

Why Does the Chimpanzee Vocal Repertoire Remain Poorly Understood? And What Can Be Done About It.

Catherine Crockford¹

¹ Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany

In: The Tai Chimpanzees: 40 years of Research. Editors: Christophe Boesch and Roman Wittig. Cambridge University Press. In Press.

Abstract

After decades of research, the origins of human speech remain little understood. One potential problem is that the vocal repertoires of humans' closest living relatives, the apes, remain poorly described. Given that the evolution of language has left few fossils, many researchers interested in this question adopt a comparative approach, examining differences and consistencies between human and animal communication. However, comparisons will remain limited in the absence of a comprehensive analysis of the vocal repertoires of the other extant apes, especially of our two closest living relatives, the chimpanzee and bonobo.

After years of observing and conducting field experiments with both western chimpanzees in the Tai Forest, Ivory Coast, and eastern chimpanzees in the Budongo Forest, Uganda, I posit several reasons why a comprehensive analysis of the chimpanzee vocal repertoire has not yet been completed, in spite of 45 years of research, and what can be done to remedy this situation. I raise four main problems and later present potential solutions: a) How do we categorise graded calls into information-specific units? b) Why are most call types emitted in most contexts? c) If different call types are combined flexibly within the same context, can calls be tied to emotional states? d) The constraints – and advantages – imposed by dense forest habitat. I also tabulate cross-site consensus in call categorisation, associated contexts of usage, and potential call functions. I also note cross-site variation in presence and absence of vocalisations.

Anecdote

After an intense three years observing Taii chimpanzees and listening to their vocalisations for my PhD, I was not to return to the Tai Forest for 17 years. On my first day back with the North Group, after walking through the forest in the dark, I arrived at a group of females as dawn was breaking. I heard through the forest a pant-hoot so familiar, a shiver of pleasure ran down my spine. This was the voice of Narcisse, one of the youngest mothers in the North Group 17 years earlier. Three minutes later, Narcisse walked into view with a baby on her back, and with her adult daughter, granddaughter, and adult son close behind her. This whole remarkable family had survived the devastating epidemics that had ravaged the group in the intervening years. The pattern of her distinctive pant-hoot had not changed in 17 years, likewise those of the other three adult females I had known 17 years earlier, Mystere, Perla, and Belle.

Even though the pant-hoot is emitted in a number of contexts, shows greater within than between individual variability, and shows group and population differences, something in the quality and the rhythm of the call is retained year in and year out and as with human voices, is a robust marker of individual identity. This begs the question, why do chimpanzees have such a robust marker of individual identity? Why do they, nonetheless, express this – and other calls - with such extensive acoustic and contextual variability?

Introduction

Aspects of human communication that are unique to our species are multiple. However, whether there is continuity or discontinuity with our communication skills and those of other primates is a point of much debate and active research. One reason that this remains unresolved is our limited understanding of the vocal repertoires and vocal usage of our closest living relatives, the chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*). To date, we do not even have a method of analysis that enables direct comparison of human and *Pan* produced vocalisations. This failure is not through lack of research effort but more demonstrates the complexity of the task at hand. The vocal repertoires of both *Pan* species are highly graded, with a complex system of usage so that most call types are emitted in most contexts, and many in a flexible combinatorial form (Crockford & Boesch 2005; Schamberg et al. 2017). This pattern has been interpreted as indicating that the calls likely convey little specific information but more likely convey emotion (Goodall 1986). However, features of the system I describe sound remarkably human – highly graded sounds, emitted in multiple contexts and in flexible combinations. Thus, the assumption that the *Pan* vocal systems are emotional and convey little context-specific information may be false and requires further assessment.

The task of delineating what is a unique vocalisation that conveys unique information however is not easy in a graded call system in a thick forest or hilly habitat, where at least for long-distance calls, observers can usually only see the signaller or the receiver, not both at the same time. Achieving this goal requires detailed observations, thorough acoustic analysis, and field experiments (Crockford et al. 2004; Herbinger et al. 2009; Crockford et al. 2017, 2018). I address four main problems that currently limit possibilities to further understand the chimpanzee vocal repertoire, and potential solutions to these problems. Here, I do not address how these problems might apply to vocal research in bonobos or other species with graded repertoires, but as some of the same problems are likely to apply, I hope these ideas will also be useful to other vocalisation researchers. The four main problems are a) call categorisation within a graded system; b) the call type and context fluidity conundrum; c) the call *combinations* and context fluidity conundrum; d) downsides – and upsides - to forest and other low visibility environments. Resolving these problems will facilitate within-site and cross-site consensus in call categorisation of chimpanzee vocalisations. Without this, we are limited in our capacity to compare repertoire usage within and across-sites. Studies already show variation in call types present across sites. Table 1, for example, shows that the voiceless ‘raspberry’ call has been noted as present in some sites and completely absent in others (Nishida et al. 2004; Pika 2014). My own observations also suggest variation in call usage across sites.

Call Categorisation within a Graded System

There are inherent problems in determining how many call types there are in a vocal repertoire. This is particularly so when the calls are not discrete, acoustically distinct units, but are graded (Hammerschmidt & Fischer 1998), such that the mean acoustic structure of a particular call type is discernible from the mean acoustic structure of another call type - like the difference between dog barks and growls, or human vowels, but the edges of the distribution of the acoustic structure cannot be discerned. In humans, categorising a sound as a /i/ or /e/ is socially learned, and depends on the language – or accent - one speaks, or the word or string of words that one utters (Hagiwara 1997). Humans (Chang et al. 2010) – and Barbary macaques (Fischer 1998) – thus use categorical perception to categorise graded calls that are associated with different contexts.

Chimpanzee calls are highly graded (Crockford & Boesch 2003), thus delineating call boundaries is problematic. Standard procedures of acoustic analysis to examine animal vocalisations (Fischer et al. 2001; Rendall et al. 1999) have rarely been used to differentiate chimpanzee call types. Of those studies, a disproportionate number have focused on the species typical long distance call, the pant-hoot (Gombe: Uhlenbroek 1996, Mitani 1992; Mahale and Ngogo: Mitani et al. 1999; Mitani et al. 1992; Tai: Crockford et al. 2004; Sonso: Notman & Rendall 2005; Kanyawara and Sonso: Fedurek et al. 2014; Fedurek et al. 2013). Even though chimpanzees have context-specific food-associated calls, which is rare and of theoretical interest in animals, as food-associated calls generally function to recruit others to join at the food source and are thus inviting competition (Heinrich & Marzluff 2017; Gros-Louis 2004; Clay et al. 2012). No study has yet conducted an acoustic analysis to identify the chimpanzee food-call from other calls in the chimpanzee repertoire, making this interesting phenomenon unavailable to non-chimpanzee researchers. Note, however, that a couple of studies have used acoustic analysis to assess whether the extensive acoustic variation noted within food-associated grunts contains context-specificity in terms of whether information about food preferences or food type is encoded in the call (Captive: Slocombe & Zuberbühler 2005; Tai chimpanzee: Kalan et al. 2015).

Jane Goodall (van Lawick-Goodall 1968; 1986) was the first to fully describe the chimpanzee call repertoire, linking calls that she could differentiate by ear to social or environmental contexts. She described 32 calls. Others have described the repertoire, ranging from 12- 31 call types (Table 1; Captive: van Hooff 1973; de Waal 1988; Gombe: Marler 1976; Kanyawara: Clark 1991; Tai: Crockford 2005). Each major call type has been classified into different call variants mainly by ear and association to specific contexts (Goodall 1986). Screams, for example, were classified by Goodall (1986) into copulation screams, SOS screams, tantrum screams and victim screams; barks into soft-bark, pant-bark, bark, waa-bark; grunts into pant-grunt, food-grunt, soft-grunt, extended-grunt, nest-grunt; hoos into hoo, various pant-hoots and huu; pants into pant, copulation-pant, and laugh. A number of these vocalisations have been further investigated in the same or different chimpanzee populations (see **Table 1**). Even though descriptions of chimpanzee vocal repertoires vary, the call names used in all repertoires are mainly made up of these five call types: screams, barks, hoos, grunts and pants, with additional modifiers indicating combinatorial calls, the context of calling, or variation in the sound of the call, such as pant-grunt, food-grunt, huu respectively (van Lawick-Goodall 1968; Goodall 1986; Mitani 1996). See **Table 1** for a summary of the call types, their associated contexts of usage and their potential function, synthesised from different chimpanzee vocalisation studies.

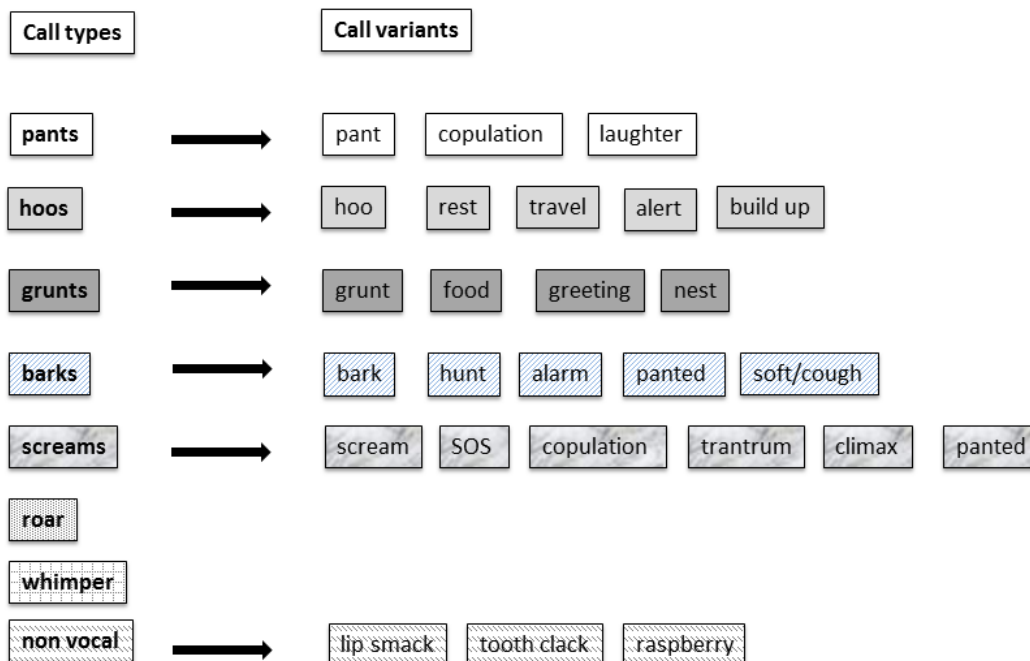
[Table 1: See additional file]

To overcome some of these long-standing problems of categorising call types, I suggest here that an easier way to organise the chimpanzee vocal repertoire is by using a hierarchical structure, centred around the major call types that are unanimously used across researchers and field sites (**Fig. 1**). The vast majority of chimpanzee calls are variants of either screams, barks, grunts, hoos, or pants (Gombe: Goodall 1986; Captivity: DeWaal 1988; Tai: Crockford 2005; **Table 1**).

A step long overdue is to confirm and describe the acoustic space occupied by each call and the acoustic markers that distinguish each from other calls using acoustic analysis. Some questions to consider include the following: Are pant-grunts, emitted by subordinates to dominants during greeting contexts, identifiable to us and chimpanzees as such because they are panted, or produced in rapid succession, or because a single grunt within a pant-grunt is acoustically differentiable from a single food-grunt? Is this call distinct from food-grunts, which are emitted as sequences of unpanted grunts, because the individual grunts in the call are distinct or because the combination of the grunt with the pant is context-specific? Since an analysis has not been conducted, we do not yet know the answer to any of these questions.

In the future, we would like to conduct acoustic analyses across the chimpanzee repertoire to examine the acoustic relationships between a) major call types and b) call variants of each call type.

Figure 1. Hierarchical representation of the chimpanzee vocal repertoire, using consensus between field sites to define call types and associated call variants.



When determining repertoire size, researchers become ‘lumpers’ or ‘splitters’, lumping acoustically similar calls together or splitting them up using different labels. Given that repertoire size is often associated with ‘contexts of production’ and ‘potential information content of calls’, repertoire size is likely to be considerably affected by research effort. Even in species typically considered to have a more discrete call system, such as chacma baboons, studies targeting grunts or barks have discerned graded acoustic differences (Rendall et al. 1999; Fischer et al. 2001). These studies used acoustic analysis to discern clusters of different call variants. They then determined if the different variants elicited different behaviour during playback experiments, when conspecifics hear each call variant from a hidden loud speaker in the absence of the caller or associated context (for explanations of field experiment methods see Wittig & Crockford 2018).

In chimpanzees, similar studies have been conducted for barks and hoos, and have revealed context-specific variation, identifying acoustically different context-specific call variants that were not previously identified (**Table 1**). For examples, using acoustic analysis, Christophe Boesch and I (Crockford & Boesch 2003) determined that the hunt-bark is context-specific and acoustically different from other barks. The hunt-bark that exists in Taï and Budongo chimpanzees has been mentioned for Ngogo chimpanzees (Mitani & Watts 1999) but has not been listed by Goodall (Goodall 1986) for Gombe chimpanzees. For Taï chimpanzees, we were also able to acoustically characterise the alarm-bark (wraa in Goodall 1986) distinguishing it from other bark variants. Likewise, in studies from Thibaud Gruber, Klaus Zuberbühler, and myself with Budongo chimpanzees, we were able to show that there is not only the ‘surprise huu’, noted by Goodall (1986), and called the alert-hoo by us, but also two other context-specific, acoustically identifiable hoos, the ‘rest’ (the soft grunt and extended grunt in Goodall 1986) and the ‘travel’ hoo (Gruber & Zuberbühler 2013; Crockford et al. 2014; Crockford et al. 2018). Playback experiments of rest-hoos or alert-hoos elicited different behavioural responses, indicating that these hoos convey different information to receivers, even when only one short, quiet hoo was played back (Crockford et al. 2014; Crockford et al. 2018). It is highly likely that further research will reveal more acoustically graded calls that nonetheless convey context-specific information to receivers.

BOX

The Benefits of Understanding Chimpanzees and their Social World.

Chimpanzees, as our closest living relatives along with bonobos, hold the potential to offer us important insights into ourselves and our species. One of the most striking facets that we share with chimpanzees – and which is perhaps the darkest and hardest for us to understand of ourselves – is that a chimpanzee, like a human, can appear deeply nurturing and empathetic one moment and can kill another in the next. They can carry, groom, and share food with a young orphan, with a cost to themselves and with no apparent immediate gain. They can be apparently altruistic, coming to the aid of others even when the act itself endangers them. Then the context changes and suddenly the same individual attacks or kills a stranger, or even kills the infant of a group member. There are perhaps not many species of animal on this planet, besides humans, that can be both empathetic and murderous. Understanding ultimate and proximate dynamics of these behavioural extremes in another species may help us to predict them better in ourselves. Understanding how chimpanzees communicate their motivations and intentions, and how communication may facilitate cooperation, are a crucial part of this process.

The Call Type and Context Fluidity Conundrum

Although hierarchical delineation of calls according to their acoustic structure may be helpful, attempting to map these into context introduces a second problem. In chimpanzees, most call types are produced in most contexts. While there is likely to be a context-specific food-grunt (Captivity: Slocombe & Zuberbühler 2005; Kanyawara: Fedurek & Slocombe 2013; Sonso: Schel et al. 2013; Tai: Kalan et al. 2015), barks, screams, and hoos are also emitted in food-contexts. Screams, which are mainly considered to be associated with a defensive reaction in aggression, are emitted during copulation (Sonso: Townsend & Zuberbühler 2009; Fallon et al. 2016), feeding, and travel (climax screams in pant hoots), in the total absence of any overt aggression. Grunts are given in food contexts, greeting contexts as a sign of subordination, and during nesting.

The pattern that most call types are emitted in most contexts led scientists to conclude early on that chimpanzee vocalisations are highly emotional and contain little context-specific information (Goodall 1986). This view was reinforced with an early research focus on the species typical long-distance call, the pant-hoot. Pant-hoots are given in many contexts: travel, food, resting, nesting, waiting, within- and between-group aggression (Goodall 1986). Even though a number of studies have shown greater within than between individual variability in pant-hoot acoustic structure (Mitani et al. 1996; Notman & Rendall 2005; Crockford et al. 2004), only a couple of studies could show some acoustic consistency with context (Notman & Rendall 2005; Uhlenbroek 1996).

However, as more studies are conducted with respect to context-specificity, the idea that chimpanzee vocalisations only convey emotion is difficult to sustain (Schamberg et al. 2018). Chimpanzees do indeed have a number of context-specific calls in their vocal repertoire. The search of context-specific calls in animal communication research has been largely limited to alarm contexts, and the search for predator-specific alarm-calls (Seyfarth et al. 1980; Price & Fischer 2014; Fischer & Price 2017). In chimpanzees, context-specific calls have been identified using acoustic analyses in a range of additional contexts, such as hunt-barks (emitted whilst hunting monkeys, Crockford & Boesch 2003) and three hoo variants emitted during rest, travel, or to hidden threats such as Gaboon vipers or snares, respectively (Crockford et al. 2018; Crockford et al. 2014).

The emerging picture that chimpanzee calls are highly graded but also context-specific – and also produced across contexts - has lead us to consider the function behind the emission of particular call types. Why emit screams – or hoos - across a range of apparently very different contexts? If chimpanzee calls are supposed to be mainly emotive, one would expect a common underlying emotion to instigate the emission of screams – or of hoos. Given the contexts of emission mentioned above, this however seems unlikely. What seems more likely is that call type may delineate a particular underlying goal, as Isaac Schamberg, Roman Wittig, and I recently suggested (Schamberg et al. 2018). Hoos as a call type, for example, may function to keep the current party of chimpanzees together. However, in dense forest habitat further information may be required to be encoded in the hoo to achieve this goal, requiring further acoustic differentiation.

For example, if a chimpanzee is resting and emits a hoo with the goal (intentional or otherwise) of staying together with present individuals, the receivers need to stay put to achieve the goal. If a chimpanzee wants

to begin to travel and has the goal of staying together with present individuals, the receivers need to also start travelling to achieve the goal. In dense forest habitat, individuals 20 m apart often cannot see each other and thus visual and other cues that could provide additional context become unreliable. Thus, if hoos emitted during resting or travelling carry acoustic markers of the rest or travel context, receivers invested in remaining with the signaller, can act appropriately (Schamberg et al. 2018).

The caller-goal framework offers a useful way to structure and understand the chimpanzee vocal repertoire. Though playback experiments have been conducted with rest- and alert-hoos, playback experiments of other vocalisations in other contexts are required to determine whether call variants convey context-specific information to receivers. Even though I recommend the use of playback experiments with chimpanzees, I also advocate using extreme caution when conducting said experiments. Our experience has shown that chimpanzees can react strongly to even a single quiet hoo, changing their travel direction, ranging, and social pattern for the day. This makes designing playback experiments that test what you want them to test a daunting task which is unlikely to work without months of detailed prior observations.

Years of observations and field experiments has helped us build associations between call types and contexts of production. We are now in the process of conducting a (non-exhaustive) vocal repertoire-wide acoustic analysis to chart the acoustic characteristics of major call types, call variants, and associated contexts of production, with a view to aiding comparison with human speech.

Call Combinations and Context Fluidity

A third problem that has hindered clear demarcation within the chimpanzee vocal repertoire is that at least half of the chimpanzee vocalisations are produced as call combinations, where strings of more than one call type are emitted in sequence (Taï: Crockford & Boesch 2005), and they are often used in relatively flexible combinations with other calls. Thus, categorising call types relative to contexts of usage is further complicated, especially as acoustic analysis is often conducted at the single unit level.

The classic example of a combinatorial chimpanzee call is the pant-hoot. This call can be divided into sections, all or only two of which may be emitted. First individual hoos can be emitted (the introduction), followed by a short-to-long series of panted hoos (the build-up), followed by a short or long series of drums, followed by one or several climax screams, hoos, or barks (the climax phase), followed by a 'let-down' phase or roar (Mitani et al. 1992; Notman & Rendall 2005; Crockford et al. 2004). Thus within a 'single' call, the pant-hoot, almost every call type within the chimpanzee repertoire can be included. A further quandary is that pant-hoots, as mentioned above, can be emitted in any number of contexts, the apparent goal is to maintain contact or recruit individuals hundreds of meters away (Eckhardt et al. 2015).

Thus, while emotion is undoubtedly conveyed in this call, to say that the emission of this call is driven by emotion seems problematic. Which emotion? The emotion associated with hoos, screams, drums, pants, or barks? Again, perhaps it is more likely that each part of the pant-hoot has a function that helps achieve a particular goal. The panted hoos in the build-up phase, for example, may be required to pump air into the air sacs to achieve the incredibly high, fundamental frequency of the climax scream. The climax scream is possibly the most powerful call in the chimpanzee repertoire, carrying the furthest and having

the highest fundamental frequency, with males achieving climax screams with a higher fundamental frequency than females (Grawunder et al. 2018), and that likely travel further through the forest. The climax scream seems designed as a contact call and indicator of benign or affiliative intent, often resulting in the recruitment of other individuals to the party, whilst travelling, resting, or within a food tree. [See (Silk et al. 2016) for a framework for examining the vocal signalling of behavioural intent in chacma baboons]. Chimpanzees rarely give climax screams in intergroup contexts, replacing them rather with climax barks in Tai chimpanzees and/or roar pant-hoots, and with roar pant-hoots in Budongo chimpanzees (personal observation). Given that intergroup encounters are almost exclusively hostile, this suggests that barks and roars are indicators of aggression, and possibly even of aggressive intent. Pant-hoots also carry robust markers of individual identity as noted in the anecdote above.

Downsides – and Upsides - to Forest Practicalities

A fourth barrier to mapping the chimpanzee vocal repertoire is the habitat in which chimpanzees live. For forest, and even savannah-living chimpanzees, much of the habitat is dense, unyielding or hilly, and requires months of training to be able to navigate it at a similar speed to a chimpanzee. Only when you can keep up with the chimpanzees, following them not from behind but at their side, can you see what they see, and are privy to their social interactions. Most chimpanzee communication happens in the minutes leading up to, or immediately after, social change, such as parties meeting or when greetings are exchanged. Here, fights may break out, copulations happen, or there is intense affiliation. Likewise, much vocal communication happens when encountering something relevant in the environment, such as a food tree or a threat. Thus missing the first minutes after a social or environmental change can often leave researchers scratching their head wondering what all the noise was about. Therefore *being able to see what the chimpanzee sees as the chimpanzee sees it* is paramount to understanding chimpanzee communication.

An additional note for all students heading out to do any chimpanzee research, especially in field sites where working together with an experienced field assistant is obligatory: be sure that you are not relying on your experienced local field assistant to see social interactions for you. Ensure that you are following the chimpanzees rather than following the field assistant. If the latter happens, you will see a lot of the field assistant and little of your study subjects.

Another huge disadvantage to understanding chimpanzee vocalisations due to dense forest habitat is that one can often only see one side of the vocal exchange – either the caller or the receiver. This makes piecing together associations between calls, context, and subsequent changes in receiver behaviour challenging, especially for long-distance calls. Thus, the study of close calls, where both signaller and receiver are often visible, and which we have shown can be nuanced and context-specific (Crockford et al. 2014, Crockford et al. 2017, 2018) may be more productive.

There is, however, an advantage that the forest habitat offers. Since visibility is often very limited, one can experience natural quasi-playback experiments every day. Several times a day your focal chimpanzee may be visually alone (all other chimpanzees are out of sight), but acoustically not alone (your focal can still hear other chimpanzees around). When you and your focal chimpanzee simultaneously hear a call, it is often possible to predict whether and how the focal will react to the call based on the 1) call type, 2) the

caller, 3) the relationship of the caller to the focal (relative dominance and bondedness), and 4) the previous recent history of social interactions between the focal, the caller, and their close associates. Whereas identifying callers from their vocalisation is not easy for all call types, pant-hoots, pant-grunts, screams, and food-grunts, some individuals can be relatively quickly and reliably identified (Mitani et al. 1996). Observations of daily ‘quasi-playback experiments’ helped us to design a playback experiment we conducted showing how chimpanzees track third-party relationships and react to calls they hear based on the four factors mentioned above (Wittig et al. 2014).

When conducting playback studies, each team member carries a two-way radio. This has given us the possibility to verify the caller identity hundreds of meters from our focal. When we hear a call we can directly ask over the radio if an observer saw and could identify the caller and determine their behaviour immediately prior to and after calling. Using this method, we have made some astonishing observations, particularly regarding the lengths chimpanzees go to offer support to their bond partners. On one such occasion with the Budongo chimpanzees, I was alone with a lactating female, Nambi, and her adolescent daughter, Nora, as both were resting. Two adolescent males, Zalu and Kwezi, showed up and started displaying at the females, a behaviour adolescent males frequently engage in as they try to manoeuvre from being treated as subordinate to dominant by adult females. After Nambi and Nora screamed, we heard pant-hoots far away and made radio contact to determine if the callers could be identified.

A field assistant, Jackson Okuti, was with the callers: two males, Nick - the alpha and a friend of Nambi, and Musa, both the beta male and Nambi’s son. Jackson reported that they were feeding in a tree in a grid reference 1 km away. Jackson heard screams from our direction at which point the two males pant-hooted, left the feeding tree, and walked for ten minutes in a straight line without stopping until they reached Nambi and Nora. Upon arriving, both males pant-hooted, drummed, and displayed, however both adolescent males had long since disappeared. Although these adolescent males posed no real threat to Nambi and Nora, their supporters left their food tree and travelled a kilometre after hearing the screams of their kin and bond partner. Our two-way radio experience showed that not responding to the screams of kin or a bond partner is much rarer than responding, with responses being either in the form of pant-hooting, barking, approaching the individual screaming or intervening. These observations suggest that screams function to recruit supporters, even over long distances, and that receiving support as a result of calling is relatively reliable, as long as supports are within earshot.

These observations, together with other studies, suggest that chimpanzee loud-calls likely represent an intricate long-range communication system conveying multiple ‘messages’. Whilst screams convey the need for support, and alarm-barks note the presence of a threat, pant-hoots may recruit others to join at food locations or in travelling, and roar pant-hoots and pant-barks may convey aggression or aggressive intent. Further studies on these and other loud calls will help test these possibilities and determine the range of functions – and information - different call types and call combinations convey.

Working with the Vocal Repertoires of Captive Chimpanzees.

It is perhaps not a surprise that the studies of the vocal repertoire of captive chimpanzees show a smaller repertoire than of their wild counterparts (**Table 1**). This is probably to be due to two factors. First, captive chimpanzees are likely exposed to fewer contexts than chimpanzees in which context-specific

calls are emitted. Whilst captive chimpanzees are exposed to food contexts and produce food grunts and pant hoots at food, like their wild counterparts, they may never experience hunting and therefore may never utter a hunt bark. Captive chimpanzees may never face an intergroup encounter and hence may rarely or never emit pant roars. If there is only one or few males in a group, and females are on contraception, males may have limited experience of male-male competition, limiting emission of pant grunts. Females on contraception may never or rarely emit copulation calls. Second, observations may be limited to environments that are noisy, such as conducting observations from public areas, making it hard to hear or record quiet vocalisations like some hoos and grunts. This will result in an under-representation of these calls in any analysis. On the positive side, chimpanzees that interact with humans may express a variety of vocal attention-getters rarely observed in their wild counterparts, specifically including variation of bilabial sounds (Hopkins et al. 2007).

Future Work and Challenges Required to Fully Delineate the Chimpanzee Vocal Repertoire

In sum, to assess whether chimpanzee communication shows continuity or discontinuity with human communication, and therefore to what degree the comparative approach is valid for examining the evolution of language, we urgently need to focus research efforts on several points. First, we will achieve more by using a common system for naming vocalisations across chimpanzee sites. Albeit this has already been achieved for the major call types, such as pant-hoot and pant-grunt, the more graded less distinctive vocalisations have more variable names across sites. An important facilitatory step is to increase the ease of vocalisation comparison across sites by conducting an acoustic analysis across the chimpanzee repertoire, using a hierarchical acoustic analysis structure, as suggested in Figure 1. Second, I suggest using detailed observations, acoustic analysis, and playback experiments to further identify a) context-specific call types and variants, and b) determine call types that are associated with particular call goals. Third, a shift in research focus from studying long-distance calls to also including short-distance calls is likely to be fruitful. The latter has the advantage that observers can see both signallers, receivers, and the associated context. Finally, for long-distance calls, using teams of observers with two-way radios to ascertain associations between calls, context, and receiver behaviour is more likely to identify call variation and function than traditional methods of following single individuals.

Table 1. Identified call types across chimpanzee populations, consensus of contexts of occurrence and likely functions.

Acknowledgements

I thank Ammie Kalan, Roman Wittig, and Christophe Boesch for their insightful comments on this chapter. I received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (Grant Agreement No 679787).

References

Chang, E.F., Rieger, J.W., Johnson, K., Berger, M.S., Barbaro, N.M. and Knight, R.T., 2010. Categorical speech representation in human superior temporal gyrus. *Nature neuroscience*, 13(11), p.1428.

- Clark A. 1991. The socio-ecology of wild chimpanzees vocal behavior in the Kibale Forest, Uganda. PhD Thesis. University of Michigan
- Clay, Z., Smith, C.L. & Blumstein, D.T., 2012. Food-associated vocalizations in mammals and birds: What do these calls really mean? *Animal Behaviour*, 83(2), pp.323–330. Available at: <http://dx.doi.org/10.1016/j.anbehav.2011.12.008>.
- Crockford C. 2005. Vocal communication in West African wild chimpanzees (*Pan troglodytes* versus): similarities and differences with humans. PhD Thesis. University of Leipzig.
- Crockford, C. et al., 2004. Wild chimpanzees produce group-specific calls: A case for vocal learning? *Ethology*, 110(3), pp.221–243.
- Crockford, C. & Boesch, C., 2005. Call combinations in wild chimpanzees. *Behaviour*, 142(4), pp.397–421.
- Crockford, C. & Boesch, C., 2003. Context-specific calls in wild chimpanzees, *Pan troglodytes* versus: analysis of barks. *Animal Behaviour*, 66(1), pp.115–125. Available at: <http://linkinghub.elsevier.com/retrieve/pii/S000334720392166X>.
- Crockford, C., Gruber, T. & Zuberbühler, K., 2018. Chimpanzee quiet hoo variants differ according to context. *Royal Society Open Science*, 5.
- Crockford, C., Wittig, R.M. and Zuberbühler, K., 2017. Vocalizing in chimpanzees is influenced by social-cognitive processes. *Science Advances*, 3(11), p.e1701742.
- Crockford, C., Wittig, R.M. & Zuberbu, K., 2014. An intentional vocalization draws others' attention : A playback experiment with wild chimpanzees.
- Eckhardt, N., Polansky, L. & Boesch, C., 2015. Spatial cohesion of adult male chimpanzees (*Pan troglodytes* versus) in Taï National Park, Côte d'Ivoire. *American Journal of Primatology*, 77(July 2013), pp.125–134.
- Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others?. *Behavioral Ecology and Sociobiology*, 28(1), 13-21.
- Fallon, B. L., Neumann, C., Byrne, R. W., & Zuberbühler, K. (2016). Female chimpanzees adjust copulation calls according to reproductive status and level of female competition. *Animal behaviour*, 113, 87-92.
- Fedurek, P., Donnellan, E. & Slocombe, K.E., 2014. Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. , pp.1345–1355.
- Fedurek, P., Schel, A.M. & Slocombe, K.E., 2013. The acoustic structure of chimpanzee pant-hooting facilitates chorusing. *Behavioral Ecology and Sociobiology*, 67, pp.1781–1789.

- Fedurek, P. & Slocombe, K.E., 2013. The social function of food-associated calls in male chimpanzees. *American Journal of Primatology*, 75(October 2012), pp.726–739.
- Fischer, J. et al., 2001. Baboon responses to graded bark variants. *Animal Behaviour*, 61, pp.925–931. Available at: <http://linkinghub.elsevier.com/retrieve/pii/S0003347200916877>.
- Fischer, J., 1998. Barbary macaques categorize shrill barks into two call types. *Animal behaviour*, 55, pp.799–807. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/9632468>.
- Fischer, J. & Price, T., 2017. Meaning , intention , and inference in primate vocal communication. *Neuroscience and Biobehavioral Reviews*, 82, pp.22–31. Available at: <https://doi.org/10.1016/j.neubiorev.2016.10.014>.
- Grawunder, S., Crockford, C., Clay, Z., Kalan, A. K., Stevens, J. M., Stoessel, A., & Hohmann, G., 2018. Higher fundamental frequency in bonobos is explained by larynx morphology. *Current Biology*, 28(20), R1188-R1189.
- Goodall, J., 1986. The chimpanzees of Gombe: Patterns of behavior. *Cambridge Mass.*
- Gros-Louis, J., 2004. The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. *Animal Behaviour*, 67, pp.431–440.
- Gruber, T. & Zuberbühler, K., 2013. Vocal Recruitment for Joint Travel in Wild Chimpanzees. , 8(9), pp.1–9.
- Hagiwara, R., 1997. Dialect variation and formant frequency: The American English vowels revisited. *The Journal of the Acoustical Society of America*, 102(1), pp.655-658.
- Hammerschmidt, K. & Fischer, J., 1998. The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system. *Ethology*, 104(3), pp.203–216. Available at: <http://www3.interscience.wiley.com/journal/122464596/abstract>.
- Herbinger, I., Papworth, S., Boesch, C. and Zuberbühler, K., 2009. Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study. *Animal Behaviour*, 78(6), pp.1389-1396.
- Hopkins, W. D., Tagliatela, J. P., & Leavens, D. A., 2007. Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Animal behaviour*, 73(2), pp. 281-286.
- Kalan, A.K., Mundry, R. & Boesch, C., 2015. Wild chimpanzees modify food call structure with respect to tree size for a particular fruit species. *Animal Behaviour*, 101, pp.1–9. Available at: <http://dx.doi.org/10.1016/j.anbehav.2014.12.011>.
- Laporte, M. N., & Zuberbühler, K., 2010. Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour*, 80(3), 467-473.

- Luef, E.M. and Pika, S., 2017. Reciprocal greeting in chimpanzees (*Pan troglodytes*) at the Ngogo community. *Journal of Neurolinguistics*, 43, pp.263-273. Marler, P., 1976. Social organization, communication and graded signals: The chimpanzee and the gorilla.
- Mitani, J.C., 1996. 18• Comparative studies of African ape vocal behavior. *Great ape societies*, p.241.
- Mitani, J.C. et al., 1992. Dialects in wild chimpanzees? *American Journal of Primatology*, 27, pp.233–243. Available at: <http://doi.wiley.com/10.1002/ajp.1350270402>.
- Mitani, J.C., Gros-Louis, J. & Macedonia, J.M., 1996. Selection for acoustic individuality within the vocal repertoire of wild chimpanzees. *International Journal of Primatology*, 17(4), pp.569–583.
- Mitani, J.C., Hunley, K.L. & Murdoch, M.E., 1999. Geographic variation in the calls of wild chimpanzees: A reassessment. *American Journal of Primatology*, 47(November 1997), pp.133–151.
- Mitani, J.C. & Watts, D.P., 1999. Demographic influences on the hunting behaviour of chimpanzees. *American Journal of Physical Anthropology*, 109(April), pp.439–454.
- Nakamura, M., Hosaka, K., Itoh, N. and Zamma, K. eds., 2015. *Mahale chimpanzees: 50 years of research*. Cambridge University Press.
- Nishida, T., Mitani, J.C. and Watts, D.P., 2004. Variable grooming behaviours in wild chimpanzees. *Folia primatologica*, 75(1), pp.31-36.
- Notman, H. & Rendall, D., 2005. Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour*, 70, pp.177–190.
- Pika, S., 2014. Chimpanzee grooming gestures and sounds: What might they tell us about how language evolved?. In *The social origins of language: Early society, communication and polymodality* (pp. 129-140). Oxford University Press.
- Price, T. & Fischer, J., 2014. Meaning attribution in the West African green monkey: Influence of call type and context. *Animal Cognition*, 17, pp.277–286.
- Rendall, D. et al., 1999. The meaning and function of grunt variants in Baboons. *Animal Behaviour*, 57, pp.583–592.
- Schamberg, I., Wittig, R.M. & Crockford, C., 2018. Call type signals caller goal: a new take on ultimate and proximate influences in vocal production. *Biological Reviews*. Available at: <http://doi.wiley.com/10.1111/brv.12437>.
- Schamberg, I., Cheney, D.L., Clay, Z., Hohmann, G. and Seyfarth, R.M., 2017. Bonobos use call combinations to facilitate inter-party travel recruitment. *Behavioral ecology and sociobiology*, 71(4), p.75.

- Schel, A.M. et al., 2013. Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, 86, pp.955–965. Available at: <http://dx.doi.org/10.1016/j.anbehav.2013.08.013>.
- Seyfarth, R.M., Cheney, D.L. & Marler, P., 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science (New York, N.Y.)*, 210(4), pp.801–803.
- Silk, J.B., Seyfarth, R.M. & Cheney, D.L., 2016. Strategic use of affiliative vocalizations by wild female baboons. *PLoS ONE*, 11, pp.1–11.
- Slocombe, K.E. & Zuberbühler, K., 2005. Functionally referential communication in a chimpanzee. *Current Biology*, 15, pp.1779–1784.
- Slocombe, K.E. and Zuberbühler, K., 2005. Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *Journal of Comparative Psychology*, 119(1), p.67.
- Townsend, S. & Zuberbühler, K., 2009. Audience effects in chimpanzee copulation calls. *Communicative and Integrative Biology*, 2(3), pp.282–284.
- Uhlenbroek C. (1996). The structure and function of the long-distance calls given by male chimpanzees in Gombe National Park. PhD Thesis. University of Bristol.
- Van Lawick-Goodall, J., 1968. A preliminary report on expressive movements and communication in the Gombe Stream chimpanzees. *Primates: Studies in adaptation and variability*.
- Van Hooff, J.A.R.A.M., 1973. A structure analysis of the social behaviour of a semi-captive group of chimpanzees. *Social communication and movement*, pp.75-162.
- De Waal, F.B., 1988. The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behaviour*, 106(3), pp.183-251.
- Wittig, R.M. et al., 2014. Triadic social interactions operate across time: a field experiment with wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 281(1779), p.20133155. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/24500174>.
- Wittig, R. M., & Crockford, C. (2018). Chimpanzees: Investigating cognition in the wild. In N. Bueno-Guerra, & F. Amici (Eds.), *Field and laboratory methods in animal cognition* (pp. 115-145). Cambridge: Cambridge University Press

Table 1. Chimpanzee Vocal Repertoire. Chapter 24, Catherine Crockford, Tai Chimpanzee Project 40 Years Book 2019

Call type	Gombe	Captivity	Kibale	Tai	Sonso	Additional Studies	Social Context	Likely Function
Screams	SOS scream			+	+		during or after begin attacked	long-distance recruitment of supporters
	Copulation scream	+	+	+	+	Townsend & Zuberbühler 2007	during copulation given by females only	possibly to incite local competition
	pant-scream			+	+		submissive greeting usually after aggressive gesture from dominant	confirm subordination
	victim scream				+	Slocombe & Zuberbühler 2005b	receiving aggression	recruit supporters
	tantrum scream scream	+	+	+	+		during a temper tantrum during aggression	
Barks	Bark	+	+	+	+			
	Pant-bark			+	+		submissive greeting with tension; when meeting or about to fusion with dominants	confirm subordination
	Soft bark (cough)		+	+	+		mild warning	halts approach of subordinates
	waa-bark	+		+	+		aggressive, often in support of another individual under attack	
	wraaa		+	alarm bark hunt bark*	alarm bark hunt bark	Crockford & Boesch 2003 Crockford & Boesch 2003	tonal bark to leopards, buffalo, pythons, dead chimpanzees short bark emitted whilst hunting	recruit others recruits other hunters
Grunts	Pant grunt	+	+	+	+	Laporte & Zuberbühler 2010; Luef & Pika 2017	submissive greeting	confirm subordination
	food grunt	rough grunts	+	deep grunt	deep grunt	Slocombe & Zuberbühler 2005a	arriving at food or feeding	recruit others to food
	food aaa call			aaa grunt	aaa grunt	Slocombe & Zuberbühler 2005a	arriving at food or feeding	recruit others to food
	soft grunt			rest hoo	rest hoo		during resting, feeding; close contact call to bond partners	maintain cohesion
	extended grunt			rest hoo	rest hoo		during resting	maintain cohesion
	nest grunt		+	hoo grunt grunt	hoo grunt grunt		initiating nesting	maintain cohesion at nesting time
Hoos	Hoo		+	+	+			
	hoo	+		alert hoo rest hoo	alert hoo rest hoo travel hoo	Crockford et al. 2012, 2017, 2018 Crockford et al. 2018 Crockford et al. 2018	puzzlement during resting and feeding, close contact call to bond partners close contact call to bond partners*	short range warning to threats maintain cohesion maintain cohesion
	pant hoot	+	+	+	+	Mitani 1992; Crockford et al. 2005; Uhlenbroek 1996; Notman & Rendell 2004; Fedurek et al. 2013; Mitani 1999;	long distance contact call	elicit contact or reunion with chimpanzees in other parties
	inquiring pant hoot arrival pant hoot spontaneous pant hoot						often accompanied by searching or waiting for a reply* especially arriving at food* singing quality often by feeding or resting individuals*	
	roar pant hoot	low hooting		+	+	Uhlenbroek 1996; Notman & Rendell 2004	within and between group aggressive	repel others
Other	laugh	panted laugh	+	+	+		play	continue play session
	cry						combination of whimper and tantrum scream*	
	whimper	+	+	+	+		distress/begging	elicit object of desire or consolation/comfort
	copulation pant		+				emitted by males during copulation	
	pant			+	+		during greetings, grooming or intense excitement such as arriving at a rich food source	affiliation
Non-vocal	squeak	+	+	+	+		threat from dominant	
	Lip smack			+	+	Fedurek et al. 2015	during grooming	continue grooming session
	tooth clack			+	+		during grooming	continue grooming session
			raspberry				during grooming*	continue grooming session
Total Calls	32	12		28	29			

Legend: Gombe: Goodall 1986; Kibale: taken from Clark 1991 from Kanywara unless indicated by*; Captivity: de Waal 1988; Tai: Crockford 2005, personal observations and studies; Sonso: CC, personal observations and studies.

Purple: verified with acoustic analysis. Green: call variants not in the Goodall repertoire

Note: most studies across sites concur with most of Goodall's (1986) vocal repertoire.

Social context: Common agreement across more than one site/researcher except where indicated by * which have only been reported in one field site/by one researcher