoped that the targeting of mother-offspring pairs would promote the opportunity for cooperation, with these dyads having high levels of tolerance which may further enable joint attention to occur.

For this experiment I again examined both species demonstration of each level of joint attention: (1) triadic attention events, (2) triadic attention with communication events, and (3) shared attention events. Since the macaques showed one instance of a shared attention event in study 1, I predicted that a more tactile stimulus would result in more cases of this behaviour in this species. For the chimpanzees, I expected to again see them demonstrate triadic attention, but could not predict whether they would exhibit shared attention events from the outcomes of study 1.

STUDY 2 - METHODS

Study sites and subjects

Data were collected from the same groups of chimpanzees and Sulawesi crested macaques as study 1, with an additional macaque group, R2, also contributing 1 trial. Group R2 was a mixed research and tourism group that ranged almost entirely in secondary growth forest. This group regularly travelled through local villages and tourism areas. As with study 1, if the identities of macaque individuals could not be confirmed and they left the experimental area, then any unknown individuals of the same age class later joining were treated as separate individuals and assigned unique ID codes. Researchers aimed to present the stimulus to as many individuals as possible in small groups (preferably dyads or family groups), so multiple exposures were not the priority. However, some individuals were exposed to objects across multiple experiments. The number of trials individuals participated in ranged from 1-2 in chimpanzees, and the number of identifiable individuals participating in macaques ranged from 1-4. However, for the macaques each experiment featured many unidentified participants who could have participated in up to 12 separate trials.

A total of 8 experiments were conducted with the chimpanzees, and 10 experiments with the macaques. A further 3 trials were filmed when the macaques encountered a foreign object naturally. Table 15 summarizes the objects presented to each species and indicates the number of individuals that engaged per trial (individuals that approached within 5m and positively interacted with the object over the entire trial period). A full breakdown of participating individuals per trial is given in Appendix 8.

Table 15. A summary of the objects presented in each trial, with the range of engaged individuals per object type (individuals that approached within 5m and positively interacted with the object).

Species	Trial type	Novel object	Number of trials where object was presented	Range of participants engaged per trial
Chimpanzees	Researcher led	Mirror ball	6	2-8
		Wooden snake	2	4
Macaques	Researcher led	Mirror ball	3	8-10
		Wooden snake	4	10-11
		Orange hippo	1	3
		Orange spoon	1	12
		Pink octopus	1	10
	Naturally found	Orange vest	2	2-10
		Green bucket	1	10

Ethical note

This study complied with the ASAB guidelines for the use of animals in research, and ethical approval was granted by the Animal Welfare and Ethical Review Body (Dept of Biology, University of York). To work with the chimpanzees, permission was granted by the Ugandan Wildlife Authority and the Ugandan National Council for Science and Technology. To work with the crested macaques at Tangkoko permission was obtained from the Indonesian State Ministry of Research and Technology (RISTEK), the Directorate General of Forest Protection and Nature Conservation (PHKA), and the Department for the Conservation of Natural Resources (BKSDA), North Sulawesi. All objects placed by experimenters were selected to be safe in the event that any participants damaged or swallowed parts of the stimuli. All objects went through strict sanitisation procedures prior to and following presentation, and researchers wore surgical masks and gloves when conducting these experiments to avoid disease transmission.

Equipment

The task involved presenting several novel objects to both species in order to elicit uncertainty. These included a lightweight reflective mirror ball (stainless steel, 9cm diameter) and a jointed wooden snake (50cm length). In the macaques, other objects presented included an orange hippo toy (approximate dimensions = 15 x 7 x 7cm), an orange spoon (silicone; approximate dimensions = 26 x 6 x 3cm) and a pink octopus toy designed for pets (corduroy, dimensions = 12.7 x 10.16 x 5.08cm). In addition, the macaques naturally came across an orange vest (a standard high visibility jacket) and a green plastic bucket (approximate dimensions = 16 x 19 x 11cm) in their territories. Researchers also used black cotton thread and a small rucksack which had an entry created into its main compartment from the bottom of the bag. The task was filmed using two Panasonic HC-VX980 camcorders with a Sennheiser MKE 400 microphone attached. Videos were later coded using Noldus Observer XT 14 event logging software (http://www.noldus.com/animal-behavior-research).

Procedure

In 4 chimpanzee trials and 5 macaque trials experimenters attempted to hide and reveal the novel objects to unaware participants. This involved researchers collecting leaves into the rucksack from the area of the intended experimental location, and then placing the rucksack 5-7 metres from the dyad on the ground. Already inside the rucksack was the novel object, which had medical tape attaching a small paper loop to it that the thread was tied to, designed so that the paper would tear as soon as a pulling force was applied to the thread. Facing away from participants the lead researcher then used the opening at the bottom of the bag to place the object, followed by the leaves to cover the object onto the ground. Retrieving the rucksack, they then walked slowly away from the participants whilst discreetly unravelling the thread until they were positioned another 5-7m away from the now hidden object. The assistant researcher observed the focal individuals during this time and warned the lead researcher if they thought individuals were watching or if the object had been spotted prematurely. Once both cameras were then positioned onto the target focal individuals, the lead experimenter gently tugged on the object to reveal it from under the leaf pile. The aim was to keep the thread attached until focal individuals approached the object, when the lead then gave a sharp pull to snap and retrieve the thread line. Although this method was effective for ensuring the subjects could not associate the objects with the experimenters present, it was extremely difficult to conduct in practice as focal individuals rarely remained in place during set up. In order to overcome this problem in 4 chimpanzee trials and 5 macaque trials experimenters simply placed the object onto the ground in a spot they believed the focal individuals were travelling toward, or that they may turn towards if resting, and then retreated 5-7m to film any interactions that took place. For this method it was also noted whether any participants witnessed the placement of the object by the experimenters. With both methods the novel objects were preferentially presented to small groups at the edge of the main party or troop opportunistically.

In the macaque populations it was also discovered that they often encountered foreign objects in their territory from human littering. The researchers therefore also documented these interactions as they mimicked the conditions that were being experimentally induced.

In all trials, including naturalistic encounters with foreign objects in the macaques, researchers filmed the entire witnessed interaction. Termination of trials occurred when individuals lost interest in the stimulus, after which objects were then retrieved by researchers. During filming researchers attempted to identify all interactants with the stimulus, and commentated any approaches or actions with the objects. The identity of any individuals that produced vocalisations were also commentated when possible.

Video coding

Videos were coded with Noldus Observer XT software in order to extract continuous details about behaviours from each interactant with the stimulus (see Table 16). I only coded periods of active engagement with the object (by at least one individual), and only positive interactions between group members and the object were considered for coding (i.e. any aggressive interactions over the stimulus were not coded, as this is not a context in which joint attention is likely to occur). I also did not code any periods where individuals were travelling whilst holding the object. Using the 'Subjects' function in Observer, I coded instances of mutual face direction (with any conspecifics), communication (facial expressions, vocalisations and gestures) and object engagement for any individual that actively engaged with the stimulus.

Table 16. Coding scheme detailing operational definitions for when the object was revealed and behaviours of interest produced by subjects during novel object experiments.
Note: Categories that were coded independently for each subject (any individual who engaged with the novel object) are distinguished by an asterisk (*).

Behaviour category	**Behaviour**	**Description**
Object revealed	Object revealed	This was selected when the researcher had placed the object in view of the focal individuals, or when the object was revealed in trials where the researchers had hidden the object (regardless of whether participants noticed it or not). This behaviour included the following modifiers concerning whether participants had witnessed the placement of the object or not: (1) reveal seen (when at least 1 individual saw the researchers place or reveal the object); (2) reveal not seen (no individuals noticed the researcher place or reveal the object); (3) unclear if reveal seen (used when it was uncertain if an individual noticed the experimenter placing or revealing the object, or for when individuals found a naturally occurring foreign object).
Trial period	No trial period	Before any individual had seen the object, or when the final individual had disengaged from the object and left the experimental area.
	Trial period	Coded from when the first individual had clearly seen the object from within 5m, until the final individual left.
Coded periods	Not coded	No individuals were engaged with the object, or were interacting with the object in a negative manner. Also activated if the object was being carried during travelling.
	Coded	When the object was in clear view with at least one individual engaged with it in a positive manner.
Engagement with object*	No object engagement	When the subject had stopped interacting with the object for 10s or more, or when they terminated their interaction with the object by leaving the experimental area or going out of sight.
	Object engagement	The individual showed object-oriented behaviours for a minimum of 3s. Example behaviours that may have indicated this included repetitive looks to the object or any physical engagement (e.g. hitting or swatting the stimulus). In order to be considered as actively

		engaging, individuals were also required to be within 5m of the stimulus.
Mutual face direction*	No mutual face looks	The subject and a partner were not simultaneously looking at each other's faces.
	Mutual face direction	The subject and a partner were simultaneously looking at each other's faces. All instances were coded. This behaviour included the following modifiers concerning whether the participant had looked to the object: (1) in the 3s before mutual face direction started; (2) in the 3s after mutual face direction ended; (3) before and after mutual face direction; (4) no looks to object; (5) unclear if looked to object. Looking to the object was defined as when the individual's face was pointing towards the stimulus, and all instances were accounted for in the 3s prior to mutual face direction onset and 3s after mutual face direction ended.
Communication availability*	Communication availability not coded	Communication availability was only coded in the 3s prior to the onset of mutual face direction, during mutual face direction and the 3s after mutual face direction ended. At all other times the behaviour 'communication availability not coded' was selected.
	All communication unavailable	When the individuals facial expressions, gestures and vocalisations could not be discerned by researchers, either due to visual obstruction, or in the case of vocalisations, due to it being impossible to identify producers of vocalisations.
	Only facial expressions available	When it was possible to identify if a facial expression was being produced. No other communicative modality was available.
	Only gestures available	When it was possible to identify if a gesture was being produced. No other communicative modality was available.
	Only vocalisations available	When it was possible to identify if a vocalisation was being produced. No other communicative modality was available.
	Facial expressions and vocalisations available	When it was possible to identify if any facial expressions and vocalisations were being produced, but the researcher could not identify if any gestures were being produced or not.
	Facial expressions	When it was possible to identify if any facial expressions and gestures were being produced, but

	and gestures available	the researcher could not identify if any vocalisations were being produced or not.
	Vocalisations and gestures available	When it was possible to identify if any vocalisations and gestures were being produced, but the researcher could not identify if any facial expressions were being produced or not.
	All communication available	When the individuals facial expressions, gestures and vocalisations could all be discerned by researchers.
Communication*	Communication not coded	Communication was only coded in the 3s prior to the onset of mutual face direction, during mutual face direction and the 3s after mutual face direction ended. At all other times the behaviour 'communication not coded' was selected.
	No communication	No signals were perceived from the subject.
	Facial expression only	A salient facial expression was produced, but no gestures or vocalisations were perceived (see Appendix 5 for a list of facial expressions included)
	Gestures only	A gesture was produced, but no facial expressions or vocalisations were perceived (see Appendix 6 for a list of gestures included)
	Vocalisations only	A vocalisation was produced, but no facial expressions or gestures were perceived (see study 1, Table 7 for a full description)
	Facial expression and vocalisation produced	When both a facial expression and vocalisation were being produced in the examined interval, with the signals having at least some overlap. No gestures were being produced.
	Facial expression and gesture produced	When both a facial expression and gesture were being produced in the examined interval, with the signals having at least some overlap. No vocalisations were being produced.
	Vocalisation and gesture produced	When both a vocalisation and gesture were being produced in the examined interval, with the signals having at least some overlap. No facial expressions were being produced.
	Facial expression, gesture and vocalisation produced	When a salient facial expression, vocalisation and gesture were being produced in the examined interval, with all the signals having at least some overlap.

Inter-coder reliability

To assess inter-coder reliability each behavioural category was double coded in a subset of videos by CW and AN. Cohen's kappa scores were calculated for all categories detailed above using the Reliability Analysis function in Observer XT.

19% of the entire experimental sample was coded (N videos = 4). For behaviour categories not specific to a subject (object revealed, trial period and coded period) the mean frequency/sequence score obtained was 0.97 and the mean duration/sequence (tolerance window = 1s) score was 1.00. For all other categories that were coded for each interactant, the mean frequency/sequence score obtained was 0.82 and the mean duration/sequence score was 0.97. In addition, NL then checked all positive instances of mutual face direction in order to ensure a conservative approach when claiming the occurrence of joint attention behaviours.

Extraction of measures

Using the Behaviour Analysis tool in Observer XT, I extracted all instances of mutual face direction during 'coded' periods. To then assess whether the species demonstrated each level of joint attention, I extracted the following behaviours from the individuals partaking in the mutual face direction behaviour: whether both of these individuals looked to the stimulus in the 3s prior to the onset of mutual face direction; and whether one or both of these individuals was communicating during the mutual face direction behaviour (where onset may have occurred prior to mutual face direction, but not after).

Statistical analysis

Due to the small number of these experiments completed, analysis via Generalized Linear Mixed Models or other statistical tests were inappropriate. Instead, I report descriptively whether subjects demonstrated each level of joint attention event. As in study 1, each analysis centred on the occurrence of mutual face direction events. In total I identified 28 mutual face direction events from 28 dyads formed from 35 individuals. None of these trials were excluded to examine the occurrence of triadic attention. For triadic attention with communication, 5 mutual face direction events (N = 3 chimpanzee and 2 macaque) were excluded as it was unknown whether at least one individual communicated. Lastly for assessing shared attention events, a further macaque mutual face direction event was excluded as it was unknown if both individuals communicated.

STUDY 2 - RESULTS

Occurrence of mutual face direction

In chimpanzees, 27 individuals were recorded to have engaged in at least one experiment, whereas for the macaques I recorded 112 engaging individuals (see Appendix 8). The total duration (seconds) of coded periods, where at least one individual was engaged, was 4711 for chimpanzees (mean duration=261, SD=324) and 3027 for macaques (mean duration=63, SD=138).

During these coded periods I identified a total of 28 mutual face direction events in all species, specifically 11 instances in chimpanzees and 17 in macaques. For the dyads involved in mutual face direction, in 4 of these cases (3 macaque), an engaged individual partook in mutual face direction with an unengaged partner (who had not yet fulfilled the criteria of 3 seconds of engagement with the laser, but all of these partners remained in the analysis as they had seen the object). Table 17 provides a summary of all mutual face direction cases.

Table 17. For the novel object experiment: descriptions of the number of dyads that engaged in mutual face direction, the amount of mutual face direction displayed from a dyad, and the mean duration of mutual face direction per species.

	N mutual face direction events	**N dyads engaged in mutual face direction**	**Range of mutual face direction instances across dyads**	**Mean duration of mutual face direction (s)**
Chimpanzees	11	8	1-4	1.3
Crested macaques	17	14	1-3	0.9

Triadic attention events

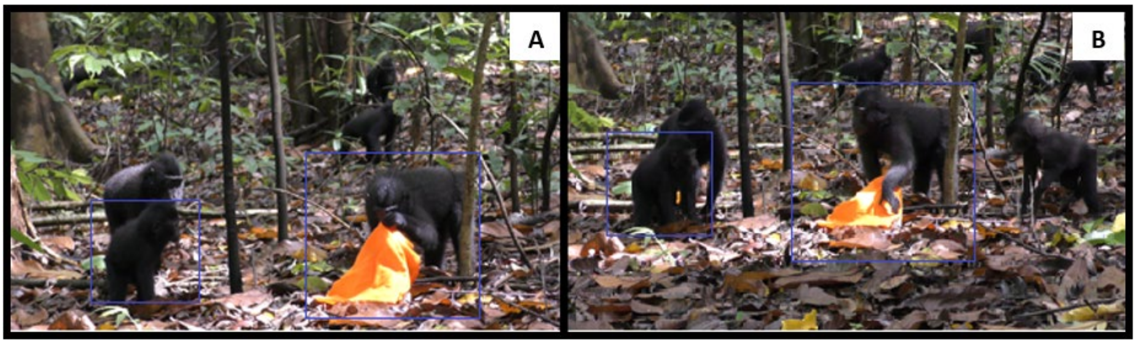
Of the 28 mutual face direction events examined here, in 21 cases both individuals had looked to the object in the 3s prior to display triadic attention (chimpanzees=7/11, macaques=14/17). In comparison to study 1, where triadic attention occurred in only 13% and 32% of chimpanzee and macaque cases, here triadic attention took place in 64% and 82% of mutual face direction cases respectively.

Triadic attention with communication events

For the 21 remaining mutual face direction instances with triadic attention, at least one individual communicated in 9 cases (N: chimpanzees=2/7, macaques=7/14). In terms of the types of communicative signals exhibited, the chimpanzee dyad produced non-tactile gestures and 1 facial expression, whereas the macaques also produced vocalisations in 3 cases and facial expressions in 1 case. As both individuals communicated in each chimpanzee event, this is described in the next section and here we give examples of macaque dyads only.

One instance of triadic attention with communication from one partner in macaques took place between two juveniles, UnkFJuv03 and UnkJuv39. Here the macaques naturally came across a reflective orange vest while travelling. UnkFJuv03 approached the object 30s prior to when the mutual face direction occurred, and was foraging nearby. Several individuals passed the object without engaging, until infant NP5B climbed the small sapling the object was placed in. Ten seconds prior to the mutual face direction instance, as NP5B was moving toward the vest, UnkFJuv03 climbed up behind him and pulled the vest down from the tree. UnkJuv39 approached during this time, and was watching UnkFJuv03 inspecting the object and started to scratch (Figure 25A). The female juvenile then looked up and the two individuals engaged in mutual face direction (Figure 25B) just after which UnkJuv39 ceased gesturing. UnkFJuv03 then continued to look at the object for another 5s before moving on.

Figure 25. Still images from the triadic attention and communication instance between UnkFJuv03 (right) and UnkJuv39 (left).



Note: The blue square highlights the dyad, and the unusual object here is the orange vest being held by UnkFJuv03. (A) shows UnkFJuv03 facing the stimulus while UnkJuv39 is inspecting the object; (B) depicts the dyad engaging in mutual face direction.

Another macaque case occurred in the R1 community between a sub-adult female, AU, and an unidentified juvenile, UnkJuv03. Here the researchers presented the macaques with a mirror ball, and the placement of the object was not seen by any individuals. AU first engaged with the object approximately 300s after it was first revealed, and 40s prior to the mutual face direction instance. UnkJuv03 did not engage until 25s prior to this instance, but almost immediately began to physically manipulate the object whilst looking toward conspecifics (Figure 26A). In the 10s prior to the event, AU approached the object within 1 metre and was examining the mirror ball and UnkJuv03 remained within 0.5 metres of the object and watched AU's engagement with the stimulus. During this time a third individual also approached, but does not interact with the object. In the 3s prior to the event, UnkJuv03 started to scratch as AU continued to watch the object (Figure 26B), and AU then turned to move away when UnkJuv03 re-attended to the object (Figure 26C). UnkJuv03 continued to scratch and turned towards AU who had also looked back towards UnkJuv03 to result in mutual face direction (Figure 26D). Following this, both individuals remained close to the object while the 3rd unidentified individual began to physically interact with the object.

Figure 26. Still images from the triadic attention and communication instance between AU (left) and UnkJuv03 (right).

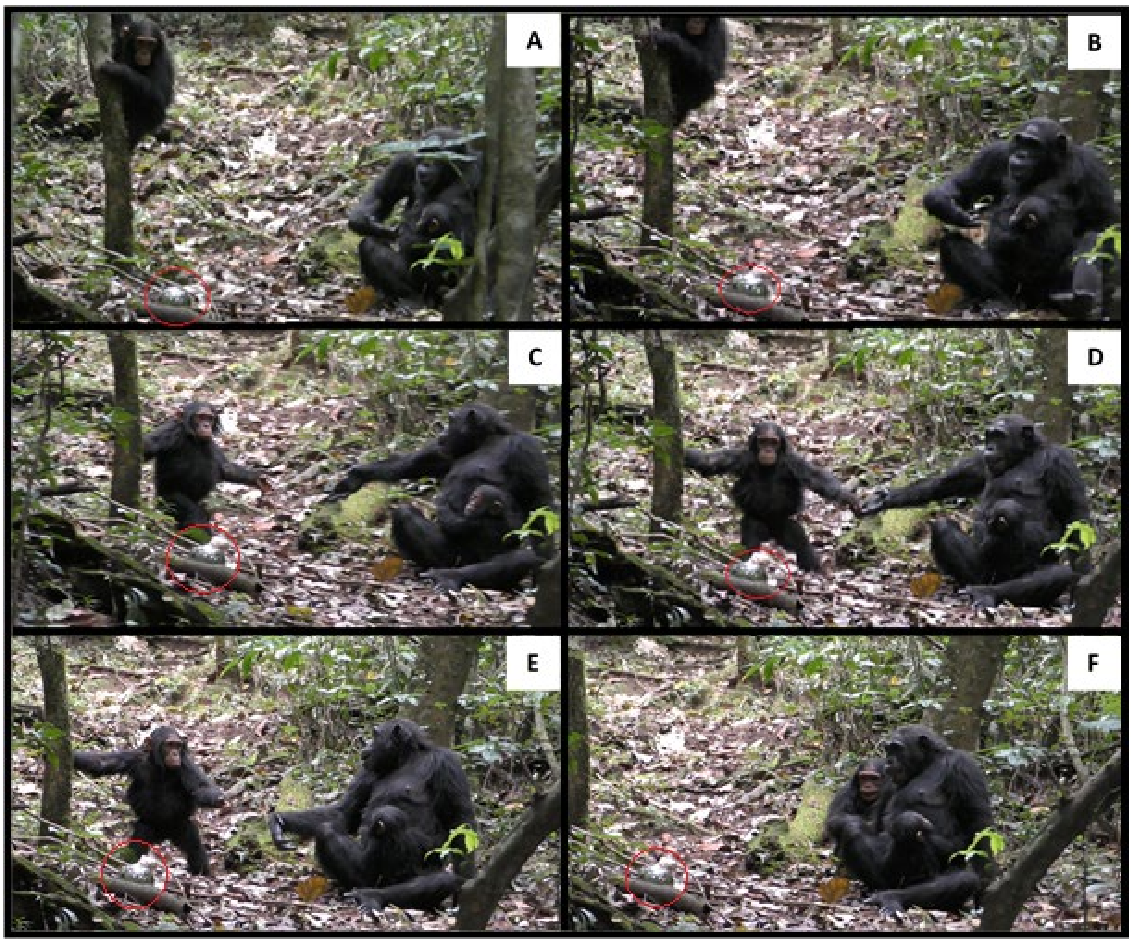
Note: The blue square indicates each member of the dyad, and the unusual object here is the mirror ball. (A) shows UnkJuv03 physically engaging with the object prior to AU's approach. (B) AU then watched the mirror ball before moving away; (C) UnkJuv03 then looked towards the mirror ball; (D) both individuals looked to each other to engage in mutual face direction.

Shared attention events

For the 21 mutual face direction instances with triadic attention, both individuals communicated during mutual face direction in 3 instances (N: chimpanzees=2/7, macaques=1/14). For the types of communicative signals exhibited, both members of the chimpanzee dyad produced non-tactile gestures and one produced a facial expression. Whereas the macaque dyads produced facial expressions and one individual also gestured. All recorded cases will now be described in detail.

The same chimpanzee dyad demonstrated two shared attention events, and only moments apart. The dyad consisted of an adult female, AI, who had her 11-month old male infant clinging to her ventrally at the time. The second member of the dyad was a 4-year old juvenile male, DS, who was unrelated to AI. All 3 individuals were watching the experimenter when a mirror ball was placed 7m away from them, just over 360s prior to the first mutual face direction period. AI got up and began to cautiously move toward the object 120s prior to the event, and sat within 1 metre of the mirror ball while DS remained distant. Thirty seconds before the first event, AI began to swipe towards the stimulus and made tactile contact, and DS began to approach while producing whimpers and a bared teeth facial expression. AI responded by also producing a bared teeth facial expression, and allowed him to mount her for reassurance. In the 10s before mutual face direction AI moved approximately 1 metre from DS, then in the 3s prior to mutual face direction they both looked to the mirror ball (Figure 27AB), before then looking up the trail where it was commentated that DS's mother was located out of frame. They then looked at each other for the first mutual face direction instance at 07:34 (duration 0.5s; Figure 27C).

Figure 27. Still images from the two joint attention events between an adult female chimpanzee, AI (right) and an unrelated male juvenile, DS (left).

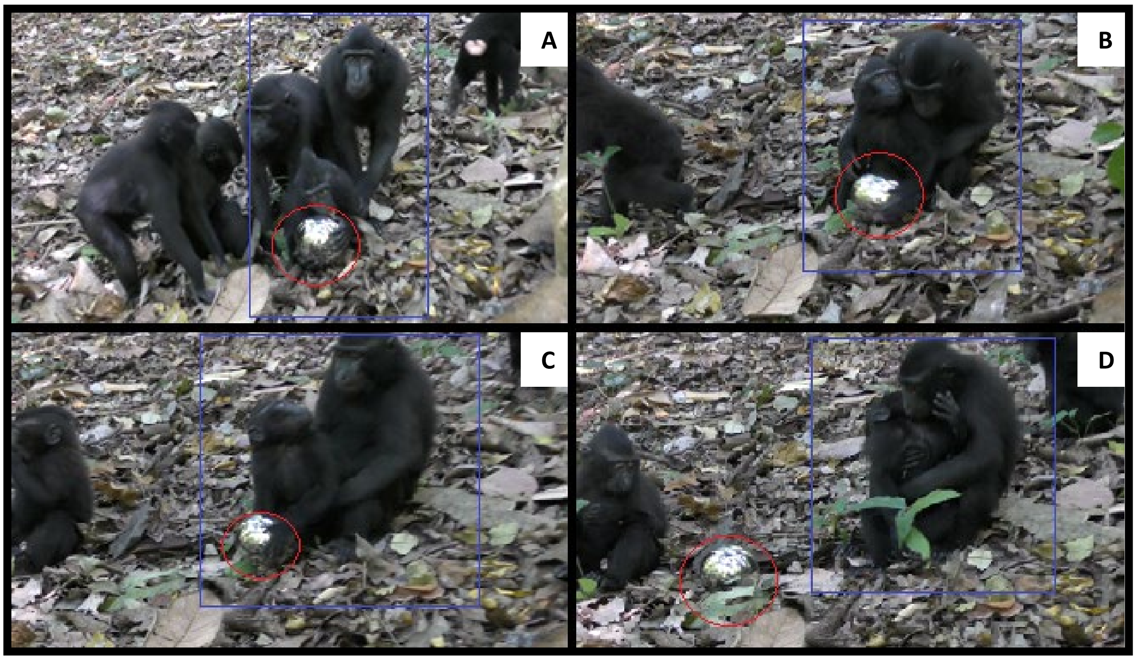


Note: The red circle highlights the position of the mirror ball in each frame. (A) DS facing the mirror ball; (B) AI facing the mirror ball; (C) DS and AI then engaged in mutual face direction as they reached towards each other and AI produced a bared teeth display; (D) Both individuals then turned back to the stimulus; (E) the dyad engaged in a second mutual face direction instance; (F) dyad look back to the stimulus and both produce bared teeth displays.

During this mutual face direction, AI reached her hand towards DS whilst simultaneously producing a bared teeth facial expression, and DS responded by reaching and touching her hand. The individuals alternated between looking to the stimulus and elsewhere (Figure 27D), and briefly dropped their hands (relinquishing tactile contact). DS then moved toward AI with his arm outstretched again, and AI reached back toward him whilst looking at his face which resulted in the second mutual face direction at 07:37 (duration 1.9s; Figure 27E). DS moved to sit in body contact with AI, and both returned their face direction towards the stimulus and produced bared teeth facial expressions (Figure 27F).

The macaque dyad that exhibited a shared attention event took place between an 11-month old male infant KA1B, and an unidentified juvenile UnkJuv33. KA1B was the first individual to engage with the mirror ball object in this trial, and did so approximately 300s prior to the shared attention event. In the 30s prior to the event, KA1B was holding the mirror ball as several other infants and juveniles were also engaged. UnkJuv33 appeared in the frame 10s prior to the event and walked toward KA1B. KA1B vocalised and appeared to attempt to grab and move the object (Figure 28A). The juvenile then put their arms around KA1B whilst observing the mirror ball (Figure 28B). KA1B looked up from the mirror ball toward UnkJuv33's face while lipsmacking, and the juvenile then looked down while lipsmacking to result in mutual face direction (Figure 28C). Both individuals then embraced (Figure 28D) and alternated between looking to the object and elsewhere, before KA1B started to aggress another nearby infant.

Figure 28. Still images from the joint attention event between an infant crested macaque, KA1B, and an unidentified juvenile, UnkJuv33.



Note: The red circle highlights the position of the mirror ball in each frame, and the blue square indicates the dyad being discussed. (A) depicts infant KA1B inspecting the stimulus before (B) UnkJuv33 approached from behind to observe the stimulus; (C) shows the subsequent mutual face direction, during which both individuals produced lipsmacks; (D) shows the dyad embracing before looking back to the mirror ball.

STUDY 2 - DISCUSSION

In line with my predictions I found higher levels of joint attention events by introducing a physical stimulus, and critically identified shared attention events in both crested macaques and, for the first time, in chimpanzees. The implementation of a physical stimulus that allowed for tactile engagement appeared to optimize joint attention events, with a much higher percentage of triadic attention events resulting from mutual face direction events than in study 1.

On examination of the recorded shared attention events, at least one member of the dyad had already been engaged for a number of minutes with the object prior to the event. This can support my prior theory that individuals are independently invested in exploring a novel stimulus alone at first, prior to being motivated to share attention about an object. It’s possible then that in study 1 the trial durations in the non-human groups were simply too short to support shared attention to occur in the chimpanzees. However, it’s also notable that all shared attention events occurred with the mirror ball stimulus despite the testing of several novel object stimuli. This stimulus may have been particularly interesting to the non-human primates as the most dynamic object with constantly changing reflections visible. The initial method (with a thread attachment) allowed for some small movement of the stimuli prior to the line being severed, but sustained movement was not possible and these trials were limited. It is notable that Tomonaga et al (2004) failed to elicit shared attention with an animated stimulus, though their study was limited to only 3 dyads. Thus, implementing a physical object in future that allows for movement or a change in appearance, and that individuals are able to interact with for a prolonged period, may still provide the most optimal conditions for shared attention to occur.

Interestingly for the macaques in both cases of shared attention events from study 1 and study 2 both members of the dyad produced lipsmacks to meet my communication criterion. Lipsmacks are a common multimodal signal that are often produced when approaching other individuals to encourage positive social interactions (Micheletta et al., 2013). It therefore could be that individuals are encouraging positive triadic engagement with the stimulus in these cases. For the chimpanzee dyad, AI and DS, I instead recorded multiple instances of bared teeth displays; a signal which has been suggested to function to reduce uncertainty and promote affiliative behaviour (Parr, Waller, Vick, & Bard, 2007). Although this signal is commonly used to appease aggressors it is frequently produced in affiliative contexts, and has been suggested to facilitate social cohesion by reinforcing friendliness (Waller & Dunbar, 2005). Here both individuals’ behaviour with the mirror ball intuitively appeared uncertain, so perhaps the dyad produced these expressions to encourage reassurance behaviours and physical affinity after experiencing an element of anxiety. This is also evident in the other communicative signals AI and DS produced during their interaction, ‘embrace’ and ‘reach’ gestures, which are both used to promote affiliative physical contact between individuals (Hobaiter & Byrne, 2014).

Despite multiple of the experiments including family groups it is notable that positive instances of shared attention did not occur in mother-infant pairs. Family groups were targeted as prior research suggested this may maximise object interactions (Lamon et al., 2018), and it was theorised that mother-offspring pairs would have a higher tolerance for each other perhaps leading to increased cooperative behaviour. However, even when the stimuli held negative connotations by imitating a snake this still did not elicit shared attention in the family groups. It is unclear what social conditions about the AI and DS trial may have fostered shared attention events, but this could suggest that the surfacing of joint attention may be dependent on the temperament of the targeted individuals, and their propensity to be neophilic or neophobic when encountering unusual objects or events, rather than the social bond between the dyad. However, I was unable to investigate the exact degree of relatedness that exists between each dyad here beyond maternal kinship, and therefore this is a component that future research should further explore.

JOINT ATTENTION GENERAL DISCUSSION

This research has demonstrated that joint attention events, even when identified with relatively strict criteria, are not unique to humans (Tomasello et al., 2005). In line with my predictions I detected quantitative differences in the proportion of mutual face direction episodes that became joint attention events across species, with humans showing elevated likelihoods of engaging in all levels of joint attention events. However, contrary to previous literature I have identified positive evidence for two non-human species displaying each level of joint attention, including shared attention events.

Tomasello et al. (2005) argued that non-human primates do not demonstrate joint attention or ‘shared intentionality’ as they lack the “motivation to share emotions, experience, and activities with other[s]” (p.1). This data contrarily indicates that crested macaques and chimpanzees can be motivated to coordinate their attention with another individual and thus share an experience, but only in rare cases. In order to ascertain why this may be the case, I explored their exhibition of the component behaviours required for joint attention events in study 1. Here it was identified that the non-human groups were both less likely to look at the faces of conspecifics than humans during the first 50 seconds of joint laser engagement, and also less likely to communicate with partners. In humans, individuals with deficits in joint attention abilities, such as those with autism spectrum condition, likewise tend to show a lack of attention to faces and reduced communication skills (Adamson et al., 2019; Riby & Hancock, 2009). Siposova and Carpenter (2019) suggest that these behavioural qualities may indicate difficulties in experiencing another individual’s attitudes or emotions during interactions, which may impede an ability to partake in shared attention. This links back to the initial assertion of Tomasello et al. (2005) which emphasises that a desire to share psychological states with others is required for shared intentionality to emerge. When examining the two recorded cases of shared attention in study 2, both dyads (AI and DS, KA1B and UnkJuv33) involve individuals showing a desire to reassure (or seek reassurance) and signal benign intent to their partner, as displayed by their communicative behaviours including lipsmacks, embraces and arm reaches (Hobaiter & Byrne, 2014; Micheletta et al., 2013). Their behaviours then may signify an acknowledgement of their partner's emotional response during the interaction, and this may be the social condition required for shared attention to arise. In order to explore this further, investigating social conditions (e.g. dominance relationships) that foster I-JA skills to emerge in non-human groups would be beneficial.

The current study marks the first claims for any monkey species engaging in joint attention events, and emphasises the need in future to widen the species that are examined for joint attention abilities. Some joint attention skills have been widely assessed throughout the primate order, such as gaze following abilities (reviewed in Rosati & Hare, 2009) but research on joint attention events has centred on chimpanzees. While chimpanzees are an important animal model for understanding human cognition (Byrne, 2000; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Rosati, 2016; Tomasello, 2014), the current findings suggest that targeting species who are more socially tolerant and communicative may be more fruitful. Bonobos, being equally close as chimpanzees in our evolutionary history, would be a valuable step to explore this possibility. Bonobos are more socially tolerant and cooperative than chimpanzees, and often outperform chimpanzees on social cognition tasks (Gruber & Clay, 2016; Hare, Melis, Woods, Hastings, & Wrangham, 2007; Herrmann, Hare, Call, & Tomasello, 2010). But more research from a variety of monkey species is also needed to determine if the phylogenetic roots of this behaviour in humans are deep in the primate lineage, or if the emergence of this capacity in the crested macaques studied here represents a case of convergent evolution. Monkey species are incredibly diverse in their social structures, and aspects of their social lives can affect their communication systems. For instance dominance style has been shown to predict the vocal output of some primate species (Kavanagh et al., 2021). In order to assess if the greater tolerance and higher levels of communication selected for joint attention in the crested macaques, data from monkey species with similar and dissimilar social structures and communicative systems are needed.

The current findings are particularly remarkable as, in comparison to previous literature, I adopted a strict operational definition for joint attention events. For shared attention I required individuals to engage in mutual face direction, and for both members of the dyad to then communicate during this interval. Surprisingly, I found no species differences in the amount of mutual face direction that occurred during control intervals. The greater number of mutual face direction episodes that were obtained from the human group compared to the non-human groups when considering the whole trial was likely therefore an artefact of longer trial durations in humans. However, communication was displayed at lower frequencies and durations in the non-human groups compared to humans in the control periods. Given the communication criteria in my operational definition for two out of three levels of joint attention events, elevated levels of communication in humans could have been an important driver for a higher proportion of their mutual face direction episodes to become shared attention events. It is particularly noteworthy that the most common facial expression displayed by humans in laser trials was smiling, which is affiliative and conveys positive affect. The macaques produce lipsmacks to signal affiliation (Micheletta et al., 2013), and the chimpanzees produce bared teeth facial expressions (Waller & Dunbar, 2005), both of which were produced in shared attention events. Therefore, positive interactions between individuals seems to be a critical factor in order for shared attention to arise.

Unlike some prior research, I did not explicitly require dyads to show intentionally communicative behaviours during any joint attention events (e.g. Leavens & Racine, 2009). Future research could usefully examine a fourth, stricter, level of joint attention that requires intentional communicative exchanges during mutual face direction (akin to ‘shared attention’ events in Siposova & Carpenter, 2018). As I only considered communicative signals produced when the signaller was looking at the face of the partner, these signals meet some of the 1st order intentionality criteria outlined in Chapter 1 including being recipient directed and being produced in association with visual monitoring of the recipient. However, another key criterion for assessing whether signals are intentionally produced is to decipher whether signals were goal directed, and whether signallers persist, elaborate or terminate the interaction if the goal is not met (Townsend et al., 2017). Concerning joint attention events, it is difficult to determine what the goal of these interactions may have been. Typically to assess the goal of signallers, researchers identify ‘apparently satisfactory outcomes’; outcomes that result in the cessation of signalling from the individual and that represent a plausible desire by the signaller (e.g. receiving grooming). Here I record too few instances of communication, in the non-human primates at least, to reliably identify an outcome that frequently satisfied the signaller’s during joint attention events.

Another approach to the issue of whether the signals I observed in joint attention events were likely to have been intentionally produced is to look for existing evidence that the signal type can be deployed intentionally by the species. For instance, human adults can unquestionably produce vocal and gestural signals intentionally and even though facial expressions have been considered as involuntary and honest expressions of emotions, it is also the case that people can exaggerate or fake expressions to regulate social interactions (e.g. smiling to be polite) suggesting a degree of intentionality (reviewed in Kret, Prochazkova, Sterck, & Clay, 2020). Human infants at 11-months old begin to coordinate their vocalisations and gestures with gaze to their caregivers face, suggesting that they may be attempting to intentionally communicate (Donnellan, Bannard, McGillion, Slocombe, & Matthews, 2020), and gestures in preverbal infants meet criteria for first order intentionality (Bates et al., 1979; Bates, Camaioni, & Volterra, 1975). The extent to which infants have intentional control over their facial expressions is, however, currently unknown. It is therefore likely that the 11-month old infants and their mothers in the current study were producing at least some of their signals intentionally. For chimpanzees, previous research has only identified two vocalisations (both alarm calls) as meeting intentional criteria (Schel et al., 2013), and the limited literature on facial expressions currently suggests they have little control over this modality (reviewed in Kret et al., 2020). In contrast, there is a substantial literature showing that ape gestures do meet criteria for first-order intentional production (Byrne et al., 2017), including the 'reach' gestures observed during the shared attention event displayed by AI and DS (Hobaiter & Byrne, 2011b). No previous research has examined intentional signal production in Sulawesi crested macaques, so it is unknown whether the lipsmacking signals that were observed in shared attention events were intentionally produced. Extrapolating previous research into the intentional use of signals indicates that at least some of the instances of shared attention I observed in humans and chimpanzees involved intentional communication, however a lack of comparable research effort into intentional signalling makes this currently unknown for the macaques.

When comparing the behaviour of human infants and their mothers separately, the mothers appeared more motivated to engage in joint attention. In 29 instances of triadic attention where the communication of both individuals was available, the mothers communicated in 100% of cases, whereas the infants produced a communicative signal in just 48% of cases. Therefore, the success of the human group to demonstrate joint attention events may stem from communicative mothers in the dyad driving these effects. Unfortunately, my sample size did not permit me to statistically examine the influence of each member of the dyad to explore this, but this is a promising avenue for future research. A beneficial next step to take would be to test joint attention events in infant-infant dyads in humans; it would be interesting to examine whether two individuals without prevalent speech and pointing signals are able to show joint attention events at levels equivalent to my non-human groups.

When designing this study my ambition was to create a paradigm to empirically test for joint attention events that allowed for fair comparisons between species. The benefit of adopting a rigorous coding scheme is the accumulation of directly comparable findings between my study groups, which were both reliable and objective. An unavoidable limitation of this approach is that I may have missed intuitively positive instances of joint attention, and on the other hand I may also have identified joint attention events which may not truly represent the sharing of attention. For instance, for shared attention events I regarded an individual's face direction towards the laser in the 3s prior to mutual face direction to be indicative that the communication taking place was about the stimulus. This was a necessary approach as I could not consider the meaning behind communicative signals because this could not be established for all signals produced by the non-human dyads. Analysing the content of the speech in the humans however, may have revealed that they were not sharing attention about the laser at all during mutual face direction instances. While applying an objective coding scheme can result in these limitations, I believe the current study is the best attempt in the literature thus far to fairly assess joint attention abilities between species. In future, using gaze instead of head direction could strengthen such assumptions, but a conservative approach using observable behaviour must continue to be applied. While intuitive cases of joint attention may be missed, impressionistic judgements about the intentions of prelinguistic infants have already been shown to be unreliable (Graham et al., 2021), and thus objective guidelines are essential for detecting joint attention in non-linguistic populations.

In my quest to generate a rigorous, yet objective operational definition for joint attention events that I could fairly apply across species, I necessarily prioritised joint attention events that rely heavily on the visual channel. Face direction is easily accessible from a 3rd person perspective and can be reliably coded, however this focus on the visual channel may have underestimated joint attention events in all groups. Gabouer and Bortfeld (2021) argued recently that many behaviours can indicate that a partner is attuned to an individual's attentional focus other than looking, including touches, nodding or verbal affirmations. Siposova and Carpenter (2019) discuss potential scenarios in the absence of communication that may still establish jointness between a dyad (labelled 'mutual awareness'). Here they offer two passengers reflexively gripping each other's hands when the lights turn off during a flight as an example. In chimpanzees then, embracing an individual after hearing neighbouring calls could demonstrate a form of joint attentional engagement. Research has also argued that touch, rather than gaze, is a preferred method of mother-infant interaction in both non-western human cultures, and in non-human species (Botero, 2016). Therefore, my focus on visually mediated joint attention likely underestimated dyads' true capacity to jointly attend in all species. As stated in the discussion for study 1, further analysis of the informational content of communicative signals may help in the absence of looking. But while body contact and touch undoubtedly also play an important role, measuring different pressures and types of touch from a 3rd party perspective is challenging, and understanding what is communicated with different types of touch in non-humans is particularly difficult. In humans at least new technology in the form of pressure sensitive suits may help us to start to better understand the role of tactile communication in joint attention events.

In conclusion, in this study at least one dyad from the three study species (humans, chimpanzees and Sulawesi crested macaques) engaged in triadic attention, triadic attention with communication, and shared attention events. Therefore, it has been demonstrated that non-human species do engage in joint attention events, and for the first time I have shown this to be true even with a stringent operational definition of jointness. Despite showing that chimpanzees and crested macaques were capable of engaging in shared attention, results from the directly comparable laser paradigm revealed important species differences. In study 1, the human dyads consistently engaged in more instances of joint attention events at all levels. When examining why this might be the case, the results revealed that in first 50 seconds of the laser trial humans displayed more of the component behaviours needed to demonstrate joint attention than the non-humans. Humans communicated and looked at their partner's face more often than chimpanzees and crested macaques, and they also engaged with the stimulus for longer, indicating greater interest in it. Although chimpanzees and macaques are capable of engaging in joint attention events, humans seem to display a higher motivation to check the attention of their partners and to communicate about objects in their environment, which may lead them to have more cases of joint attention events. In study 2, the communicative signals displayed by the chimpanzee and macaque dyads who engaged in joint attention events gave or elicited reassurance, and seemed to act as an acknowledgement of their partner's response to the stimulus. This suggests that uncertainty may be a key context for eliciting joint attention events in non-human primates. These findings challenge the assertion that only humans engage in joint attention events: chimpanzees and crested macaques can share attention about external objects, they are just significantly less likely to do so than humans.

CHAPTER 5: General discussion

This dissertation has comprehensively examined two chimpanzee communicative signals, as well as an important aspect of social cognition that is intimately connected to language development in humans. First, this thesis investigated a functionally referential chimpanzee vocalisation, and revealed that the likelihood of producing rough grunts on arrival at a food source varied with community membership, sex, age, ecological and social factors. Next, the examination of the exaggerated loud scratch gesture failed to replicate published findings of the referential function of this gesture in three wild chimpanzee communities, indicating such a function is not ubiquitous to the species. Finally, my two studies on the examination of joint attention events showed, for the first time in the literature, that non-human primates do share attention with conspecifics in their natural environments, albeit rarely.

Summary of research findings

My examination of chimpanzee rough grunt production aimed to redress the existing focus in the literature on adult males, and to examine this behaviour for the first time in an extensive cross-site comparison. This approach was a critical next step for elucidating the function of these calls, as assuming these vocalisations are produced in a uniform manner across demographic classes encouraged a perspective that adult males from single-sites are representative of the species. Here I examined data from five wild chimpanzee communities, with adult males, adult females and non-adult individuals to investigate the production of rough grunt vocalisations during arrival at a feeding site. The results of this investigation provided the first evidence for genuine population-level differences in the production of this vocalisation, which suggests that habitat ecology or cultural differences can affect the production of communicative signals. I also identified several sex differences in calling behaviour: males called more often than females, appeared to be more sensitive to ecological characteristics of the feeding site than females, and possibly vocalised to recruit females to the feeding site. Female calling was not sensitive to any of the ecological or social variables I tested, meaning the function of arrival rough grunt production in adult females remains elusive and requires further study. Moving forward, it will be critical that studies continue to consider how the different social lives and fitness costs or benefits may differentially affect the communicative signals in each sex. Finally, this chapter provided novel insights into the development of these vocalisations from infancy to sub-adulthood. Research on the ontogeny of chimpanzee communicative signalling is sparse, but this study provided important evidence that a social learning or vocal contagion mechanism may underlie the development of this call type.

I can suggest several valuable next steps for this research area; first would be to further investigate the function of these calls in adult females. Future studies should examine a balanced data set of mothers and non-mothers to allow for more conclusive evidence on whether the call production in nursing mothers (where nutritional intake is more critical) differs to females without offspring. A future study should also consider the oestrus status of females, as this could provide a deeper insight into potential social correlates of their calling behaviour since female association patterns change considerably with oestrus status (Machanda, Gilby, & Wrangham, 2013; Matsumoto-Oda, 1999). In male individuals, it would be beneficial for future work to discriminate between rough grunts produced in isolation and rough grunt/pant hoot call combinations, and investigate if these call types hold separate functions. Finally, regarding young chimpanzees, studies would benefit from recording rough grunt production with more fine-grained temporal information, in order to test robustly if juveniles are mirroring the calling patterns of their mothers. It would also be interesting to investigate if any other specific individuals influence the call production of young chimpanzees (e.g. older siblings), and this may help to discriminate between a social learning versus a vocal contagion mechanism if specific individuals appear to be mirrored. Overall, this chapter has set a precedent for future studies to adopt an approach which is sensitive to the ecological and demographic differences in chimpanzee communities that may impact communicative signalling behaviour.

The second empirical chapter investigated the proposed referential function of the exaggerated loud scratch gesture, which was the first claim of a naturally occurring, habitually used referential gesture in wild chimpanzees. This finding from Pika and Mitani (2006) suggested important aspects of continuity between the referential abilities of humans and our closest living relatives, but was only tested in a single community of chimpanzees and no inter-observer reliability for the observations was available. Thus, whether this function was ubiquitous to the species was unknown. The goal of this chapter was to assess whether this gesture did indeed function referentially in communities outside of the Ngogo community using rigorous methods. For this study I included data from three wild communities alongside the published data from Ngogo, and examined the grooming interactions in male and female individuals from 4-years old upwards. The results of this study revealed that a referential function (indicating the location the signaller wanted to be groomed) was specific to the Ngogo community: signallers at other sites received grooming in the scratched location at comparatively low rates, and did not appear to pursue this goal. This finding emphasises how single-site studies can lead to premature assumptions concerning the ubiquity of behaviour. Instead with this study (as in chapter 2) I showed how cross-site comparisons can reveal remarkable population-level differences, here in the usage of a gestural signal. At Kanyawara I then tested several alternative hypotheses, and identified that in this community the exaggerated loud scratch functioned to initiate grooming, reengage partners in grooming, or to request grooming during a bout. Conducting a comprehensive examination of several goals here led to the discovery of the highly flexible use of this gesture. Future research needs to test if these functions are stable across communities, and continue to examine the behaviour of both the signaller and recipient during entire grooming bouts to do so. With these findings the search resumes for a habitually used, naturally occurring referential gesture in non-humans. In the absence of a gestural signal that directs the attention of another to specific objects, events or locations in their environment, arguments can be made that the motivation to produce referential signals in the gestural domain is a uniquely human trait. With this study, by adopting a method that allowed for direct comparisons between communities, I identified subtle group-specific differences in the use of a gesture, and my findings at Kanyawara indicate that the function or meaning of this chimpanzee gesture may be quite flexible and dependent on the intricacies of the immediate context.

A recurrent issue in the comparative literature is a lack of directly comparable work between-species, which is unproductive as it exacerbates difficulties in attempts to trace the evolutionary origins of a behaviour. My final empirical chapter sought to address this issue in the joint attention literature, with the goal of conducting an experiment on joint attention events which allowed for fair between-species comparisons to assess if this ability is uniquely human. I presented the moving light of a laser as a novel stimulus to dyads in their natural environment in order to directly compare the joint attention abilities of wild chimpanzees, wild Sulawesi crested macaques, and human mother-infant dyads from the UK and Uganda. As a follow-up I then presented novel physical objects to the non-human primates. Across the two studies dyads of all three species exhibited the highest level of joint attention, shared attention events, although this was rare in the non-human groups. By designing an experiment which was appropriate for each species in their natural environments, I can conclude that joint attention events, even when identified with a relatively strict operational definition, are not a uniquely human ability. The laser experiment also revealed that humans showed more of the component behaviours required for joint attention events; humans looked at the faces of their partner more, and exhibited more communication between dyads in particular. By breaking down the operational criteria that I used, I was able to assess where these species differences arose. This study was also the first to examine joint attention events in a monkey species. The Sulawesi crested macaques studied here showed comparable, if not better, engagement in joint attention events compared to chimpanzees, which have previously dominated this area of research. The performance of the macaques here provides a useful avenue for future research by suggesting that more tolerant and communicative species may be more likely to share attention with conspecifics. With this research I have challenged the theoretical perspective that joint attention is a human unique trait, but this study has also revealed important species differences that likely contribute to the greatly elevated levels of engagement in joint attention in humans compared to the non-human primate species that I studied. This chapter has emphasised the need for fair between-species comparisons before claiming social cognitive abilities as uniquely human.

Studying chimpanzee communication: research impact and future directions

This thesis aimed to address several problems in the current literature surrounding chimpanzee communication, and first was able to demonstrate that multi-site research is fundamental for studying the communicative behaviour of this species. My findings in chapter 2 and 3 indicated that aspects of production for two communicative signals differed considerably between communities. More research needs to be conducted to understand why these population-level differences arise. For instance, to understand if ecological disparities can account for the behavioural differences between communities (Byrne, 2007; Kalan et al., 2020), as they may do for rough grunt production, or whether community-specific behaviours stem from social learning mechanisms (Whiten, 2000), as they may do for the function of the exaggerated loud scratch. Although single-site studies can provide valuable insights into behaviour, it needs to be habitually acknowledged that these insights may be limited to the studied population, and efforts need to be made to conduct the directly comparable research elsewhere. An increase in collaborative effort between research groups and field sites would facilitate this goal, but there are many challenges with such an approach. Researchers can be reluctant to share hard-earned data with other research groups, especially if the new angle can bring their original research into question. Collaborations can also take many months or years to organise in order to examine whether existing data was comparably collected. This was a particularly challenging aspect of this thesis, and at times I was forced to exclude data due to small differences between study site methods (e.g. in chapter 2: what constituted arriving to a feeding site). Given the logistical difficultly of collecting sufficient data for a single project in multiple communities, or in combining existing data, the optimum approach is instead for field sites and research groups to align their data collection practices from the offset. More online platforms are being created to enable this effort, for instance the OSF (https://osf.io), ManyPrimates (https://manyprimates.github.io) and PhyloPsy (https://www.phylopsy.org). Concerning the study of communication, an effort to bridge gaps between vocal and gestural research methods would be advantageous for studying several language traits, such as intentionality. The collection of continuous focal video footage using a camera with high quality external microphone would be a simple way to better facilitate collaborative efforts here, as this can maximise the number of questions that can be asked of the data. Currently this method is sometimes avoided due to how time consuming video coding continuous recordings can be; ideally technological advances will one day permit researchers to mark events of interest in real time during filming to enable faster data extraction with video footage, while also preserving the continuous video for future projects.

This thesis has also stressed the importance of chimpanzee research moving away from a primarily male perspective. Chapter 1 highlighted the vastly different life histories of males and females of this species, and how striving to maximise their fitness may then lead to differences in their behaviour. It is therefore short sighted to assume that the communication of adult males is representative of the species. In particular, the impact that the social lives of females may have on their communication is relatively unexplored. Formerly the social lives of the dispersing sex of a species were considered to be less rich than the philopatric sex due to an absence of kin (Sterck, Watts, & Van Schaik, 1997), and female chimpanzees were assumed to only form strong relationships with their offspring (Mitani, 2006). Now, research indicates that females do form strong social bonds (Langergraber, Mitani, & Vigilant, 2009; Lehmann & Boesch, 2009) that likely hold adaptive value for themselves, and their offspring (Foerster et al., 2015). Since female chimpanzees are the dispersing sex, their arrival in a new community presents a unique opportunity to observe the formation of social bonds in adulthood, and their adaptation to behaviours of the local community. With our findings regarding population-level differences in communication, and existing literature detailing the variability in female sociality between communities (e.g. the increased gregariousness of females at Taï National Park compared to Gombe and Kanyawara; Riedel, Franz, & Boesch, 2011), it's possible that females adapt their communicative behaviour to align with their new group. This could be using a gesture to support a different function in a new community, or perhaps even structural changes to their vocalisations, as has been witnessed following the merging of two groups in captivity (Watson et al., 2015). Females with dependent offspring also, unlike males, have constant social partners available whom they are likely highly attuned with, perhaps reducing the need to use communication to recruit non-kin and to coordinate activities with others. While some signals may be rarely produced by female individuals (e.g. pant hoots) this should not result in them being ignored in the literature. My study on rough grunts is a testament to the fact that the function of signals produced more frequently by males may not extrapolate to females.

It is equally important to study chimpanzee behaviour from an ontogenetic perspective, to understand the social pressures or mechanisms that promote the development of specific behaviours. For instance, interactional experience with non-mother conspecifics appears to impact the development of communication, such as gesture frequency and repertoire size, and the emergence of intentional signalling (Fröhlich, Müller, Zeiträg, Wittig, & Pika, 2017; Fröhlich, Wittig, et al., 2019). My chapter examining rough grunts also revealed that a social learning or vocal contagion mechanism may support the emergence of these calls during juvenility. While critical for understanding behaviour (Tinbergen, 1963) a developmental approach is challenging. Using longitudinal datasets is the optimal method for observing behaviour over development, but this requires several years of research effort, and often single research sites cannot provide sufficient data given the small number of infants born each year in communities. Powerful ontogenetic approaches thus heavily rely on multi-site data, and would benefit from greater collaboration between field sites and research groups.

A greater collaborative effort may also foster new opportunities to examine other species alongside chimpanzees, but it will be critical that researchers ensure they are conducting fair between-species comparisons, otherwise the evolutionary history of traits will remain elusive. My chapter on joint attention highlighted how it is unhelpful to claim traits as uniquely human before sufficient comparative evidence is available, and there are several shortfalls that studies need to overcome to avoid this. First, it's important that operational definitions can encompass directly observable behaviour in other species, and are based on reliable observations. For instance, in the realm of joint attention, Hobson and Hobson (2007) suggested that partners exchanging 'sharing looks' was sufficient in the absence of overt communicative behaviour to infer that that partners knew they were attending to something together. However, Graham et al. (2021) found that sharing looks could not be reliably distinguished from checking looks in prelinguistic human infants, and therefore it's highly unlikely that this behaviour would be detectable in another species to measure joint attentional engagement. For my examination of joint attention then, it was critical that overt communicative signals (gestures, vocalisations, facial expressions) were used to indicate the jointness of the interaction. My study also demonstrated the merit of conducting relatively simple experiments which encourage the observation of naturalistic behaviour in a species, and can be directly transferable between species. This is more informative of their natural propensity to demonstrate social-cognitive skills than some extensive captive studies. For example, a previous joint attention study compared chimpanzee and human infants, but used the same developmental scales (e.g. Bayley Scales of Infant Development; Bayley & Reuner, 1969) for both species without any adaptations to be more species-appropriate for the chimpanzees, thus requiring these individuals to understand the verbal requests of human experimenters for instance (Bard et al., 2014). Observations of the behaviour of wild individuals with no human interference is the optimal way to understand their natural skills, however relying solely on natural occurrences requires extensive work, and rare behaviours would be at risk of being prematurely claimed as absent. Instead, field experiments which are sensitive to natural behaviour of a species and mimic potential contexts in the natural world (e.g. study 2 of the joint attention chapter mimicked natural encounters with foreign objects in the Sulawesi crested macaques) may be the best approach to understanding the social cognition of a species.

Creating paradigms and operational definitions that are sensitive to the species are important for fair between-species comparisons, but aside from the adopted paradigm and definitions, there are other approaches studies can take to maximise our understanding of how behaviours evolved. Firstly, studies should aim to investigate more than the presence or absence of a trait, by breaking down the components parts of a behaviour to truly understand where species difference lie. Using such an approach in chapter 4 of this thesis revealed that communication in particular appears to be key to foster the occurrence of joint attentional engagement. Secondly, studies comparing non-human to human samples need to consider recruiting a representative sample for their human group. The exclusive use of WEIRD (Henrich et al., 2010) human samples is not representative as different cultures may foster or encourage the development of abilities (implicitly or explicitly) to different extents. For instance, infants in Uganda have been found to engage in less social play than infants in the UK, and social play is an important context which provides opportunities to develop communication and joint attention skills (Holden et al., in review). Therefore, diverse samples in both the human and non-human groups are vital in comparative datasets. Finally, researchers, particularly investigating social cognition, need to widen their scope to include more monkey species in their studies. Given the potential influence of social traits on social cognition and communication (e.g. social tolerance on vocal output; Kavanagh et al., 2021), broadening the primate species investigated past the great apes is key as it provides a greater range of social ecology which may have supported the emergence of a social cognitive ability. While these suggestions may pose more logistical challenges for collecting data, it seems essential for informative comparisons and ultimately achieving the goals of conducting comparative research.

Conclusion

Chimpanzees have a rich communication system, and studying this provides valuable insights to help us understand the evolutionary origins of human language. However, components of language cannot be fully understood using a comparative approach if a restricted view of the species is presented. This thesis has provided important evidence that cross-site comparisons and representative data from a species is imperative to understand the production and function of communicative signals. Chapter 2 revealed that community membership, sex, age, ecological and social factors affected the likelihood for chimpanzees to produce functionally referential food calls, ‘rough grunts’. Chapter 3 showed that a referential function for the exaggerated loud scratch gesture is not ubiquitous to the species, but may be culturally specific to one community. Finally, chapter 4 demonstrated for the first time that non-human species are capable of sharing attention with conspecifics in their natural environments. I hope these findings will encourage the systematic employment of cross-site and cross-species comparisons, and the use of representative study samples in non-human and human species. To forge progress in our understanding of language evolution, collaborations between research groups, study sites and disciplines are likely to be of paramount importance.

APPENDICES

Appendix 1: Description of data and summary of contributions.

In the following table chimpanzee groups are indicated in bold type, macaque groups with an asterisk (*) and human groups with italics. All data was analysed by Nicole Lahiff, with GLMM models also assessed by Claudia Wilke and overseen by Roger Mundry.

CHAPTER 2: Social and ecological correlates of food-associated calling in male, female and non-adult chimpanzees			
Group	**Data Type**	**Data collector(s)**	**Data coder(s)**
Kanyawara	Real-time manual recorded observations of feeding and vocal behaviour	Nicole Lahiff, Claudia Wilke, Junior Whiteley, Joseph Mine, Elliot Arnold	Nicole Lahiff
Ngogo central		Nicole Lahiff, Claudia Wilke, Junior Whiteley, Maggie Hoffman, Elliot Arnold	
Ngogo west			
Sonso		Anne Schel	
Tai South		Ammie Kalan	Nicole Lahiff, Franziska Wegdell
CHAPTER 3: Is a referential gesture ubiquitous to wild chimpanzees? An exploration of alternative functions for the exaggerated loud scratch gesture			
Kanyawara	Video recordings of entire grooming bouts	Nicole Lahiff and Claudia Wilke	Nicole Lahiff and Claudia Wilke
Sonso	All-occurrence video recordings of gesture production	Catherine Hobaiter	Nicole Lahiff, Claudia Wilke, Abbie Naylor and Katie Slocombe
Waibira			
Ngogo	Coded data in excel file (analysed material)	Simone Pika	Simone Pika
CHAPTER 4: Are joint attention events uniquely human? A comparative study with Humans (homo sapiens), Chimpanzees (Pan troglodytes schweinfurthii) and Sulawesi Crested Macaques (Macaca nigra)			
Kanyawara	Video recordings of experiments	Nicole Lahiff, Claudia Wilke, Junior Whiteley, Elliot Arnold and Maggie Hoffman	Nicole Lahiff, Claudia Wilke, Abbie Naylor, Luke Townrow, Katie Ryan, Lucy Dunn and Daisy Whitwood
Ngogo central			
Ngogo west			
PB1b*		Kirsty Graham, Andre Pasetha, Claudia Wilke and Katie Slocombe	
R1*			
R2*			
British		Nicole Lahiff, Eve Holden, Joanna Buryn-Weitzel, Kirsty Graham, Sophie Marshall, Charlotte Knapper, Rhiannon Pierce, Rebecca Anderson, Molly Bowns, Lucy Dunn, Megan Earl, Harold Green, Charlie Ives, Yujin Lee, Anna Nador, Ellie Parker, Harshanaa Patel, Barbara Sodomkova, Emma Standley, Sonnie Tan, Maisie Thurman, Joseph Vogliqi, Daisy Whitwood, Caitlin Woods	Nicole Lahiff, Claudia Wilke, Abbie Naylor, Luke Townrow, Katie Ryan, Eve Holden, Lucy Dunn, Daisy Whitwood, Rebecca Anderson and Barbara Sodomkova
Ugandan		Eve Holden, Joanna Buryn-Weitzel, Kirsty Graham, Claudia Wilke, Edmund Donnellan, Maggie Hoffman, Sophie Marshall, Charlotte Knapper, Charlie Ives, Josephine Paricia, Santa Atim, Michael Jurua, Helen Biroch, Florence Tusiime, John McCutcheon, Emma Sopelsa-Hall.	

Appendix 2: Calculating friendship indices.

The formulae detailed here describe how the strength of social relationships between chimpanzees were determined in chapter 2, using the methods of Schel et al. (2013). The composite friendship index (CFI; based upon Gilby & Wrangham's 'composite association index', 2008) includes three independent measures of dyadic association: party level association, grooming frequency and nearest neighbour association. All three of these measures will be detailed below. In the following descriptions 'chimp A' always denotes the focal individual, and friendship indices were calculated with all other adult members of the community (with each member being represented individually by chimp B). Focal individuals must have had a minimum of 12 hours of focal observation time during the study period to enter into these analyses.

For party level association (PLA) I used simple ratio index (Cairns & Schwager, 1987) to assess the proportion of time that a dyad (chimp A, chimp B) was observed in the same party together. This was calculated using 15-minute scan data which is part of the long-term data collection at Kanyawara, and was collected by AS at Sonso. PLA was calculated as:

$$\mathrm{PLA_{ab}} = \frac{\mathrm{P_{ab}}}{\mathrm{P_a} + \mathrm{P_b} - \mathrm{P_{ab}}}$$

Here, P_{ab} is the number of parties containing chimp A and B together, P_a is the number of parties containing chimp A, and P_b is the number of parties containing chimp B. In the denominator, P_{ab} is subtracted to avoid counting individuals twice because P_a and P_b already considers parties which contain both individuals together. To enable meaningful comparisons across the indices, each value was then standardised by dividing chimp A and B's PLA score by the mean of all dyads PLA scores in the community (PLA_{ab}/PLA_{mean}).

For grooming frequency, I used all-occurrence grooming records for all focal individuals and calculated the grooming rate between chimp A and B with:

$$\mathrm{Groom_{ab}} = \frac{\mathrm{A_f B_g}}{\text{Focal duration A}}$$

where A_fB_g is the duration of grooming between focal chimp A and B, and the denominator is the duration of focal observation time of A. As before, each value was then standardised by dividing chimp A and B's grooming frequency score by the mean of all dyads grooming frequency scores in the community ($Groom_{ab}/Groom_{mean}$).

For the final measure, nearest neighbour (NN) association, I used the rate that chimp A was the nearest neighbour (within 10m) to chimp B. The spatial proximity between the dyad was calculated as follows:

$$\mathrm{NN_{ab}} = \frac{\mathrm{A_fB_{nn}}}{\text{Focal duration A}}$$

In this formula A_fB_{nn} is the number of 15-minute scans where chimp B is the nearest neighbour within 10m of focal chimp A. The denominator is the duration of the focal observation time of chimp A. As before, each value was then standardised by dividing chimp A and B's NN score by the mean of all dyads NN scores in the community (NN_{ab}/NN_{mean}).

As each of the indices described thus far is an independent measure of dyadic association, next an overall composite index was calculated from these independent measures to capture a dyad's overall tendency to associate. This was done by using the standardised scores, with the following formula:

$$\mathrm{CFI_{ab}} = \frac{(\mathrm{PLA_{ab}}/\mathrm{PLA_{mean}}) + (\mathrm{Groom_{ab}}/\mathrm{Groom_{mean}}) + (\mathrm{NN_{ab}}/\mathrm{NN_{mean}})}{3}$$

Finally, I calculated mean and standard deviation CFI values for each focal individual (chimp A) using their dyadic CFI scores with all chimp B's. Standard z scores were then calculated to capture the direction and magnitude of their relationships in comparison to the remainder of the community. To calculate a z score between chimp A and chimp B, I used the following formula:

$$Z\ \mathrm{score_{ab}} = \frac{\mathrm{CFI_{ab}} - \text{mean } \mathrm{CFI_a}}{\text{SD of } \mathrm{CFI_a}}$$

Here CFI_{ab} is the composite friendship index between chimp A and B, and the mean CFI_a is the average of all dyadic CFI values between chimp A and the rest of the adult members in the community. The denominator was then the standard deviation of these values.

Appendix 3: Extended model results for chapter 2.

Here I tabulate the model estimates, standard errors, and confidence interval for each model in chapter 2.

Model 1: Community and sex effects on rough grunt production

Table 1. Results of the model investigating the probability for individuals to rough grunt, dependent on sex and community.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
Intercept	-2.989	0.645	-5.957	-1.725			(1)	-3.379	-2.587
sex(2)	1.644	0.876	-0.463	3.453			(1)	0.717	2.171
Community Ngogo Central(3)	1.531	0.795	-0.032	3.078			(1)	1.191	1.865
Community Sonso(3)	1.010	0.682	-0.376	2.581				0.651	1.344
communityTai South(3)	-0.415	0.736	-1.741	1.103				-0.773	-0.169
age.at.event(4)	0.051	0.166	-0.255	0.346	0.094	1	.759	0.007	0.140
sex(2): community Ngogo Central(3)	**-3.359**	**1.228**	**-7.999**	**-0.761**	**11.479**	**3**	**.009**	**-4.415**	**-2.421**
sex(2): community Sonso(3)	-0.397	0.928	-2.274	1.674				-0.909	0.537
sex(2): communityTai South(3)	-1.033	1.008	-3.023	1.348				-1.543	-0.106

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with sex, where ‘female’ was the reference category; (3) This term was dummy coded with community, where ‘Kanyawara’ was the reference category. The indicated test refers to the overall effect of community; (4) Terms which have been z-transformed to a mean of zero and a standard deviation of one. Rows in bold text reflect significant variables (*p*<.05)

Model 2: Ecological effects on adult male food calling behaviour

Table 2. Results of the model investigating the probability for a male to rough grunt, exploring the influence of ecological variables.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
Intercept	-1.607	0.610	-3.142	-0.479			(1)	-2.155	-1.359
part.eaten(2)	0.182	0.313	-0.440	0.821	0.336	1	.562	-0.048	0.399
chimp.min(3,4)	**0.514**	**0.123**	**0.275**	**0.782**	**18.131**	**1**	**<.001**	**0.392**	**0.611**
Community Ngogo Central(5)	**-1.311**	**0.966**	**-12.249**	**0.486**	**10.949**	**3**	**.012**	**-2.098**	**-0.895**
Community Sonso(5)	1.084	0.637	-0.078	2.701				0.836	1.641
communityTai South(5)	0.485	0.728	-0.802	2.231				0.213	1.023
age.at.event (3,4)	0.054	0.183	-0.326	0.425	0.089	1	.766	-0.023	0.230
number.adult. IDs.present. focal.arr(3)	**-0.246**	**0.120**	**-0.504**	**-0.017**	**4.241**	**1**	**.039**	**-0.308**	**-0.185**

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with part.eaten, where 'fruit' was the reference category; (3) Terms which have been z-transformed to a mean of zero and a standard deviation of one; (4) terms which were log-transformed; and (5) These terms where dummy coded with community, where Kanyawara was the reference category; the indicated test refers to the overall effect of community. Rows in bold text reflect significant variables ($p<.05$)

Model 3: Effects of social environment and vocal behaviour on adult male food calling

Table 3. Results of the model investigating the probability for a male to rough grunt, exploring the influence of social variables and vocal behaviour.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
Intercept	-2.479	1.210	-6.091	-0.297			(1)	-3.904	-1.789
total.males.on .focal.arrival(2)	-0.426	0.301	-1.176	0.149	1.965	1	.161	-0.533	-0.251
total.females. on.focal. arrival(2)	**-0.541**	**0.237**	**-1.207**	**-0.118**	**5.577**	**1**	**.018**	**-0.732**	**-0.413**

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
isp.arrive.with.focal.YN(3)	0.329	0.452	-0.515	1.385	0.558	1	.455	-0.016	0.644
isp.already.present.YN(4)	-0.231	0.473	-1.304	0.726	0.249	1	.618	-0.669	0.055
highrank.arrive.with.focal.YN(5)	0.742	0.706	-0.539	2.218	0.942	1	.332	0.443	1.425
highrank.already.present.YN(6)	-0.282	0.469	-1.443	0.628	0.360	1	.549	-0.625	-0.001
m1.focalPH.3min.focal.arr(7)	**2.027**	**0.440**	**1.306**	**3.505**	**24.904**	**1**	**<.001**	**1.764**	**2.463**
m1.otherPH.3min.focal.arr(8)	-0.169	0.531	-1.521	0.977	0.104	1	.747	-0.712	0.176
m1.nonfocalRG.3min.before.focal.arr.YN(9)	0.022	0.397	-0.773	0.853	0.003	1	.957	-0.536	0.382
community(10)	1.854	1.232	-0.437	5.311	2.237	1	.135	1.038	3.243
age.at.event(2)	*0.962*	*0.761*	*0.070*	*2.333*	*3.803*	*1*	*.051*	*0.407*	*1.602*
focal.rank(2,11)	**0.847**	**0.388**	**0.242**	**1.927**	**4.730**	**1**	**.030**	**0.667**	**1.181**
chimp.min(2,11)	**0.807**	**0.277**	**0.385**	**1.636**	**9.531**	**1**	**.002**	**0.714**	**1.118**

Key: (1) this value was not included, as this has a very limited interpretation; (2) Terms which have been z-transformed to a mean of zero and a standard deviation of one; (3) This term was dummy coded with isp.arrive.with.focal.YN, where 'no' was the reference category; (4) This term was dummy coded with isp.already.present.YN, where 'no' was the reference category; (5) This term was dummy coded with highrank.arrive.with.focal.YN, where 'no' was the reference category; (6) This term was dummy coded with highrank.already.present.YN, where 'no' was the reference category; (7) This term was dummy coded with m1.focalPH.3min.focal.arr, where 'no' was the reference category; (8) This term was dummy coded with m1.otherPH.3min.focal.arr, where 'no' was the reference category; (9) This term was dummy coded with m1.nonfocalRG.3min.before.focal.arr, where 'no' was the reference category; (10) These terms where dummy coded with community, where Kanyawara was the reference category; (11) terms which were log-transformed. Rows in bold text reflect significant variables (*p*<.05).

Model 4: Ecological effects on adult female food calling behaviour

Table 4. Results of the model investigating the probability for a female to rough grunt, exploring the influence of ecological variables.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
Intercept	-2.127	0.557	-3.389	-1.260			(1)	-2.306	-1.835
part.eaten(2)	-0.230	0.331	-0.896	0.330	0.458	1	.498	-0.363	0.143
chimp.min(3,4)	*0.290*	*0.156*	*0.001*	*0.629*	*2.826*	*1*	*.093*	*0.216*	*0.342*
Community Ngogo Central(5)	**1.257**	**0.512**	**0.350**	**2.394**	**9.807**	**4**	**.044**	**0.981**	**1.581**
Community Ngogo West(5)	1.415	0.629	0.199	2.791				0.664	1.953
Community Sonso(5)	0.552	0.511	-0.300	1.633				0.274	0.822
Community Tai South(5)	0.361	0.466	-0.450	1.387				0.086	0.633
mother.of. dependents(6)	0.489	0.397	-0.219	1.308	1.593	1	.207	0.328	0.619
age.at.event *(3,4)*	0.016	0.144	-0.263	0.319	0.016	1	.901	-0.063	0.135
number.adult. IDs.present. focal.arr*(3)*	0.023	0.139	-0.249	0.295	0.030	1	.862	-0.048	0.148

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with part.eaten, where ‘fruit’ was the reference category; (3) Terms which have been z-transformed to a mean of zero and a standard deviation of one; (4) terms which were log-transformed; and (5) These terms where dummy coded with community, where Kanyawara was the reference category; the indicated test refers to the overall effect of community. Rows in bold text reflect significant variables (*p*<.05)

Model 5: Effects of social environment and vocal behaviour on adult female food calling

Table 5. Results of the model investigating the probability for a female to rough grunt, exploring the influence of social variables and vocal behaviour.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
Intercept	-2.268	0.707	-22.794	-1.033			(1)	-32.027	-1.908
total.males.on.focal.arrival(2)	-0.002	0.340	-3.002	1.987	0.00	1	.995	-4.343	0.159
total.females.on.focal.arrival (2)	0.348	0.298	-0.852	3.207	1.423	1	.233	-6.153	0.503
isp.arrive.with.focal.YN(3)	**1.040**	**0.492**	**0.161**	**10.171**	**4.755**	**1**	**.029**	**0.814**	**9.403**
isp.already.present.YN(4)	-0.183	0.509	-5.562	2.437	0.131	1	.717	-0.380	1.979
highrank.arrive.with.focal.YN(5)	-0.538	0.592	-8.716	1.452	0.835	1	.361	-1.063	6.910
highrank.already.present.YN(6)	0.394	0.581	-1.919	6.002	0.465	1	.495	-0.141	7.251
m1.otherPH.3min.focal.arr(7)	-05.64	0.632	-8.619	0.793	0.851	1	.356	-3.848	-0.147
m1.nonfocalRG.3min.before.focal.arr.YN(8)	**0.967**	**0.495**	**0.048**	**10.641**	**4.568**	**1**	**.033**	**0.482**	**9.584**
community(9)	0.486	0.619	-4.338	2.746	0.635	1	.426	-2.151	0.789
age.at.event(2)	-0.039	0.186	-2.032	1.563	0.044	1	.835	-2.624	0.048

Key: (1) this value was not included, as this has a very limited interpretation; (2) Terms which have been z-transformed to a mean of zero and a standard deviation of one; (3) This term was dummy coded with isp.arrive.with.focal.YN, where 'no' was the reference category; (4) This term was dummy coded with isp.already.present.YN, where 'no' was the reference category; (5) This term was dummy coded with highrank.arrive.with.focal.YN, where 'no' was the reference category; (6) This term was dummy coded with highrank.already.present.YN, where 'no' was the reference category; (7) This term was dummy coded with m1.otherPH.3min.focal.arr, where 'no' was the reference category; (8) This term was dummy coded with m1.nonfocalRG.3min.before.focal.arr, where 'no' was the reference category; (10) These terms where dummy coded with community, where Kanyawara was the reference category. Rows in bold text reflect significant variables (*p*<.05).

Model 6: Effects of sex and age on young chimpanzee food calling

Table 6. Results of the model investigating the probability for young chimpanzees to rough grunt, dependent on sex and age.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
Intercept	-0.944	0.354	-1.957	-0.081			(1)		
sex(2)	-0.685	0.444	-1.749	0.310			(1)	-1.456	-0.653
age.at.event(3)	-0.040	0.375	-0.865	0.875			(1)	-0.437	0.273
chimp.min(3,4)	0.006	0.200	-0.408	0.465	<.001	1	.975	-0.089	0.212
total.adults.on.focal.arrival(3)	-0.062	0.236	-0.595	0.474	0.504	1	.478	-0.379	0.089
sex:age.at.event(3)	*0.950*	*0.531*	*-0.002*	*2.201*	*3.622*	*1*	*.057*	*0.524*	*1.409*

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with sex, where 'female' was the reference category; (3) Terms which have been z-transformed to a mean of zero and a standard deviation of one; (4) terms which were log-transformed. Rows in bold text reflect significant variables (*p*<.05)

Model 7: Effects of mother vocalisations on the food calling of offspring

Table 7. Results of the model investigating the probability for offspring to rough grunt, dependent on whether the mother produced a rough grunt.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
Intercept	-4.785	1.222	-217.855	-3.597			(1)		
mother RG during/after arrival(2)	**5.885**	**1.203**	**4.850**	**531.617**	**61.176**	**1**	**<.001**	**5.311**	**24.981**
sex(3)	-1.095	1.074	-44.407	3.940	1.128	1	.288	-20.910	-0.452
z.age.at.event(4)	-0.637	0.538	-13.966	1.166	1.472	1	.225	-1.192	0.414
Community Ngogo Central(5)	*-2.025*	*1.444*	*-79.126*	*1.495*	*5.383*	*2*	*.068*	*-3.790*	*-1.084*
communityTai South(5)	*1.327*	*1.213*	*-21.021*	*58.982*				*-0.092*	*20.938*

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with mother RG during/after arrival, where 'no' was the reference category; (3)

This term was dummy coded with sex, where 'female' was the reference category; (4) Terms which have been z-transformed to a mean of zero and a standard deviation of one; (5) These terms where dummy coded with community, where Kanyawara was the reference category. The indicated test refers to the overall effect of community. Rows in bold text reflect significant variables (*p*<.05).

Appendix 4: Extended model results for chapter 3.

Here I tabulate the model estimates, standard errors, and confidence interval for each model in chapter 3.

Model 1: Referential function

Table 8. Results of the reduced model investigating the probability for the partner to groom within 5cm of the location scratched by the target individual.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**X^2**	**df**	***P***
intercept	-3.339	0.930	-6.190	-1.728			(1)
communityNgogo(2)	**2.184**	**0.524**	**1.330**	**3.815**	**22.624**	**3**	**<.001**
communitySonso(2)	0.680	0.654	-0.648	2.259			
communityWaibira(2)	0.392	0.763	-1.667	2.076			
rank.class.difflower(3)	**1.469**	**0.703**	**0.027**	**3.597**	**7.752**	**2**	**.023**
rank.class.diffsame(3)	1.765	0.675	0.476	3.684			
target.rank.classlow(4)	1.648	0.747	0.158	3.664	5.588	2	.061
target.rank.classmiddle(4)	0.350	0.512	-0.734	1.527			

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with community, where 'Kanyawara' was the reference category. The indicated test refers to the overall effect of community; (3) This term was dummy coded with rank.class.diff, where 'higher' was the reference category. The indicated test refers to the overall effect of rank class difference; (4) These terms where dummy coded with target.rank.class, where 'high' was the reference category. The indicated test refers to the overall effect of target rank class. Rows in bold text reflect significant variables (*p*<.05).

Model 2a: Grooming initiation

Table 9. Results of the reduced model investigating the number of exaggerated loud scratches given by the target individual in the 20s before dyadic grooming, compared to the number during dyadic grooming.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**X^2**	**df**	***P***
intercept	-5.325	0.293	-6.049	-4.913			(1)
period(2)	**-2.096**	**0.373**	**-3.082**	**-1.427**	**26.834**	**1**	**<.001**
rank.diff(3)	-0.146	0.175	-0.475	0.174	0.707	1	.400
CAI(3)	0.121	0.171	-0.226	0.451	0.494	1	.482

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with period, where 'before' was the reference category; (3) Terms which have been z-transformed to a mean of zero and a standard deviation of one. Rows in bold text reflect significant variables (*p*<.05).

Model 2b: Grooming initiation; grooming role

Table 10. Results of the reduced model investigating the probability for the target individual to become the groomer when dyadic grooming started, with this being predicted by whether or not the target individual produced an exaggerated loud scratch before grooming started.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**X^2**	**df**	***P***
intercept	-0.265	0.260	-0.836	0.221			(1)
target ELS(2)	**1.564**	**0.615**	**0.487**	**3.172**	**7.632**	**1**	**.006**
rank difference(3)	**0.833**	**0.255**	**0.396**	**1.544**	**11.525**	**1**	**<.001**

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with target individual ELS, where 'no' was the reference category; (3) Terms which have been z-transformed to a mean of zero and a standard deviation of one. Rows in bold text reflect significant variables (*p*<.05).

Model 3: Grooming re-initiation when in pause

Table 11. Results of the reduced model investigating the number of exaggerated loud scratches given by the target individual during active grooming and during pauses.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**X^2**	**df**	***P***
intercept	-10.033	0.490	-13.310	-9.397			(1)
period(2)	4.197	0.485	3.452	7.228			(1)
rank.diff(3)	0.018	0.166	-0.312	0.381	0.011	1	.916
CAI(3)	-0.875	0.401	-1.784	-0.233			(1)
period(2)*CAI(3)	**0.783**	**0.417**	**0.092**	**1.781**	**4.365**	**1**	**.037**

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with period, where 'groom' was the reference category; (3) Terms which have been z-transformed to a mean of zero and a standard deviation of one. Rows in bold text reflect significant variables (*p*<.05).

Model 4a: Requesting a favourable grooming switch

Table 12. Results of the reduced model investigating the number of 'favourable switches' in the 10s after a target individual produces an exaggerated loud scratch, compared to the number during the remainder of the dyadic grooming bout.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**X^2**	**df**	***P***
intercept	-3.983	0.168	-4.410	-3.739			(1)
period(2)	**-1.724**	**0.188**	**-2.013**	**-1.305**	**32.390**	**1**	**<.001**
rank.diff(3)	-0.141	0.131	-0.403	0.116	1.089	1	.297
CAI(3)	0.082	0.133	-0.190	0.324	0.367	1	.545

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with period, where 'afterELS' was the reference category; (3) Terms which have been z-transformed to a mean of zero and a standard deviation of one. Rows in bold text reflect significant variables (*p*<.05).

Model 4b: Requesting a favourable grooming switch; goal-directed behaviour

Table 13. Results of the full model investigating the probability for the target individual to show persistence, elaboration or grooming termination when they had elicited a 'favourable' grooming switch from the partner (goal met) or not.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
intercept	-1.929	0.457	-8.994	-1.300			(1)	-8.062	-1.613
goal met(2)	**-2.959**	**1.119**	**-16.344**	**-1.515**	**15.156**	**1**	**<.001**	**-18.936**	**-2.715**
rank difference(3)	0.327	0.239	-0.181	1.136	2.058	1	.151	0.197	0.463
CAI(3)	-0.045	0.246	-0.606	0.422	0.034	1	.854	-0.238	0.186

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with goal met, where 'no' was the reference category; (3) Terms which have been z-transformed to a mean of zero and a standard deviation of one. Rows in bold text reflect significant variables (*p*<.05).

Model 5: Requesting a favourable grooming switch; goal-directed behaviour

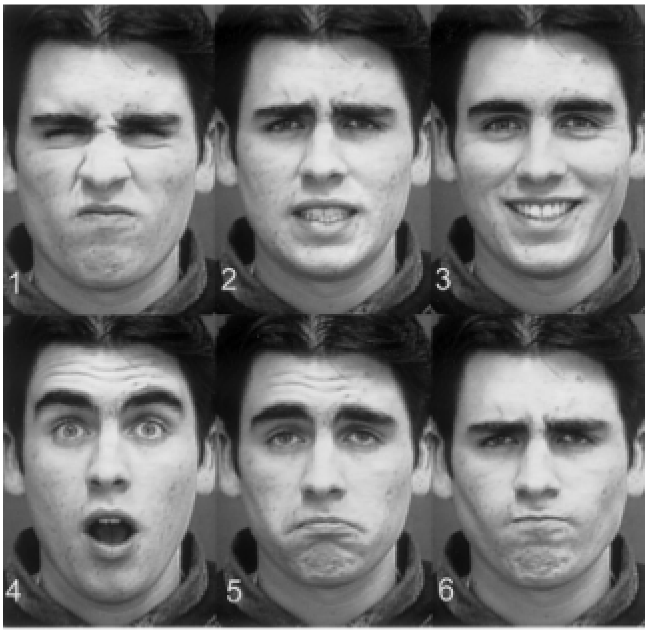
Table 14. Results of the reduced model investigating the number of exaggerated loud scratches produced by the target individual.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*
intercept	-7.153	0.179	-7.511	-6.833			(1)
rank.diff(2)	0.073	0.089	-0.107	0.246	0.617	1	.432
CAI(2)	-0.037	0.086	-0.231	0.131	0.191	1	.662

Key: (1) this value was not included, as this has a very limited interpretation; (2) Terms which have been z-transformed to a mean of zero and a standard deviation of one.

Appendix 5: Descriptions of coded facial expressions.

This item includes facial expressions that were coded in each study species in chapter 4. While all the below facial expressions were considered, my coding in chapter 4 did not differentiate between facial expression type (only expression present/expression absent/expressions unavailable).

Focal Individual	Definition/Picture
Human - mothers	There is strong evidence for the universal facial expressions of six emotions – anger, disgust, fear, joy, sadness, and surprise. I also coded a blend of the facial expressions joy and surprise (often associated with gasping) – this involved an open mouth, smile and eyebrows raised. Figure 1 shows exemplars of each of these expressions that I then used to code facial expressions in my data.  **Figure 1.** Basic human facial expressions: 1) Disgust; 2) Fear; 3) Joy; 4) Surprise; 5) Sadness; and 6) Anger. Images sourced from Schmidt & Cohn (2001) Lip-point This expression was understood to be common in the communities I examined in Uganda. It is a pouting facial expression, used as if to direct attention. See video for example: https://www.youtube.com/watch?v=6dpVEEwNFuA
Human - infants	Cry face/negative face A common infant reaction to negative situations. This involved lowered brows, lip corners pulled to the side and a variable degree of mouth opening and cheek raising (Oster, 2005). Their eye's may have been narrowed, squinted or squeezed closed (see Figure 2). These criteria

for negative-affect expressions were defined based on previous research by a variety of investigators of infant “cry faces” and negative emotional expressions (e.g. Messinger, 2002)

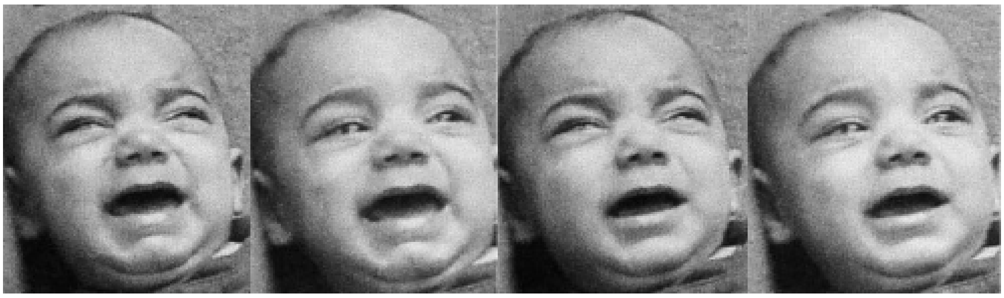


Figure 2. Exemplars of infant cry/negative face sourced from Messinger (2002)

Pouting

Pouting expressions often occur when infants appear to be trying to prevent crying. Here the brows would be raised and angular in appearance over narrowed eyes. The nasolabial folds would have been prominent, and the mouth corners were down-turned in a “horseshoe” shape (Oster, 1978). The chin was raised, and the mouth would usually have been closed (Figure 3).

Figure 3. Exemplars of infant pouting expressions sourced from Sullivan & Lewis (2003)

Smiling

A common infant reaction to positive situations. This involved cheek raising, lip corners pulled up to the side, and often with an open mouth. See Figure 4 for examples here.

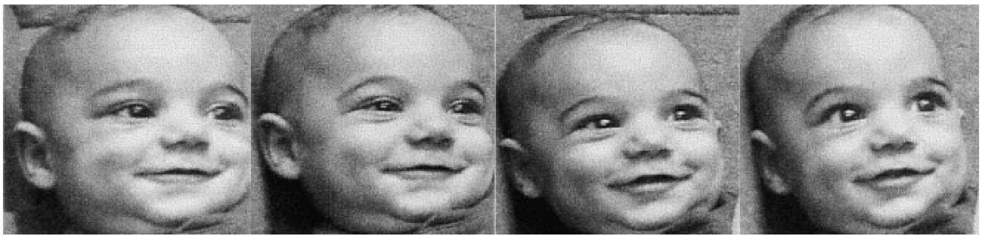


Figure 4. Exemplars of infant smiling expressions sourced from Messinger (2002)

Laughter or play face

Wide-open mouthed, gaping enjoyment expressions occur with characteristic vocalizations known as laughter (Figure 5). In intense forms of this expression, the lips may be rolled inward as the jaw gapes. Either form signals high excitement and positive arousal. Such expressions haven been called “play face” because they appear to be the human equivalent of a primate expression of the same quality (Preuschoft & van Hooff, 1997)

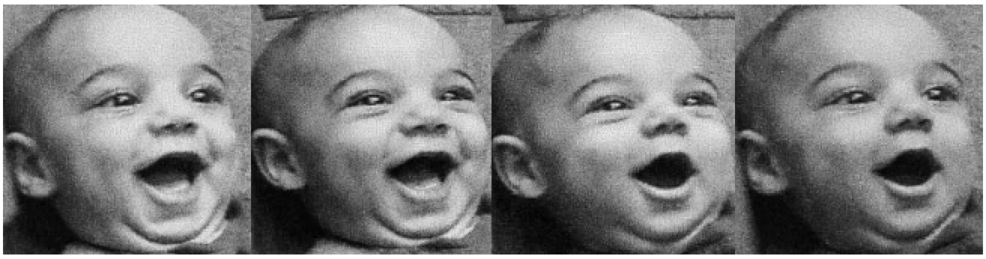


Figure 5. Exemplars of infant laughing or play face expressions sourced from Messinger (2002)

Surprise

Brows are raised and prominently arched. The eyes are widened so that the white of the sclera is more evident than in relaxed interest (Figure 6). The mouth gapes with jaw slackened, assuming an “o” shape, and may have been accompanied by abrupt, momentary stilling of other ongoing behaviour.

Figure 6. Exemplar of infant surprise facial expression sourced from Sullivan & Lewis (2003)

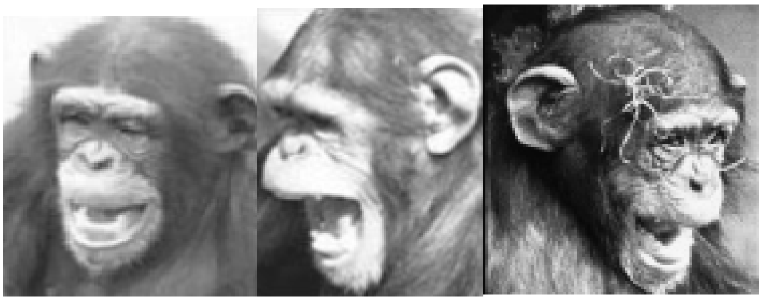
Fear

Not a very common expression in infants; when it has been observed it has been remarked as a negatively toned surprise expression involving brow straightening, tensed lower eyelids and/or lateral movement of the mouth corners (Figure 7).

	 **Figure 7.** Exemplars of infant fear expressions sourced from Sullivan & Lewis (2003) Disgust When the infant had narrowed or closed eyes, often with mouth gaping to eject bad-tasting substance. Nose wrinkling and upper lip raising are components of the full disgust reaction, but can occur alone as a less intense form of the reaction (Rosenstein & Oster, 1988). A closed mouth, either with corners down or retracted lips, is also a feature associated with milder aversive reactions. Figure 8 depicts examples of disgust expressions during infancy.  **Figure 8.** Exemplars of infant disgust expressions sourced from Sullivan & Lewis (2003)
Chimps – mothers and infants	**All images and descriptions for chimpanzee facial expressions were sourced from Parr & Waller (2006) and Parr et al. (2007)** Bared teeth display Open mouth, lips parted, a raised upper lip and retracted lip corners to reveal the teeth. 

Play face

Lowered jaw, lip corners stretched with the mouth open.

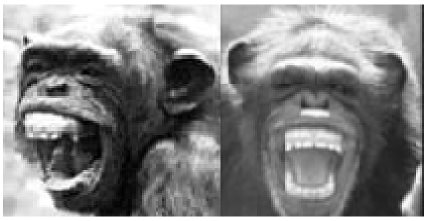


Pant hoot face

Here the lips would have been funnelled and parted, usually with the mouth open.

Scream face

Raised upper lip with lip corners pulled back, exposing the upper teeth. Mouth is wide open.



Pout

Here the chin would have been raised, with the lips funnelled and parted.

	Whimper Lip corners retracted, and lips funnelled and parted.  Ambiguous face A facial expression was produced, but not similar to, or a variant of, any of the other listed facial expressions.
Macaques – mothers and infants	Bared teeth display The upper and lower lips are vertically retracted to present the teeth, and is often accompanied by flattening the ears and raising the scalp (Whitehouse, Micheletta, Kaminski, & Waller, 2016). Image sourced from Waller, Whitehouse, & Micheletta (2016)  Yawn When males opened their mouths wide to deliberately expose their canines. The mouth would be opened slowly with head tilted back until the canines were revealed, and then their mouth would be quickly snapped shut. Image sourced from Micheletta, Whitehouse, Parr & Waller (2015) 

Teeth-chattering

When individuals rapidly opened and closed their mouths with their teeth exposed.

Lip-smacks

Here the lips were pursed, and the lower jaw would move up and down rapidly and rhythmically to produce a smacking sound. This excluded small lip or mouth movements made during grooming interactions. Figure 9 demonstrated the component parts of a lipsmack facial expression.

Figure 9. The component parts of lipsmack facial expressions (from left to right) scalp retraction, lipsmacks with scalp retraction, and lipsmacks with scalp retractions and head turns. Images sourced from Micheletta et al. (2013).

Greeting/scalp retraction

Ears are usually flattened with scalp retraction, and can be accompanied by teeth chattering.

Play face

Relaxed open mouth, similar to the chimpanzee play face. Image sourced from Micheletta, Whitehouse, Parr & Waller (2015)

Appendix 6: Descriptions of coded gestural signals.

This item includes gestural signals that were coded in each study species in chapter 4. While all the below gestures were considered, my coding in chapter 4 did not differentiate between gesture type (only gesture present/gesture absent/gesture unavailable).

Gesture	Definition
Human– mothers and infants	The following gesture descriptions were sourced from: Blake, O'Rourke, & Borzellino (1994); Carpenter, Mastergeorge, & Coggins (1983); Crais, Douglas, & Campbell (2004); O'Neill, Bard, Linnell, & Fluck (2005) Pointing When their finger was extended towards an object or event in the environment. Raising palms upwards When both palms were lifted in an upwards motion; usually used to emphasise a question (e.g. "where has it gone?"). Request reach When the subject reached out their hand to request an object. Shaking head When individual's shook their head from side to side to indicate 'no'. Nodding head When individual's nodded their head up and down to indicate 'yes'. Shrugging When individual's raised and lowered their shoulders. Waving Either with open or closed hand, waving from side to side. Blow kisses Bringing their own hand up to the mouth to kiss before moving the arm outwards, as if 'blowing kisses'

	Tactile gestures This could include hitting, slapping or grab-pulling (tug) which had to be delivered with some force (must have been salient) or to have occurred repeatedly. This category also included embracing (hugging another with both arms), nuzzling (rubbing their head or face on another in an affectionate way) and kissing.
Human– mothers only	The following gestures were coded only for the mothers (sourced from: O’Neill, Bard, Linnell, & Fluck, 2005) Indicate An object or event was singled out through movements of the head or hand towards the object or event, or direct contact with (i.e. tapping or touching) the object or location of the event. Beckoning Beckoning with either the whole hand or the index finger. Clap hands When the subject clapped their hands together.
Human– infants only	The following gestures were only coded for the infants (sourced from: Blake, O’Rourke, & Borzellino, 1994; Carpenter, Mastergeorge, & Coggins, 1983; Crais, Douglas, & Campbell, 2004) Reaching Arm extended, hand open, with the palm either facing down or with the hand opening and closing towards the intended person or object. Offer When the infant reached out and gave a toy or object to another person. Eye-contact was maintained during the interaction (did not include dropping the toy). Raising arms/carry requests Extending arm(s) upwards to signal a desire to be carried. One or both arms were raised toward another person. Show When an arm was extended to show an object in hand.

Chimp – mothers and infants	All chimpanzee gestures were selected from the Byrne et al. (2017) "St. Andrews Catalogue of great ape gestures" Arm(s) raise The signaller raised their hand(s) or arm(s) vertically above their shoulder. I excluded events here that resulted in scratching, or holding onto objects (e.g. tree branches during grooming) Exaggerated loud scratch (termed Big Loud Scratch) Defined as loud exaggerated scratching movement on the signaller's own body. For this I included the operational criteria used in chapter 3 of this thesis: the scratch needed to be a minimum of 15cm in length, and at least 2 strokes; the movement needed to be the whole arm and not just from the wrist. Scratches were not included if they resulted in self-grooming (pulling hair or examining own hand after scratch). Embrace When the signaller wrapped their arm(s) around a recipient and maintained physical contact. However, cases of clinging/nursing were excluded (needed to be briefer than this) Reach hand/wrist Arm was extended to the recipient with their hand in open, palm exposed position (no contact) or with wrist or back of hand extended towards recipient Tactile Here I compiled numerous tactile gestures which are outlined by Byrne et al. (2017) including hitting, slapping, pushing or grab-pulling (tug). These gestures needed to be delivered with some force (must have been salient) or have occurred repeatedly.
Macaques – mothers and infants	Names and descriptions for gestures for the Sulawesi crested macaques were taken from the Macaca Nigra Project long term data. Missed hit When an individual attempted to hit another individual but did not touch them, similar to 'swat' in chimpanzees (Byrne et al., 2017).

Support shake
When an individual was stood on a branch or another object, and would shake or jump on this support. It is a “show off” behaviour, similar to ‘object shake’ in chimpanzees (Byrne et al., 2017).

Hug
When an individual used one or both hands/arms and wrapped them around the body of another; ‘embrace’ in chimpanzees (Byrne et al., 2017).

Mock bite
A soft bite on the body of a social partner in an action of play or copulation.

Hip holding
When an individual placed their hand on or grasped the hips of another, often accompanied by affiliative behaviours

Reach
As for the chimpanzees, with an arm extended toward a recipient.

Scratch
Defined as vigorous and fast scratching on the individuals own body with their hand or foot, which involved movement of their whole arm or leg (not just small movements of their fingers or hand/foot). Cases were excluded if they were part of self-grooming.

Head flick
When the individual’s head was flicked back in a quick motion.

Tactile
A compilation of numerous tactile gestures including hitting, slapping, pushing or grab-pulling (tug). These gestures needed to be delivered with some force (must have been salient) or have occurred repeatedly.

Appendix 7: Extended model results for chapter 4.

Model 1: Triadic attention events

Table 15. Results of the model investigating the probability for there to be triadic attention with mutual face direction, exploring the influence of species.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
Intercept	-0.060	0.327	-31.923	-0.835			(1)	-18.621	-1.935
speciesHuman(2)	2.127	0.954	0.750	31.967	7.696	2	.021	1.658	18.551
speciesMacaque (2)	1.294	1.002	-0.458	30.738				0.800	17.783

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with species, where 'chimpanzees' was the reference category. The indicated test refers to the overall effect of species.

Model 2: Triadic attention with communication events

Table 16. Results of the model investigating the probability for there to be triadic attention with mutual face direction and communication, exploring the influence of species.

Term	Estimate	SE	Lower CI	Upper CI	X^2	df	*P*	min	max
Intercept	-2.009	1.101	-33.237	-0.511			(1)	-18.603	-1.669
speciesHuman(2)	1.929	1.136	0.165	33.135	6.091	2	.048	1.590	18.523
speciesMacaque (2)	0.587	1.366	-73.332	31.403				-0.128	17.183

Key: (1) this value was not included, as this has a very limited interpretation; (2) This term was dummy coded with species, where 'chimpanzees' was the reference category. The indicated test refers to the overall effect of species.

Appendix 8: Summary of experimental trials conducted in chapter 4, study 2.

The following table provides a summary of the objects presented in each experimental trial (study 2, chapter 4), with the number of engaged individuals per trial and a breakdown of the age and sex classes of participating individuals. Within each trial, maternally related kin are indicated with an asterisk (*). If more than one family group was present, the second family is indicated with by double asterisks (**).

Novel object	Number of participants that engaged	Participant IDs	Sex	Age class
Chimpanzees, researcher led				
Mirror ball	3	FC*	Female	Juvenile
		HZ	Male	Juvenile
		NU*	Female	Juvenile
Mirror ball	4	CI*	Female	Infant
		KZ*	Female	Juvenile
		SP	Female	Juvenile
		PN*	Female	Adult
Mirror ball	8	WJ**	Male	Infant
		WC*	Male	Juvenile
		WO*	Female	Juvenile
		WZ**	Male	Juvenile
		BO	Male	Adult
		NP	Female	Adult
		WA**	Female	Adult
		WL*	Female	Adult
Mirror ball	2	DS	Male	Juvenile
		AI	Female	Adult
Mirror ball	2	OTB*	Male	Juvenile
		OM*	Female	Adult
Mirror ball	2	TZ*	Male	Infant
		TR*	Female	Juvenile
Wooden snake	4	AO*	Male	Infant
		AE*	Female	Juvenile
		AN*	Female	Juvenile
		AL*	Female	Adult
Wooden snake	4	TZ*	Male	Infant
		OL	Female	Juvenile
		TR*	Female	Juvenile
		TG*	Female	Adult
Macaques, researcher led				
Mirror ball	8	UnkJuv02	Unknown	Juvenile

		UnkJuv03	Unknown	Juvenile
		UnkFSubAdu01	Female	Sub-adult
		UnkFSubAdu02	Female	Sub-adult
		UnkAdu01	Unknown	Adult
		UnkAdu02	Unknown	Adult
		UnkAdu03	Unknown	Adult
		AU	Female	Sub-adult
Mirror ball	10	KP6B	Male	Infant
		UnkInf01	Unknown	Infant
		UnkInf02	Unknown	Infant
		UnkInf03	Unknown	Infant
		UnkJuv18	Unknown	Juvenile
		UnkJuv19	Unknown	Juvenile
		UnkJuv20	Unknown	Juvenile
		UnkJuv21	Unknown	Juvenile
		UnkMSubAdu01	Male	Sub-adult
		HA	Female	Adult
Mirror ball	10	JA1B	Male	Infant
		KA1B	Female	Infant
		QP4B	Male	Infant
		UnkInf16	Unknown	Infant
		UnkJuv32	Unknown	Juvenile
		UnkJuv33	Unknown	Juvenile
		UnkJuv34	Unknown	Juvenile
		UnkJuv35	Unknown	Juvenile
		XP4B	Male	Juvenile
		YP5B	Male	Juvenile
Wooden snake	10	UnkJuv04	Unknown	Juvenile
		UnkJuv05	Unknown	Juvenile
		UnkJuv06	Unknown	Juvenile
		UnkJuv07	Unknown	Juvenile
		BG	Male	Adult
		FP	Female	Adult
		UnkFAdu01	Female	Adult
		UnkFAdu02	Female	Adult
		UnkFAdu03	Female	Adult
		UnkFAdu04	Female	Adult
Wooden snake	11	UnkInf13	Unknown	Infant
		UnkInf14	Unknown	Infant

		UnkInf15	Unknown	Infant
		UnkFJuv01	Female	Juvenile
		UnkFJuv02	Female	Juvenile
		UnkJuv27	Unknown	Juvenile
		UnkJuv28	Unknown	Juvenile
		UnkJuv29	Unknown	Juvenile
		UnkJuv30	Unknown	Juvenile
		UnkJuv31	Unknown	Juvenile
		UnkFAdu05	Female	Adult
Wooden snake	10	CA2B	Male	Infant
		UnkInf17	Unknown	Infant
		UnkInf18	Unknown	Infant
		CP5B	Male	Juvenile
		KP6B	Female	Juvenile
		UnkJuv36	Unknown	Juvenile
		UnkJuv37	Unknown	Juvenile
		UnkJuv38	Unknown	Juvenile
		UnkFSubAdu03	Female	Sub-adult
		FM	Male	Adult
Wooden snake	10	UnkInf25	Unknown	Infant
		UnkInf26	Unknown	Infant
		UnkInf27	Unknown	Infant
		UnkFJuv04	Female	Juvenile
		UnkFJuv05	Female	Juvenile
		UnkJuv41	Unknown	Juvenile
		UnkJuv42	Unknown	Juvenile
		UnkJuv43	Unknown	Juvenile
		UnkFSubAdu04	Female	Sub-adult
		UnkMAdu01	Male	Adult
Orange hippo	3	FP6B	Female	Infant
		KP6B	Male	Infant
		UnkJuv01	Unknown	Juvenile
Orange spoon	12	CA2B	Male	Infant
		UnkJuv08	Unknown	Juvenile
		UnkJuv09	Unknown	Juvenile
		UnkJuv10	Unknown	Juvenile
		UnkJuv11	Unknown	Juvenile
		UnkJuv12	Unknown	Juvenile
		UnkJuv13	Unknown	Juvenile
		UnkJuv14	Unknown	Juvenile
		UnkJuv15	Unknown	Juvenile

		UnkJuv16	Unknown	Juvenile
		UnkJuv17	Unknown	Juvenile
		UnkAdu04	Unknown	Adult
Pink Octopus	10	FP6B	Female	Infant
		UnkInf04	Unknown	Infant
		UnkInf05	Unknown	Infant
		UnkInf06	Unknown	Infant
		UnkInf07	Unknown	Infant
		UnkJuv22	Unknown	Juvenile
		UnkSubAdu03	Unknown	Sub-adult
		UnkSubAdu04	Unknown	Sub-adult
		UnkSubAdu05	Unknown	Sub-adult
		HG	Male	Adult
Macaques, naturally found				
Green Bucket	10	FP6B	Female	Infant
		UnkInf08	Unknown	Infant
		UnkInf09	Unknown	Infant
		UnkInf10	Unknown	Infant
		UnkInf11	Unknown	Infant
		UnkInf12	Unknown	Infant
		UnkJuv23	Unknown	Juvenile
		UnkJuv24	Unknown	Juvenile
		UnkJuv25	Unknown	Juvenile
		UnkJuv26	Unknown	Juvenile
Orange vest	2	UnkSubAdu01	Unknown	Sub-Adult
		UnkSubAdu02	Unknown	Sub-Adult
Orange vest	10	NP5B	Male	Infant
		UnkInf19	Unknown	Infant
		UnkInf20	Unknown	Infant
		UnkInf21	Unknown	Infant
		UnkInf22	Unknown	Infant
		UnkInf23	Unknown	Infant
		UnkInf24	Unknown	Infant
		UnkMInf01	Male	Infant
		UnkMInf02	Male	Infant
		UnkFJuv03	Female	Juvenile

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