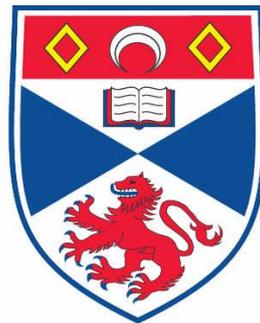


**Coordination of joint activities and communication in
wild chimpanzees (*Pan troglodytes*) of the Budongo
Forest, Uganda**

Caroline Mullins



**This thesis is submitted in partial fulfilment for the degree of
Doctor of Philosophy at the University of St Andrews**

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1. This statement of collaboration acknowledges the contribution of Anne M. Schel, of the École Normale Supérieure, in providing playback stimuli which the playback experiments presented in chapter five relied upon, and of Pawel Fedurek, of the Université de Neuchâtel, in carrying out one playback experiment.

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I, Caroline Mullins, hereby certify that this thesis, which is approximately 45 000 words in length, has been written by me, and that it is the record of work carried out by me or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a candidate for the degree of Doctor of Philosophy in October 2009; the higher study for which this is a record was carried out in the University of St Andrews between 2009 and 2014.

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Abstract:

Evidence from captive studies suggests that chimpanzees (*Pan troglodytes*) lack the motivation to complete cooperative tasks and there is little evidence for communication that coordinates their behaviour during joint actions or whether individuals have a shared motivation towards the same goal. Two types of behaviour where individuals are argued to engage in joint activity are investigated in the Sonso community of wild chimpanzees in Budongo Forest Reserve, Uganda: joint travel and group hunting. This study presents evidence from naturalistic observations, and also a playback experiment to further investigate hunting behaviour. Joint travel appears to have no coordinating signal or behaviour on a local level, although the use of pant-hoot vocalisations to coordinate long-distance group travel is supported. In group hunting, bark vocalisations are associated with initiating a group hunt, indicating their potential role in coordination of joint action. Bark production also appears to be affected by the social composition of other hunters, with more barks being produced when other hunters are closer affiliates, suggesting flexibility in call production. The field experiment exploring joint action in group hunts utilises the alarm calls of the chimpanzees' prey species- the Colobus monkey (*Colobus guereza*). Alarm calls produced by the monkeys when they were being hunted by chimpanzees and in response to an eagle stimulus were played back to dyads of affiliated males, and their vocal and behaviour responses recorded. Results firstly indicate that chimpanzees recognise different Colobus predator alarm. Furthermore, half of the trials with the Colobus hunting alarm elicited a vocal response of barks from both of the males in the experiment, along with joint movement in the direction of the playback. These initial results from a novel field experiment suggest that the bark vocalisation is associated with the initiation of joint action in the context of group hunting.

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Chapter 1: General introduction to coordination of joint activities and communication in the wild chimpanzees of Budongo, Uganda

1.1 Introduction

There are a set of social-cognitive and social-motivational skills possessed by humans which are suggested to have a complexity not found in other primates, or indeed any other animal species (Richerson & Boyd, 2005). How these skills evolved and whether they really are unique to humans is the subject of much debate amongst scientists from many disciplines including biologists, psychologists and anthropologists. Current theory proposes that, stimulated by an increase in cooperative behaviour and motivations, these skills paved the way for the evolution of human-unique features such as linguistic symbols and cultural institutions (Tomasello, Carpenter, Call, Behne, & Moll, 2005). The species-wide use of symbolic language and cumulative culture (where innovations and behaviour learned within the social group are built upon and specific to that group) are widely accepted as uniquely human traits, but the cognitive and motivational underpinnings of such behaviour may include skills that are shared with other species.

If cooperative behaviour and motivations were the driving force of language and cultural evolution in humans, then it might be expected by comparison that the more complex forms of cooperative actions could involve more complex coordination and communication in other species. One of the most widespread examples of cooperation in wild animals occurs during group hunting behaviour. In mammals, only one group of lionesses (*Panthera leo*), wolves (*Canis lupus*), bottle-nosed dolphins (*Tursiops truncatus*) and chimpanzees (*Pan troglodytes*) have been described to hunt collaboratively with complex coordination of movements and differing individual strategies (Bailey, Myatt, & Wilson, 2013; Gazda, Connor, Edgar, & Cox, 2005). However, it is yet under-researched and not obvious from current natural observations what cognitive mechanisms or coordinating communication underlies complex cooperative behaviour and its development.

It has been suggested that an increase in complexity of cooperation (in hunting) may require greater cognitive capacities (Boesch & Boesch-Achermann, 2000), which is an opinion shared by those investigating other species' cooperation in laboratory experiments. For example, rooks (*Corvus frugilegus*) cooperate to get a food reward, but will not wait to perform their part depending on when their potential partner enters the room (Seed, Clayton, & Emery, 2008). Spotted hyaenas (*Crocuta crocuta*) coordinate in space and time in cooperative laboratory tasks, but do not show collaboration in the wild (Drea & Carter, 2009). By way of explanation, Drea and Carter indicate how the 'biological preparedness' of an animal's evolutionary life history for complex cooperative skills is absent in hyaenas, and further how complex collaborative skills may require years of practice and thus only occur in long-lived and highly encephalised species- such as chimpanzees (Boesch, 2002). Chimpanzees engaging in group hunting behaviour therefore represent an ideal species for comparing complexity of coordination and communication during complex cooperative activities and, as they are the most genetically related species to humans, may further contribute to arguments about the evolution of human-unique behaviour by comparison with human behaviour (Laland & Brown, 2011).

Human intentional communication represents one of the social-cognitive skills important in the evolution of human-unique communication and symbolic language, and is different from other animals' in that it is dependent on 'shared intention' or a 'joint attentional frame' (Tomasello and Carpenter, 2007). It has been suggested that this skill was built upon with human's unique motivation to share experiences or information, resulting in language and referential gestures such as pointing. There are two aspects of 'shared intentionality' which are considered as unique cognitive and motivational traits in humans – firstly, the sharing of mental states, and secondly, the motivation to share a goal with another (Tomasello, 2008). The cognitive aspect will be discussed initially, followed by the motivational aspect and how they can be observed in the communication between individuals during joint action.

1.1.1 Sharing mental states

Shared intentionality, according to Tomasello and Carpenter (2007), refers to “collaborative interactions in which participants share psychological states with one another”. Examples of collaborative activities displaying shared intentionality might include group hunting, or playing a game of football, where individuals take on different roles, have the same goal in mind, and may communicate¹ to coordinate their actions in order to achieve that goal. The authors also consider that shared intentionality is involved in less complex joint actions in humans, for instance ‘taking a walk together’, where individuals also share a mental state about their goal in walking together (Tomasello, 2008, p. 7). However, if one were to observe the behaviour of this couple, it would not be clear that they shared a psychological state; they would need to be asked about their goals directly to see if they did indeed have the same goal when walking together.

One method for looking at how human behaviour, such as joint actions involving shared intentionality, has evolved or developed is by comparison with other animal species that display similar behaviour (Laland & Brown, 2011, pp. 198-202). However, a major problem that is encountered when comparing how humans coordinate joint action with cases of animal joint action - for example the many group-living species across the animal kingdom that seemingly coordinate travel (King & Sueur, 2011) - is that it is not possible to ask them about their mental states and understanding of others’ mental states during this joint activity. It may be the case, therefore, that this key aspect of the definition of shared intentionality in human joint action, namely that participants *share*

¹ A biological approach is taken when considering communication in this paper, based on Maynard Smith and Harper’s (2003) emphasis on the adaptive relevance of signals and their effects on the receiver, but using specifically Scott-Phillips’ definition of a cue as “any act or structure that (i) affects the behaviour of other organisms; and (ii) which is effective because the effect has evolved to be affected by the act or structure; but which (iii) did not evolve because of those effects” and a signal as “any act or structure that (i) affects the behaviour of other organisms; (ii) evolved because of those effects; and (iii) which is effective because the effect (the response) has evolved to be affected by the act or structure”, and communication as “the completion of corresponding signals and responses” (Scott-Phillips, 2008).

psychological states with one another, may never be objectively discriminated in non-human animals² (Boinski & Campbell, 1995).

But why is a mentalistic understanding of another's intentions necessary so that actions carried out with another can be considered 'shared' (Tomasello, 2008; Tomasello *et al.*, 2005)? The disembodied view of intentional understanding is explained further by Tomasello and Carpenter (2007) when they say that true 'common psychological ground' requires '*knowing together that they are experiencing the same thing*'. If we instead think of intentions as a physically observable action by a subject on an object in the world (Gómez, 2009), then common ground - otherwise known as 'common knowledge' (Whiten *et al.*, 1999) or 'mutual knowledge' (Barrett, Henzi, & Rendall, 2007) - becomes something we can observe in the behaviour of individuals who are acting on the same object or towards the same outcome (i.e. have the same 'goal'). A 'shared intention' might therefore be observed between two or more individuals engaged in joint action by looking for coordination of behaviour, and specifically communication to achieve this coordination. Joint action is defined from now on as any behaviour involving two or more individuals acting towards the same goal. Coordination includes any signal or behaviour that causes the actions of individuals to be coordinated in space or time, or that causes different actions to be coordinated towards the same goal.

1.1.2 Communication during joint activities and motivation

Communicative acts can reveal something about an individual's commitment to the same goal and motivation to share this goal with another. For example, if an individual engages in actions and communicative attempts to re-engage a recalcitrant partner, along with any other signals given that initiate or maintain joint behaviour, such communication can be seen as coordinating joint action and indicate that the signaller is motivated to carry out the action jointly.

² No species other than humans have been demonstrated as capable of understanding that other beings have mental states or 'beliefs', i.e. theory of mind (Call & Tomasello, 2008; Tomasello & Rakoczy, 2003).

Communicative actions on the part of the signaller, however, are not necessarily indicative of a shared motivation on the part of the receiver if they (the receiver) perform no communicative acts themselves. This study therefore tries to limit observations to joint activities which would be impossible to achieve without both participants having the same goals, as per Tanner and Byrne (2010). In this way, a shared motivation is assumed between individuals acting towards the same goal. Although such an assumption does not necessarily satisfy Tomasello's idea of 'motivation to share a goal' between partners (Tomasello, 2008), it does satisfy a more broadly applicable idea of shared motivation as one that is observable when individuals engage in joint action towards the same goal.

Tomasello's shared motivation may require communication between joint actors that refers specifically, or referentially, to the goal itself (Tomasello & Carpenter, 2007). However, true referentially (with symbolic meaning) in signals is only considered possible between humans using language, unless a concept of referentiality is used which remains neutral about underlying mental processes (Marler, Evans, & Hauser, 1992). Therefore, although within Tomasello's framework the term 'joint motivation' should really be used instead of 'shared motivation', this study will use the two terms interchangeably as they occur in the literature on animal communication.

This thesis will also view communication occurring within the framework of joint activities where participants have a joint motivation as 'coordinating communication'.³ If communication were found which initiates or maintains joint activity, it would be possible to look further at concomitant behaviour occurring during signalling, such as audience effects, looking behaviour (e.g. audience-checking), attention-getting and persistence or elaboration in communicative acts. Such actions are thought to offer clues as to the flexibility of signal production, which can also be used to infer intentionality

³ The concept of communication which functions to coordinate should be kept distinct from Tomasello's idea of 'cooperative communication' as the sharing of information e.g. pointing referentially (Tomasello, 2008).

(Hobaiter & Byrne, 2011; Laporte & Zuberbühler, 2010; Leavens, Russell, & Hopkins, 2005; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013b).

Nevertheless, some signals given during joint activity may not necessarily function to coordinate the behaviour of specific individuals directly. They may instead have a more general function, for example creating a 'mutual emotional frame' within which animals synchronize individual behaviour (Bates & Byrne, 2010). Such changes in emotion are possible to assess through physiological measures, for example in levels of the stress hormone cortisol (Bakeman & Adamson, 1986) or self-directed behaviour which both indicate arousal (Kutsukake, 2003). However, differences in 'emotional state' do not exclude the possibility of cognitive control of behaviour; they could represent a proximate stage in physiological or psychological changes linked just as readily to the production of an innate or of a flexibly-produced signal.

Physiological measures which can be considered as representing a motivational or emotional state are not mutually exclusive to physiological changes which may be occurring as a consequence of communication and specific behaviour responses (Marler *et al.*, 1992). Therefore, this study will not include measurements of physiological changes associated with signalling and joint actions, as flexibility of signal production and coordination of actions cannot be 'explained' by changes in emotional state. The study will, however, pay attention to the potential effect of a 'mutual emotional frame' by distinguishing between communicative signals associated with joint activities that involve only two individuals, and those that involve larger groups.

The literature on joint activity in laboratory experiments with chimpanzees will now be reviewed, followed by studies on captive populations which have tried to avoid some of the problems presented in experiments by observing spontaneous acts of sharing and collaboration. A description of field studies which extend the captive work into ethologically valid contexts will reveal how a detailed focus on communication is missing from previous work on behaviour during joint activities, finally leading to an explanation of the research carried out with the Sonso community of chimpanzees, at the Budongo field station in Uganda, for this study.

1.2 Joint actions in laboratory experiments

Laboratory experiments have been carried out by Tomasello and Carpenter (2007) testing human infants and chimpanzees for specific behaviour thought to be relevant to those activities that require shared intentionality, including both helping and cooperative activities. They have found evidence for shared intentionality in 12-15 months old children, but not in captive chimpanzees. The experiments looked for communicative attempts to re-engage a partner who interrupts joint action. The experimental tasks used to test participants were defined as 'joint cooperative activities' using Bratman's (1992) three requisites. The definition includes the idea of cooperation in a joint action by requiring that participants:

- 1) are mutually responsive to one another;
- 2) pursue a shared goal; and,
- 3) coordinate their plans of action for pursuing said goal (exemplified by an understanding of role-reversal).

The requirements were applied to joint action experiments in the first instance by whether subjects are considered mutually responsive- if they are attentive to each other (looks) and show 'awareness of gaze'. Secondly, in pursuing a shared goal it should be noted that although actions can be different, the outcome of the actions should be the same for the cooperating individuals. Thirdly, the individuals should have an understanding of role reversal, or understand that the goal cannot be achieved without both participants carrying out their required action.

Evidence for joint cooperative activity - using Bratman's three criteria - will now be discussed from work with captive chimpanzees and other primates. This will provide a background on theoretical frameworks used, methodologies for testing them, and whether laboratory experiments with chimpanzees can really show if they engage in and coordinate joint action with a shared motivation.

1.2.1 Mutual responsiveness

Experiments with captive chimpanzees provide conflicting evidence for joint attention and flexibility in signalling during joint actions in the cooperative-communicative context. An example of flexibility in signal production depending on audience attention was shown by Povinelli et al. (2003) who found that chimpanzees change the gestures they use to get a human partner to give them a food reward depending on whether the human is looking at the desired object or a non-desirable distracter. This example relates to a task where there is no shared goal, and conflicts with evidence from Hirata and Fuwa's cooperation study (2007) which, although firstly showing that chimpanzees use vocalizations and gestures to gain the attention of a human partner needed for a cooperative task, secondly showed that this did not seem to be dependent on the attentional orientation of the partner. The same study gave pairs of chimpanzees the task of having to pull on a rope on either side of a block to bring food within reach. With a chimpanzee partner, there was some monitoring of the other's behaviour (looking) and waiting for them to fulfil their part of the task, but no eye-contact or communicative attempts as with the human partner. This suggests that mutual responsiveness was missing from chimpanzee cooperative experiments without a human partner.

The difference between eye contact and communicative attempts in the experiments between a chimpanzee pair and a human-chimpanzee pair is explained by Bakeman and Adamson's (1984) distinction between 'passive joint engagement' and 'coordinated joint engagement'. During triadic play situations of human infants with peers or mothers, passive joint engagement involves only joint interaction with an object, whereas in coordinated joint engagement there is evidence that the partners are mutually responsive to each other as per Bratman's first requirement for defining behaviour as a 'joint cooperative activity' given above. For example, the infant looking at their play partner may also vocalise, smile or gesture at them during the joint action (Bakeman & Adamson, 1984). This distinction is in concordance with a view that the captive chimpanzees' behaviour during the experiment was coordinated more in the manner of 'tuning forks' - with individuals in synchrony when working towards similar but

individual goals - rather than a 'sharing' of goals which has been emphasised by Call (2009) as a uniquely human propensity.

In sum, Hirata and Fuwa's results suggest that captive chimpanzees were learning to coordinate their behaviour through a behaviour conditioning mechanism, with any signals utilised having been conditioned to be associated with predictable behaviour results from the human partner, and not representative of an intentional communicative attempt (Hirata & Fuwa, 2007). This argument for associative learning in captive chimpanzees can be applied to other experiments where individuals appear to change their communicative behaviour depending on the attentional state of a human. For example, it can be applied when chimpanzees increased vocalisations to a human holding a banana when they are facing away from them, as opposed to increasing gestures to a human oriented towards and thus able to see them (Hostetter, Cantero, & Hopkins, 2001). Here, the results could indicate a conditioned response to the orientation of the human, and not necessarily awareness of their attentional state. Therefore, captive chimpanzees (especially those raised by humans) may not be showing some socio-communicative abilities because they have higher cognitive abilities. They may show the behaviour because they have been conditioned to respond to ritualised experimental set-ups in a way that will induce a reaction from humans, and is ultimately likely to result in gaining a food reward (Barrett, 2011). The results of laboratory experiments where chimpanzees seem to show high socio-communicative skills should therefore always be interpreted with caution when the experiment involves ritualised training and rewards-based tests with human experimenters.

Another difficulty that is common to studies on captive chimpanzees is that of sample size. As the authors of the above chimpanzee cooperation study concede, only one chimpanzee-chimpanzee pair and one chimpanzee-human pair were tested and so all generalised conclusions should be drawn with caution (Hirata & Fuwa, 2007).

Other recent laboratory experiments investigating joint actions (using a slightly larger sample of six pairs of chimpanzees) show that they do actually use gestures such as poking an arm through a division, clapping hands or beating the division panel, or

produce vocalisations such as whimpering and screaming, as a request to obtain an out-of-reach tool from a chimpanzee partner (Yamamoto, Humle, Tanaka, & Plaistow, 2009). Ultimately, however, as these experiments involve requests for help from one individual working towards their own goal, and not a coordination of joint actions towards the same goal, the extent to which such communication can be considered in the context of joint activity is not immediately clear as there is no shared goal.

Recent laboratory experiments on human children and chimpanzees have led Warneken and colleagues to suggest a dichotomy between helping behaviour and cooperative joint activities, and between the motivational and cognitive abilities required for each (Warneken & Tomasello, 2007). Helping behaviour is present in both species: Warneken found that both captive and semi-captive chimpanzees and human infants of 15 months would help experimenters to obtain out-of-reach objects. This is suggested to be a ‘more basic social skill’ (requiring only that a partner be induced, or ‘coerced’ to act towards the actor’s goals) than joint cooperative activity. To test for joint cooperation in subjects, Warneken designed four joint tasks based on ‘play’ scenarios, such as obtaining an object from a tube or box that had to be manipulated by two individuals at the same time to work. These tasks were said to require a coordination of goals, joint attention and shared intentions, all of which were found in children of 12 and 18 months, but not in chimpanzees (Warneken, Chen, & Tomasello, 2006). In light of Warneken’s study, the later section of this discussion aimed at discerning joint activities in wild chimpanzees will consider the difference in goals between helping and joint cooperative activities as they relate to the potential coordination of joint actions and shared motivation in wild chimpanzee behaviour (pp. 15-18).

1.2.2 Shared goals: coordinating communication and re-engagement

Tanner and Byrne (2010) have recently reported triadic and collaborative interactions during spontaneous social games between western gorillas (*Gorilla gorilla*) at the San Francisco Zoo. Videos of these games show that most were collaborative in that partners had ‘shared behaviour patterns, coordinated action, and complementary and

reversible roles'. This evidence from gorillas differs from a previous claim of Warneken and colleagues (2006), that, attempts to re-engage a human partner who disengages during cooperative 'play' tasks represents a uniquely human form of communication: a communication with shared goals which involves 'shared intentionality'. In Warneken's study, human infants made vocalisations and gestures whilst monitoring the experimenter when they stopped participating in the joint action, whereas the three chimpanzees tested made no such attempts. The finding of both gestures and action in gorillas to re-engage partners, hints that the results of Warneken et al. (2006), which show no communicative attempts to re-engage a human partner during social games, may have arisen due to the unsuitability of the task for the animals tested. The authors acknowledge that the chimpanzees tested were not interested in the games being played, which indicates that the subjects did not in fact have a shared goal with the experimenter. This disinterestedness in the task, taken alongside the very small sample size of only three chimpanzees tested, represents a flaw in the methodology. Further experiments with chimpanzees involving tasks which they fully engage in are necessary to draw more far-reaching conclusions about chimpanzee behaviour.

Further evidence for coordination and re-engagement in apes, where researchers were looking specifically for shared intentionality, comes from Pika's observations of triadic games between captive bonobos (*Pan paniscus*) and humans. These observations showed bonobos making communicative attempts to re-engage a human partner during 'cooperative games' (Pika & Zuberbuhler, 2008). Although the activities observed were simple (one was joint splashing in a water pool and another rolling a ball out to the partner who then returned it to the bonobo) and involved few individuals, the authors suggest their results show that the bonobos participating in the games were mutually responsive to their partner and were pursuing a shared goal when they communicated to re-engage the partner (Tomasello *et al.*, 2005). Of special significance here is that they are cases of *spontaneous* socio-communicative behaviour that did not result in the animal receiving a food reward. This is more concordant with the literature on experiments with human infants who participate in games seemingly for the 'joy of sharing the experience' with the adult partner (Tomasello, 2008).

That bonobos are considered a more socially tolerant species than chimpanzees (Hare, Melis, Woods, Hastings, & Wrangham, 2007) could be relevant in the comparative analyses of experiments with bonobos, as it has been argued that the increase in tolerance towards others allowed the evolution of highly cooperative and communicative behaviour in humans to occur (Hare & Tomasello, 2005; Pickering & Dominguez-Rodrigo, 2010). However, for the purposes of comparison with chimpanzee communication within the framework of joint action, it should be noted that the extent to which the bonobos are coordinating their actions towards a shared goal in the triadic games of Pika's study is debatable. For example, it is unclear whether, even when the game involves another object, the joint behaviour can be considered to have an external shared goal when the goal of the activity is still the social interaction between the pair themselves. Relevant laboratory experiments investigating joint cooperative activities are therefore still lacking for both bonobos and chimpanzees.

1.2.3 Coordinating plans of action

The requirement for coordinating plans of action in Bratman's criteria for joint cooperative action is the trickiest to apply to observations of animal behaviour. It is difficult to see how individuals coordinating their 'plans of action' would look any different to individuals coordinating their action. An example from human behaviour would be individuals carrying out a planned strategy to score a goal in football after a free kick, compared to individuals responding to a miss-hit ball and the positions of other players in order to score a 'chance' goal. Even the proposed example of an observation showing an understanding of role reversal, for example by taking on different roles, could simply represent an individual changing their role *ad hoc* in response to environmental conditions without any necessary planning.

Indeed, it is unclear whether chimpanzees even possess the cognitive ability to form a plan of action for the future. Suddendorf and colleagues (2009) analysed the results and methodology of recent laboratory experiments and found little convincing evidence for future planning in apes. Chimpanzees do not plan for future exchange of tokens for a

reward, although there does seem to be some ability of chimpanzees to save a tool for an action task an hour later (Osvath & Osvath, 2008). However, future planning in cooperative tasks involving joint action, which have a social dimension, is not ruled out and the authors conclude with a general call for further research rather than stating that such capacities do not exist in the great apes (Suddendorf *et al.*, 2009).

The investigation of future planning is beyond the scope of the present study, which will therefore not consider ‘coordinating a plan of action’ as a requirement for the consideration of behaviour as joint action, but only require that coordination of the joint action has occurred. In this way all insinuations about mental states in the definition of joint actions are avoided, and inferences about cognitive devices such as intentionality are restricted to *post-hoc* analyses of observed behaviour.

A recurring problem of captive experiments is that the future ‘goal’ of the participants’ actions in the experiment may not in fact be what is planned by the experimenter. The motivation of the participant may be directed at something other than what the experiment designed it to be (c.f. Warneken *et al.*, 2006 where chimpanzees were not interested in the cooperative task and therefore may not have been motivated to behave in a way that would reveal skills being tested for, like re-engagement communication). Here, naturalistic observations and experiments on behaviour in the wild may have an advantage over artificial, human-conceived experiments. In regularly observed joint activities in wild chimpanzees, such as group hunting to catch a monkey or travelling together to the same location, the shared goal is assumed to be more obvious. In these cases, communication produced before or during the behaviour that initiates or coordinates that activity becomes a relevant and observable variable, along with measuring different outcomes of joint action.

Of interest to the focus of the present thesis, there has been some contention over whether wild chimpanzee behaviour has been shown to fulfil any of Bratman’s requisites, especially with regards to group hunting (Boesch, 2005). Wild chimpanzees live in varied social and physical environments, and so the application of Bratman’s strict requirements to any joint activities they carry out may be difficult. That subjects

are mutually responsive and look at each other can be observed when dyads are in close proximity and on the ground, but when distances increase to more than 10m, visibility in the Budongo forest is very poor and as, especially during e.g. hunting, focal individuals are likely to be moving fast and greater than 10m from the observers, looks may not be possible to record with accuracy. Consequently, looking behaviour can only be compared in this study between individuals which are close enough to the observer and in conditions of visibility that are good enough for accurate recordings.

Another problem is that partners may be mutually responsive to each other aurally (through vocal communication) without needing to be in sight of each other. This would render the requirement of looks and awareness of the other's gaze obsolete. Indeed, communication through auditory channels may also be used to coordinate their joint action- Bratman's third requirement given above. This problem is noted as a confounding factor in results throughout this study. That the chimpanzees are pursuing a common goal will only be assumed from their behaviour during long-established and well-defined joint activities, each of which will be discussed in detail in the next section.

1.3 Testing in the field: behaviour observations and experiments

The overall aims of this study, to explore the communication between chimpanzees which have a joint motivation to engage in a joint action and whether this coordinates the joint action, were tested in a wild chimpanzee community living in the Budongo Forest, Uganda. Observations are interpreted within a behaviour framework (avoiding meta-representational mental models), which allows comparison with previous studies in humans and non-human (i.e. non-linguistic) animals- in this case our closest living genetic relatives, the chimpanzee. Such a framework offers the potential to compare the results from chimpanzees with human coordination during joint activities, which may contribute to hypotheses about the evolutionary origins of behaviour in a last common ancestor. Methods for defining behaviour as joint action will now be discussed, as well as the social framework within which they occur. Potential joint action behaviour in the chimpanzees of Budongo will then be analysed and their inclusion in this study justified.

1.3.1 Defining joint action from natural behaviour observations

In order to investigate what communication is used by individuals engaged in joint activity, and whether this functions to coordinate their activity, a clear idea is needed of what behaviour can be defined as joint action, as there can be many approaches to describing behaviour⁴ (Tinbergen, 1963). The term cooperation is frequently used by observers of natural behaviour in animals to describe joint actions during group hunting or defence, but has also been used to describe behaviour such as mutual grooming in primates (Bailey *et al.*, 2013; Boesch, 1994; Muller & Mitani, 2005; Silk, 2005). It seems that the term cooperation may be misleading as it is often used as an evolutionary concept that is separate from a description of observable behaviour. For example, the definition of cooperation by Hamilton (1964) describes behaviour as cooperative on an ultimate and evolutionary level depending on whether it increases the reproductive

⁴ Tinbergen (1963) describes 4 questions which can be asked when looking at animal behaviour: 1) *evolution (phylogeny)*; 2) *ontogeny (development)*; 3) *survival value (ultimate function)*; and 4) *causation (proximate function)*.

fitness of the individuals involved. The operational definition of cooperation used by Boesch (1989) does not consider the ultimate function (survival value) of joint activity behaviour. It instead focusses on the proximate function (causation) by examining mechanisms for coordinating joint actions in wild chimpanzees, for example communication. Thus joint action as defined in this study is also described by Boesch's operational definition of cooperation as 'two or more individuals acting together to achieve a common goal' (Boesch & Boesch, 1989). This allows for direct comparison of joint action in this study with cooperation described in Boesch's studies.

This definition can accommodate instances of joint action when the goal is not achieved, for example group hunts that are not successful. Just as the definition of communication as the *successful* completion of a signalling act may result in the omission of signalling acts from data if they are not apparently received (Aureli *et al.*, 2008), so defining cooperation according to its successful outcome may omit from data behaviour that is operationally cooperative (Boesch & Boesch-Achermann, 2000). This means that coordinated behaviour towards the same goal will be considered as joint action if, *on average*, it results in specific and predictable joint behaviour outcomes that can be interpreted by observers as a shared goal.

1.3.2 Social considerations during joint actions

Chimpanzees individually recognise other chimpanzees and behave differently when in proximity to certain individuals, with such a series of interactions being described as a 'relationship' between them (Hinde, 1976). Some proximate measures of these relationships, for example self-directed behaviour (Kutsukake, 2003), show that anxiety is lower when nearest neighbours are more familiar individuals (measured by proximity times and agonistic/affiliative interactions). Such reductions in stress can be linked to the 'emotional reactivity' hypothesis of Hare and colleagues (2007), whereby individuals are more cooperative with those they are more tolerant of (i.e. have reduced fear and anxiety around). If this is the case, then according to Tomasello's (2008) theory, joint actions and coordinating behaviour could be qualitatively different within a

species when an individual is interacting and communicating with a familiar and ‘cooperative’ partner compared to others.

The importance of an individual’s social environment for communication is supported by recent field experiments with wild chimpanzees. In these experiments, chimpanzees displayed flexibility in vocal production depending on the caller’s affiliative relationship with the receiver (Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013a). That such differences in signal production may exist between different social partners is further supported by laboratory experiments on captive chimpanzees in Leipzig, where individuals engaged in a collaborative task perform better with a partner who shares food outside of the experimental context (Melis, Hare, & Tomasello, 2006b), and individuals also specifically try to recruit partners which were previously seen to be successful cooperators (Melis, Hare, & Tomasello, 2006a). These results highlight the importance on including individual identity and social relationships as factors in research on communication. In order to account for this potential source of variation in signalling, this study will include measures of social relationship (including dominance and affiliation) between individuals engaged in joint action.

Affiliative male dyads can be defined using measures of party membership, proximity, grooming, agonistic support and other affiliative behaviour; closely bonded males are often not simply kin-related (Langergraber, Mitani, & Vigilant, 2007). Female chimpanzees are not reported to have as strong social bonds with each other as the males have with other males (Boesch & Boesch-Achermann, 2000; Nishida, 1968) and thus have fewer instances of cooperation observed in the wild (Muller & Mitani, 2005). However, females remain very closely bonded to their direct kin within the group (Goodall, 1986; Reynolds, 1968) and mother-offspring groups can even separate themselves from the main group for long periods (Reynolds, 2005). Thus motivation to engage in joint action within these smaller groups may be very high, particularly in contexts where kin selection is an active force (Hamilton, 1963), such as for anti-predator behaviour, examples of which may include small family groups travelling together in close proximity. These sex differences and their potential effect on coordinating joint action during travel will be discussed further in chapter 3 (pp. 45).

1.3.3 Observing joint actions in natural settings

In light of recent studies showing that chimpanzees are more skilful in competitive paradigms than cooperative tasks (Hare & Tomasello, 2004), it seems possible that negative results from studies investigating joint actions in captive chimpanzees (for example, as discussed on pp. 10, Warneken *et al.*, 2006) may result from limitations in the experimental paradigm rather than actual cognitive deficits in chimpanzees. This possibility is compounded when evidence from bonobos is compared to chimpanzee studies. Bonobos are known to engage more in triadic games and perform better in cooperative tasks in captivity than chimpanzees when the food reward is easy to monopolize (Hare *et al.*, 2007). However, chimpanzees performed as well as bonobos when the food source was not easily monopolised compared to a non-divisible food reward, emphasising the importance of making experimental paradigms relevant to the species' natural behaviour repertoire. It could simply be that the experiments used in captivity do not offer the environmental or social set-up required for the cooperative activities individuals naturally engage in to occur, as they do in the wild.

Kingstone (2009) compares results from investigations into social attention in nonhuman primates in the laboratory versus the wild, most prominently citing the example of lemurs in a naturalistic environment, which were shown (by attaching a small telemetric gaze-tracking device to the subjects) to co-orient with other lemurs they looked at during normal daily activity (Shepherd & Platt, 2008). Even more strikingly, a recent study on lemurs by Ruiz and colleagues has effectively thrown into question results from all laboratory object-choice tasks requiring gaze-following (Ruiz, Gómez, Roeder, & Byrne, 2009). The experimental paradigm utilised showed how, simply by combining observations of whether co-orientation had occurred with whether subjects chose the primed box containing a food reward, lemurs did indeed use information gained by gaze following in a foraging context. Such a positive result had not been found in previous experiments with lemurs. The warning is poignant: when testing for use of socio-communicative cues by an animal in their subsequent behaviour, be sure to check that your focal animal has received the signal. This could be checked by

recording looks at the signaller by the receiver; however, in the case of auditory communication, signals and replies can be exchanged without such looks towards the partner. Therefore, observing overall behaviour of signaller and receivers before and after supposed communicative attempts, looking particularly for coordination of movement and monitoring of partners, could be more likely to reveal communication specific to contexts involving joint activity, where individuals have a 'common ground' or joint motivation towards the same goal.

This study will focus on two contexts in which wild chimpanzees are likely to engage in joint actions, and in which communication between individuals could reveal joint motivation and a shared goal. The following section will examine other potential joint actions found in wild chimpanzee behaviour, before discussing the main contexts focussed on in this study: joint travel and group hunting.

1.4 Joint action: natural observations in chimpanzees

Chimpanzees are a social species, and as such carry out many different activities with other individuals in the wild (Marler, Bateson, & Hinde, 1976). Some potential joint actions in wild chimpanzees are now discussed, including food sharing, agonistic support, and group defence, joint travel and group hunting.

1.4.1 Food sharing

Food sharing in wild chimpanzees seems to involve communication which draws many parallels with the work of Yamamoto and colleagues (2009) investigating communication and cooperation in captive chimpanzees. Natural observations of food sharing in the wild include communicative behaviour which has been described as begging or harassment. Such behaviour has been shown as a key factor in obtaining food or not from non-kin (Gilby, 2006; Slocombe & Newton-Fisher, 2005). The evidence from field observations has been interpreted on an evolutionary-level to indicate that meat sharing involves complex forms of cooperation. It has been claimed that food sharing is explained by varying levels of altruism, including a cognitively rich monitoring of costs and benefits required for reciprocal altruism⁵; or at least a good memory for past interactions with specific individuals and a system for rewarding support received in different contexts (Byrne, 2007; Langergraber *et al.*, 2007; Mitani & Watts, 2001).

Despite the speculation on evolutionary causes for food sharing, the aspect of behaviour which is of interest to this study, namely proximate mechanisms modulating sharing behaviour, is under-researched, as Hirata and co-authors (2007) suggest. It is not clear whether individuals are mutually responsive, indicated if communication is being employed by *both actors* to coordinate food exchanges, rather than one individual signalling (for example with begging gestures) until they receive food. However, the

⁵ Altruistic behaviour is defined as behaviour that benefits another organism, not closely related, while being apparently detrimental to the organism performing the behaviour, benefit and detriment being defined in terms of contribution to inclusive fitness; reciprocal altruism occurs when there is non-random dispensation of altruism depending on the altruistic tendencies of the recipient (Trivers, 1971).

goals of interacting individuals are unlikely to be the same in the case of food sharing after begging behaviour, where both individuals want the food for themselves. In the case of active food sharing, their actions might be considered more as a helping behaviour (where one individual helps another towards their goal) than a joint activity with a shared goal (a distinction discussed on pp. 10). Food sharing does not generally seem to represent behaviour where individuals are acting together towards the same goal. Therefore, in accordance with the operational definition of joint activity, food sharing will not be included as a joint action in this study.

1.4.2 Agonistic support

Another type of behaviour observed in wild chimpanzees which has been said to involve cooperation is alliance formation during agonistic encounters, which is often accompanied by specific vocalisations (Muller & Mitani, 2005; Nishida, 1983). However, a similar argument applies to social alliance formation in agonistic encounters as with food sharing: agonistic support where one partner may be helping the other by supporting the protagonist or receiver of aggression in their own goals does not mean the partners are necessarily acting towards the same goal. It can be unclear from their behaviour whether individuals are, or even could be theoretically, working together towards a shared goal. Whilst it is certainly possible that agonistic support could be considered as joint action, for example in the form of two individuals chasing another at the same time which they would not do individually whilst being mutually responsive, such occurrences were so rarely observed during the study period that they will not be included for this study.

1.4.3 Group defence

Another case of potential joint action in wild chimpanzees comes from observations of collaborative defence during inter-group conflict (Boehm, 1992). Group defence indicates a shared goal as individuals from one community will only act against another community if other individuals are engaged in the same activity. The Kanyawara community of chimpanzees at Kibale National Park, Uganda have preferred coalition

partners for group defence, which has been shown by differential responses of individuals to playback of other group 'pant-hoots' where coordinated travel responses depend on the presence of certain other individuals (Wilson, Hauser, & Wrangham, 2001).

Goodall makes no mention of socio-communicative vocalisations or gestures during inter-group encounters in her seminal book on the Gombe chimpanzees. Her description of patrolling mentions only that compact groups travel silently, often pausing to look around and listen. The only mention of contact between those in the group occurring when there is a sudden sound like a twig cracking, whereupon they "may grin and reach out to touch or embrace one another", which is a fear reaction and may not represent communication that indicates mutual responsiveness (Goodall, 1986).

Boesch and Boesch-Achermann (2000) describes his focal community's reactions to other-group encounters in Tai in more detail. Due to the dense nature of the Tai forest, initial contact tends to be auditory, and the reaction of the males to this noise is described similarly to Goodall's above, as they gather together, sometimes uttering little screams. In a more interpretative description the males are also said to 'reassure' each other while giving soft screams, although exactly what behaviour reassuring entails is not described. The males are also described as 'seeking reassurance' when travelling towards an attack, as well as turning towards a following male "with a fearful open-grin face" (Boesch & Boesch-Achermann, 2000, p. 139). It is further suggested that the chimpanzees are coordinated vocally during certain attacks on stranger groups by using "attack calls", although these are also not described any further and a literature search has not revealed any other references to such a call (Boesch & Boesch-Achermann, 2000, p. 141).

Herbinger and colleagues (2009) describe vocalisations and gestures given by the whole group after playback experiments of other community pant-hoots at Tai, but do not give information on communication between specific individuals concomitant with their subsequent actions. We know they are producing certain calls (including hoots) and gestures (mostly hunching, grinning, and mounting/embracing) but not whether

individuals are mutually responsive or whether these could be coordinating subsequent action. The Sonso community in Budongo are surrounded on all sides by other communities of chimpanzees, but unfortunately only one is currently being habituated (Samuni, Mundry, Terkel, Zuberbühler, & Hobaiter, 2014), and so group encounters where interactions are seen in detail are so rare that group encounters are not included in this study.

1.4.4 Joint travel

Chimpanzees live in communities with a fission-fusion dispersal system, where they frequently split up into very different group sizes of different composition and with varying time periods apart (Symington, 1990). Wrangham (2002) suggests in a theoretical paper that, in the absence of other constraints, for example low predation pressure on chimpanzees, the optimal foraging strategy for apes (i.e. that increases their survival value) is to feed alone, only joining others at larger food sources where feeding competition is reduced. Whatever the selection pressures influencing such behaviour strategies, a picture is emerging from the primate literature indicating that species living in a societal structure where they have to remember individuals and information about them over varying and sometimes extensive periods of absence, may have increased computational abilities in this respect (Barrett, 2011).

Despite research investigating the cognitive consequences of fission-fusion dispersal, it is not known how such movements are coordinated. Are individuals, for example, travelling in random distributions with random associations depending on food availability and other environmental or landscape features, as theorised by Wrangham (2002)? Or are their associations more socially-driven, involving joint action where individuals have a shared goal and are mutually responsive, which may be the case when food is abundant (Bates, 2005; Gilby & Wrangham, 2008)? The latter option for travel association, which is suggested to influence sub-group formation and travel in Sonso chimpanzees, may be more likely to be coordinated through communication that initiates joint travel or recruits specific individuals to travel in small groups.

Some observations of wild chimpanzees in Tai have shown one alpha male using drumming on tree buttresses to coordinate group movement and specify direction (Boesch, 1991b). Although this behaviour has only been observed for one male and even then for only a limited period of time (as much of his group was later killed), the detail of description and complexity of the signal suggest that some wild chimpanzees use communication for coordinating travel, and that there is a flexibility in signal use and learning within individuals (Bates & Byrne, 2010).

Goodall first made note of possible signals used to coordinate travel in small groups in Gombe (Goodall, 1986, pp. 133-141). Loud scratches and looks towards an infant were recorded from female chimpanzees before travel, as well as waiting for others to follow, sometimes with a soft or extended grunt vocalisation. There were also six observations where branch-shaking was apparently linked to travelling behaviour. The main conclusion drawn from these observations was that coordination of individuals travelling in small parties in Gombe is in need of systematic research.

Recent work by Gruber in the Budongo Forest Reserve distinguishes a very specific soft, low-pitched vocalisation (termed a 'travel-hoo') which is apparently produced specifically to recruit other individuals to travel (Gruber & Zuberbühler, 2013). A critique of the methodologies used in this study will be included in chapter 3, but despite its flaws the study does present the possibility that vocalisation are being used to coordinate joint travel in chimpanzees on a local level in small groups.

Joint travel will be investigated in this study as behaviour in wild chimpanzees where coordination of a joint activity may be occurring. The ability of researchers to ascertain from behaviour whether joint travel involves a shared goal with mutually responsive individuals or not will be discussed further in chapter 3, with special attention paid to potential sex differences in how travel is coordinated.

1.4.5 Group Hunting

In the Budongo chimpanzees, group hunting where more than one individual acts together hunting prey (a shared goal) was not seen for over 16 years of observation, then was observed infrequently between 1994 - 2002 (Reynolds, 2005). Rates suddenly increased in the last ten years, which is a pattern of emergence similar to that seen in other groups (Boesch & Boesch-Achermann, 2000). Budongo now has rates and patterns of group hunting comparable to all other field sites for which seasonal hunting 'crazes' are described, for example of hunting every day for about 10 weeks (Muller & Mitani, 2005). Debates have already been held over whether and to what extent the socio-communicative components required to fulfil Tomasello's definition of shared intentionality are occurring during group hunts, but communication during hunts has not been directly tested and so cannot reliably contribute to either side of the argument at the moment (Boesch, 1994, 2005; Tomasello *et al.*, 2005). This study aims to provide results that can contribute to this discussion.

Goodall (1986) was the first to make note of the cooperative aspect of hunting observed in the chimpanzees at Gombe. These have been described as conforming to a definition of cooperation which requires increased success due to two or more chimpanzees acting towards the same goal at the same time (Tomasello *et al.*, 2005). Busse (1978) describes hunts in Gombe as being an 'incidental result of fortuitous encounters between chimpanzee groups and potential prey animals'. Indeed, many of the descriptions of group hunts do not include descriptions of behaviour that might lead one to believe the chimpanzees are mutually responsive to one another or coordinating their actions. The collection of observations related by Goodall (1986), however, includes some descriptions of communication between individuals that convey a strong sense of coordination of joint action to achieve their goal.

One male, Goblin, after watching baboon infants playing, stood below a tree under two other males with hair erect. He apparently looked between the males and the baboons, whereupon the two males descended, one embraced Goblin, grinning and squeaking, then 'all three slowly approached the young baboons'. It is not clear from this

description whether the glancing between the baboons and the two male chimpanzees was an active attempt to signal his hunting intention, or just monitoring of both groups' behaviour and waiting for the others to synchronise their behaviour with his as expected from previous similar instances. Either way, the description still evidences a case where an individual appears to adjust its own behaviour to coordinate its actions with others by waiting (which is comparable to Warneken's experiment with human children and chimpanzees, where waiting is a behaviour variable indicative of a form of shared intentionality during a cooperative activity (Warneken *et al.*, 2006)). Another example Goodall gives which may represent communication of intent involved the male Figan, who, 'after gazing intently into a thicket where a sow and piglets had run, looked back at Jomeo and gave the characteristic branch shake that is normally used to summon females during consortships. Jomeo at once hurried over, both males entered the thicket, and a piglet was captured' (Goodall, 1986). The description suggests mutual awareness with social monitoring and intentional gestural communication in order to recruit a partner to hunt.

Complex cooperative hunting, where different individuals take on different roles, has been described for the Taï National Park chimpanzees (Boesch & Boesch, 1989). In this community, hunting success is much higher when a group hunts (89% success) compared to an individual (16%), and a critical factor of 'the presence of other group members' has been identified for initiating a hunt. Chimpanzees have even been observed to go on hunting 'patrols' in groups at Taï and Ngogo (Boesch & Boesch, 1989; Goldberg & Ruvolo, 1997b). Boesch defines a 'group hunt' as any hunt where two or more hunters act towards the same prey (or group of prey) at the same time. 'Hunters' are defined as any individual who plays an active part in the hunt, by climbing up to the canopy height where the prey is located and looking or orienting towards them (Boesch & Boesch, 1989).

In the most detailed descriptions of hunts from habituated wild chimpanzees, Boesch suggested that the majority of group hunts occurring at Taï were 'collaborative', with four coordinated roles taken by hunters towards the same prey: *drivers* who initiate a hunt and drive prey in a constant direction, *blockers* who climb trees to block certain

escape routes, *chasers* who run under prey and try to capture them, and *ambushers* who silently climb to a concealed place in the path of the fleeing prey ready to capture them (Boesch and Boesch-Achermann, 2000).

Some group hunts, although operationally cooperative, are proposed to consist of less complex levels of organisation between hunters than the performing of different complementary actions, as described in Table 1.1 below. Bailey and colleagues (2013) have provided a more detailed update to the definitions of complexity provided by Boesch (1989). However, the descriptions still lack information about what forms of communication are needed to coordinate actions and how they might be used.

Table 1.1. Operational definition of cooperation for group hunts describing four levels of organisation with growing complexity between hunters, taken from Bailey et al. (2013) which was adapted from Boesch’s original definitions (Boesch & Boesch, 1989).

Table 1 Definitions of the different levels of cooperative hunt complexity taken from Boesch and Boesch (1989) in combination with our additions

	Old definition (Boesch and Boesch 1989)	Suggested additions to definitions
Passive	None	The presence of other predators in some way increases the individual hunting success of others without them intentionally interacting or paying attention to each other’s actions during the hunt. There is no focal prey animal except by chance and food is rarely shared. For example, one hunter may accidentally scare prey into the path of another. Hunters intentionally hunt in the same location as others
Similarity	All hunters concentrate similar actions on the same prey, but without any spatial or time relation between them; however, at least two hunters always act simultaneously. Similar actions are varying elements of pursuing a prey, i.e., stalk or chase	Timing and orientation are primarily in response to the behaviour of the prey, not that of other hunters. The kill is shared. For example, all members of a group of hunters start chasing the prey at the same time
Synchrony	Each hunter concentrates in similar actions on the same prey and tries to relate in time to each other’s actions. Hunters may begin at the same <i>time</i> or adjust their speed to remain in time	Hunters synchronise the timing of their movements in relation both to each other and the position and behaviour of the prey. Prey is shared
Coordination	Each hunter concentrates in similar actions on the same prey and tries to relate <i>in time and space</i> to each other’s actions. Hunters may begin from different directions or adjust their position to remain coordinated	It must be clear that the positioning relative to one another is not incidental, for example, if prey are approached from different directions, individuals must have spread out at some point to positions that allow such an approach rather than be individuals arriving at the scene from different start points. For example, fanning out along a front to flush prey or encircling prey such that all individuals have a similar role. Prey is shared
Collaboration	Hunters perform different <i>complimentary</i> actions, all directed towards the same prey. Examples are driving, blocking escape way and encirclement	There must be clear role differentiation resulting in team-like behaviour. The same individuals may perform the same specialised roles repeatedly in different hunts (see Anderson and Franks 2001). Timing and positioning are much more strongly based on each others’, rather than on the prey’s, behaviour than during lower levels of cooperation. For instance, a group of lions observe prey as a group, then fan out and surround it and take on different complimentary roles (ambushers and drivers) during the hunt (Schaller 1972; Stander 1992a, b). Prey is shared

Of interest for this study is that all of the above categories as described by Bailey and colleagues, excepting *similarity* and *passive* hunts, involve coordination of action in time or space, or coordination of different activities. In terms of observations of joint actions, all higher levels of complexity could potentially involve some form of communication to coordinate each individual's actions. Such coordinating signals could be given to initiate joint action, to maintain the joint action in a specific place or time, or to signal changes in complimentary actions towards the goal (applies only to cases where individuals perform different actions towards the same goal).

The highest level of hunting complexity in chimpanzees has only been observed frequently (211 times) at one field site (Taï), compared to six collaborative hunts being observed at Gombe, and none at Mahale, although there is no representative data for Budongo, Bossou or Kibale field sites (Boesch & Boesch-Achermann, 2000). The authors propose that the variation in hunting strategies between sites may be due to the fact that the application of complex strategies is only beneficial to individuals in the group when hunting success is increased. This scenario may be unique to the Taï forest where the preferred prey species (red Colobus monkeys, *Procolobus badius*) live high in the canopy making it unlikely that solo chimpanzees would be able to capture them. Although the absence of red Colobus and a lower canopy level could mean that highly complex strategies are not needed in Budongo (Goldberg & Ruvolo, 1997a), a sharp increase in the frequency of chimpanzee groups hunting guereza Colobus monkeys⁶, (*Colobus guereza*) has recently been observed in the Sonso community at Budongo, making it an ideal field site for researching hunting behaviour further.

Some researchers who have described group hunting in chimpanzees operationally concluded that the behaviour is not at all cooperative, most commonly citing individualistic explanations where each chimpanzee takes on the role it sees will allow it to achieve its own goals at that time (Busse, 1978; Gilby, Eberly, & Wrangham, 2008; Melis *et al.*, 2006a; Tomasello *et al.*, 2005). Such explanations certainly do not support the idea that shared motivation or joint action is involved in chimpanzee hunting. They

⁶ Henceforth called Colobus monkeys.

seem instead to fit in with the least complex category of cooperative hunting defined by Boesch (1989) as *similarity*, with no coordination of actions. However, as is equally lacking in Boesch's descriptions, they also do not address the issue of how much active coordination or communication is involved when taking on these different roles- for example monitoring others' behaviour and using 'recruiting' gestures or vocalisations. The present study attempts to address this gap in research on chimpanzee hunting behaviour.

The fourth and fifth chapters will investigate the vocalisations and behaviour of hunting chimpanzees, firstly through dissemination of data collected on naturally occurring hunts observed in the Sonso community, and secondly from a playback experiment designed to elicit a shared coordinated response from an affiliative chimpanzee dyad in the hunting context.

The field site where research was carried out and the chimpanzee community studied will be introduced firstly in the chapter two. The third chapter will describe the results of investigations into coordination of joint travel behaviour.

Chapter 2. Sonso study site, the chimpanzee community, and measures of dominance and affiliation.

Abstract

The study site in the Sonso region of the Budongo Forest Reserve is introduced first in this chapter. The chimpanzee community under investigation is then described, including demographic details and general aspects of their life history relevant to the study. A measure of dominance is calculated for the male chimpanzees from pant-grunts, a signal given only to more dominant individuals, which were produced during the study period. Affiliation between individuals is also calculated using a combined measure adapted from other studies that includes party (group) membership, a measure of proximity, and a measure of grooming between each dyad of individuals.

2.1 Sonso study site

Data were collected between January - April 2010, September 2010 - October 2011, and July - August 2012 from the Sonso community in the Budongo Forest Reserve, Uganda. The field site, shown in figure 2.1, is at the southernmost edge of a 428km² moist, semi-deciduous tropical forest in the West of Uganda (1°44' N, 31°33' E), with a mean altitude of 1100m (Eggeling, 1947; Gilby, Eberly, Pintea, & Pusey, 2006; Plumptre, 1996). The forest was selectively logged for Mahogany and *Cynometra* hardwood trees for 60 years, with the Sonso study site mainly being logged between 1947 and 1952. The activity left a mosaic of forest types including many indigenous fig trees and some invasive species, such as mango trees and *Broussonetia papyrifera*, that constitute a significant portion of the chimpanzee community's diet (Plumptre, 1996). The study site was set up by Reynolds in 1990 under the Budongo Forest Project (Reynolds, 1992), using buildings converted from the old saw mill, and has continued as a chimpanzee research centre until the present time. The project is now called the Budongo Conservation Field Station (BCFS), funded mainly by RZSS (the Royal Zoological Society of Scotland), and undertakes conservation efforts with local communities in addition to research with multiple species (www.budongo.org).

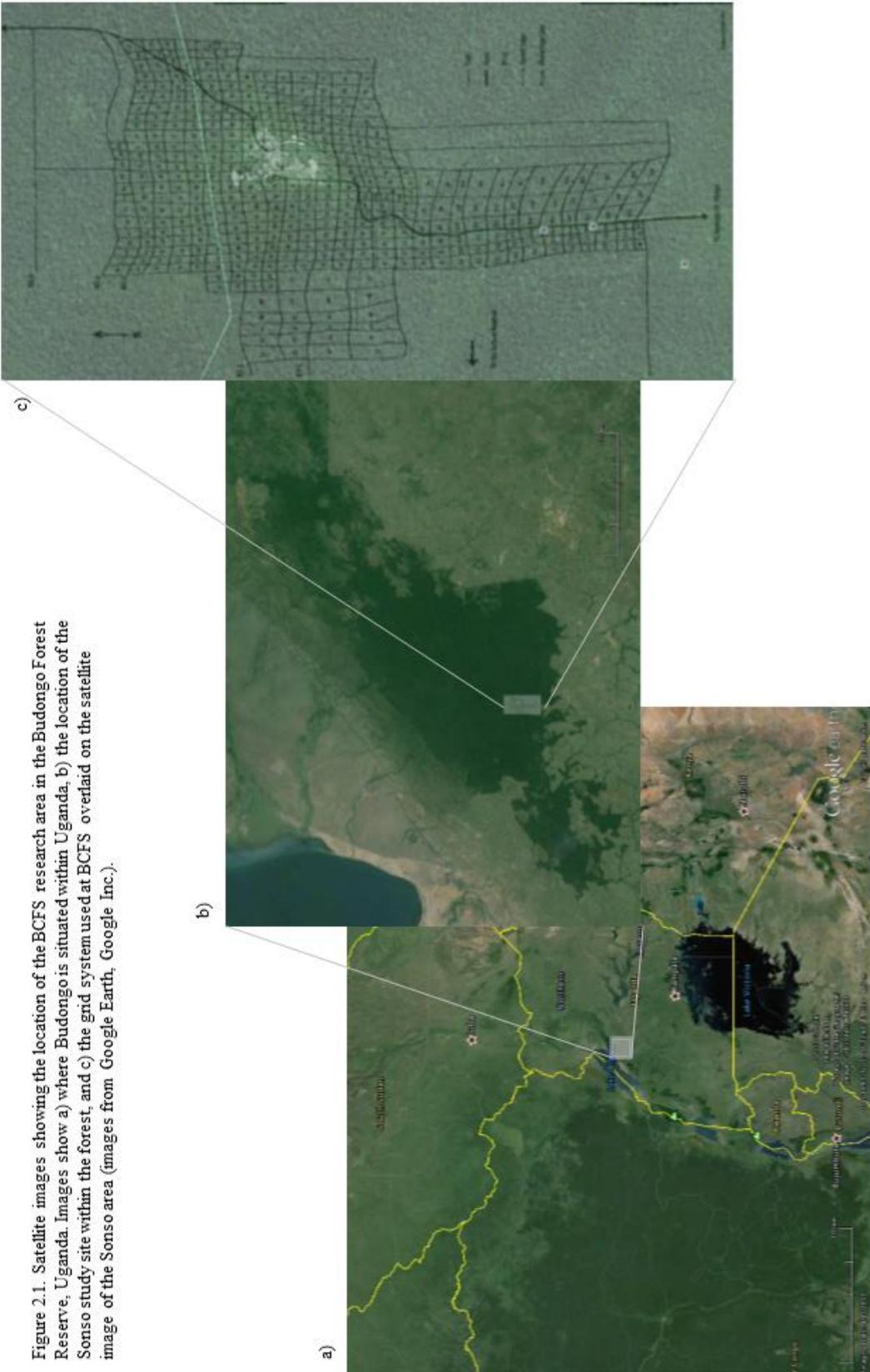


Figure 2.1. Satellite images showing the location of the BCFS research area in the Budongo Forest Reserve, Uganda. Images show a) where Budongo is situated within Uganda, b) the location of the Sonso study site within the forest, and c) the grid system used at BCFS overlaid on the satellite image of the Sonso area (images from Google Earth, Google Inc.).

2.2 Sonso chimpanzee community

Chimpanzees in the Budongo Forest, Uganda belong to a subspecies called *Pan troglodytes schweinfurthii* (Goldberg & Ruvolo, 1997b). They live in patriarchal communities (Nishida, 1968) with a fission-fusion structure, which can greatly affect the behaviour data collected from individuals depending on party size and social composition (Goodall, 1986; Newton-Fisher, 2003; Wrangham, Clark, & Isabirye-Basuta, 1992). Party composition was therefore a part of all observations recorded in Sonso, determined by identifying all individuals within 35m of the centre of a group of chimpanzees- which in practice is approximated as all individuals within sight, when collecting data in a dense forest with poor visibility (Newton-Fisher, Reynolds, & Plumtre, 2000). A field assistant, Jackson Okuti, who has worked with the community for 7 years, taught the main observer (CM) individual identities, common chimpanzee behaviour and how to recognise different vocalisations during a pilot study (January-April 2010), and was always present in the field to assist with individual identification and behaviour observations for the following two years during which this research was conducted.

The Sonso community was habituated without food provisioning and followed for research purposes for more than 30 years (Reynolds, 2005). Their home range centres on the research camp- through which they regularly walk- and extends south to the edge of the forest where a small farming village, Nakafungo, is located (Newton-Fisher, 2003). Contact between Sonso chimpanzees and villagers can occur when mango trees are fruiting in the village, but interactions remain visual and no aggression has been recorded between species in the history of the project.

The alpha and other adult and sub-adult males form the main 'central' party while females generally have slightly different but overlapping ranges and move in family groups or with one or two other females and their respective families. The community tends to come together and form larger groups when productive fig trees are fruiting in the dry season- a fission-fusion social group structure (Reynolds, 2005). During the study period of January 2010-September 2012 Sonso community consisted of 73

individuals: 23 adult females, 11 adult males, 11 sub-adult females, 3 sub-adult males and 25 juveniles/infants which were observed more than once in the Sonso community. Adults were defined as over 15 years and sub-adults between 10 and 15 years of age (categories from Goodall, 1986). One male, ZD became a sub-adult during the study, and so is included in male dominance analyses and affiliation measures. Appendix 1 contains a complete list of Sonso chimpanzees in the community.

The hierarchical system of the community is such that adult males are always more dominant than females, probably due to the sexual dimorphism of the species, but alliances and the presence of dominant, related individuals can affect the behaviour outcome of competitive interactions (De Waal, 1989). Relationships characterised by positive social interactions between individuals, comparable to human ‘friendships’, have many different definitions in the primate literature (Silk, Cheney, & Seyfarth, 2013). Those aspects of relationships which are important for considering whether individuals would have the motivation to cooperate with each other have been extracted for chimpanzees in the context of group hunting and joint action: ‘allies’ are defined as two or more individuals who form alliances, or ‘cooperate’, where they direct aggression jointly towards others (Mitani, Merriwether, & Zhang, 2000; Nishida, 1983); ‘affiliates’ are defined simply as those individuals associating, grooming and spending time in proximity to each other (Mitani *et al.*, 2000; Muller & Mitani, 2005; Nishida, 1968). Alliance formation, although likely to be a strong predictor for cooperative motivation, is relatively rare during intra-male conflict at Sonso, and there was not enough data to utilise this measure. Therefore affiliation was used by creating a composite measure of party association, grooming and proximity, adapted from studies by Gilby and Schel (Gilby & Wrangham, 2008; Schel *et al.*, 2013a).

2.3 Dominance hierarchy

2.3.1 Introduction

Chimpanzee males have a linear dominance hierarchy which consists of the alpha male at the top, then higher, middle and lower- ranking males (Goodall, 1986). All adult males are higher ranking than females and sub-adult males can be dominant or subordinate to females (although at the time of the present study no sub-adult males were seen to be submissive to a female (Schel *et al.*, 2013a). Hierarchies are often calculated in chimpanzees by looking at the production of a specific vocalisation, the pant-grunt, which is thought to be a sign of respect given only by submissive to dominant individuals (Goodall, 1986; Noe, de Waal, & van Hoof, 1980). Other behaviours and signals given during agonistic interactions can also be used, such as screams and physical attacks (Newton-Fisher, 2004; Noe *et al.*, 1980), but these can be more complicated and may be influenced by other factors than the dominance relationship between a dyad, as for example alliances and audience effects of other chimpanzees can alter this behaviour (Laporte & Zuberbuhler, 2010; Newton-Fisher, 2004). It has recently been reported from Budongo, as was suggested for male chimpanzees at Mahale (Hayaki, Huffman, & Nishida, 1989), that pant-grunt production can also be affected by the audience present, with the presence of the alpha male repressing pant-grunt production by females to other males (Laporte & Zuberbuhler, 2010). However, as such audience affects would only effect the frequency of calling and not the direction of pant-grunt being produced during encounters, only pant-grunts were used to calculate a linear hierarchy here.

2.3.2 Methods

Pant-grunts are a relatively rare vocalisation amongst male chimpanzees, with the exception of the alpha male who receives the majority of these signals (Newton-Fisher, 2004). During the present study period, January 2010- September 2012, the alpha- NK- received 1483 out of 1905 pant-grunts recorded *ad-libitum* (all-occurrence) from individual focal follows by researchers carried out daily between 07:00-16:30 for the

long-term database at BCFS (CM, AS, GM, SM, JK, MD, and JC)⁷. Where an individual produced a pant-grunt upon encountering another individual, they are recorded as having ‘lost’ the encounter. The method of data collection and slow production rate has led to an often sparse data set for pant-grunts, missing some individuals’ dyadic interactions with other group members. Jameson, Appleby, and Freeman (1999) presents a method for calculating linear or near-linear dominance hierarchies suited to such datasets with many missing interactions. They take the BBS model from Batchelder, Bershad, and Simpson (1992) which, assuming normality in the distribution of dominance that underlies observed dominance behaviour, allows each animal to be assigned a scale score, $s(a_i)$:

(1)

$$s(a_i) = [\alpha(2W_i - N_i)/2N_i]$$

where $\alpha = \sqrt{2\pi} = 2.50663$ (a constant from the Taylor expression of the normal distribution), W_i is the number of encounters which individual a_i won, and N_i is the total number of dominance encounters involving individual a_i . This scale score represents the number of encounters the individual won as a function of all its agonistic encounters. These initial scale scores are then used in the following equation which is applied recursively to each individual, giving a new scale score each time.

(2)

$$s(a_i) = [2(W_i - L_i)/N_i] + Q_i$$

where W_i is the number of encounters which individual a_i won, L_i is the number of encounters which individual a_i lost, N_i is the total number of dominance encounters involving individual a_i , and Q_i is the mean scale score of all the individuals which a_i interacted with agonistically. Q_i is re-calculated each time from the new scale scores for each individual to create the next scale score $s(a_i)$ from the second equation above.

When the scale scores stabilise, a linear hierarchy has been reached.

⁷ CM refers to the author, Caroline Mullins; AS refers to fellow researcher Anne Schel; GM SM JK MD and JC refer to field assistants Geresomu, Sam, Jackson, Monday and Jacob respectively.

2.3.3 Results

Table 2.1 below shows examples of the second equation being applied recursively to create new scale scores per individual for each iteration. The alpha male, NK, was removed from the analyses, as his special status makes him an outlier which would violate the assumption used in this test: that dominance is distributed normally across individuals. The sub-adult ZG was also not included as he spent a lot of time away from the male parties and was not treated as other males due to a severe snare injury and stunted growth. ZD, a male who became a sub-adult during the study period, is included in the analysis, but no focal data is available for him and his ranking is based on a smaller data set than for the other males. His most likely position in the hierarchy is therefore last, and not second-to-last as prediction by the final iteration of the scale scores shown in table 2.1, which may be accounted for by the larger data set recorded for PS compared to ZD. NK was therefore ranked at number one, and the other adult and sub-adult males were ranked according to their position in the table, with MS at the top ranking number two, and so on down the list.

Table 2.1. Dominance hierarchy for Sonso males calculated as per Jameson *et al.* (1999) using pant-grunt data collected *ad lib.* and from individual focal follows during the period January 2010-September 2012.

ID	initial $s(a_i)$	$s(a_1)$	$s(a_2)$	$s(a_3)$	$s(a_4)$	$s(a_5)$	$s(a_6)$	$s(a_7)$	$s(a_8)$	$s(a_9)$
ms	1.25	1.82	1.75	1.78	1.79	1.80	1.81	1.82	1.84	1.85
zf	1.12	1.52	1.45	1.49	1.49	1.51	1.52	1.53	1.54	1.55
hw	1.08	1.45	1.38	1.42	1.43	1.44	1.45	1.47	1.48	1.49
kt	0.93	1.05	0.94	0.99	0.99	1.00	1.02	1.03	1.04	1.05
sq	0.45	0.61	0.58	0.60	0.61	0.62	0.63	0.65	0.66	0.67
fd	0.32	0.53	0.54	0.55	0.56	0.58	0.59	0.60	0.61	0.62
sm	-0.45	-0.57	-0.53	-0.53	-0.52	-0.51	-0.50	-0.49	-0.47	-0.46
zl	-0.77	-0.87	-0.77	-0.79	-0.76	-0.75	-0.74	-0.73	-0.72	-0.70
fk	-1.05	-1.38	-1.26	-1.28	-1.26	-1.25	-1.23	-1.22	-1.21	-1.20
kz	-1.13	-1.56	-1.43	-1.44	-1.42	-1.41	-1.40	-1.39	-1.38	-1.36
ps	-1.24	-1.80	-1.71	-1.71	-1.70	-1.68	-1.67	-1.66	-1.65	-1.64
zd	-1.25	-1.72	-1.63	-1.64	-1.62	-1.61	-1.60	-1.59	-1.58	-1.56

2.4 Affiliation measures

2.4.1 Introduction

The index for affiliation between dyads of chimpanzees used in the present study utilises aspects of Gilby and Wrangham's (2008) 'combined association index' (CAI) and Schel et al.'s (2013a) 'composite friendship index' (CFI). The new index bases the calculations for its measures on those found in Gilby and Wrangham's (2008) methods to assess association, which were in turn derived from the simple ratio index described by Cairns and Schwager (1987), but adds a measure of grooming between individuals as per Schel et al. (2013a). Grooming is an easily observed positive social interaction between individual chimpanzees which plays an important role in maintaining long-term relationships in male chimpanzees (Mitani, 2009). As such, the addition of a grooming index to those of party-level association and proximity gives a richer data set for assessing affiliation between dyads, as defined by Mitani et al. (2000) and here called the 'composite index of affiliation' (CIA).

2.4.2 Methods

The individual composites of the CIA are broadly similar to those used separately by Machanda et al. (2013) and are presented below. All measures were calculated using 5 minute instantaneous scan samples collected during continuous focal follows of all adult and sub-adult chimpanzees in the Sonso community (Altmann, 1974). Individuals were chosen for focal observation in a pseudo-randomised order and full-day follows were conducted (during the working day utilised at BCFS from 07:00- 16:30) to avoid biases in data collection based on time of day, general activity or location.

Data collected during scan samples consisted of: subject ID; general activity (resting/feeding/travelling/social-behaviour/self-grooming); location (on the ground/in a tree (>3m height)/on a path (dirt or road)/on a log or low-branch below 3m height); vocalisation produced (see table 3.1); social behaviour (grooming/physical

aggression/sex/displays/solicitation/play-for more details see appendix 2.2); social partner ID; neighbour ID of individuals within 0, 2, 5, 10 and 10+m; and any other comments. Table 2.2 shows the number of scans and total focal-time for data collection for each male in the Sonso community.

Table 2.2. Number of scans and focal time for Sonso adult males (and two sub-adults) from individual focal-follows conducted during the period of January 2010- September 2012.

ID code	Number of scans	Focal time (hours)
FD	136	24.06
FK	288	40.34
HW	173	23.39
KT	241	36.65
KZ	234	24.05
MS	258	31.52
NK	270	45.11
PS	159	19.33
SM	149	24.20
SQ	216	30.48
ZF	209	30.04
ZG	46	6.76
ZL	139	25.25

2.4.2.1 Party association

The party association index (PAI) represents the proportion of party scans in which a dyad was seen together:

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

where P_{ab} is the number of party scans in which individuals A and B were seen together, P_a is the number of parties containing A, and P_b the number of parties containing B. P_{ab} is subtracted from the denominator as P_a and P_b already include those parties where A and B were seen together.

2.4.2.2. 5m spatial proximity

The 5m proximity index (5MI) is a measure of spatial proximity representing the frequency with which individuals were within 5m of each other:

$$5MI_{ab} = \frac{A_f B_{5m} + B_f A_{5m}}{A_f B_p + B_f A_p}$$

where $A_f B_{5m}$ is the number of scans where the focal individual A was within 5m of B, $B_f A_{5m}$ is the number of scans where focal B was within 5m of A, $A_f B_p$ is the number of scans where A was the focal and B was in the same party, and $B_f A_p$ is the number of scans where B was the focal and A was in the same party. Including the number of scans where the partner was in the same party as the focal individual in the denominator ensures the 5MI measure is independent of the party association index, and allows for dyads that are rarely seen in the same party to nonetheless have a high 5MI value if when they are seen together, they are frequently in close proximity.

2.4.2.3 Grooming

The grooming index (GI) is a summation of all grooming events (both unidirectional and allo-grooming) between dyads observed during 5 min scans of focal individuals. Looking separately at the weighting of allo- to unidirectional grooming and at the relative direction of grooming events can reveal more information about the value of the relationship to each individual in the dyad (Mitani, 2009; Silk *et al.*, 2013), but would require a lot more data than is contained here (grooming of any kind was only observed between 28 male dyads out of 66 during scans).

$$GI_{ab} = \frac{A_f B_g + B_f A_g}{A_f B_p + B_f A_p}$$

where $A_f B_g$ is the number of scans where the focal individual A was grooming with B, $B_f A_g$ is the number of scans where the focal individual B was grooming with A, and $A_f B_p$ and $B_f A_p$ are the number of times A and B were the focal and the other was in the

same party, as for the 5MI ratio. Machanda et al. (2013), using a similar measure, only calculated the grooming index for dyads who were within 5m of each other in at least 10 focal scans. This ensures that the index is not disproportionately influenced by only a few observations of close proximity. However, from the current data set, only 22 out of 66 possible male dyads were within 5m proximity to each other in 10 or more scans, meaning that 2/3 of the male dyads would not have a GI value to include in the CIA. As grooming is an important measure to make the CIA an index of affiliation and not simply association, the GI used here controls for party level association only. This means that the GI value is not independent of the 5MI measure, but it is still independent of the PAI measure, so dyads that are rarely in the same party can still have a high grooming index value (all dyads have more than 10 scans where they are in the same party) and vice versa.

2.4.2.4 Combined index of affiliation

The combined index of affiliation (CIA) was calculated by first standardising the three indices described above by dividing by the mean index value from all dyads. Each of the indices then represents the value of the measure between the dyad compared to all male-male dyads in the group. The three indices were then added and divided by 3 to get the CIA for each dyad.

$$CIA_{ab} = \frac{PAI_{ab}/PAI_{mean} + 5MI_{ab}/5MI_{mean} + GI_{ab}/GI_{mean}}{3}$$

A dyad with an index value that was greater than 1 has a level of affiliation greater than the average for all dyads. The method described above provides a combined index similar to that of Gilby and Wrangham (2008).

2.4.3 Results

The results of the calculations for the combined index of affiliation are presented in table 2.3 below. All adult males were included in the analysis of dyadic relationships, as

well as two sub-adults (N = 13), so that the measure could be used in analyses of group hunting behaviour of males in chapters 4 and 5. The individual ZD was not included as a focal animal during data collection, so values for dyadic relationships with ZD are one-sided and not used in calculating the mean indices for standardising the values.

Table 2.3. CIA (combined index of affiliation) calculated for all adult male dyads in Sonso during the study period January 2010- September 2012. Values for the sub-adult males ZD and FK are included as they were included in dyads for the experiment in chapter 5. Highlighted values are >1 and represent affiliation greater than the average.

CIA	fd	fk	hw	kt	kz	ms	nk	ps	sm	sq	zf	zl	zd
fd	.	1.74	1.11	0.66	0.23	0.07	0.09	0.35	0.44	2.92	1.27	0.60	0.29
fk	.	.	1.33	1.07	0.50	1.97	1.77	0.34	0.22	1.39	1.92	0.06	0.02
hw	.	.	.	1.17	1.70	0.27	0.95	0.53	0.73	2.30	0.66	1.00	0.33
kt	0.65	0.99	2.64	0.22	0.36	1.28	1.49	0.77	0.37
kz	1.83	1.01	0.21	0.29	0.34	1.68	1.05	0.27
ms	2.12	0.28	0.47	0.98	1.52	1.23	0.35
nk	0.14	0.85	1.30	3.72	0.45	0.48
ps	4.06	0.53	0.33	0.27	0.34
sm	0.32	0.38	0.48	0.62
sq	0.18	1.65	1.44
zf	0.59	0.48
zl	3.32

2.4.4 Summary

A linear dominance hierarchy and dyadic affiliation measures have been calculated for all adult and sub-adult males in the Sonso community present during the study period. These measures allow analyses of communication during the coordination of joint action in the following chapters using variables representing the relationship between individuals involved in the joint action. The first instance of a potentially coordinated joint action in wild chimpanzees, joint travel, is presented first in chapter 3.

2.5 Research approval

Ethical approval for this study was obtained from the ethics committee of the Department of Psychology and Neuroscience at the University of St Andrews. Permission to carry out research was obtained from the Ugandan Wildlife Authority (UWA) and the Ugandan National Council for Science and Technology (UNCST) (see Appendices 4-6).

Chapter 3: Joint travel and coordination in wild chimpanzees

Abstract

Communication associated with joint travel is explored in this chapter, using three data sources - scans, focal follows and video recordings of behaviour. These methods offer more comprehensive details of small-group travel behaviour in Sonso chimpanzees than a previous study. Scan data provided no evidence for a vocalisation type that is systematically associated with general travelling behaviour, although in males pant-hoots included as part of displays were produced more during travel than during other activities, supporting previous studies which implicate pant-hoots and drumming as long-distance coordinating signals. A one minute predeparture period was analysed from travel initiations recorded during focal follows which showed no evidence for a vocalisation type that is specifically associated with the initiation of small-group travel more than any other call type in Sonso chimpanzees. In males, pant-hoots were produced at a higher rate than the average (from all behaviour observations) in the one minute predeparture period, but were not associated with local coordination of joint travel. Video data showing the initial stages of travelling from resting or feeding behaviour found no significant association between vocal production, or pausing, or looking at a partner, and subsequent following behaviour of partners, which appears not to be related to the age of the partner or, in females, with whether the traveling partner was their offspring. In summary, the data presented in this chapter provided no evidence for vocalisations that locally coordinate joint travel behaviour in the current cohort of chimpanzees in Sonso. Further observations are suggested to expand the social and environmental factors controlled for during analyses of travel coordination and communication, and to include gestures as potentially coordinating signals.

3.1 Background

3.1.1 Introduction

This chapter will look at the travelling behaviour of chimpanzees in Sonso, and whether there is any evidence for coordination using communication. Joint travel is defined as occurring when two or more individuals travel together in proximity. Joint travel is considered to be a joint action if, on average, individuals travelling in proximity travel to the same location, or goal. If joint travel is coordinated using signals, evidence is expected to show initiators of travel communicating in order to alter the travel behaviour of another individual, rather than the individual simply following the cue of the already travelling initiator (a distinction exemplified in sheep travel by Ramseyer, Boissy, Dumont, & Thierry, 2009). Signals might also be used to maintain joint travel when an individual is already moving, or to recruit specific individuals to travel.

As described in the background information of chapter one, the limitations of using joint travel as an example of joint action in chimpanzees are the same as for humans travelling together. Human joint travel was described by Tomasello and colleagues as an example of shared intentionality involving shared mental states (Tomasello *et al.*, 2005). However, when observing joint travel behaviour in chimpanzees, it is not possible to ask individuals about their thoughts and goals during the activity as it is with humans. This raises an issue with chimpanzee joint travel in that communication observed, which could be given as evidence for coordination towards a shared goal during joint travel, could rather show that the individuals are maintaining proximity to one another for social reasons. In this case, the criteria for ‘joint action’ that individuals share a goal may not always be fulfilled. However, as a previous study has stated evidence for a specific vocalisation used to recruit other individuals to travel that is not used to maintain proximity during other activities (Gruber & Zuberbühler, 2013), and as

a shared goal during joint travel cannot be ruled out, this study includes joint travel as a possible joint action.⁸

3.1.2 Chimpanzee joint travel

In chimpanzees, two or more individuals often travel together to visit different resources and rest in the same area, but this travel is not restricted to the whole group as chimpanzees are a fission-fusion species (Bates, 2005; Goodall, 1986). Fission-fusion describes a group structure whereby individuals come together and divide into smaller subgroups, also called parties (or single individuals) depending on their activity and the location of different resources available (Kummer, 1971). Regarding behaviour, this means chimpanzees fit in with the definition of a high degree of ‘fission-fusion dynamics’ proposed by Aureli and colleagues (2008), in that chimpanzees exhibit large variation in both spatial cohesion and individual membership of subgroups over time.

Although group travel coordination has been studied in detail for many primate species, especially different baboon species, only Guinea baboons (*Papio papio*) appear to have a similar high degree of fission and fusion dynamics suitable for comparison with chimpanzee travel behaviour. Unfortunately, Guinea baboons are also the least studied of this monkey family, and it is not yet known how they coordinate group movements (Fischer & Zinner, 2011). A wide range of species, from wolves to geese to gorillas, exhibit behaviour before group travel including vocalisations and stereotyped movements suggested to coordinate group travel, but many methods and varying terminology have been used in studies on these species (for a comprehensive review see King & Sueur, 2011). A recent symposium of the International Primatological Society collated and discussed much of the work on group movements and travel coordination, producing a set of recognised and generally applicable definitions (Pyritz, King, Sueur, & Fichtel, 2011). The definitions used in this study will now be described.

⁸ For comparison, a recent review of group travel in primates indicated that there is no evidence for shared intentionality in other group-travelling primates, defined according to Tomasello’s strict requirements for shared mental states (Fischer & Zinner, 2011).

This thesis looks at behaviour most likely to apply to a fission-fusion dispersal pattern, where travelling groups vary in composition and size. The analyses focus on potential coordination between individuals in small groups, where two types of behaviour are looked at. The first is predeparture behaviour, which is defined as behaviour performed before the departure of the initiator, and which makes the timing of departure predictable. The second is recruitment behaviour, which is defined as behaviour which increases the probability that other group member will join a certain activity (Bourjade & Sueur, 2010).⁹ For analysing small group coordination, both measures can be recorded with respect to specific travel partners and their subsequent behaviour.

A recent study by Gruber and Zuberbühler (2013) looked at joint travel coordination with the same study group of chimpanzees at Sonso, but serious flaws in methodology make the use of their results unreliable. These problems are referred to in the methods section of the current chapter. A crucial theoretical error in the Gruber study stems from the absence of a defined predeparture period. A defined predeparture period, as used in the current thesis and in all previous joint travel studies in other species (King & Sueur, 2011), is required in order to obtain reliable and replicable data on communication between individuals prior to travel. Without such a defined time period, data are open to biases in the recording of signals produced at varying times before travel, particularly when the observer is expecting, for example, one specific call type to be associated with travel behaviour.

3.1.3 Sex differences in chimpanzee travel behaviour

When analysing joint travel in chimpanzees, there are likely to be sex differences in travel coordination as a result of differences in travel pattern and range usage between males and females with young offspring. Males in Sonso tend to include visiting the

⁹ In terms of whole-group travel, predeparture vocalisations are thought to reflect the motivation of the group as a whole rather than signals directed at specific individuals, as collective action is only achieved after a 'quorum' threshold of performers (i.e. a certain number of individuals in the group) is reached (Pyritz *et al.*, 2011).

edges of their territory as part of their daily foraging activity (Bates & Byrne, 2009), rather than regularly engaging in specific boundary ‘patrols’ as other wild chimpanzee communities have been observed doing (Boesch & Boesch-Achermann, 2000; Mitani & Watts, 2005). For males, travel decisions in Sonso are thought to be based primarily on social considerations, rather than visiting specific food sources (Bates, 2005). This makes the possibility that they are maintaining proximity during travel through communication (and thus coordinating joint travel) a question worthy of investigation. Females with dependent offspring are also likely to maintain cohesion during travel, although the underlying motivation may be different to males. Differences in motivation may occur as females and their offspring remain in near-permanent proximity until the offspring reach sub-adulthood, whereas males can change preferred affiliative partners more flexibly (Mitani *et al.*, 2000).

3.1.4 Coordinating signals

Decisions to travel together (in proximity and towards the same destination), then, could easily be made *ad hoc* by one individual which follows the movements of a preferred affiliative partner. However, this movement together may be coordinated (i.e. if both individuals are moving towards the same goal, be that of travelling to the same location or simply of remaining in proximity, and wish to do this jointly). Evidence of this coordination may be observed as a signal given before travel, a signal given in the initial stages of travel, and recruitment behaviour when waiting for the partner to join before travelling on.

To investigate whether such behaviour occurs, the communication of chimpanzees was examined when two or more individuals started moving in proximity and travelling together. Males and females were analysed separately. Types of communication considered included vocalisations (see table 3.1) and, for the initiation period of travel or recruitment to travel coded from videos, pauses in travel and looks towards a travel

partner¹⁰. It was predicted overall for both males and females that the ‘hoo’ vocalisations would be produced more during travel than feeding or resting behaviour, and that vocal production would be affected by social composition of the audience.

Table 3.1. Vocalisation repertoire used for recording field observations of Sonso chimpanzees in the Budongo Forest, Uganda from January 2010 to September 2012; descriptions based on Slocombe (2005) and Marler and Tenaza (1977).

Vocalisation name	Acoustic description
Bark	Loud, low-pitched vocalisation with sudden onset; energy concentrated in lower harmonics; graded from a grunt and into a squeak
Cough	Unvoiced, low-pitched bark
Drumming	Non-vocal, low frequency, long-distance (up to 1km) sounds produced by hitting tree buttresses with hands or feet (Arcadi, Robert, & Boesch, 1998)
Hoo	Soft-hoos are low-pitched short calls given singularly or in short bouts (see grunts in (Marler & Tenaza, 1977)); loud-hoos have higher amplitude and duration
Laughter	Low-pitched exhalations, irregular grunts and wheezes on inhalations (reminiscent of, but not identical, to human laughter)
Pant	Rapid panting with phonation on inhalation and exhalation; usually unvoiced, quiet and low-pitched
Pant-grunt	Low-pitched sound voiced on both inhalation and exhalation; quieter and faster than a pant-hoot
Pant-hoot	Loud call voiced on both inhalation and exhalation, consisting of four phases: an introductory phase (of hoo calls); a build-up phase (of increasingly loud hoos); a climax phase (screams and roars); a let-down phase (hoos with decreasing energy); display pant-hoots include drumming or branch-shaking
Rough-grunt	Most often a pulsed grunt with relatively slow tempo; can range from low-pitched grunts to high-pitched tonal squeaks; given in context of food

¹⁰ Looks, or back-glances increase recruitment success in Rhesus macaques (*Macaca Mulatta*) (Sueur & Petit, 2008).

Scream	High-pitched loud harmonic call with varying tonal quality (even in the same individual); often graded into shorter screams called ‘squeaks’
Whimper	A series of quiet hoo vocalisations in which pitch and amplitude rise and ebb; can be pure tone or harmonic series

A specified predeparture period was analysed from video footage and audio recordings for signals between individuals and their subsequent behaviour. It was predicted that: a specific call-type, the ‘hoo’, would be produced more than other call-types in the predeparture period and in the initiation of travel; that hoo’s would be produced more in the predeparture period compared to the production rate during all other behaviour; and that calls would be produced more during the predeparture period when an individual was within sight of other chimpanzees than when the focal was alone.

It was also specifically noted during focal follows when an individual was seen to start travelling within 10m behind an individual and in the same direction (‘following’ them¹¹) and these events were analysed for any preceding communication. It was predicted that hoo vocalisations would be produced during follow events more than other vocalisations and that hoo production by a travelling individual would be more likely to result in a potential travel partner following within 10m of the initiator.

In further analyses of the initiation of travel from video recordings, it was expected that hoo’s, pauses in travel and looks towards a travel partner would increase with higher initial distances of travel partners, and be more likely occur when the travel initiation results in a follow event than not.

¹¹ The definition of ‘following’ differs to other studies of collective movement in monkeys which rely on a threshold number of individuals in a group moving in the same direction as an initiator (Ramseyer *et al.*, 2009). This study seeks to look specifically for dyadic communication between individuals considered to be doing an activity together, which can only be recorded if they are both within visual range, i.e. within 10m of each other and the observers.

3.2 Methods

3.2.1 Study group

Data were collected in Budongo between September 2010 and December 2011 using full-day focal follows (between 7am and 4:30pm) of adult male and female chimpanzees, which are described in chapter 2. An all-occurrence method of recording signals between individuals during focal follows was needed to remove biases due to observer pre-conceptions and expectations of signals associated with travel (Altmann, 1974). The fission-fusion group dynamic and wide ranging behaviour meant that individuals were chosen for focal follows on a pseudo-random basis, where individuals in parties were initially searched for in the morning according to a random schedule, and later individuals were chosen according to which was the most ‘under-sampled’ within a party (Fragaszy, Boinski, & Whipple, 1992).

3.2.2 General travelling behaviour

Instantaneous scan samples were conducted every five minutes during focal follows (as described in chapter 2.4.2) in order to accurately compare the proportion of time individuals spent in different general activities and their proximity to other individuals during the behaviour (Altmann, 1974). When extracting data for analysis, general behaviour used for comparison were resting, feeding and travelling. Scans where the focal individual was engaged in a social interaction were not included in these analyses, as by definition they already include individuals looking at, interacting with, and potentially communicating with another (this also excluded all grooming interactions). The two-letter codename (see appendix 1) for each individual was listed at distances of 0, 2, 5, 10 and 10+ metres from the focal individual during a scan, which allowed the analyses to be put in the context of other nearby individuals. Number and demographic composition of individuals in contact and within 10m proximity to the focal animal were calculated, including adult males, adult females, offspring of females, and

grouping unrelated infants, juveniles and sub-adults as ‘juveniles’¹² for this particular analysis.

Most juveniles and infants in the Sonso community have been genetically assessed for paternity with the Sonso males (see appendix 1), but have not been included as offspring for these analyses. This is because it is still unclear whether males can recognise their offspring, with conflicting evidence of paternal kin recognition from different field sites in Tai, the Ivory Coast and Ngogo, Uganda (Langergraber *et al.*, 2007; Lehmann, Fickenscher, & Boesch, 2006). However, the most recent study from Gombe, Tanzania, which is the first to compare adult male association with young males from infancy through to juveniles and sub-adult age, found no effect of paternity on the proportion of time spent in the same party or (from preliminary results due a smaller sample size) on the frequency of affiliative or agonistic interactions (Wroblewski, 2010). All non-adult offspring are therefore counted as unrelated juveniles for the male analyses.

3.2.3 Overall vocalisation frequencies, predeparture vocalisations and pauses in travel

During focal follows, all-occurrence continuous data on an individual’s behaviour was collected and time-stamped at each change in activity (behaviour state, as described in chapter 2.4.2) or new behaviour event (for full description of behaviour see appendix 2.2). Behaviour events recorded were social behaviour and partner ID, vocalisations, individual IDs in contact, within 2m, 5m, 10m or more than 10m, location and environment details, and other comments. This allowed *post hoc* extraction of vocal and social information from specific time frames related to the transition in behaviour state from resting or feeding to travelling. This method provides unbiased data on social and communicative events associated with travel initiation, unlike the methodology previously used to look at joint travel in Sonso chimpanzees, where the observer used an *in situ* method for classifying travel events while following a focal individual, and

¹² The group ‘juveniles’ consists of unrelated non-adult chimpanzees with which a focal chimpanzee (an adult male or female) was theoretically less likely to communicate and coordinate travel with compared to with their offspring or another adult chimpanzee.

then recorded vocalisations and social data relating to travel initiation only from those instances (Gruber & Zuberbühler, 2013).

Vocalisations were also recorded on an all-occurrence basis in the current study, with all call-types being given equal importance during observation. This method differs to the Gruber study on joint travel in Sonso where vocalisations relating to travel initiation were not recorded from a defined predeparture period, but instead whenever the observer thought a specific call, the ‘travel hoo’, was produced, at any stage during travel. These ‘travel hoos’ were classified as distinct from other hoo vocalisations *in situ* rather than through *post-hoc* acoustic classification of all hoo-type vocalisations produced during different behaviour states from all individuals. Furthermore, their acoustic analyses for discriminating this ‘travel hoo’ as distinct from other hoo vocalisations included 10 samples from only one female and one male chimpanzee in the group, meaning the results could have been an over-interpretation of the data.

During analysis in this study, a travel event was defined as when an individual continuously travelled (with no break of more than five seconds) for at least 30 seconds¹³ after a period of rest or feeding for at least five minutes¹⁴. A rate of vocal production per hour was then calculated for each call type during travel for comparison with an overall baseline vocalisation rate for each call type during individual focal follows. In order to show whether any vocalisations were associated with the initiation of a travel event, vocal production in the time period one minute prior to travelling was compared for males and females when they were alone or in proximity to other individuals¹⁵. Travel initiations which included a ‘pause’ (counted as a change in behaviour state from travelling for less than 30s, to resting for less than 30s, before

¹³ 30 seconds of continuous travel represents a distance of 24m when travelling at an average speed of 0.8m/s, the average speed of an adult chimpanzee (Pontzer & Wrangham, 2004); this roughly represents the midpoint between the average visual range- 10m- and the average spread of a travel party- 35m- in Sonso (Newton-Fisher, 2004).

¹⁴ Five minutes was chosen to coincide with the rest of this study as representing the minimum time period for a continuous behaviour to be considered as unrelated to previous behaviour.

¹⁵ This one minute predeparture period coincides with the ‘initiation phase’ defined by Gruber as ‘the period between cessation of the previous activity and the beginning of the subsequent ‘movement phase’ (movement defined as travelling 10m), which was described as ‘typically lasting for about one minute’ (Gruber & Zuberbühler, 2013).

travelling again for more than 30s) were also recorded, as well as any vocalisations produced at each of these stages.

3.2.4 Travelling 'follow' behaviour observations and vocalisations

A separate event was recorded during focal follows when the focal individual 'followed' or was 'followed by' another individual during travel, thus allowing specific comparisons of vocalisations and social information from the one minute period prior to the act of social travel irrespective of previous activity and time spent travelling. Follows were defined as an individual travelling less than 5m from the focal animal in the same direction (not more than 45° divergent from the focal animal's travel direction) for at least 10m. It should be noted that these follows were coded *in situ* during data collection making them potentially more susceptible to subconscious observer bias when the observer recording data is expecting a certain result (Altmann, 1974). The analyses should thus only be considered in concert with the previous section which extracted travel initiations from a complete dataset of raw behaviour and vocalisation observations, and with the following section describing video recordings of travel initiations.

3.2.5 Video recordings of travel initiations

Video data were collected whenever environmental conditions allowed using a Panasonic SD90 HD video camera with attached Sennheiser MKE400 microphone. The camera had a 'pre-record' feature, which allowed the user to record the five-second period before, as well as the behaviour of interest, in this case any start of travel. Videos were only used if (1) the focal individual was clearly visible and close enough to hear any vocalisations, (2) all other individuals in-sight were known, (3) the focal had been resting or feeding for at least one minute before travelling, (4) the individual travelled on for at least 30 seconds or until out-of-sight of their original position (whichever came first), and (5) the individual did not pause for more than one minute, or start another activity during pauses, before travelling on. Videos were coded for dyadic interactions, between the focal and one other individual, as the narrow field of view and ability of the

observer to comment on interactions only extended to one other individual outside of the camera frame. Videos of travel initiations were coded for the ID of their partner, defined as nearest neighbour (including juveniles and infants of females, but not including the infant if it was already being carried by the mother upon travel onset), and their distance when they started moving. It was also recorded whether the focal looked towards their partner, and vocalisations of the focal animal and their partner (a) in the five second period prior to travel onset, (b) during short travel movements before pausing, (c) during pauses-defined as stopping for less than one minute, and (d) during the travelling on period. The number of pauses, distance from partner, and whether they followed or were followed by their partner when they went on to travel were also coded (see appendix 2.1).

3.2.6 Statistical analyses

Statistics were carried out using SPSS 19.0 statistical software package (SPSS Inc. an IBM company). Tests were non-parametric when assumptions of normality for parametric tests were not met. Two-tailed tests were conducted at 0.05 level of significance. Exact methods were used when expected values fell below five and the Bonferroni correction (Rice, 1989) in SPSS analyses used for multiple comparisons of frequencies. Individual ID was introduced as a random factor in GLMM tests to control for the effect of individual ID. This prevents the loss of data through averaging results for individuals, and GLMM tests are generally robust when data are not normally distributed or variance is not equal.

3.3 Results

3.3.1 Introduction

In this section, I will first present data on general travelling behaviour in the Sonso chimpanzees. Specifically, I will look for any vocalisation types that are associated with travel. I will then look at behaviour and potential communication in the predeparture period before travel. This will include a brief look at the recordings of travel events that include pauses. I will also examine the behaviour associated with specific follow events recorded during focal observations. Finally, video recordings of travel initiations will be explored in terms of vocalisations, pausing and follow behaviour.

3.3.2 General travelling behaviour

General behaviour was recorded from 3760 scan samples conducted during full-day follows of 26 different individuals (12 adult males, 1 sub-adult male and 13 adult females). Results (from 12 males and 10 females with at least 20 scans each) revealed a sex difference in the proportion of time spent alone or in proximity (within ten metres) to another individual when resting, feeding or travelling. The results, illustrated in figure 3.1 below, show that males were more likely than females to have no other individual within ten metres of them during feeding and travelling, but this difference was not significant during resting (Mann-Whitney U tests comparing males and females, using average probability of being alone per individual, N= 12, 10; for feeding: male median = 0.548, IQR = 0.22 female median = 0.814, IQR = 0.32, T = 17.000, p = 0.003; for travelling: male median = 0.481, IQR = 0.30 , female median = 0.833, IQR = 0.27, T= 11.000, p = 0.001; for resting: male median = 0.605, IQR = 0.30, female median = 0.747, IQR = 0.30, T = 32.000, p = 0.067).

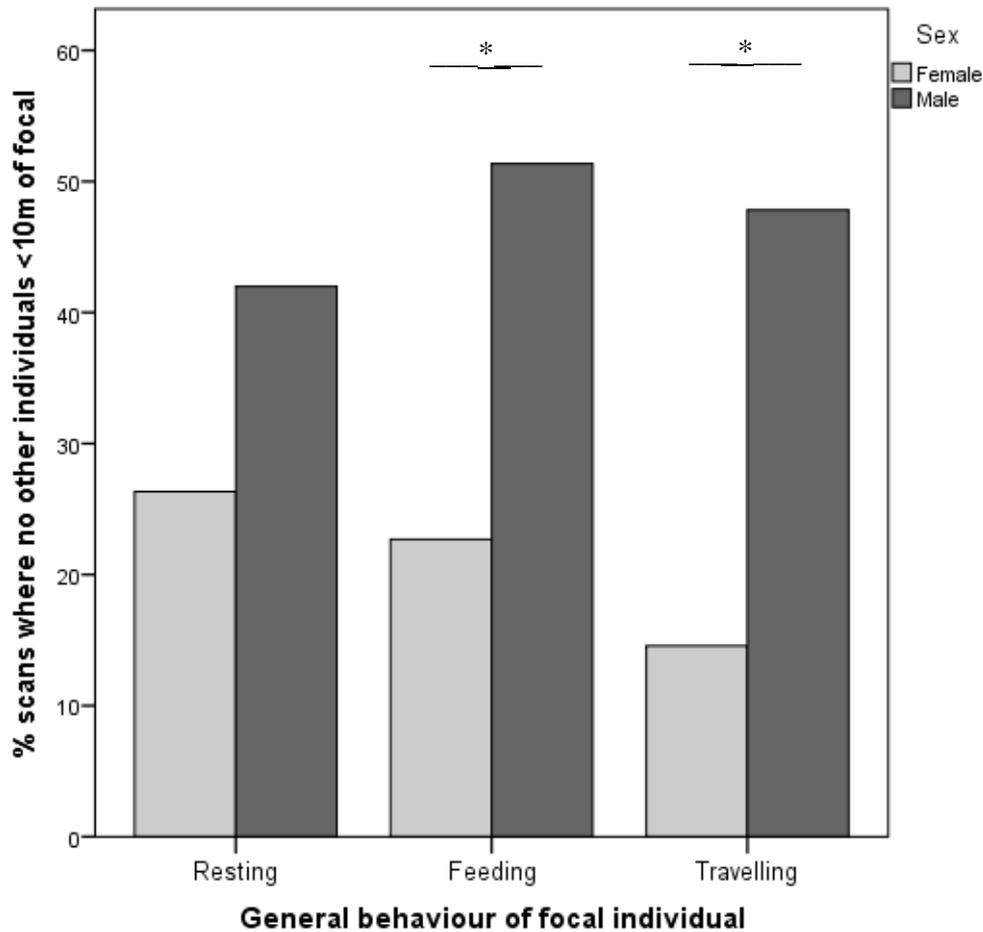


Figure 3.1. Sex difference between the proportions of time spent resting, feeding and travelling with no other individuals within ten metres of the focal chimpanzee (Mann-Whitney U tests comparing males and females, using average probability of being alone per individual, for resting: $N = 12, 10$; feeding: $T = 17.000, p = 0.003^*$; travelling: $T = 11.000, p = 0.001^*$).

The demographic compositions of individuals within 10m of female focal animals during resting, feeding and travelling activities are presented in figure 3.2. Females spent a significantly greater proportion of their time with their own offspring than with any other demographic group in all general activities (Wilcoxon signed-rank test showed that females were in proximity to offspring significantly more than to males, females and juveniles: $N = 10, p = 0.002, Z = -2.803$ for females during resting, feeding and travelling behaviour, for males during feeding, and for juveniles during resting and travelling behaviour; $N = 10, p = 0.002, Z = -2.805$ for males during resting and travelling, and for juveniles during feeding behaviour). Comparing the general behaviour of the focal female with the frequency of offspring within 10m proximity

revealed no significant differences between resting, feeding or travelling behaviour and offspring proximity (Kruskal-Wallis test: $N = 10$, $d.f. = 2$, $\chi^2 = 1.172$, $p = 0.557$).

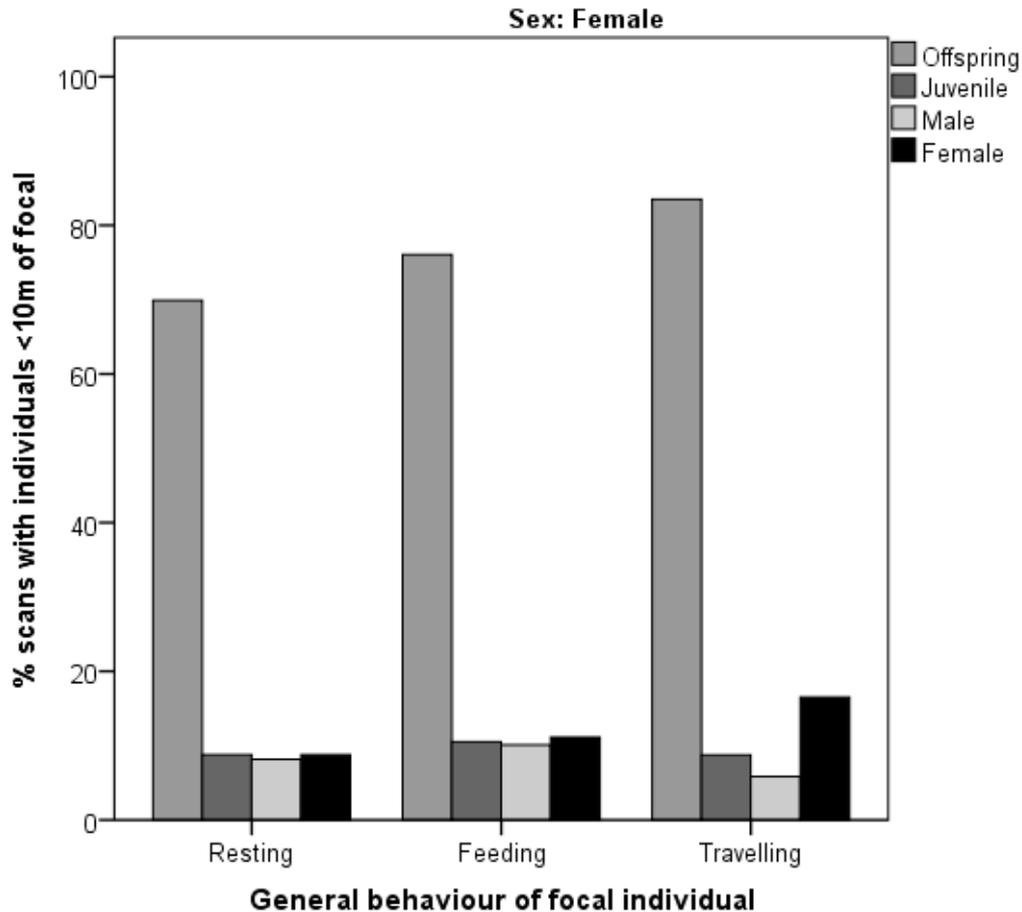


Figure 3.2. Females spent the greatest proportion of their time resting, feeding and travelling with offspring than with non-kin juveniles (including infants), adult males and adult females within ten metres of the focal chimpanzee.

After controlling for individual differences (by averaging results per ID), there was no significant effect of general activity on the proportion of scans with individuals in 10m proximity for males. Specifically, comparing the general behaviour of the focal male with the frequency of individuals within 10m proximity revealed no significant differences between resting, feeding or travelling behaviour and proximity (Kruskal-Wallis test: $N = 12$, $d.f. = 2$, $\chi^2 = 0.000$, $p = 1.000$). However, there was a trend for males to spend a greater proportion of their time with other adult males than with

females or juveniles in all activities, as seen in figure 3.3. Medians and interquartile ranges for these analyses are shown in table 3.2.

Table 3.2. Median and interquartile range of the number of individuals within 10m proximity to a focal male or female during resting, feeding and travelling behaviour.

Sex	General Behaviour	Individuals in proximity	Median individuals <10m proximity	Interquartile range
Male	Resting	All neighbours	1.1898	.67
	Resting	females	.2767	.18
	Resting	males	.4670	.31
	Resting	juveniles	.0582	.13
	Feeding	All neighbours	.9558	.35
	Feeding	females	.1928	.10
	Feeding	males	.3493	.23
	Feeding	juveniles	.0970	.12
	Travelling	All neighbours	.9143	.40
	Travelling	females	.1583	.16
	Travelling	males	.3798	.31
	Travelling	juveniles	.1659	.16
Female	Resting	All neighbours	1.4378	.72
	Resting	females	.0648	.13
	Resting	males	.0369	.12
	Resting	juveniles	.0501	.10
	Resting	offspring	.7472	.30
	Feeding	All neighbours	1.4157	.99
	Feeding	females	.0656	.10
	Feeding	males	.0479	.20
	Feeding	juveniles	.0619	.13
	Feeding	offspring	.7886	.33
	Travelling	All neighbours	1.6771	1.31
	Travelling	females	.0313	.21
Travelling	males	0.0000	.17	
Travelling	juveniles	.0476	.21	
Travelling	offspring	.8333	.30	

The trend for males to spend a greater proportion of time in proximity to other males compared to females or juveniles was a statistically significant effect for all except males and juveniles in proximity during travelling behaviour (Wilcoxon signed-rank

test showed that during resting behaviour: adult males were in proximity to other males significantly more than to females, $N = 12$, $Z = -2.510$, $p_{\text{exact}} = 0.009$ or juveniles, $N = 12$, $Z = -2.903$, $p_{\text{exact}} = 0.001$; during feeding behaviour: adult males were in proximity to other males significantly more than to females, $N = 12$, $Z = -2.667$, $p_{\text{exact}} = 0.005$ or juveniles, $N = 12$, $Z = -3.059$, $p_{\text{exact}} = 0.000$; during travelling behaviour: adult males were in proximity to other males significantly more than to females, $N = 12$, $Z = -2.756$, $p_{\text{exact}} = 0.003$ and non-significantly more than to juveniles, $N = 12$, $Z = -1.784$, $p_{\text{exact}} = 0.084$).

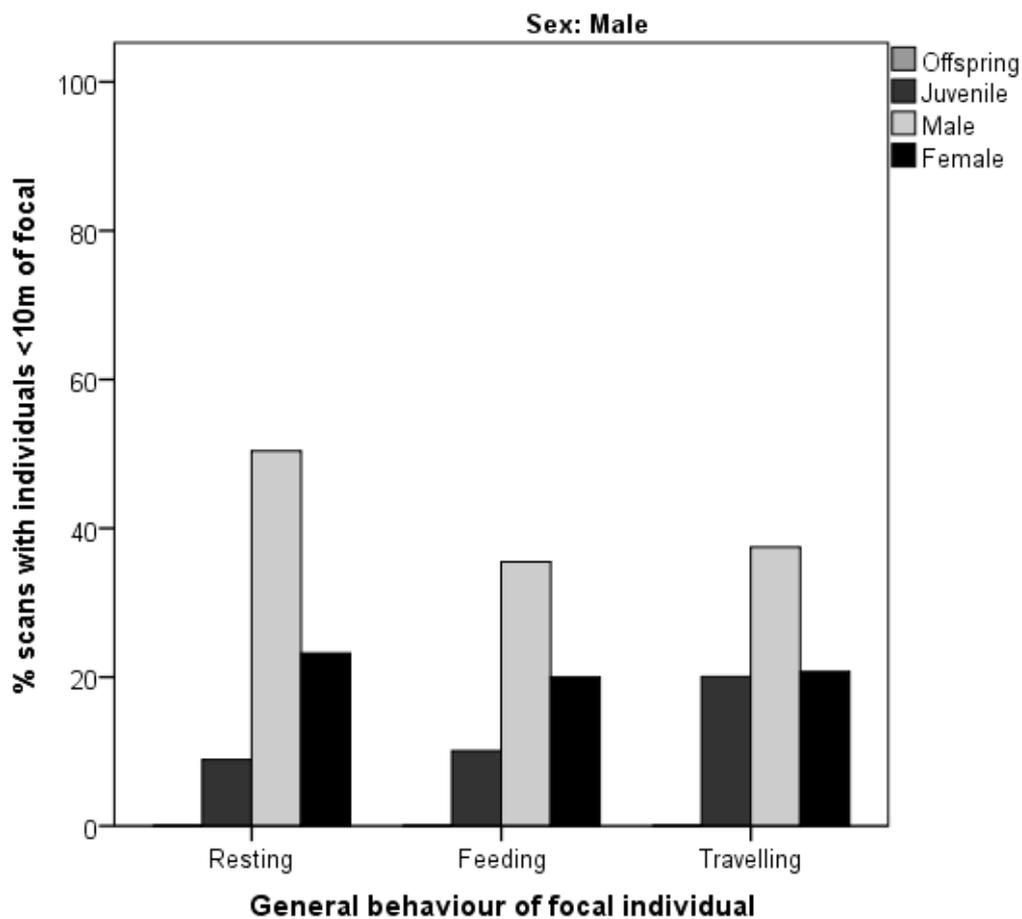


Figure 3.3. Proportion of time spent by males resting, feeding and travelling with non-kin juveniles (including infants), adult males and adult females within ten metres of the focal chimpanzee (male offspring, as determined by genetic analyses, were not included as offspring in these results).

3.3.3 Overall vocalisation frequencies, predeparture vocalisations and pauses in travel

3.3.3.1 Overall vocalisation frequencies

A total of 1634 vocalisations were recorded during 598 hours of focal observation. In order to compare vocalisation frequencies produced during different types of general activity, the data were restricted to include only those observations where the focal individual was in-sight of the observer and close enough that the observer could hear soft vocalisations produced. This gave 1566 vocalisations in total (summarised in table 3.3), 327 from females in 118 hours of observation and 1239 from males in 232 hours of in-sight focal observation.

Table 3.3. Summary of different vocalisation types per general behaviour state recorded during focal follows of adult male and female chimpanzees in Sonso, Uganda.

General behaviour	bark	display pant hoot	drumming	hoo/grunt	pant	pant grunt	pant hoot	rough grunt	scream	whimper
Resting	26	10		271	22	66	103	8	12	6
Feeding	11			159	1	42	70	122	4	1
Travelling	11	65	5	212		76	84	26	17	3
Self-grooming				19	1	5	6			
Social interaction	2			44	1	18	15		20	2
Grand Total	50	75	5	705	25	207	278	156	53	12

Rough grunts (i.e. ‘food grunts’) were produced most often during feeding compared to any other activity (table 3.3) and were discounted from current analyses investigating travel vocalisations at this stage, as they are only associated with feeding behaviour and so are unlikely to coordinate joint travel where both individuals are travelling and not feeding. Pant-grunts were excluded as they serve a social function which is likely to outweigh any systematic differences in behaviour state of the caller (Goodall, 1986). Hoos (which include grunts), pant-hoots and display pant-hoots were produced most often during travelling and are therefore looked at with regards to travelling behaviour in more detail.

Table 3.4. Median calling rates per hour and interquartile range of display pant hoots, pant hoots and hoo/grunts produced by males and females during resting, feeding and travelling behaviour.

Sex	General Behaviour	Vocalisation	Median calling rate (per hour)	Interquartile range
Male	Resting	display pant hoot	0.044	0.051
	Resting	pant hoot	0.396	0.308
	Resting	hoo/grunt	0.743	0.749
	Feeding	display pant hoot	0.000	0.000
	Feeding	pant hoot	0.241	0.226
	Feeding	hoo/grunt	0.567	0.591
	Travelling	display pant hoot	0.213	0.226
	Travelling	pant hoot	0.291	0.187
	Travelling	hoo/grunt	0.398	0.730
Female	Resting	display pant hoot	0.000	0.000
	Resting	pant hoot	0.091	0.194
	Resting	hoo/grunt	0.461	0.867
	Feeding	display pant hoot	0.000	0.000
	Feeding	pant hoot	0.000	0.095
	Feeding	hoo/grunt	0.114	0.239
	Travelling	display pant hoot	0.000	0.000
	Travelling	pant hoot	0.000	0.235
	Travelling	hoo/grunt	0.322	1.164

Table 3.5. Wilcoxon signed-ranks tests comparing rates of display plant hoot, pant hoot and hoo/grunt vocalisations per individual during travel compared to resting and feeding behaviour. 'b' denotes positive ranks and 'c' denotes negative ranks. Significant effects (** <0.01) are seen in males where display pant hoots are produced more during travelling compared to resting or feeding behaviour.

		Display pant hoot		Hoo/grunt		Pant hoot	
Sex		Travel-rest	Travel-feeding	Travel-rest	Travel-feeding	Travel-rest	Travel-feeding
Male	Z	-2.934 ^c	-3.059 ^c	-.628 ^b	-.356 ^c	-.978 ^b	-1.007 ^c
	P _{exact}	.001**	.000**	.569	.765	.365	.359
Female	Z	-1.000 ^c	-1.000 ^c	-1.478 ^b	-1.859 ^c	-.560 ^b	-.734 ^c
	P _{exact}	1.000	1.000	.160	.078	.641	.563

Females showed no significant differences in the rate of producing hoos, pant-hoots or display pant-hoots during resting, feeding or travelling behaviour, after controlling for focal ID and comparing the rates of each call type during different general activities¹⁶ (see tables 3.4 and 3.5). Testing the males, displayed in figure 3.4, revealed a significant difference in rate of display pant-hoot productions when travelling compared to resting (travelling median = 0.213, IQR = 0.226, resting median = 0.044, IQR = 0.051; Wilcoxon signed-ranks test: $N_{\text{males}} = 12$, $Z = -2.934$, $p_{\text{exact}} = 0.001$).

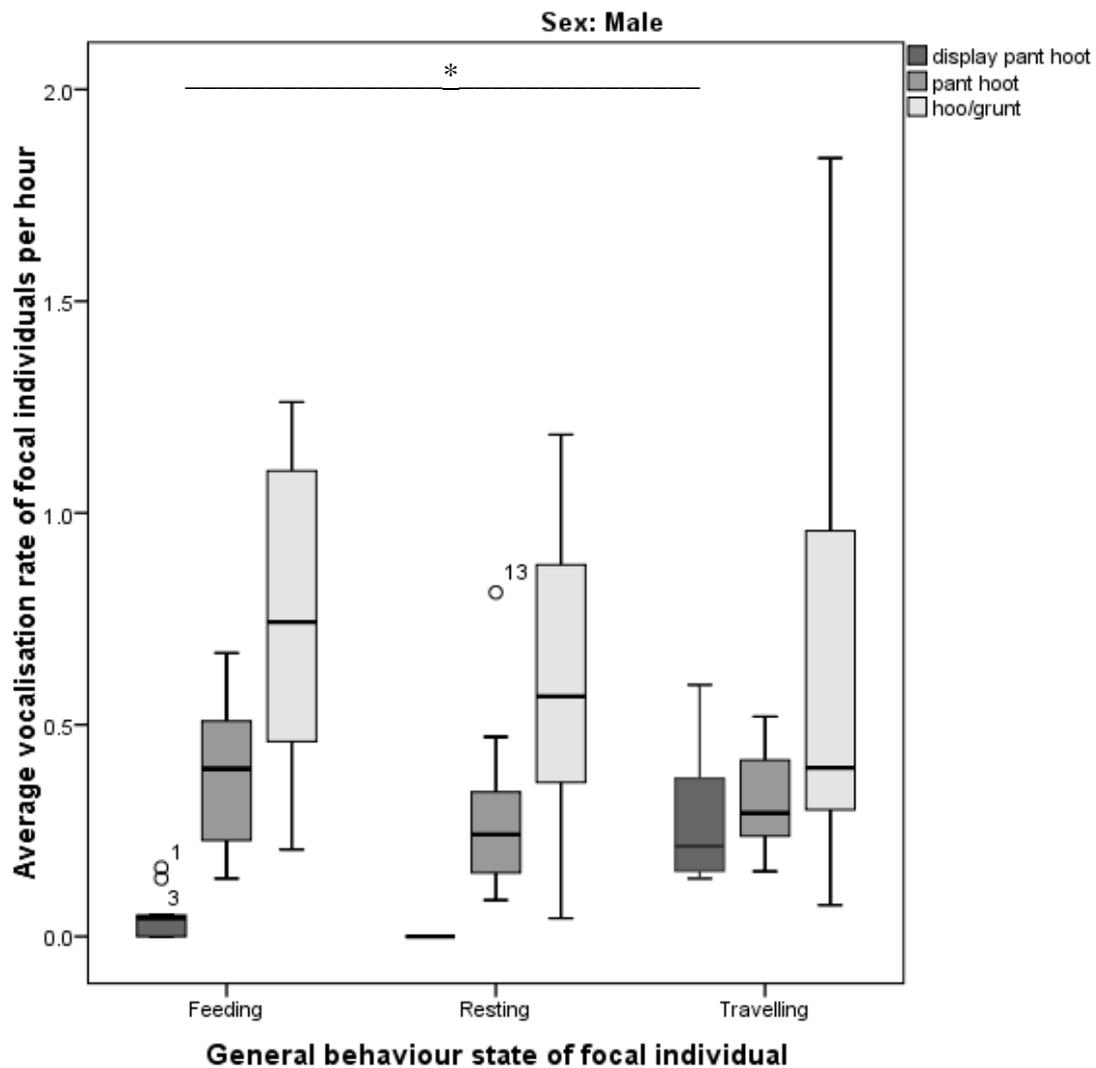


Figure 3.4. Number of display pant-hoots, pant-hoots and hoo vocalisations produced by male chimpanzees during resting, feeding and travelling behaviour in. There is a significant increase in rate of display pant-hoot production when travelling compared to resting (Wilcoxon signed-ranks test: $N_{\text{males}} = 12$, $Z = -2.934$, $p_{\text{exact}} = 0.001^*$).

¹⁶ Rates of calling calculated from focal times for each individual.

3.3.3.2 Predeparture period

Data on the predeparture period of one minute prior to travelling were analysed by looking firstly at vocalisations produced in this predeparture time and, secondly, by looking for any evidence of pauses in the travel initiation with concomitant vocalisations. In total, 327 travel initiations were recorded from 13 males and 11 females, with an additional 13 travel initiations including pauses.

(a) vocalisations

The number of each vocalisation type recorded during the predeparture period is shown in Figure 3.5. It can be seen that the number of travel initiations which were preceded by any vocalisation in the previous minute was small for both females and males: 11 out of 76 for females and 43 out of 251 for males. Hoo and pant-grunt¹⁷ vocalisations were produced most often in both sexes, with pant-hoots also being produced more in males, as can be seen in figure 3.5. For females, then, pant-grunts and hoo vocalisations represent the calls most likely to be a candidate for a predeparture signal, but there is no significant difference between the production rate of pant-grunts or hoo (pant-grunt median = 0.000, IQR = 6.667; hoo/grunt median = 6.667, IQR = 15.000; Wilcoxon signed rank test: $N = 11$, $p_{\text{exact}} = 0.563$, $Z = -0.738$). For males, pant-hoots, pant-grunts and hoo vocalisations were produced most often, but there was no significant difference in the production rate per hour between the call types (pant-grunt median = 2.500, IQR = 4.831; hoo/grunt median = 2.609, IQR = 3.556; pant-hoot median = 3.333, IQR = 6.000; Wilcoxon signed rank test between pant-hoots and pant-grunts: $N = 13$, $p_{\text{exact}} = 0.515$, $Z = -0.712$; between pant-hoots and hoo: $N = 13$, $p_{\text{exact}} = 0.984$, $Z = -0.590$; between pant-grunts and hoo: $N = 13$, $p_{\text{exact}} = 0.750$, $Z = -0.357$)¹⁸. This means that there was no significant difference in the likelihood of any one call type analysed to be

¹⁷ Pant-grunts were included here for comparisons between call production, as although the social function they serve in chimpanzees (Goodall, 1986), may be related to the travel initiation, if it concerns the approach of a more dominant individual which may subsequently affect the focal individual's travel decisions.

¹⁸ Averaging the results per ID code to account for variation in individual propensity to vocalise or not revealed the same pattern of insignificant effects.

produced more than another in the one minute prior to travel initiation for either males or females.

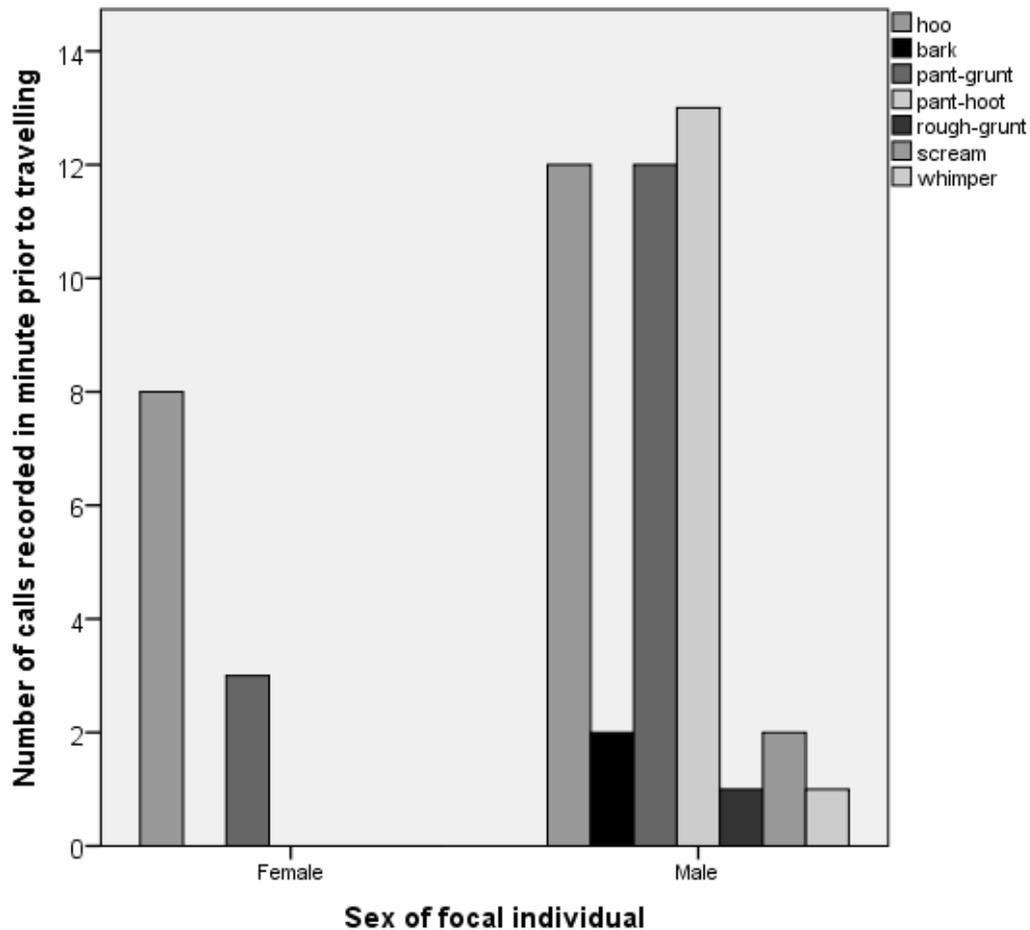


Figure 3.5. Raw numbers of different vocalisation types recorded during the minute before travel by female and male chimpanzees under focal observation.

In females, hoo and pant-grunt production in the one minute prior to travel initiation was not significantly different to the expected baseline rate of vocalisation production for each individual (baseline vocalisation rates for hoo median = 1.238, IQR = 2.737; pant-grunt median = 0.439, IQR = 0.624; pant-hoot median = 0.264, IQR = 0.500; Wilcoxon signed rank test for hoo: $N = 11$, $p_{\text{exact}} = 0.123$, $Z = -1.600$; for pant-grunts: $N = 11$, $p_{\text{exact}} = 0.910$, $Z = -0.178$). Males produced significantly more pant-

hoots and pant-grunts during the predeparture period than their expected baseline rate (baseline vocalisation rates for hoo median = 2.116, IQR = 2.403; pant-grunt median = 0.586, IQR = 0.461; pant-hoot median = 0.907, IQR = 0.555; Wilcoxon signed rank test for pant-hoots: $N = 13$, $p_{\text{exact}} = 0.021$, $Z = -2.275$; for pant-grunts: $N = 13$, $p_{\text{exact}} = 0.042$, $Z = -2.045$), although the higher rate of hoo vocalisations observed in figure 3.5 was revealed as non-significantly different to their baseline production rate (Wilcoxon signed rank test for hoots: $N = 13$, $p_{\text{exact}} = 0.455$, $Z = -0.804$).

The number of individuals within 10m of the focal chimpanzee did not differ significantly with hoo/grunt vocalisation production during the predeparture period in females or males (GLMM including number of individuals within 10m proximity as a fixed factor and individual ID as a random factor for females: mean individuals <10m when vocalised = 1.50, s.d. = 1.604, when not vocalised = 1.46, s.d. = 1.450, $N = 58$, d.f. = 7, $F = 0.574$, $p = 0.774$; for males: mean individuals <10m when vocalised = 0.58, s.d. = 0.793, when not vocalised = 0.86, s.d. = 1.302, $N = 231$, d.f. = 7, $F = 0.311$, $p = 0.949$). There was also no significant effect between pant-hoot vocalisation production and the number of individuals in proximity to males before travel initiation (mean individuals <10m when vocalised = 1.15, s.d. = 1.405, when not vocalised = 0.83, s.d. = 1.276; GLMM: $N = 231$, d.f. = 7, $F = 1.367$, $p = 0.220$), while females produced no pant-hoots in the predeparture period. As can be seen in figure 3.6, for males the mean number of individuals within 10m is higher when they produce a pant-grunt vocalisation than when they do not (mean individuals <10m when vocalised = 2.33, s.d. = 2.270, when not vocalised = 0.77, s.d. = 1.171; GLMM: $N = 231$, d.f. = 7, $F = 6.067$, $p = 0.000$). For females there were fewer individuals in proximity when pant-grunts were produced (mean individuals <10m when vocalised = 1.00, s.d. = 1.000, when not vocalised = 1.48, s.d. = 1.473; GLMM: $N = 58$, d.f. = 7, $F = 2.491$, $p = 0.026$).

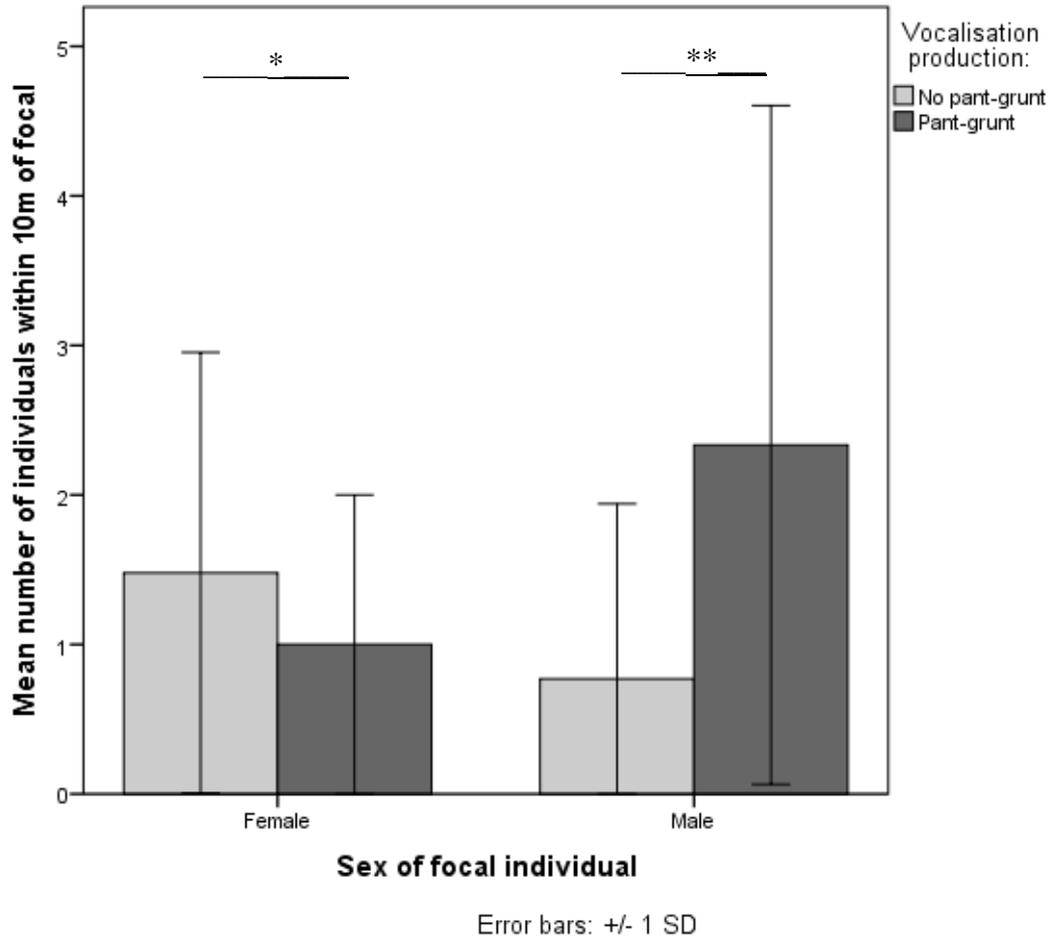


Figure 3.6. The mean number of individuals within a 10m radius of the focal male or female chimpanzee in the minute prior to a travel event and whether the focal animal produced a pant-grunt vocalisation or not. For males, the mean number of individuals within 10m is higher when they produce a pant-grunt vocalisation than when they do not (GLMM including number of individuals within 10m proximity as a fixed factor and individual ID as a random factor: $N = 231$, $d.f. = 7$, $F = 6.067$, $p = 0.000^{**}$). For females, the mean number of individuals within 10m is lower when they produce a pant-grunt vocalisation than when they do not (GLMM: $N = 58$, $d.f. = 7$, $F = 2.491$, $p = 0.026^{**}$).

b) pauses and vocalisations

There were only 13 pauses during the initiation of travel (where travelling and pauses of between five and 30 seconds occurred prior to a travel event of greater than 30 seconds, and where subjects had been resting or feeding for greater than 5 minutes prior to the

first travel event), 7 for males and 6 for females. For the males, only one pant-hoot was given during the pause, when three other males were in-sight but more than 10m away, and no other vocalisations were produced. For females, two hoo vocalisations and one pant-hoot were given in the predeparture period (all with no other individual in-sight of the focal animal); no vocalisations were produced during the pauses. The sample sizes were too small for statistical analyses, but pauses and vocalisations during the initial stages of travel will be analysed further from video recordings in part 3.3.5 of this chapter.

3.3.4 'Follow' behaviour observations and vocalisations

Looking at all 187 recordings of follow events throughout travelling behaviour reveals that males were followed 46 times and were the follower of another individual 60 times, whilst females were followed more often than males at 61 times, and were followers only 20 times. The proportion of times an individual was a follower versus being followed was significantly different between the sexes (male median = 0.588, IQR = 0.450; female median = 0.338, IQR = 0.470; Mann-Whitney U test: $N_{\text{males}}=13$, $N_{\text{females}}=12$, $T = 40.000$, $p_{\text{exact}} = 0.037$). Only 9 (11%) follow events with females involved an individual that was not their offspring, so each analysis was carried out separately for males and females.

Analysing the frequencies of different vocalisation types produced in the minute prior to a follow event revealed that hoo vocalisations were produced in 29 (15.5%) out of the 187 cases while all other vocalisation were produced fewer than 5 times in total (see figure 3.7) This represented 18 (17.0%) from males and 11 (13.5%) from females.

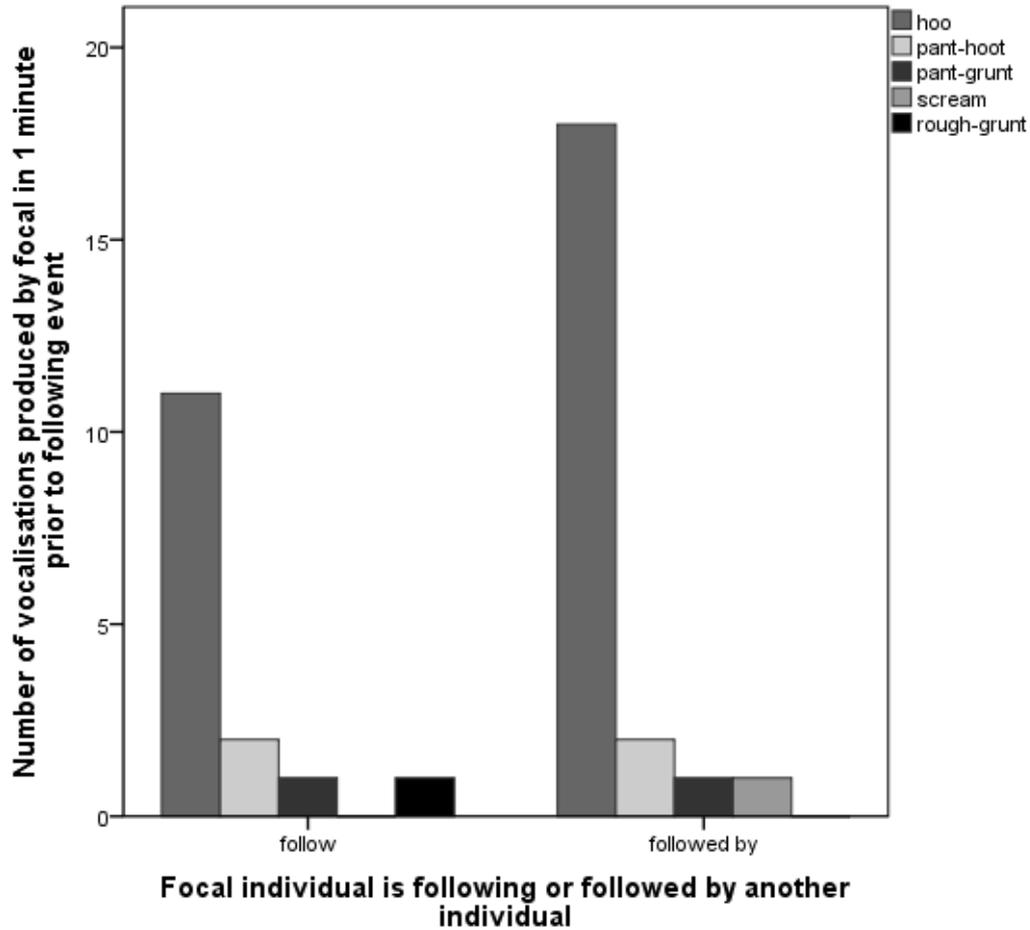


Figure 3.7. The total number of vocalisations produced by focal chimpanzees during the one minute period prior to a follow event.

Hoo vocalisations were produced by the focal in the minute prior to a following event significantly more often than other vocalisation types for both males and females. Wilcoxon signed rank test in females, where $N = 12$, comparing hoo vocalisation rate (median = 0.047, IQR = 0.211) with pant-hoots, pant-grunts, screams and rough grunts (all medians = 0.000, IQR = 0.000) all gave: $p_{\text{exact}} = 0.031$, $Z = -2.214$; and in males, where $N = 13$, comparing hoos (median = 0.154, IQR = 0.333) with: pant-hoots (median = 0.000, IQR = 0.000): $p_{\text{exact}} = 0.039$, $Z = -2.103$; pant-grunts (median = 0.000, IQR = 0.000): $p_{\text{exact}} = 0.031$, $Z = -2.207$; screams (median = 0.000, IQR = 0.000): $p_{\text{exact}} = 0.016$, $Z = -2.375$; rough grunts (median = 0.000, IQR = 0.000): $p_{\text{exact}} = 0.016$, $Z = -2.386$. However, comparing the rate of hoo vocalisation production in the minute prior

to a follow event for each individual with their baseline rate for that call, revealed that although the trend was slightly stronger in males than in females, neither sex showed a significant increase in rate of calling compared to their baseline rate (Wilcoxon signed rank test comparing hoo rate with baseline hoo rate per individual for males: hoo median = 8.571, IQR = 25.00; baseline median = 2.116, IQR = 2.40; N = 13, $p_{\text{exact}} = 0.094$, Z = -1.712; for females: hoo median = 2.500, IQR = 19.88; baseline median = 1.157, IQR = 2.48; N = 12, $p_{\text{exact}} = 0.123$, Z = -1.600)

Hoo production was also compared with whether the focal was a follower or was followed after calling or not. There was no significant difference between whether or not an individual gave a hoo vocalisation prior to following or prior to being followed by another individual (Mann-Whitney U test for males: median when followed = 0.000, IQR = 0.40; median when follower = 0.000, IQR = 0.46; $N_{\text{followed, follower}} = 12, 12$, T = 69.500, $p = 0.919$; for females: median when followed = 0.000, IQR = 0.21; median when follower = 0.000, IQR = 0.07; $N_{\text{followed}} = 11$, $N_{\text{follower}} = 9$, T = 42.000, $p = 0.497$).

3.3.5 Video recordings of travel initiations

A total of 77 travel initiations were video recorded in areas of high visibility and to a high enough quality for accurate coding: N = 57 from 12 females and N = 20 from 8 males. For females, 49 travel events were social, in that at least one individual (other than an infant already in contact with the mother) was in-sight of the focal animal. The male travel initiations included 5 cases where the focal individual was alone, leaving 15 that were social. Only one clear gestural signal was given by a female in the videos analysed. The female, NB, stood up from resting, looked and reached with her hand involving physical contact with the offspring juvenile's arm during the first two steps of travel, then continued to travel without looking behind. The offspring was sleeping with head down and lifted their head on contact, sat up and followed in the same direction after 25 seconds when the female was more than 15m distance. No vocalisations were given by either party. Analysis of vocal signalling is focussed on from video recordings of travel and is restricted to hoo vocalisations because hoos (including grunts) were the

only vocalisation type to be produced more than once by a focal animal in total (12 times in total).

Hoo vocalisations were no more likely to be produced at any stage during the start of travel when with another individual than when alone (Mann-Whitney U test for males: $N_{\text{alone}} = 3$, median = 0, $N_{\text{social}} = 6$, median = 0, IQR = 0.20; $T = 9.000$, $p_{\text{exact}} = 1.000$; for females: $N_{\text{alone}} = 3$, median = 0, $N_{\text{social}} = 12$, median = 0, IQR = 0.21; $T = 12.000$, $p_{\text{exact}} = 0.516$). For males, there was also no significant difference between whether the focal animal paused or not when with a potential travel partner in sight or not (Mann-Whitney U test for males: $N_{\text{alone}} = 3$, median = 0.333, $N_{\text{social}} = 6$, median = 0, IQR = 0.58; $T = 6.000$, $p_{\text{exact}} = 0.524$). Female focal animals were significantly more likely to pause when there was a potential travel partner in sight than when they were alone (Mann-Whitney U test: $N_{\text{alone}} = 3$, median = 0, $N_{\text{social}} = 12$, median = 0, IQR = 0.50; $T = 4.000$, $p_{\text{exact}} = 0.044$). Comparing the distance between the focal female and their potential travel partner at the start of travel when they paused ($N = 31$) with when they did not pause ($N = 26$), revealed that females more likely to pause when their travel partner was further away (mean distance when paused = 10.65m, s.d. = 4.424, mean distance when not paused = 3.69, s.d. = 4.297; GLMM including distance to partner as variable, pausing or not as a fixed factor and focal individual ID as a random factor: $N = 57$, $F = 17.774$, $p = 0.000$). For females, only two travel initiations involved an individual not their offspring, so a further comparison of calling behaviour and pauses between offspring and unrelated travelling partners was not possible from these data.

Only the 64 social travel initiations were used when comparing following behaviour. Not all of the social travel initiations involved the focal individual following or being followed by another, so comparisons were made with the potential signals for recruiting others used in other studies: looks at partner, pauses in travel and hoo vocalisations (Gruber & Zuberbühler, 2013). Descriptive statistics comparing signals and following behaviour are shown in table 3.6.

Table 3.6. Sample size (N), median and interquartile range of probability of three potential signals produced during travel initiations where the focal was not followed, was followed, or was the follower of their travel partner, for males and females.

Sex of focal	Signal type	Following behaviour of focal	N	Median	Interquartile range
Female	Pause	No follow	4	1.00	1
		Followed by partner	12	1.00	1
		Follower of partner	1	0.00	
	Hoo/grunt	No follow	4	0.00	1
		Followed by partner	12	0.00	0
		Follower of partner	1	0.00	
	Look at partner	No follow	4	0.00	1
		Followed by partner	12	1.00	1
		Follower of partner	1	0.00	
Male	Pause	No follow	4	0.00	1
		Followed by partner	3	0.00	
		Follower of partner	2	0.00	
	Hoo/grunt	No follow	4	0.00	0
		Followed by partner	3	0.00	1
		Follower of partner	2	0.00	
	Look at partner	No follow	4	1.00	1
		Followed by partner	3	1.00	1
		Follower of partner	2	1.00	

For females, the probability of looking, pausing or producing hoo vocalisations at any stage of travel initiation was not significantly affected by whether the individual was following, being followed or not by their potential travel partner (Kruskal Wallis test for hoo signals: d.f. = 2, $\chi^2 = 0.402$, $p_{\text{exact}} = 1.000$; for looks: d.f. = 2, $\chi^2 = 3.562$, $p_{\text{exact}} = 0.126$; for pauses: d.f. = 2, $\chi^2 = 2.423$, $p_{\text{exact}} = 0.298$). For males, the probability of looking at a potential travel partner or producing a hoo vocalisation was also not significantly affected by whether the individual was following, being followed or not (Kruskal Wallis test for hoo signals: d.f. = 2, $\chi^2 = 0.714$, $p_{\text{exact}} = 1.000$; for looks: d.f. = 2, $\chi^2 = 1.750$, $p_{\text{exact}} = 0.500$). However, for males, the probability of pausing was

significantly higher when they followed their travel partner compared to being followed or no follow behaviour (Kruskal Wallis test for pauses: d.f. = 2, $\chi^2 = 6.250$, $p_{\text{exact}} = 0.040$);), although the sample size of 15 here for males is very small and included some data points from the same individual, so results should be interpreted with caution (figure 3.8).

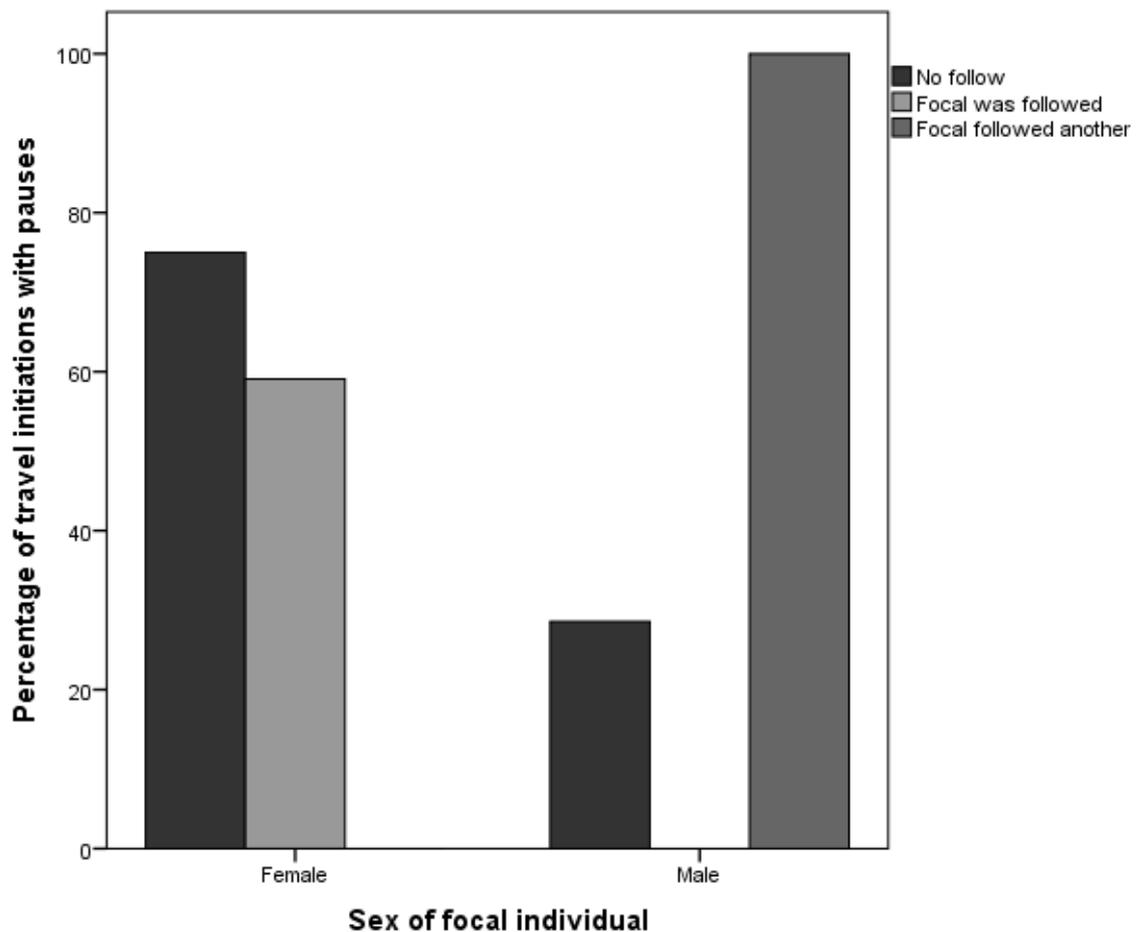


Figure 3.8. The percentage of travel initiations with pauses where the focal individual was followed, followed another, or no follow was observed for females and males. The difference in males between pausing when following another individual compared to being followed or not was significant, although from a small sample size (Kruskal Wallis test for pauses: $N = 3, 2, 4$, d.f. = 2, $\chi^2 = 6.250$, $p_{\text{exact}} = 0.040$).

Pearson correlations were carried out for females and males to test whether an individual produced more signals when they paused (which would be expected if pauses

indicate waiting), testing if a higher number of pauses was related to the number of hoos produced by the focal or the number of looks the focal gave towards their social partner. There were no significant correlations found for either females or males for number of pauses with hoos or with looks. Whether or not an increase in hoos was accompanied by an increase in looks was also tested. Again, there were no significant correlations found for either females or males (see table 3.7). For females: mean number of pauses = 1.257, s.d. = 0.934; mean number of hoos = 0.125, s.d. = 0.250 mean number of looks to partner = 0.981, s.d. = 0.775. For males: mean number of pauses = 0.217, s.d. = 0.349; mean number of hoos = 0.100, s.d. = 0.167 mean number of looks to partner = 1.200, s.d. = 1.166.

Table 3.7. Pearson correlation test results for male and female pauses, looks and hoo vocalisations during social travel initiations. No significant correlations were found between any of the variables.

Females	Number of pauses with hoos	Pearson Correlation	0.216
		Sig. (2-tailed)	0.106
		N	12
	Number of hoos with looks	Pearson Correlation	0.164
		Sig. (2-tailed)	0.222
		N	12
	Number of looks with pauses	Pearson Correlation	0.117
		Sig. (2-tailed)	0.386
		N	12
Males	Number of pauses with hoos	Pearson Correlation	0.292
		Sig. (2-tailed)	0.212
		N	6
	Number of hoos with looks	Pearson Correlation	0.148
		Sig. (2-tailed)	0.599
		N	6
	Number of looks with pauses	Pearson Correlation	0.121
		Sig. (2-tailed)	0.667
		N	6

3.4 Discussion

3.4.1 Introduction

The results will now be discussed, starting with general travelling behaviour in the Sonso chimpanzees and the vocalisation types that may be associated with travel on a local and more global level. This will include a brief discussion of the recordings of travel events which include pauses. I will also examine the behaviour associated with specific follow events recorded during focal observations. The video recordings of travel initiations are then discussed, and more specifically the lack of a significant difference found between producing vocalisations, pausing, or looking towards a partner when alone compared to with other individuals during the initial stages of travel. Final conclusions are then drawn from this data about coordination of joint travel in Sonso chimpanzees.

3.4.2 General travelling behaviour

The sex differences found between the proportion of time spent in proximity to other individuals during different general activities can have a large influence on how social travel behaviour is analysed and interpreted. Females in Sonso spend a significantly lower proportion of their time more than ten metres from another individual than males during all activities (Figure 3.1). This is because juveniles and infants are included as nearest neighbours and social partners during data collection, and all the adult females in the study community have juvenile or infant offspring which accompany them throughout the day to different feeding sites until they nest at night¹⁹. The scan results showed this effect, as focal females spent significantly more time with their offspring than with males, females or unrelated juveniles. The inclusion of infants and juveniles as proximal neighbours, and thus as subjects for communication, in this thesis differs

¹⁹ One female, WL, without offspring of her own adopted an orphaned female at the beginning of the study period, carrying it when travelling and suckling it (even without milk), and generally treating it the same as other mothers treated their offspring.

from other studies looking at travel and vocalisations in chimpanzees (Gruber & Zuberbühler, 2013; Laporte & Zuberbuhler, 2010). Although offspring are unlikely to have an effect on pant-grunt production in adult females, as pant-grunt are only produced towards more dominant individuals (Goodall, 1986; Laporte & Zuberbuhler, 2010), it may be problematic to discount offspring as the ‘intended recipient’ of signals during social travel situations, when mother-offspring family units are those most likely to travel together in close proximity.

Sex differences in travel behaviour are also important to consider within the framework of chimpanzee’s patrilineal societal structure, where females spend more time alone in family groups and males spend more time with other adult males with whom they form stable affiliative bonds, enabled by their remaining in the same community throughout their lifetime (Goodall, 1986; Mitani, 2009). Figure 3.2 indicated that males spent the highest proportion of their time in proximity to other males than with females or juveniles. However, after controlling for individual identity, this difference was not found to be significant. The lower proportion of time spent with other males during travel compared to resting could indicate that maintaining proximity during travel itself may not be as important to the male chimpanzees than being in the same place when they spend time feeding or resting. However, individual differences seem to render any trends in differences non-significant. This indicates that some individuals contributed more to the differences than others, and that association patterns with other males, females or juveniles are not generalised during different activities in adult male chimpanzees.

Previous research into the use of loud, long-distance calls, such as pant-hoots, by chimpanzees in Budongo may influence the interpretation of results (Notman & Rendall, 2005). Pant-hoots have been found to be acoustically different upon arrival at abundant food sources in Sonso, with the calls containing different elements when travelling and arriving at food sources, or joining other community members (Notman & Rendall, 2005). Pant-hoots may therefore render the use of localised coordinating signals for travelling in proximity unnecessary, provided that individuals have no predatory pressure to travel close together, and can generally locate others from long-

distance pant-hoots or from food-grunts (Schel *et al.*, 2013a). Such coordination is made possible if individuals' pant-hoots are distinctly recognisable by other members of the community (Marler & Hobbett, 1975; Mitani, Gros-Louis, & Macedonia, 1996), and such a possibility is supported by research indicating that pant-hoots are indeed produced more often at a food source when alliance partners are in the area (Mitani & Nishida, 1993).

3.4.3 Overall vocalisation frequencies and predeparture vocalisations

The overall data on vocal production and the focal individual's behaviour state when vocalising (from focal follows) supports the view that loud vocalisations might be the most important for coordinating male group travel (Mitani & Nishida, 1993; Notman & Rendall, 2005). This was shown as the only vocalisation to increase significantly during travel behaviour compared to resting or feeding for males was the 'display pant-hoot' (a pant-hoot produced at the same time as display behaviour, such as swinging branches and drumming on trees). The same effect was not seen for females, which might be related to their tendency to travel in small family groups and remain dispersed, or simply to their lower dominance positions compared to males²⁰.

Hoo (and grunt) vocalisations are produced at the highest rate compared to other call types in all activities, which will be discussed later in relation to the perception of call associations with certain activities.²¹ The following analyses use focal data to look at behaviour during the one minute predeparture period before travel. This allows a more subtle approach than with general associations to look at whether any signals were associated with localised travel initiation and potentially coordinating travel of the focal and other individuals within a 10m radius.

²⁰ Display behaviour is most often associated with exhibition of dominance over others (Newton-Fisher, 2004).

²¹ A travel hoo that is distinct from other hoo vocalisations has not yet been reliably ascertained, as the results of Gruber and Zuberbühler (2013) compare calls from only two individuals.

In females, only hoos and pant-grunts were produced with any regularity before travel, while males produced hoos, pant-grunts and pant-hoots. Neither males nor females showed any significant difference between producing the different call types in the one minute period prior to travel. As pant-grunts are produced socially upon encountering more dominant individuals, it seems unlikely that they are being used to coordinate travel, so it is still possible that females were using hoo vocalisation as a signal to travel. However, the rate of calling in the predeparture period did not differ significantly from the overall rate of producing that call for each individual, meaning that the higher rate of hoo production is consistent with a higher rate of producing hoo vocalisations compared to other call types throughout an individual's day. These data therefore indicate that there is no vocalisation produced in the predeparture period that is specifically associated with the initiation of travel.

In males, the rate of production of pant-hoot vocalisations, although not significantly higher than pant-grunts or hoos, was significantly higher than the baseline pant-hoot production rate. Pant-hoots may therefore be considered to be associated with the predeparture period of travel initiation more than during other behaviour in males. This result is in concordance with the previous discussion points relating loud vocalisations to travel in males, and with other studies (Arcadi *et al.*, 1998; Notman & Rendall, 2005). However, their calling rate was still relatively low during the predeparture period (only 13 out of 251 observations) compared to predeparture vocalisations suggested to coordinate group travel in other primate species. For example, 5% of the predeparture periods contained pant-hoots in male chimpanzees in this study, compared to 20% containing grunts in gorillas (*Gorilla gorilla*)²² and 75% containing trills in white-faced capuchins (*Cebus capunicus*)²³. Males also produced pant-grunts at a higher rate than baseline during the predeparture period, but this is more likely to be as a result of approaching dominant individuals than a travel signal as described for the females above.

²² Percentage of 1 minute predeparture periods containing grunts calculated from median call-number of 3 during a 15 minute predeparture period in Gorilla Group 5 (Stewart & Harcourt, 1994).

²³ Percentage of 1 minute predeparture periods containing trills calculated from mean call rate per minute in 10 minute pre-departure period (Boinski & Campbell, 1995).

3.4.4 Travelling 'follow' behaviour observations and vocalisations

Following behaviour events were more likely to be preceded in the previous minute by hoo vocalisation than any other call type for both males and females. The rate of calling, however, was not significantly greater than the baseline rate of producing hoo vocalisations for either sex. This effect was seen with the travel initiation data and, in the same way, probably occurs because hoo (including grunt) vocalisations were the most frequently produced call type observed during focal follows (table 3.2). The higher rate of hoo production compared to other calls, coupled with the increased likelihood of an observer hearing and recording a soft vocalisation when the focal chimpanzee is nearby on the ground during rest or travel compared to other behaviours, may contribute to the perception that hoo vocalisations are associated with and specific to travel initiation more than other vocalisations (Gruber & Zuberbühler, 2013). The data in the present study do not support such an association.

It should be noted that the data on follows used here were not limited to the initiation of a travel event, but also included follows where individuals were already travelling. Therefore any vocalisations produced prior to the follow may be just as readily associated with a motivation to increase proximity as opposed to initiating joint travel. There was no significant difference between whether hoo vocalisations were produced before being followed as opposed to before following another individual. This suggests that even if the hoo vocalisation were associated with travelling together in proximity, it does not represent a signal to 'recruit' an individual into joint travel any more than it acts as a cue to their own action in following another. These possible differences in interpretation, along with the possible bias from using a method of data collection which requires *in situ* interpretation of behaviour, makes 'following behaviour' events the least reliable of the methods presented in this chapter for assessing joint travel coordination. In terms of looking for potential 'recruit to travel' signals, the video recordings taken during focal follows are most suitable as they allow the number of pauses, vocalisations and monitoring (looking behaviour) of a potential travel partner to be compared during the initial stages travelling.

3.4.5 Video recordings of travel initiations

Video data represent the most accurate description of behaviour during travel initiation for adult females in Sonso, although the small number of suitable video recordings for adult males was not large enough to draw firm conclusions from. The precise reasons for the difference in number of useable video recordings between the sexes is not clear, but may be partly influenced by the dominance display and other social behaviour exhibited by males when travelling, which can very quickly take them out of sight and obscured by vegetation during filming.

Similar to the focal and scan data, hoo vocalisations were the only call type to be produced with any regularity during the initial stages of travel shown in video recordings of males and females. However, there was no difference between whether a hoo vocalisation was produced when an individual was alone compared to when they were with a potential travel partner, suggesting that the call was not being produced as a signal directed at another individual to coordinate travel. There was also no difference in the probability of focal males to pause during the initial stages of travel initiation when they were alone or with another individual. This suggests that pausing (for less than a minute) is not necessarily a good candidate for a recruiting signal in males, as it also occurred when individuals were alone. However, females were more likely to pause when they initiated travel with others compared to when alone, and this was found to be linked to the distance of the potential travel partner- the potential travel partner was further away when the female paused compared to when they did not pause. The subsequent effect of these pauses on the following behaviour of the travel partner can help to elucidate whether such pauses can be considered signal or not.

Specifically considering the outcome of whether the three potential recruiting signals (looks, pauses and vocalisations) were given, as suggested by Pyritz *et al.* (2011), the data from video recordings found no interaction between any of the potential signals produced by the focal individuals and whether they were the follower, or were followed or not by their partner (although for males there was actually a decrease in the

probability of being followed when pausing, compared to following their partner or no following behaviour being observed).

There are some problems with the inclusion of looks as a signal, or even an indication of monitoring behaviour, which I will briefly discuss here. Looks have been considered as a recruitment signal in studies looking at travel coordination in monkeys and chimpanzees, and have recently been suggested as an intentional signal (Gruber & Zuberbühler, 2013; Sueur & Petit, 2010). When repetitions of looks between an individual and a location (i.e. gaze alternation) is considered along with other signal production, such as vocalisations, and with demonstrated persistence, or escalation of a behaviour until a specific outcome is achieved in a communicative partner, looks can be an important indicator of the attentional state of a signaller. When found in concert with the aforementioned behaviour, looks can potentially fulfil criteria for intentionality in an animal signal (Leavens & Hopkins, 1998; Schel *et al.*, 2013b). However, the ability of an observer in the field to accurately judge all look directions and durations from a primate without video recordings is limited, especially in dense forests. It is also unclear to what extent looking behaviour is a reliable indicator of whether a chimpanzee is actively monitoring another individuals' behaviour or not. Considering only the monitoring of travel behaviour, this could just as easily be achieved by listening to the movements of another individual as they travel through dense vegetation- especially if they are descending from the canopy- as by monitoring the individual visually.

In a further analysis, the few specific cases where pauses, hoos and looks were produced together, which might be considered as persistence or an 'escalation' of signal production by the signaller until a goal was achieved, were compared. There were no significant correlations between any of the potential signals, indicating that there was no persistence of signal production during the initial stages of travel. For example, an individual did not look more or vocalise more after they had paused three or four times, which might be expected if they were 'waiting' for a partner to join in travel.

A potentially important consideration concerning travel events recorded on video for the males is that chimpanzee males in Sonso utilise their daily foraging pattern to visit the

edge of their territory, sometimes including patrolling behaviour (Bates & Byrne, 2009). Patrols occur when a group of males (and sometimes females) move in close proximity, or in a straight line, and in silence at the boundary of their territory (Watts & Mitani, 2001). The main confounding factor for observing travel coordination during visits to the edge of the territory or on patrols is the size of the group (Mitani & Watts, 2005). Large numbers of potential recipients of a signal and many individuals stopping and starting travel in different places make it difficult to distinguish which individuals are initiating, following or signalling about travel. For future studies it would be interesting to compare predeparture and travel behaviour between individual males when they are travelling in small groups (of two or three) and larger groups (of ten or more) when they are at the edge of their territory compared to in their central home range²⁴. It could be that males are more likely to locally coordinate their travel when at the edges of their territory compared to in the middle. This might happen because the edges of their territory have a higher risk of dangerous conflict with neighbouring communities (Goodall, 1986), so individuals may be more likely to stay quiet and close together, making the use of soft vocalisations, looks or gestures more appropriate than loud pant-hoot vocalisations and rough grunts.

3.4.6 Overall conclusions

In summary, the data presented in this chapter provide no evidence for a vocalisation type that is systematically associated with general travelling behaviour, with travel initiation²⁵, or of the local coordination of travel seen in following behaviour in the current cohort of female chimpanzees in Sonso. In adult (and one sub-adult) males, pant-hoot vocalisations are the most probable call type associated with travel initiation and, when produced with displays, with travel behaviour in general (but not with localised travel coordination in the form of increasing probability of following behaviour). As pant-hoots are a loud vocalisation that can be heard for hundreds of metres, further data on the subsequent travelling behaviour of the entire group,

²⁴ Territory is defined as the entire area defended by the community; home range is defined as the area used most often by the community.

²⁵ Neither of these were directly tested in Gruber and Zuberbühler (2013).

including relative positions of all individuals in the group and their social relationship with the caller, are needed to explore the association of pant-hoots with travel in male chimpanzees.

The data presented here do not rule out the possibility that certain environmental or social factors, such as visibility, vegetation type, location within territory and general position relative to other individuals, might be affecting the production of signals that coordinate actions before travelling or increase the likelihood of a caller being followed. For example, females may only produce hoo vocalisations when visibility is low due to dense vegetation, or at the edge of their territory where it is more important to maintain proximity for protection from other communities. These questions could be assessed in future studies by including vegetation type, GPS location data and whole-group location data as variables in analyses. It is also possible that signals other than vocalisations (for example gestures, or combinations of gestures and calls) are being used to locally coordinate travel movements, which would require a greater sample of video recordings of individuals' travel departures from a longer study period in the future.

Any of these variables could have been weighted one way or the other to give the different results (suggesting that soft hoo vocalisation are used to coordinate localised travel decisions) obtained from the same field site by Gruber and Zuberbühler (2013). It is also possible that some individual chimpanzees contributed more to the data set than others in the two studies, and that these individuals had a significant impact on the results, although only one female died at the beginning of the present study and so was not included in results. Even one chimpanzee can have a large impact on what communication is observed and how a group coordinates travel, as was seen with the one alpha male in Tai where group travel was initiated after he drummed on various tree buttresses in the direction of travel (Boesch, 1991b; Boesch & Boesch-Achermann, 2000). This possibility should be tested by repeating observations of joint travel behaviour in Sonso chimpanzees with a different cohort of individuals, using a strict methodology where *all* travel and communicative behaviour is recorded from focal follows of specific individuals, as per the present study (i.e. without recording observations dependent on an *in situ* interpretation of travel events in the field).

Putting travel communication back into the context of joint cooperative activities reveals a problem with the interpretation of travel communication between mother and offspring, or even between affiliative male dyads, in that the motivation for producing signals when offspring fail to follow could stem from anxiety about the offspring being above a certain distance from them, and not by a motivation to travel together *per se*. The number of females and age range of infant offspring in Sonso was not large enough to compare communication and coordination in joint travel depending on the level of 'independence' (i.e. time and distance spent away from mother) of the infants. This would be interesting to examine with a larger data set than the current study, by comparing whether looks, pauses and vocalisations by females decrease upon travel initiation with infant travel partners of increasing independence.

Furthermore, expanding observations of male joint travel to include looking at coordinated travel towards a specific food source (e.g. a known fruiting tree) between un-related affiliative dyads compared to non-affiliated dyads may reveal differences in communication used in the two groups. Non-affiliated dyads might be expected to vocalise (coordinate) and look less than affiliated dyads if joint travel to the location were a joint action as opposed to the individuals having their own goals. This could provide information about the extent to which male chimpanzees have the motivation to travel 'together' in the wild, especially if an interruption method is used based on Warneken's experiments with human infants and adult chimpanzees, i.e. distracting one partner from a joint task (in this case travelling) and looking for evidence of communicative attempts to re-engage that partner (Warneken *et al.*, 2006). Further evidence that travelling together could be truly considered a 'joint cooperative activity' according to Bratman's (1992) second requisite that participants 'pursue a shared goal', could also come from instances where vocalisations act to alter (or coordinate) the behaviour of both individuals suggested to be engaged in the joint travel and not just one, which could be seen by collecting video data on male travel behaviour for a longer time period (over many years).

In conclusion, the present study found that although female chimpanzees were more likely to pause during travel initiation when their offspring were further away before travel, this had no effect on follow behaviour and there was no vocalisation or looking behaviour to suggest that subsequent travel was locally coordinated. Male chimpanzees did not vocalise, pause or use looks to coordinate travel initiation on a local level from the current data set, but pant-hoots are associated with male travel and need further research into whether they contribute to long-range coordination of travel, and whether this can be considered 'joint cooperative action'. This evidence is contrary to a previous study suggesting a local coordination of joint travel in wild chimpanzees using the hoo vocalisation (Gruber & Zuberbühler, 2013). In light of this study's results, further research was suggested to investigate whether more complex social or environmental variables might influence the production of coordinating signals during joint travel. It may be that, as the results presented here suggest, coordination of joint travel is generally achieved without specific signal production. The remainder of this thesis is therefore devoted to the investigation of communication and coordination during a more complex joint cooperative activity than joint travel which has been observed in Sonso chimpanzees: group hunting behaviour.

Chapter 4. Natural hunt observations and coordination of joint action

Abstract

Coordination of group hunting behaviour was investigated by analysing descriptions of hunts from my data as well as those from the long-term database. Bark vocalisations were associated with group hunting more than other vocalisations. They were more likely to be given by those initiating the hunt (who were also the least dominant), and may have been produced flexibly depending on affiliative relationships with other hunters. The data analysed indicated that the bark vocalisation has some role in the coordination of group hunts by affecting the initiation of hunts. Individuals were more likely to take an active chasing role in the hunt if their affiliation level was higher with the other hunters present. Individual strategies did not affect the production of barks, signifying that vocalisations are not coordinating different hunting strategies by simple association with either chasing or observing strategies. Neither were they associated with the potential recruitment of out-of-sight affiliated individuals who were not already hunting, although it is suggested that these results require further research. The increase in bark production seen when an individual is hunting with close affiliates supports the theory that the motivation towards joint action in hunting behaviour is socially affected and associated with a flexibility in vocal production. Playback experiments were suggested that could investigate the role of bark vocalisations in the initiation of joint action and coordination of movement in the context of group hunting,

4.1 Introduction

This chapter is concerned with looking at naturally occurring hunts in the Sonso community of chimpanzees in the Budongo Forest Reserve, asking predominantly what can be determined about their communication and coordination of behaviour from naturalistic observations. In this introduction I will first summarise the evolutionary approaches that have been taken in previous studies researching chimpanzee group hunts and how these might affect communication and coordination during a group hunt. I will then consider how individuals might be coordinating behaviour with each other during group hunts and specifically how communication might be used to achieve this.

4.1.1 Evolutionary approaches to studying group hunting behaviour

One of the mechanisms that may influence how we interpret communicative behaviour during group hunts is the functional (or adaptation) factor- i.e. how the behaviour increases an animal's fitness (Tinbergen, 1963). No chimpanzee studies to date have recorded hunting behaviour long enough to determine the effects of successful group hunting and meat eating on *evolutionary* fitness and reproductive success. Some proxy measures of individual fitness (and reproductive fitness) have, however, been recorded by estimating energy reward gained from meat-eating (or micronutrient reward from even a scrap of meat), sex rewards after meat sharing, and an assumed fitness increase from strengthening and maintaining affiliative bonds (Gilby *et al.*, 2006; Gomes & Boesch, 2009; Muller & Mitani, 2005; Nishida, Hasegawa, Hayaki, Takahata, & Uehara, 1992; Tennie, Gilby, & Mundry, 2009). These fitness benefits, and an assumed cost from the dangers of hunting potentially dangerous prey with teeth²⁶, have been extrapolated into models. These models are used to determine whether the cooperative behaviour evolved through reciprocal altruism, mutualism, or sexual selection (Boesch, 1994; Gilby & Connor, 2010; Stanford, Wallis, Mpongo, & Goodall, 1994; Trivers, 1971).

²⁶ The costs of hunting have never, to my knowledge, been quantified for chimpanzees in a publication.

The evidence from different chimpanzee study sites shows variation in hunting behaviour and calculated benefits between sub-species, within sub-species, and even between groups in the same population (Gilby *et al.*, 2006; Uehara, 1986). This variation seems to support the inclusion of hunting as a culturally learned behaviour (Whiten *et al.*, 1999) which may include benefits and increases in fitness that can vary between groups and populations. Such benefits may in turn depend heavily on a single individual's influence on the behaviour of some or all members of the group (Gilby *et al.*, 2008) or on interactions between certain individuals with strong affiliation (Muller & Mitani, 2005). As such, group hunting is a highly relevant behaviour for investigating communication and coordination between the individuals involved.

Discussions about the evolutionary and fitness benefits of hunting in groups may not be the most helpful starting point for studying coordination of group hunting when it is not yet known what signals are produced and how they are used to communicate during a hunt. However, the adaptive function of hunting behaviour may influence how individual chimpanzees communicate during group hunts, which may not necessarily be related to coordination of actions (Tinbergen, 1963). For example, consider how the meat reward (benefit) is shared after the hunt. If an active hunter vocalises a lot when chasing and capturing a monkey and they are a low-ranking male without allies present, they are likely to lose the meat unless they can run away with it quickly enough to escape other males. Therefore, if individuals vocalise upon capture (or imminent capture), they may do this differently depending on their dominance or alliance position with respect to other hunting group members - specifically depending on the presence and position of more dominant individuals.²⁷

Sonso chimpanzees have shown flexibility in vocal production depending on the presence of dominant allies and affiliates, for example by modulating screams and food grunts (Slocombe *et al.*, 2010; Slocombe & Zuberbuhler, 2007), or in the presence of alpha individuals, for example pant-grunt production to other individuals (Laporte &

²⁷ For example, the alpha male in Sonso was observed to steal meat by threatening others eight times over the 2 year observation period in Budongo, and always obtained meat when he was present.

Zuberbuhler, 2010). Therefore, considering the flexibility in call production depending on social factors, and the influence others individuals might have on calling described in the previous paragraph, this study will include dominance and affiliation relationships between hunters when they vocalise during group hunts.

This chapter used data on group hunts to examine the immediate behaviour responses and proximate mechanisms that may be involved in coordinating behaviour of chimpanzees during group hunts. If communication is occurring in the form of signals between individuals to coordinate their behaviour, the possible ways this could happen should first be discussed. I will now suggest some methods to determine how, whilst avoiding any mind-reading requirements, the behaviour of individuals engaged in a group hunting activity may be influenced by the vocalisations and gestures of other individuals engaged in the same activity (Marler *et al.*, 1992; Seyfarth & Cheney, 2003).

4.1.2 Coordination and communication

Before hunting activity commences, communication may be used to signal motivation to hunt to other group members, in a similar way to the signals produced before joint travel are used in other species (King & Sueur, 2011). Alternatively, one individual might simply start hunting alone and be followed by others, without any communication for coordination being used. Once two or more individuals' attention is focussed on prey, vocalisations and gestures may function as a signal to approach monkeys, coordinate timing or location of approach, or even to signal different strategies of each individual involved. Once they are committed to a group hunting activity by moving towards prey, individuals may vocalise or gesture when changing direction or changing hunting strategy. It would be difficult to distinguish whether such a signal could be linked to a specific receiver's change in behaviour when there are many potential receivers engaged in changing travelling behaviour in different locations. Vocalisations given once a hunt is in progress will therefore only be considered in relation to the

potential motivation of the signaller as they carry out a specific behaviour, and not the reactions of receivers²⁸.

Looking at the behavioural and environmental contexts of the signaller and receiver can allow associations to be made between specific signals and their social and environmental context of production during group hunts. This is reflected in the data collection protocol which includes *ad lib* sampling of all individuals' social behaviour while they are hunting, location in relation to the prey, each other, and the physical environment, as well as recording specific vocalisations and the behaviour of the signaller. A discussion of which hunting behaviour actions and which signals are theoretically important to the question of how chimpanzees are communicating and potentially coordinating group hunts now follows, before the stating of formal hypotheses to be tested.

4.1.3 Behaviour observations and vocalisations

The vocal repertoire of chimpanzees is graded, often making specific calls difficult to distinguish without acoustic analysis (Marler *et al.*, 1976). However, a more general and approximate grouping of call-types that can be recognised by all human observers is used at the Budongo field site. This allows reliable classification *in situ* when observing naturally occurring hunts. Vocalisations are placed into broad categories when recorded by long-term field staff, including a 'bark' vocalisation (see table 3.1). Special attention is given during analysis of hunting data to a vocalisation that is potentially specific to the hunting context, termed the 'hunting bark'.

Hunting barks in Tai chimpanzees are a distinct call characterised by a significantly shorter duration than other barks, and are mostly given by those already involved in the hunt (Boesch & Boesch-Achermann, 2000; Crockford & Boesch, 2003), but may also function to recruit others to start hunting or be given during a pause in the hunt when the caller wants to continue (*pers. comm.* Cathy Crockford). Hunting barks have yet to

²⁸ Both a signal and response are needed to consider a behaviour as communication (Scott-Phillips, 2008).

be acoustically discriminated as a distinct call type in Budongo and so, in the absence of specific criteria for classifying them separately from other barks, all bark vocalisations, including waa-barks, were grouped together into one call-type when recording observations in this study.

Bark vocalisations can vary in volume but all bark-types are considered loud vocalisation that can be heard by all individuals in the party and so can include many different receivers (Crockford & Boesch, 2003; Marler & Hobbett, 1975). The dispersed, elevated and fast-paced nature of a hunt, together with poor visibility, make it unlikely that an individual's gaze direction while they are vocalising- a factor that could indicate intended recipient or intentionality in signalling- can ever be accurately recorded in a wild chimpanzee hunt. That such directed communication is occurring during group hunts cannot be summarily ruled out, although the data on natural observations of group hunts will not address the issue.

It may also be relevant to look at the proportion of individual behaviour strategies in those hunting together. This could be another factor influencing vocalisations. An increase in vocalisation intensity has been proposed as a mechanism for converging emotional states and coordinating foraging activity in those involved in direct communication in an irruptive, nomadic songbird, the red crossbill (*Loxia curvirostra*) (Cornelius, Breuner, & Hahn, 2010). If such a mechanism were also at work in the chimpanzees when hunting, it might be expected that the rate of calling by those actively involved in the hunts should be higher compared to those who are not.

In the following data analyses, an overview of the hunting behaviour of Sonso chimpanzees in Budongo will be described, including hunting strategies and success rates, and vocalisations produced during group hunts (4.3.1). It is predicted that bark vocalisations will be associated with group hunting more than other vocalisations, will be produced more in larger hunting parties, and may increase the success of hunts. Individual differences in hunting strategies are then analysed and it is predicted that preferred strategies will be related to dominance levels and affiliative bonds with other hunters (4.3.2). Finally, I will explore the vocalisations produced during hunts, looking

at how vocalisations might coordinate hunting behaviour by analysing individuals' relationships with others in the hunt, their relative dominance to each other, and a potential measure of their *motivation* to hunt (whether they initiated the hunt or not) (4.3.3). Bark vocalisation are predicted to be produced more often when an individual initiates a hunt than when they join a hunt, an effect which will be independent of their social relationship with other hunters if the vocalisation is linked most strongly to motivation to hunt. If the bark has a potential recruiting function when produced during the hunt, it is also predicted that barks will be produced more often when affiliated individuals have not yet joined the hunting party than when affiliates are already hunting together.

4.2 Methods

Hunting behaviour was observed using *ad lib.* sampling by all researchers in the Sonso community 97 times from January 2009 to August 2012 (average 2.2 per month). 66% of these hunts were recorded with detailed descriptions of the individuals involved and their behaviour. An individual focal follow was being conducted on an animal which started hunting three times (Altmann, 1974). The low instance of individuals that were being focal-followed when they engaged in hunting behaviour meant that all-occurrence recordings from hunts taken *ad lib* had to be used to get a meaningful number of observations (19 hunts from personal observations and 64 hunts in total including long-term data). The long-term data includes observations by other researchers and the team of field assistants including GM, MD, JC, SM, and JK. The field assistants have been assessed with data collection reliability tests by BCFS (www.budongo.org) to ensure reliability of identity classification, and researchers are always accompanied by a field assistant.

Where possible, a Marantz professional digital sound recorder (model: PMD660) with a Sennheiser (model: MKH416T) microphone was used to record during the hunt and for the observer to narrate chimpanzee behaviour during the hunt. A Panasonic HD90 digital camcorder was used for filming the hunt where possible, but where events were not visible in the trees, commentary on an individual's proximity to others and their positions in the trees or on the ground relative to the focal animal and to the prey was recorded. Individuals in the party were noted (or taken from 15 minute scan samples for the long-term data) before the hunt began, then behaviour observations were recorded *ad lib*, taking point samples from any individual when a new behaviour was observed (Altmann, 1974). All observations were recorded using a Palm TX handheld device, on a time-stamped spreadsheet of behaviour, or constituted hand-written descriptions of events.

Individuals were classified as hunters if they were described carrying out any behaviour where they were following the prey, either on the ground or in the trees, with their attention on the prey. This includes those individuals observing from the ground, as per

Watts and Mitani (2002), which were previously described as bystanders by Boesch (2002) and not included as hunters in his analyses. Group hunts were classified as any hunting behaviour from two or more individuals.

Behaviour recorded from hunters included: vocalisations; travelling (climbing trees, chasing monkeys, travelling below trees on ground) in relation to the prey or other hunters, and direction with location on grid system; waiting (in trees, on ground, in canopy) in relation to prey or hunters and canopy composition; looking at prey, canopy or other hunters; interaction with monkeys (threatening, fighting, catching, killing, grabbing and throwing down from tree); social interactions between chimpanzees; feeding, social and meat sharing behaviour if prey were killed; and any additional notes.

Where the point samples taken from an individual during a hunt included their position in the forest and in relation to the monkey, as well as their behaviour towards the monkey, their behaviour was assigned to different categories. The potentially different strategies described by Boesch (2003) are given below with added definitions which were used in this study to make them more objectively classifiable when checked against video recordings of an individual's behaviour during a hunt as well as compared to *in situ* observations from the field. The categories are described in table 4.1.

Table 4.1. Definitions of chimpanzee hunting strategies as defined by Boesch (2002) and updated for this study.

Strategy	Definition from Boesch (2002)	Updated definition
<i>Driver</i>	follows prey in a given direction without catching them	<i>initiator</i> is the first chimpanzee to approach within <20m the prey and move towards it for >5 seconds (without trying to capture the prey itself), or until they or another chimpanzee approaches <10m the prey or the prey is captured
<i>Blocker</i>	places himself in a tree so as to block the progression of the prey	<i>blocker</i> changes general activity and climb a tree (without feeding from the tree) in order to be positioned in the path of the moving prey, but >10m from the prey at that time
<i>Chaser</i>	moves quickly after the prey trying their best to catch up with them	<i>chaser</i> follows <10m behind or below prey while trying to capture it
<i>Ambusher</i>	places himself in a position where no prey is yet and where he cannot easily be seen, and he will rush towards the prey as soon as it enters his tree	same as blocker, but must produce no vocalisations and be in a position where visibility is low (e.g. <20% visible pixels from video still of the chimp, compared to baseline average) and no monkeys are <20m
<i>Observer</i>	not described	follows hunt >10m from prey on ground whilst looking at prey²⁹

The ambusher category is unlikely to be accurately observed in the field without clear video footage of the entire hunt, including the positions and visibility of all hunting individuals and monkeys in the trees, and so is not included in this study. The term ‘ambush’ was occasionally used by field assistants in the long-term data (SM), but upon questioning the observer, it was revealed that the individual’s behaviour could not be distinguished from a ‘blocker’.

²⁹ This category was not included as a hunting strategy by Boesch, but as Watts and Mitani (2002) argue, bystanders on the ground who are observing the hunt may easily and at any time join the chase in the canopy or chase down a fallen monkey, so should not be excluded from involvement.

For the long-term data recordings used, point observational samples were included only if the individual's behaviour was described adequately enough (i.e. sufficiently accurate in my judgement, based on the detail of the written account of the hunt and questioning the observer) to be assigned one of the three broad strategies of chaser, blocker or observer. Individuals taking on more than one strategy during a single hunt were not included in analyses on strategies as these samples could not be considered independent. Whether an individual was an initiator was recorded separately from chaser, blocker and observer strategies. This was because 'initiator' describes action prior to actual hunting behaviour and all initiators subsequently took on chaser, blocker or observer roles.

Hunting strategies were important to consider in relation to communication and coordination as they may reveal something about the motivation of hunting individuals. First of all, initiators can be considered to show the highest motivation to hunt, and so signals produced by initiators to receiving individuals could be associated with motivation to engage in joint hunting behaviour. The three hunting strategies can then be equated to differing levels of involvement in the hunt. Then, in terms active involvement (and risk), chasers are the most active, followed by blockers and then observers. These categories will therefore be used to compare individuals' vocal behaviour in relation to their investment in the hunt. They will also be used to compare strategies of individuals depending on the presence/absence of affiliated or more dominant individuals.

4.2.1 Statistical analyses

Statistical analyses were carried out using IBM SPSS Statistics 19.0.0. All tests were two-tailed and have the significance set at $\alpha = 0.05$. Data were analysed using non-parametric tests if they failed the Shapiro-Wilk test of normality; otherwise parametric tests were used, including GLMM tests. Non-parametric tests included Chi-square or Fisher exact tests for comparing frequencies between groups, Spearman's rank test for correlations and Mann-Whitney U (Wilcoxon rank-sum) tests for ordinal or interval/ratio data. G-tests of independence were carried out in Excel using a formulae template available online (<http://udel.edu/~mcdonald/statgtestind.xls>). These tests are

similar to Chi-square analyses but give a further statistic representing independence of results based on identity. In this way, the effect of individual identity on communication and behaviour could be assessed. Social factors which differed for each individual in a hunt were then tested for their effect on hunting strategy used or vocalisations produced using multinomial logistic regression tests. Individual identity was included as a factor to remove pseudoreplication.

4.3 Results

I will start this section by giving an overall picture of hunting by Sonso chimpanzees through analyses of observed hunts, followed by a detailed look at the different hunting behaviour and vocalisations recorded as point samples throughout the hunts. I will then examine individual differences in hunting behaviour and vocalisation, with a final analysis to explore links between hunting behaviour and vocalisations produced during hunts.

4.3.1 Overall group hunting observations summary

I recorded 19 hunts where at least some part of the hunt itself was observed during January 2010-April 2010 and September 2010-October 2011. Three hunts were solo (16%), only one of which was successful (rate of 0.33), and 16 were group hunts (84%) involving two or more chimpanzees in the hunt. Seven of these group hunts were successful, all resulting in the capture and eating of Colobus monkeys, giving a mean success rate of 0.44.

Combining my own data with descriptions from the BCFS project's long-term data gave a total of 64 hunting accounts from February 2009-August 2012 (all involving Colobus monkeys). Five of these were solo hunts (8%), three of which were successful (rate of 0.60), and 59 were group hunts (92%). 41 of the group hunts were successful, giving a mean success rate of 0.69. These results are summarised in table 4.2 below.

Table 4.2. Number of hunts with detailed descriptions of individual behaviour from personal data and from personal data combined with data from the long-term database at BCFS, giving the proportion of solo and group hunts and their success rates.

Data Source	Total hunts	Percentage solo hunts	Success rate of solo hunts	Percentage group hunts	Success rate of group hunts
Personal data	19	16%	0.33	84%	0.44
Long-term data	64	8%	0.6	92%	0.69

To see if the number of hunters affects the success rate of group hunts, the mean number of hunters for successful hunts was compared to unsuccessful hunts (number of hunters in successful hunts failed the Shapiro-Wilk test for normality: $T = 0.925$, d.f. = 41, $p = 0.01$). There was no significant difference between number of hunters in successful compared to unsuccessful hunts (mean number hunters: successful hunt = 5.95 s.d. = 3.19, $N = 41$; unsuccessful hunt = 5.33 s.d. = 2.79, $N = 18$; Mann-Whitney U test: $W = 499$, $N_{hunts} = 59$, $p = 0.496$).

4.3.2 Individual differences in hunting strategies

When comparing different strategies, ‘blocker’ was described at a much lower rate (29 times) than either ‘chaser’ or ‘observer’ (145 and 102 respectively), and was performed at a lower rate than either chaser or observer for all but one individual. The blocking described was across 15 different individuals, with the highest rate- four times- accounting for only 14% of the individual’s strategies. The low rate of blocking observations made it difficult to compare signalling between this strategy and the others, as the sample size is too small. All further analyses of hunting strategy compare only observer and chasing behaviour, which are especially relevant for looking at differences in level of activity in hunting behaviour, as they represent different levels of involvement in the hunt with its concomitant risk.

Comparing only the chaser and observer strategies, table 4.3 shows that FK, SM, and FD most often take on the strategy of chaser, whereas NK and ZF are more often observers, and that these differences between chaser and observer preferences are significant.³⁰

³⁰ Only individuals observed in at least ten different group hunts were included in analyses to compare individual differences in strategies.

Table 4.3. Frequency of chasing and observing strategies compared with individual hunter identities (IDs) using a G-test. Heterogeneity G-value is significant, suggesting the ratio of chaser to observer strategies is different between individuals, so data cannot be pooled between individuals (heterogeneity $G=75.74$, $d.f.=9$, $p<0.001$).

Hunter ID	Chaser	Observer		G-value	d.f.	P-value
FD	21	7		7.33	1	**0.01
FK	28	1		31.50	1	**0.00
HW	16	14		0.13	1	0.71
KT	17	11		1.30	1	0.25
MS	8	11		0.48	1	0.49
NK	8	21		6.04	1	**0.01
SM	21	1		22.36	1	**0.00
SQ	14	9		1.10	1	0.30
ZF	3	19		12.97	1	**0.00
ZL	9	8		0.06	1	0.81
			total G	83.26	10	**0.00
pooled	145	102	pooled G	7.52	1	**0.01
			heterogeneity G	75.74	9	**0.00

** significant to 0.01 level

The heterogeneity G-value is significant ($G = 86.15$, $d.f. = 9$, $p < 0.001$) so the null hypothesis that different individuals take on the chaser and observer strategies with equal probability is rejected. As the different individuals' data sets are significantly different from each other, data on strategies should not be pooled but looked at for each individual hunter instead (McDonald, 2009).

4.3.2.1 Dominance and affiliative relationships and hunting strategies

Given the results above, it is important to look at whether aspects of individuals that are different in each hunt might be contributing to the differences in strategies used.

Dominance levels and affiliative relationships relative to other hunters are of particular interest. A multinomial logistic regression test was therefore used to assess how much variation in strategy used (chaser or observer) could be accounted for by social factors

in hunters. Individual hunter identity ('hunter ID') was included as a fixed factor to remove variation due solely to individual identity. Their relative dominance rank compared to other individuals in each hunt, their mean affiliation level with fellow hunters (CIA) in each hunt and age were then included as covariates in a main effects model.

Relative dominance showed the strongest effect on variation (Wald statistic = 5.37, $N = 229$, $p = 0.021$) with every increase by 1 in relative dominance representing an increase of 1.4 times the number of observers (this is independent of age). Affiliation also showed a significant effect on number of observers (Wald statistic = 4.43, $N = 229$, $p = 0.035$) but in the opposite direction, meaning that individuals were more likely to take an active chasing role in the hunt if their affiliation level was higher with the other hunters present.

Comparing the mean preferred strategies for each hunter also showed that more dominant individuals are more likely to observe from the ground, rather than chasing the monkey through the canopy. This is shown in figure 4.1, where there is a significant correlation between the proportion of hunts where an individual was more active in the hunt by chasing the monkeys, compared to observing it from the ground, and their dominance rank (median relative dominance rank = 0.260, IQR = 7.66, median rate active hunting = 0.547, IQR = 0.46; Spearman's rank test: $r_s = -0.770$, $N_{\text{hunters}} = 10$, $p = 0.009$). The age of males is strongly correlated with their mean relative dominance in a hunt (median age = 19.000, IQR = 5.50; Spearman's rank test: $r_s = 0.871$, $N_{\text{hunters}} = 10$, $p = 0.001$). However, the age of hunters is not correlated with their success rate (median success rate = 0.704, IQR = 0.05; Spearman's rank test: $r_s = -0.228$, $N_{\text{hunters}} = 10$, $p = 0.526$). Neither is the age of the hunter correlated with whether the individual catches the prey (median rate of catching prey = 0.259, IQR = 0.20, Spearman's rank test: $r_s = -0.499$, $N_{\text{hunters}} = 10$, $p = 0.142$), or whether the individual has a share of the meat after a successful hunt (median probability of obtaining meat = 0.321, IQR = 0.17, Spearman's rank test: $r_s = 0.350$, $N_{\text{hunters}} = 10$, $p = 0.322$).

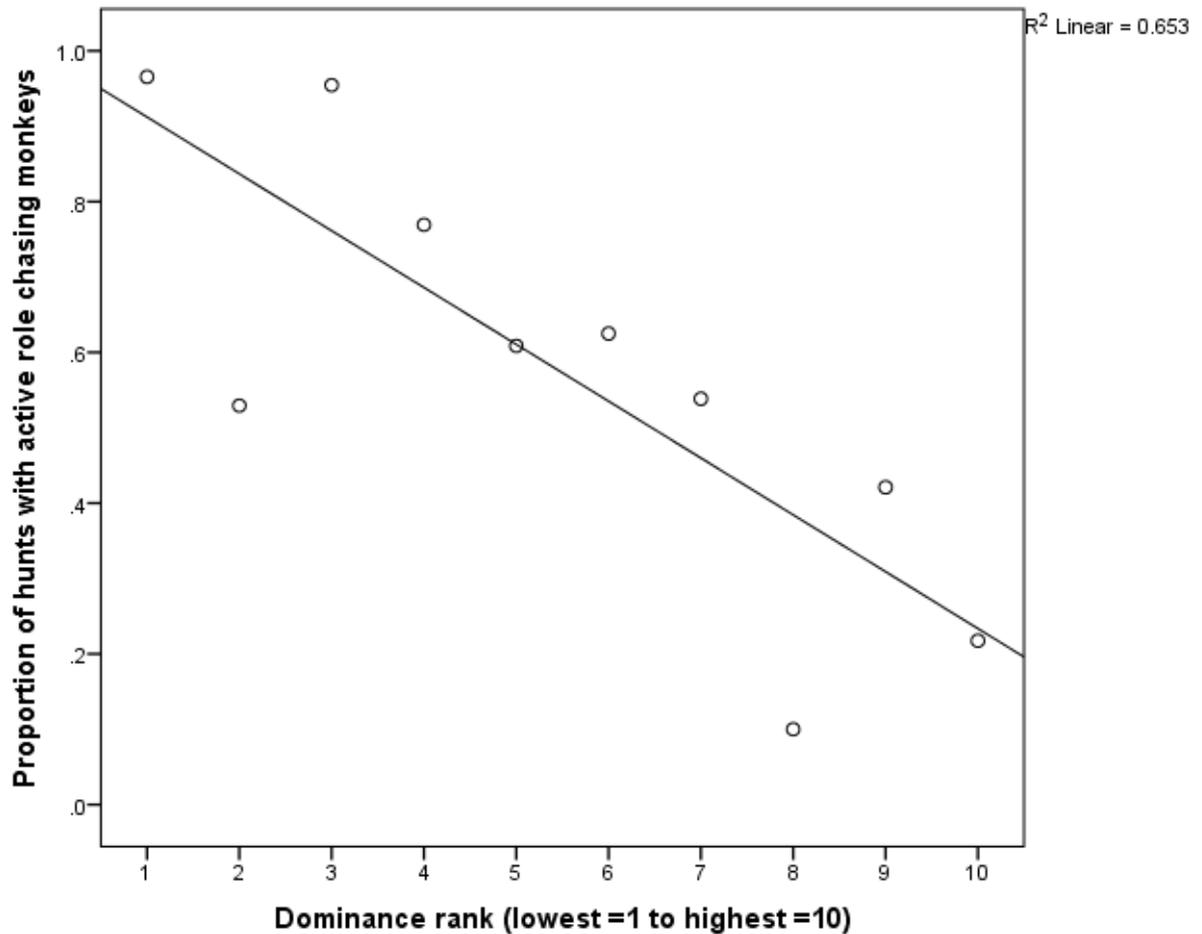


Figure 4.1. Proportion of hunts in which an individual had an active role chasing monkeys compared to their dominance rank. Spearman's rho was -0.77, $p = 0.009$ for $N = 10$ group hunting males.

4.3.3 Individual differences in vocalisations produced during the hunt

A total of 285 point samples were recorded from 52 hunts where vocalisations were included in the recording procedure for the hunt and included the identity of the caller. Hunts where vocalisations were not included in the descriptions of individual hunting behaviour were not included in analyses. Where a vocalisation was heard but the caller was not observed, this was recorded as unknown and not included in analyses. When comparing different vocalisations, data points were only used if only one vocalisation type was recorded for the individual during the hunt, to ensure independence of samples.

For each individual ($N = 10$), the mean number of hunters was slightly higher if they vocalised during the hunt than if they remained silent (mean number hunters when individual vocalised = 7.69 s.d. = 3.14; when individual did not vocalise = 7.58 s.d. = 3.56). Breaking down the vocalisations into different call types reveals that it is the bark vocalisation causing this effect (see figure 4.2): hunting parties were significantly larger when an individual barked (mean = 8.38 s.d. = 3.15) than when individual did not bark (mean = 7.49 s.d. = 3.52; Wilcoxon signed ranks test: $Z = -2.244$, $N_{hunters} = 10$, $p_{exact} = 0.021$).

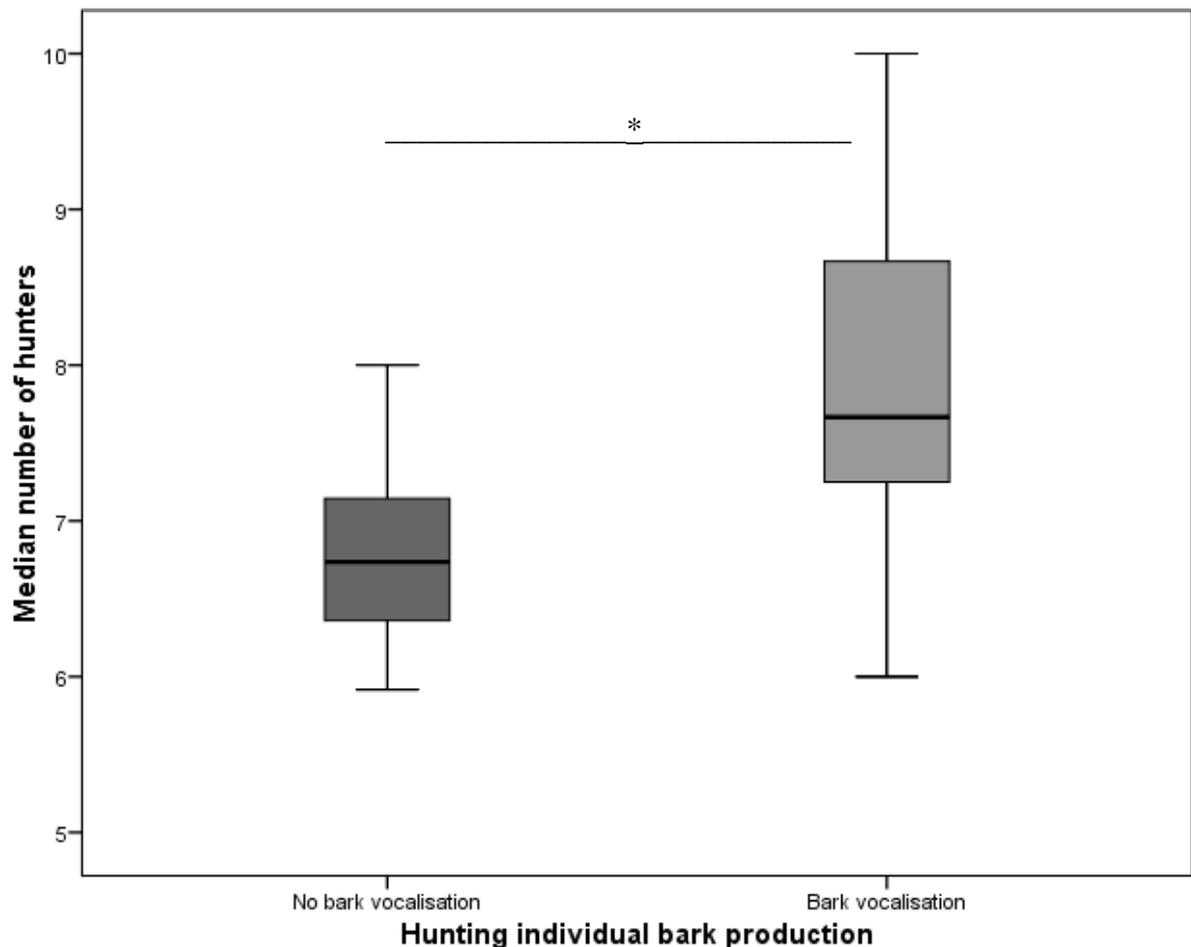


Figure 4.2. Median number of hunters when an individual produced a bark vocalisation during the hunt is significantly higher than when they produced no bark vocalisation (Wilcoxon signed ranks test: $Z = -2.244$, $N_{hunters} = 10$, $p_{exact} = 0.021^*$).

The other recorded vocalisations were produced at too low a rate to be compared with number of hunters (and no call-type other than barks was produced by all individuals at least once during a group hunt, see table 4.4). There were only 6 additional instances where barks were described as being produced before the hunt started, which was not enough to reliably compare number of hunters between groups where a bark was given before a hunt or during one.

Table 4.4. Number of vocalisations produced by different hunters during group hunts from the combined data.

Hunter ID	Number of barks	Number of pant-hoots	Number of screams	Number of whimpers	Number of hoo/grunts
FD	5	1	2	0	0
FK	8	1	3	1	0
HW	4	1	2	0	0
KT	4	0	3	0	1
MS	3	0	0	0	0
NK	3	1	0	0	0
SM	7	1	9	0	2
SQ	6	0	1	0	0
ZF	4	0	0	0	0
ZL	2	0	1	0	0
Total number of vocalisations	46	5	21	1	3

My data (from sound recordings) showed that 90% of individuals have a higher rate of vocalising during group hunts than being silent. Using a G-test, the heterogeneity G-value is non-significant, suggesting there is no significant effect of individual ID on vocalisation rate, and that data on vocalisations can be pooled between individuals. Pooled G-value is non-significant ($G= 2.12$, $d.f.= 1$, $p= 0.09$), but shows a trend for vocalising more than being silent during hunts (see table 4.5 below).

Table 4.5. Frequency of vocalising or not during a hunt from my data compared with individual hunter identities (IDs) using a G-test (no differences are significantly different from an expected proportion of 50:50). Heterogeneity G-value is non-significant, suggesting the ratio of being silent to vocalising during group hunts is not dependent on hunter ID and data can be pooled between individuals, but there is no overall effect ($G= 2.12$, $d.f.= 1$, $p= 0.09$).

Hunter ID	vocalise	silent		G-value	d.f.	P-value
FD	7	5		0.33	1	0.56
FK	7	3		1.65	1	0.20
HW	5	3		0.51	1	0.48
KT	3	3		0.00	1	1.00
MS	3	1		1.05	1	0.31
NK	3	2		0.20	1	0.65
SM	5	2		1.33	1	0.25
SQ	3	3		0.00	1	1.00
ZF	3	2		0.20	1	0.65
ZL	3	4		0.14	1	0.70
			total G	5.41	10	0.86
pooled	42	28	pooled G	2.82	1	0.09
			heterogeneity G	2.59	9	1.00

The effect of individual identity on rates of calling was compared for the long-term data combined with my data and the heterogeneity G-test repeated in order to assess whether different individuals are simply more prone to vocalise than others in the combined data set. Table 4.6 shows that 80% of individuals were silent significantly more than vocalising. Only one individual (SM) has a higher rate of vocalising during group hunts, but it is non-significant. Table 4.4 shows that this is likely due to the high number of screams recorded from this individual; SM produced screams at least three times more often than any other individual.³¹

³¹ The rate of screaming is low or zero for all individuals during group hunts except SM, and without this data point, the number of screams produced during hunts is $\frac{1}{4}$ the number for barks. Therefore analyses comparing individual identities and vocalisations will use only barks, which is the only vocalisations type to be recorded from all individuals.

Table 4.6. Frequency of vocalising or not during a hunt (from combined data set) compared with individual hunter identities (IDs) using a G-test (from long-term data combined with CM data). Heterogeneity G-value is non-significant, suggesting the ratio of being silent to vocalising during hunts is not dependent on individual ID and data can be pooled. The pooled G-value shows that individuals are more likely to be silent during a group hunt than to vocalise (G=42.43, p=0.00; * are significant with $p < 0.05$ and ** are significant with $p < 0.01$).

Hunter ID	vocalise	silent		G-value	d.f.	P-value
FD	7	17		4.30	1	*0.04
FK	10	18		2.32	1	**0.00
HW	5	21		10.59	1	**0.00
KT	6	17		5.48	1	*0.02
MS	3	15		8.73	1	**0.00
NK	4	18		9.64	1	**0.00
SM	11	8		0.48	1	0.49
SQ	7	13		1.83	1	0.18
ZF	4	13		5.02	1	*0.03
ZL	2	12		7.92	1	**0.00
			total G	56.30	10	**0.00
pooled	59	152	pooled G	42.43	1	**0.00
			heterogeneity G	13.87	9	0.79

The heterogeneity G-value is non-significant, suggesting the ratio of being silent to vocalising during hunts is not independent between individuals and the samples from different individuals can be pooled. The pooled G-value shows that from the long-term data, individuals are more likely to be silent during a hunt than to vocalise (G= 42.43, d.f.= 1, p= 0.00). The difference between vocalisations recorded from my data and the combined long-term data is illustrated in figure 4.3 below.

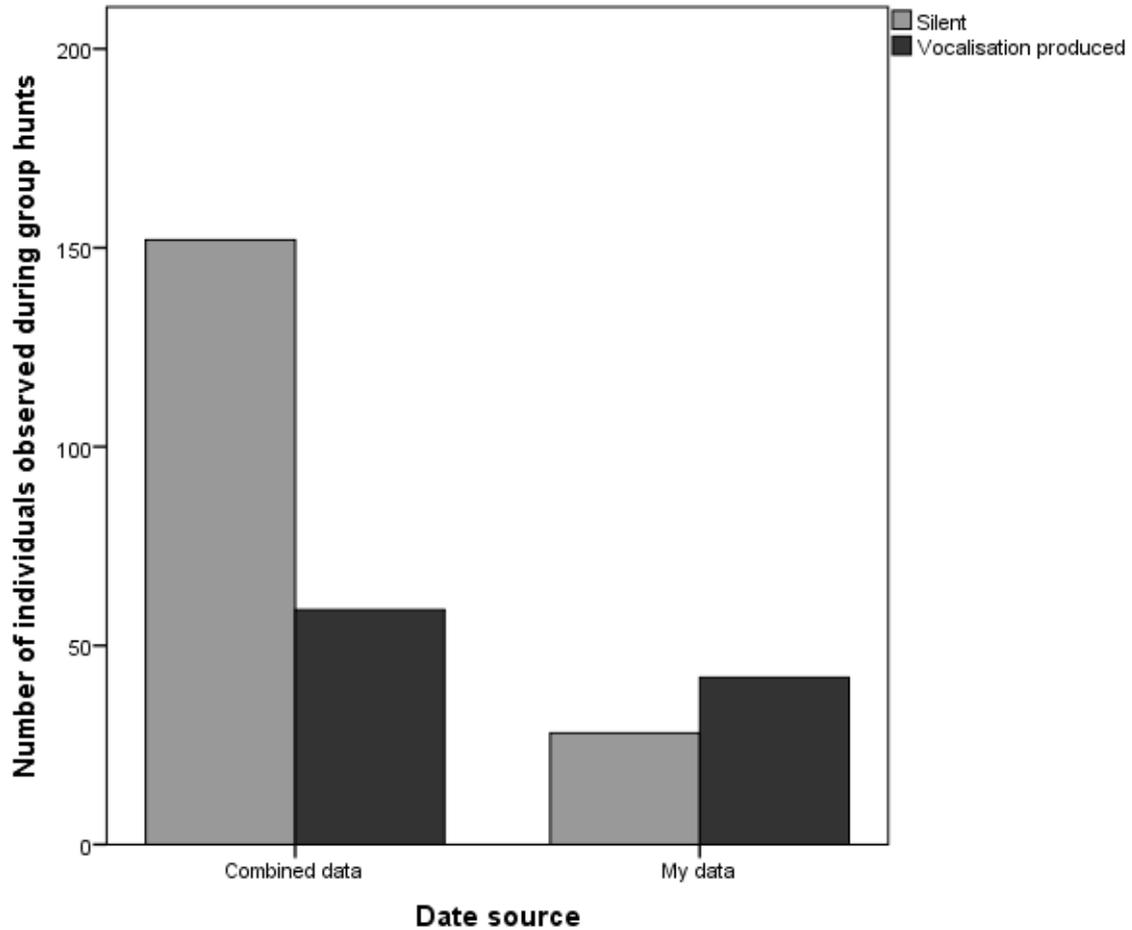


Figure 4.3. Number of individuals observed to vocalise compared to remaining silent during group hunts recorded from my data compared to the combined long-term data from BCFS.

4.3.3.1 Initiation of hunts and coordination: individual differences in vocalisations

No individual initiated hunts with a probability greater than 1 s.d. lower or higher than the overall mean initiation rate ($N = 167$, mean = 0.38, s.d. = 0.488). However, individual identity was found to have a significant effect on the number of hunts initiated compared to the number of hunts joined (Fisher exact test: $F = 19.848$, d.f. = 9, $N = 167$, $p = 0.016$)³². Table 4.7 shows that FK and SM initiated more of the hunts they took part in than the overall average (FK: $N = 24$, mean = 0.71, s.d. = 0.464; and SM: $N = 16$, mean = 0.63, s.d. = 0.500 respectively; overall mean = 0.38, s.d. = 0.488).

³² Using Bonferroni correction in SPSS 19.0 crosstabs.

Table 4.7. Mean proportion of hunts initiated for individual hunters (cases excluded where initiation of hunt was not seen, $N_{\text{total}} = 167$), showing that FK and SM initiated the hunts at a higher rate than the overall average.

Hunter ID	Mean	N	Std. Deviation
FD	.35	20	.489
FK*	.71	24	.464
HW	.32	19	.478
KT	.29	17	.470
MS	.25	12	.452
NK	.24	17	.437
SM*	.63	16	.500
SQ	.35	17	.493
ZF	.17	12	.389
ZL	.31	13	.480
Overall	.38	167	.488

Comparing the frequency with which vocalising individuals initiate a hunt to those that do not initiate the hunt reveals that individuals are more likely to be an initiator of a group hunt when they produce bark vocalisations than when they do not (median initiation rate when barked = 0.675, IQR = 0.45; median initiation rate if not barked = 0.258, IQR = 0.26; Wilcoxon signed-ranks test: $Z = -1.988$, $N_{\text{hunters}} = 10$, $p_{\text{exact}} = 0.049$) figure 4.4. The same effect is not seen when comparing hunting strategies with whether an individual barked or not (GLMM testing variable ‘strategy’ with bark production as a fixed factor and hunter ID as a random factor: $N = 199$, $F = 0.875$, $p = 0.351$; mean probability of hunter taking on observer strategy when barked = 0.32, s.d. = 0.471; mean when no bark = 0.49, s.d. = 0.502), i.e. chasers are no more likely to vocalise than observers from the ground.

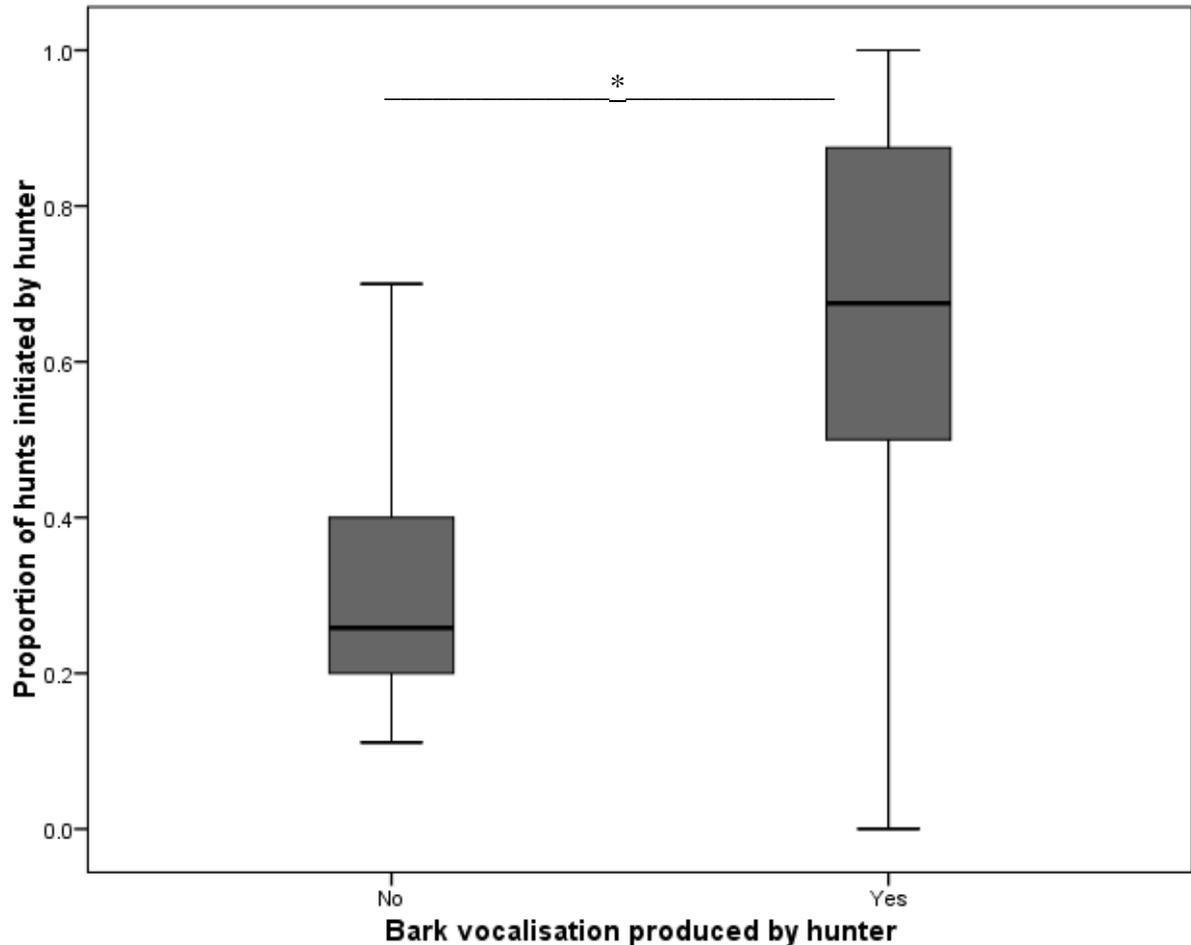


Figure 4.4. Shows the proportion of hunts during which a bark vocalisation was produced when an individual initiated or did not initiate a hunt (Wilcoxon signed-ranks test: $Z = -1.988$, $N_{\text{hunters}} = 10$, $p_{\text{exact}} = 0.049^*$).

4.3.3.2 Social influences on vocal production

To explore the effect individual identity and social relationships with other hunters on vocalisations produced, dominance ranks and affiliation measures (CIA) were calculated per hunt for each individual relative to the other individuals involved in the hunt. Only males with known affiliation and dominance relationships, and with more than ten different hunt observations, were used in the analyses ($N = 10$). Relative dominance ranks were calculated per hunt for each individual involved in the hunt relative to the other males' dominance ranks in that hunt (ranks less dominant than

average for the hunt were negative, more dominant than average were positive). The relative dominance rank for each male during a hunt was significantly lower when the individual barked (median = -0.186, IQR = 4.94) than when an individual did not bark (median = 0.251, IQR = 4.33; Wilcoxon signed-rank test: $Z = -2.293$, $N = 10$, $p = 0.020$) figure 4.5. There was no significant effect of an individual's mean CIA measure per hunt on bark production (Wilcoxon signed-rank test: $Z = -1.172$, $N = 10$, $p = 0.275$).

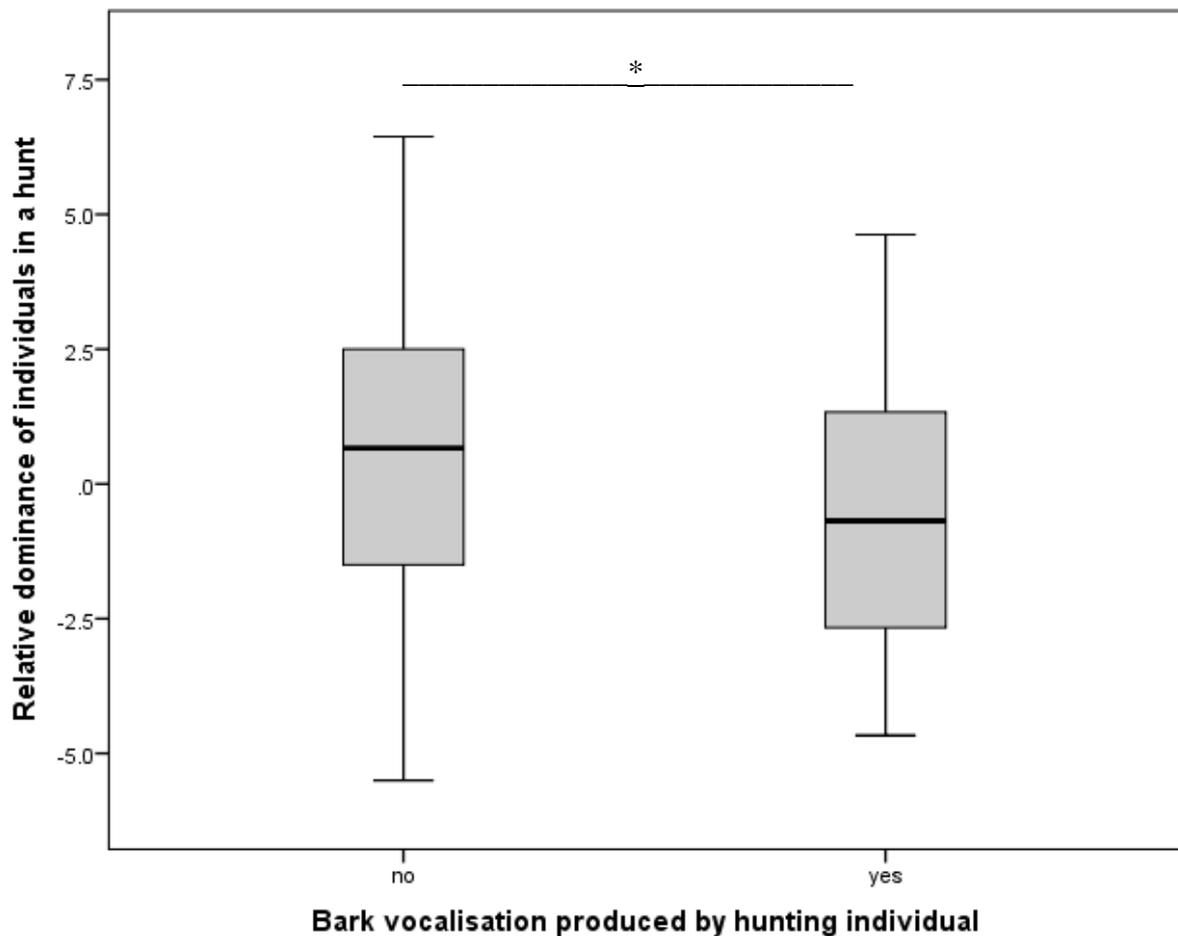


Figure 4.5. The relative dominance rank of an individual relative to other males in the hunting party (calculated for each hunting male) compared to the production of a bark vocalisation during the hunt. Relative dominance is significantly lower when individuals bark than when no bark is produced (Wilcoxon signed-rank test: $Z = -2.293$, $N = 10$, $p = 0.020$).

In order to look at whether barks have a possibility of being used to recruit out-of-sight individuals, the percentage of an individual's total affiliation which was attributable to fellow hunters compared to individuals not present (i.e. individuals that were not hunting, but were in the same travelling party before the hunt and could have heard a loud bark vocalisation which can reach out-of-sight individuals in the forest) was calculated for each individual during a hunt. The proportion of the CIA representing an individual's fellow hunters was significantly higher when the individual barked (median = 67.967, IQR = 24.92) than when an individual did not bark (median = 35.415, IQR = 48.09; Wilcoxon signed-rank test: $Z = -2.599$, $N = 10$, $p = 0.006$) figure 4.6.

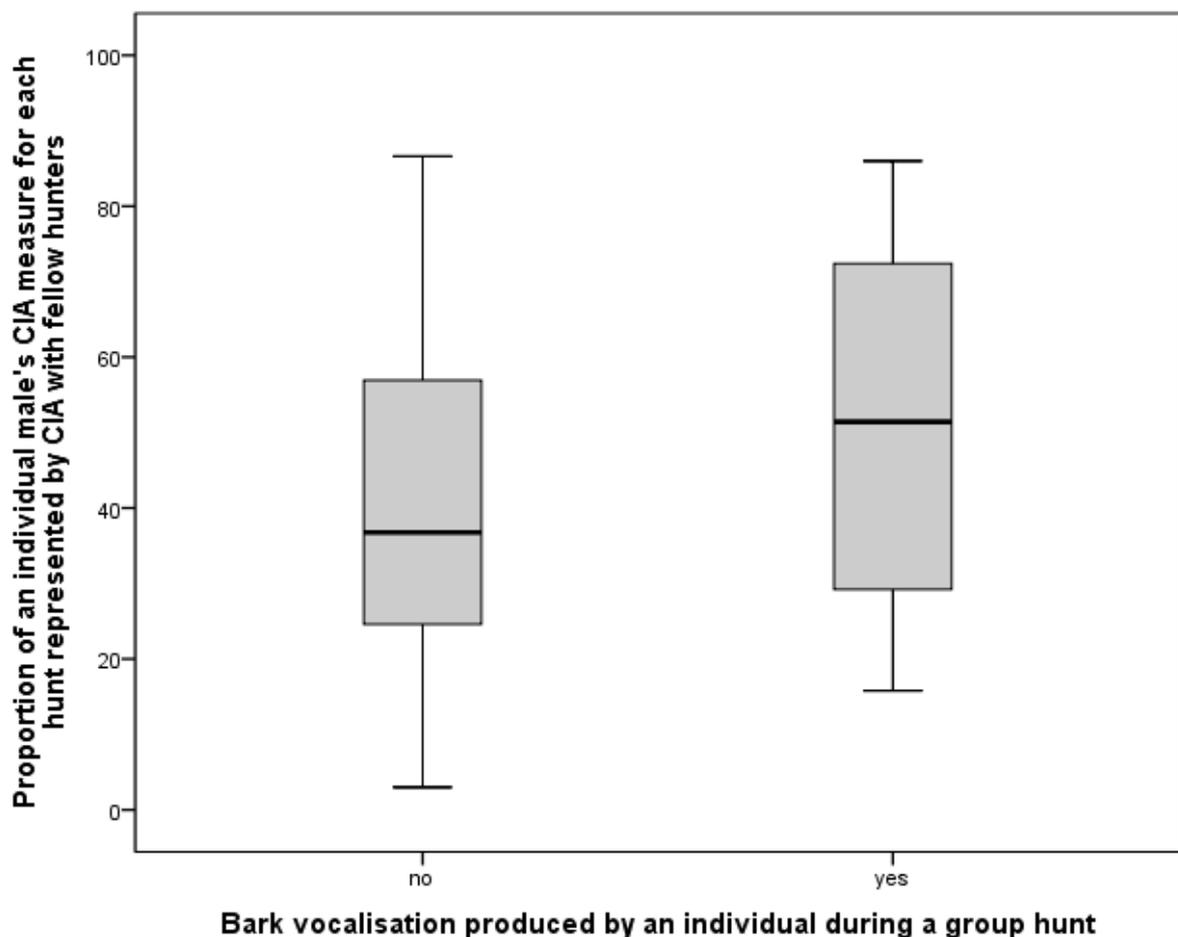


Figure 4.6. The mean percentage of affiliation (CIA) values represented by male affiliates within the hunting party rather than out-of-sight affiliative males (calculated for each hunting male) with the production of a bark vocalisation during each hunt. Boxes represent the inter-quartile range and whiskers represent 95% confidence intervals.

Looking again at what features of individuals might be contributing to the differences in bark production, dominance levels and affiliative relationships relative to other hunters are compared in a multinomial logistic regression test. Individual hunter identity ('hunter ID') was included as a fixed factor to remove variation due solely to individual identity and control for pseudoreplication. Their relative dominance rank, mean affiliation level with fellow hunters (CIA) and whether they initiated the hunt or not were then included as covariates in a main effects model. Hunt initiation showed the strongest effect on variation (Wald statistic = 5.84, $N = 140$, $p = 0.016$) with every increase by 1 in rate of initiation representing an increase of 0.31 times the probability of bark production. Relative affiliation also showed a significant effect (Wald statistic = 5.62, $N = 140$, $p = 0.018$), meaning that individuals were more likely to produce a bark vocalisation during the hunt if their affiliation level was higher with the other hunters present than when it was lower. Relative dominance had no significant effect. The difference in effect of relative dominance on bark production in this test compared to figure 4.5 can be attributed to the strong correlation between dominance rank and rate of initiation (Pearson correlation: $N = 10$, $Z = -0.776$, $p = 0.008$). Individuals that initiate hunts more are the lowest ranking, meaning that when the effect of initiation on bark production is removed in the logistic regression, there is no remaining effect due to dominance alone.

Bark production had no significant effect on whether an individual obtained meat after a successful hunt (median probability of meat reward after barking = 0.183, IQR = 0.35; after not barking = 0.380, IQR = 0.16; Wilcoxon signed-ranks test: $Z = -1.580$, $N = 10$, $p_{exact} = 0.131$).

4.4 Discussion

The results of data analyses on natural hunt observations are now discussed, starting with overall rates of group hunting compared to solo hunts, number of hunters and success rates. Potential biases in the long-term data collection will also be intimated. A discussion of individual differences in hunting strategies then follows, including the effects of dominance and affiliation levels with other hunters. Potential coordination of hunting behaviour will then be discussed, including the production of barks during hunt initiation, with a final discussion on how individual differences in dominance and affiliations levels may affect signalling behaviour during group hunts.

4.4.1 Overall analyses

Most hunts observed in Budongo were classified as group hunts involving two or more individuals. Group hunts were consistently more successful than solo hunts, but the number of hunters did not differ significantly between successful and unsuccessful hunts. This result contrasts to group hunting at the Tai chimpanzee field site which found an increase in success with more hunters (Boesch & Boesch, 1989).³³ However, comparison of overall hunting observations between personal and long-term data may indicate two biases in data collection from the long-term data collection, to under-report both solo hunts and unsuccessful hunts. These biases should be taken in consideration when interpreting results.

The percentage of recordings described as solo hunts was double from personal recordings (16% solo compared to 8% group hunts), a difference indicating under-reporting of solo hunts in the long-term data. Although it would be interesting to compare solo hunt rates of certain individuals with their group hunt involvement, a lack

³³ The results of (Boesch & Boesch, 1989) were calculated by assigning a minimum number of hunters requirement for the hunt to be included in analyses comparing hunting party size with success, which was not done in these analyses as larger hunting party sizes were not common in Budongo. Another difference making comparison difficult is that hunts in Tai also tended to involve the capture of multiple monkeys, which is rarer in Budongo.

of data and the described potential bias precludes such an aim. The success rate of group hunts was more than 50% higher in the long-term data than personal data (0.69 from combined data compared to 0.44 from personal data), suggesting a tendency in the project's long-term observation team to under-record unsuccessful hunts. Such a bias towards recording successful hunts would affect any analyses of correlations between success rate of group hunts and the number of hunters, individuals involved, and vocalisation data. Conclusions drawn that include success rate are therefore tentatively drawn and acknowledge the need for a more rigorous method of data collection for the long-term dataset.

4.4.2 Individual strategies in hunting behaviour

Individual differences in hunting strategies are important as they may effect coordination and communication during hunts. Individual hunters were shown to vary in how frequently they used different hunting strategies. Looking at individual features of hunters relative to other hunters revealed that relative dominance showed the strongest effect on variation. Individuals that were more dominant compared to other hunters present were more likely to be observers than chasers, and this was shown to be a general effect of dominance rank independent of other hunter identity. The reason for this is unclear. One explanation – that more dominant individuals do not need to be more actively involved in a hunt as they can steal meat after the hunt easily is not supported, as dominance has no subsequent effect on whether the individual obtained a piece of meat from the hunt.

Another explanation is that the age of males is strongly correlated with their dominance rank and mean relative dominance in a hunt, so the effect of dominance on an individual's chosen strategy could, in reality, be an effect of experience due to age (as suggested by Boesch (1994)). However, there is no separate measure for experience here,³⁴ so the question of experience would need re-assessed from Sonso chimpanzees

³⁴ Sonso males are mostly young, under 20 years so the field site lacks long-term data on their hunting experience and preferred hunting strategies.

in the future.³⁵ Comparing hunting strategies of individuals after a change in dominance hierarchy would allow this problem to be investigated further. However, the data presented at this stage indicate that older, more dominant individuals use strategies with a lower associated level of investment and risk.

The effect of relative affiliation on hunting strategy showed that individuals were more likely to take an active chasing strategy in the hunt if their affiliation level was higher with the other hunters present. This result presents the interesting idea that individuals prefer to take on the physically more active and risky hunting strategy with individuals they are more affiliative with, supporting the idea that group hunting has a social function, for example strengthening bonds, and is not simply about gaining the food reward (Gilby *et al.*, 2006; Muller & Mitani, 2005).

4.4.3 Vocalisations

The long-term data indicated that individuals were more likely to be silent during a group hunt than to vocalise. This is in contrast to personal data showing a non-significant trend for individuals to vocalise rather than be silent during group hunts. The difference may be due to inconsistent observation effort for vocalisations between different observers and suggests that long-term data should not be used to compare overall numbers of vocalising frequency during group hunts until stricter data collection protocols are in place for all observers. This does not preclude the (cautious) use of current data to make comparisons between individual behaviour and vocalisation types where they have been recorded. This is done with the assumption that there was no systematic bias in which call-types were recorded from certain individuals. The assumption is made based on the results from my data and the long-term data which both showed no direct effect of individual identity on vocalisation rates recorded.

³⁵ It is interesting to note for comparison with results from other field sites that there was no effect of age, dominance or hunting strategy on an individual's probability of obtaining meat after the hunt, and that meat was shared in all group hunts observed, even if some theft also occurred.

This section will now discuss how vocalisations may have been used to coordinate group hunts, including whether barks were used in the initiation of hunts or to recruit others to hunt, and finally social factors of individuals relative to other hunters that might have affected their use of signals in a joint activity.

(i) shared motivation and coordination of group hunts

If group hunts represent joint action with a shared motivation towards the prey, there was expected to be an interaction between the number of hunters involved in a hunt, and whether an individual produced a vocalisation. Hunting groups are slightly larger when an individual produces a bark vocalisation than when they do not vocalise. This result supports the work of Crockford and Boesch (2003) from the Tai chimpanzees which linked barks to group hunting behaviour, and further associates the call with higher arousal and a potentially shared motivation to hunt as a group.

The difference between the group sizes when bark vocalisations are produced cannot show whether an individual barks because there are already more individuals hunting, or whether barking is produced to encourage others to join the hunt (a recruiting signal). There were not enough data to draw any conclusions about whether a bark was produced before a hunt began and the subsequent hunting party size (barks were recorded only six times *before* the chimpanzees started moving towards the monkeys in the trees). It is suggested that playback experiments using barks recorded during group hunts should be used to try and elucidate whether barks can initiate hunting behaviour or act as a recruiting signal to other individuals. Possible effects seen from playback experiments might be either increasing the likelihood that receivers will move to join in hunting behaviour, or increasing the likelihood that receivers will join in producing bark vocalisations (which may in turn affect the hunting and vocalisation behaviour of other individuals).

As a means for investigating the possibility that barks could be used as a vocalisation directed towards specific individuals to recruit them to join the hunt, the percentage affiliation of those involved in the hunt compared to absent individuals was associated

with bark production. Recent field experiments show that other chimpanzee vocalisations- rough grunts and alarm hoos/barks- are produced more often in the presence of individuals with a high dyadic friendship index (Schel *et al.*, 2013a; Schel *et al.*, 2013b). The results presented here show that more barks were produced when affiliation was higher with fellow hunters compared to affiliation level with those that were not hunting. This suggests that the bark vocalisation was produced more often when affiliates were already within the hunting party, and was not directed at affiliated individuals who were not yet hunting as a recruiting signal. A problem with this conclusion is that the exact location of absent individuals was not always known, so it was not completely certain whether the hunting individuals could have known that absent individuals were near enough to hear a vocalisation or not.

Evidence that bark vocalisations are more likely to be produced by initiators than by non-initiators of a group hunt supports the theory that bark calls are produced by individuals who are highly motivated to hunt. This conclusion is supported by the multinomial logistic regression model which showed that initiating the hunt gave the strongest effect on the variation in hunting males' bark production, independent of individual identity, dominance and affiliation measures. The result also supports the idea that barks might be used to coordinate the initiation of a hunt. Playback studies where barks which were recorded during group hunting behaviour could help to show if barks produced before hunting behaviour elicit bark production in other individuals or instigate hunting behaviour in receivers. The acoustic analysis of Taï chimpanzee barks by Crockford and Boesch (2003) showed greatest variation in the duration of bark vocalisations- a factor associated with motivational state in the signaller more than potential referential specificity of a call (Marler *et al.*, 1992). With this in mind, it would be interesting to see whether more than one individual's bark must be heard before a group hunt is initiated, as suggested for the *quorum* threshold proposed to coordinate group travel in other primates (Pyritz *et al.*, 2011).

There may be some occasions in natural hunts observations where bark vocalisations would not be suitable to initiate a hunt, for example during hunting patrols (Boesch & Boesch, 1989), where individuals remain silent and utilise apparent 'stealth tactics'. In

these cases, communication signalling the initiation of a hunt, or commitment to a common goal prior to commencement of hunting behaviour, would be subtle and discreet; in fact, more like gestures, or soft hoo vocalisations. Playback experiments would be very unlikely in these situations if a requirement was for a hunting patrol to already be in progress. However, the use of high-definition video cameras during focal follows in the day-to-day observations of chimpanzee groups should make the likelihood of recording such behaviour more probable, and ultimately comparable between all the long-term study sites in the future.

A further comparison would be to record whether individuals only follow others into a hunt if they vocalise themselves, which would support the idea of the bark representing a jointly-held emotional state and commitment to the hunt, rather than a signal that directly influences behaviour and strategies during the hunt. The data from this study do not support the notion that barks are coordinating specific strategies during the hunt, as there was no association between bark production and chaser or observer strategies. If barks can be said to represent the motivation to hunt, this also suggests that motivation to hunt is not necessarily related to physical investment and the risk level involved in the individuals' hunting strategy.³⁶

(ii) social influences on vocalisations during group hunts

An interesting result emerging from the logistic regression is that the relative affiliation of an individual during a hunt with other hunters (independent of number of hunters) seems to account for a significant proportion of the variation in bark production. This shows that, independent of individual identity, dominance, and whether they initiate a hunt, an individual is more likely to bark when its dyadic relationships with fellow hunters is more affiliative. The result suggests that individuals may be modulating their production of barks depending on their affiliative relationship with fellow hunters, which is a conclusion in line with recent studies by Schel and colleagues (Schel *et al.*,

³⁶ If motivation to hunt is not related to the risk or investment in a hunt, this can provide a proximate explanation for the evolutionary problem proposed by some authors of why individuals engage in a risky behaviour if the reward is not always in proportion to their investment (Busse, 1978; Mitani & Watts, 2001). An evolutionary explanation has already been proposed by Tennie *et al.* (2009).

2013a; Schel *et al.*, 2013b) showing that alarm calls and food grunts are produced more for more affiliative receivers.

It is difficult to conclude from this data whether barks given during hunts might function to signal something specific about coordinating action to other hunters, but the increase in bark production seen when an individual is hunting with close affiliates supports the theory that the motivation to hunt is socially affected and associated with a flexibility in vocal production. Further playback experiments where barks recorded from hunting individuals are presented to specific receivers would help to elucidate how they affect the behavioural response of the receiver. According to the data presented in this study, differences should be found between responses if the playback vocalisation is from an affiliative individual compared to a non-affiliate. Responses expected to be affected include whether the receiver initiates hunting behaviour or not, whether they join in with the same vocalisation, and whether they engage in a specific hunting strategy.

In conclusion, evidence from natural hunt observations suggests that the bark vocalisation is associated with hunting behaviour, and is produced differentially depending on the number and affiliative relationship between hunters. These results indicate that the bark vocalisation is a candidate signal for coordination of a joint action, and appears to be involved in the initiation of hunting behaviour, although evidence is lacking for whether it has a role in coordinating specific actions of individuals during the hunt. A playback experiment is now presented in the next chapter which aims to simulate the initiation of a hunt to dyads of chimpanzees by playing Colobus monkey alarm calls when hunted, in order to investigate the communication between specific individuals during coordination of a potential joint response to the playback vocalisation.

Chapter 5. Initiation of joint action with a playback experiment

Abstract

Chimpanzees in captivity appear to lack the motivation to complete cooperative tasks. When they participate in joint actions, there is no evidence for communication used to coordinate actions towards a shared goal. Wild chimpanzees in Budongo engage in a joint activity- group hunting- for which it is unknown if they communicate to coordinate their actions. Evidence from naturalistic observations suggests the bark vocalisation is associated with group hunting, is more likely to be given by those initiating the hunt, and may be flexibly produced depending on affiliative relationships with other hunters. A novel field experiment is presented here which utilises the alarm calls of the chimpanzees' prey species - the Colobus monkey - to explore coordination of joint action between chimpanzees in response. Alarm calls produced by the monkeys when they were being hunted by chimpanzees and in response to an eagle stimulus were played back to dyads of affiliated males and their vocal/behaviour responses recorded. Results show that chimpanzees respond with different levels of attention to Colobus hunting alarms and Colobus eagle alarms, which indicated that they can discriminate between the two call types. Furthermore, half of the trials with the Colobus hunting alarm elicited a vocal response of bark vocalisations from both of the males in the experiment, prior to initiating joint movement in the direction of the playback. Such joint responses were not observed for other predator alarms. Additional trials are needed to confirm the difference in joint action response to Colobus eagle and hunt alarms, but results indicate that bark vocalisations are associated with the initiation of joint hunting activity, but not subsequent movements towards the goal. Barks are therefore considered as representative of the shared motivation of participants to join a hunt, and further experiments are suggested to see whether other signals are used to coordinate joint actions and strategies during actual hunting activity.

5.1 Introduction

A novel field experiment is now introduced that aims to investigate communication between wild chimpanzees in the context of coordinated behaviour. This was considered an important area for research with wild populations as current theory derived from laboratory experiments suggests that chimpanzees perform poorly at coordinated tasks (compared to humans and other *Pan* species)- possibly because they lack the motivation to cooperate- and that they fail to communicate when they do manage to coordinate their actions (Hare *et al.*, 2007; Hare & Tomasello, 2004; Melis *et al.*, 2006b). The very fact that chimpanzees in captivity appear to lack the motivation to complete the cooperative tasks assigned them hints that questions of cooperation would better be researched with chimpanzees in their natural environment where they can respond with their full range of natural behaviour, as discussed in chapter 1.

The experiment presented here takes advantage of a natural context where chimpanzees might cooperate in Budongo: group hunting of Colobus monkeys (*Colobus guereza*). The previous chapter found that bark vocalisations were associated with group hunting more than other vocalisations. They were more likely to be given by those initiating the hunt (who were also the least dominant), and may have been produced flexibly depending on affiliative relationships with other hunters. These results suggest that the bark vocalisation may have some role in the coordination of group hunts by affecting the initiation of hunts. Barks did not seem to be associated with specific hunting strategies of chasing monkeys in the trees or observing from the ground. Neither did they seem to be associated with the potential recruitment of out-of-sight affiliated individuals who were not already hunting, although this finding needs further research. Playback experiments were suggested to assess the role of bark vocalisations in the initiation of joint action and coordination of movement in the context of group hunting, and this is what the current chapter aims to achieve.

5.1.1 Playback experiments in the field

Playback experiments offer the advantage of allowing systematic investigation into subjects' responses to different stimuli. Compared to natural observations of chimpanzee responses to Colobus alarms, playback experiments allow the observer to be 'in the right place at the right time' for filming specific individuals on presentation of a specific stimulus (Cheney & Seyfarth, 1980). Furthermore, social responses to another individual can be measured by introducing control measures, such as only presenting the stimuli to a subject when a specified individual is also present within a certain distance and when no others are nearby (Hopp & Morton, 1998, p. 334). The more control measures included, the more exact your interpretation of resulting behaviour can be. However, increasing the number of criteria for the experiment to be carried out concomitantly decreases the chances of encountering such conditions in the natural setting. This means that well-designed field experiments with controls are difficult to carry out and it can take a long time to collect sufficient data for analysis.

Carrying out playback experiments with captive populations of chimpanzees would alleviate this 'time constraint' unique to field studies, but would also remove all advantages of observing animals in their natural environment. The playback experiments which are now presented simulate chimpanzee hunts of Colobus monkeys and would not be possible with captive chimpanzees or those in sanctuary environments. This is because observing a reliable and appropriate response from the chimpanzees requires that the experimental set-up and vocalisation being broadcast could *naturally* be occurring in that situation. Chimpanzees only hunt monkeys in groups when in the wild. This playback experiment was therefore carried out with wild chimpanzees in the Budongo forest, where the rate of group hunting has increased in recent year (as discussed in chapter 4).³⁷

³⁷ The study is also being continued as a collaborative project with P. Fedurek in order to increase sample size.

5.1.2 *Colobus monkey alarms*

Colobus monkeys in the Budongo Forest produce different alarm calls depending on whether the perceived threat is a ground or aerial predator (Schel, Tranquilli, & Zuberbühler, 2009). Two distinct alarm responses have been recorded from the Colobus monkeys in Budongo when they were presented with an eagle call stimulus and a leopard call stimulus. When the alarms were subsequently played back to other Colobus groups, they resulted in different behaviour and vocal responses from conspecifics (Schel, Candiotti, & Zuberbühler, 2010). A third alarm call that, although given less often than other alarms, is distinct from the ground and aerial predator alarms is given by adult male Colobus when they are hunted by chimpanzees (*pers. comm.* A.M Schel).

Colobus monkeys normally remain silent and inconspicuous in the presence of chimpanzees and humans (Schel *et al.*, 2009), but alarm calls are produced by males when they are actively hunted by a group of chimpanzees. Indeed, this is often the means by which the chimpanzee long-term observers in Budongo can identify the location of a hunt. The Colobus alarm call is thought to have an anti-predator function (Schel *et al.*, 2010), and this may explain why the alarm is given during hunts by Chimpanzees but rarely to the mere presence of chimpanzees, when monkeys generally stay silent and unobtrusive (Marler, 1972).

The Colobus predator alarm calls are called roars, which are loud and low-pitched vocalisations, also produced as part of ‘dawn choruses’ (Schel *et al.*, 2009; Schel & Zuberbühler, 2012). The roars consist of a series of roaring phrases, which have the same acoustic structures between predator types (although these phrases differ acoustically from those in morning choruses) (Schel & Zuberbühler, 2012). Although individual phrases are identical in predator alarms, the *sequence* of roaring phrases was shown to differ between two predators, with responses to leopard calls containing fewer phrases and sometimes being preceded by a ‘snort’, and responses to eagle calls containing more roaring phrases (Schel *et al.*, 2009). The alarm roars produced by Colobus monkeys when they are being hunted are similar to those given in response to a leopard call, but differ acoustically in frequency (calls given during hunts are higher

pitched) and duration (calls are shorter during hunts) (*pers. comm.* A.M. Schel, from nine samples).

It is currently unknown whether chimpanzees can distinguish between the alarm roars of the Colobus monkeys produced in response to different predator stimuli, and whether they recognise the alarm given in response to being hunted by chimpanzees. Other primate species and birds have been shown to recognise and respond appropriately to the alarm calls of other species (Hauser & Wrangham, 1990; Rainey, Zuberbühler, & Slater, 2004; Zuberbühler, 2000). It seems likely that this ability would extend into the great ape species as well (Zuberbühler, 2001). If recognised, the alarm roar given by Colobus in response to eagles should hold little or no interest for the chimpanzee males, provided they are resting or feeding and not already engaged in a ‘hunting patrol’ or looking for potential prey (Boesch, 1994), because aerial predators are not a threat to the larger-sized apes (Goodall, 1986).

Colobus alarms given to leopards should also attract little attention from the chimpanzees as leopards have not been seen in the Budongo Forest Reserve for decades, and certainly not in the lifetime of the current adult male cohort of the Sonso community (Reynolds, 2005). However, leopards remain a serious threat to wild chimpanzees in other field sites, for example Taï (Boesch, 1991a), and encounters can elicit vocal alarm responses and other anti-predator or social behaviour (see summary: Klailova *et al.*, 2013). The Colobus monkeys in Budongo have also not encountered leopards for many years, but still respond appropriately to a ground predator alarm as though there were a threat (Schel *et al.*, 2010). It is therefore possible that chimpanzees might show increased vigilance to a potential ground predator upon hearing the Colobus leopard alarm roar compared to the eagle alarm, and seek social reassurance (Goodall, 1986).

5.1.3 Playback experiments

By carrying out playback experiments using Colobus monkey alarms as stimuli, two main lines of questioning will be followed: (1) do chimpanzees recognise the different Colobus alarm roars; and (2) if chimpanzees recognize whether the Colobus hunt alarm

indicates a hunted individual that is alarm-calling, (a) will the chimpanzees react with joint action in the direction of the playback or not; and (b) will they use communication to coordinate a joint response?

In order to answer these questions, dyads of affiliative male chimpanzees were presented with three alarm vocalisations recorded from Colobus monkeys: eagle alarms, leopard alarm and hunt alarms (produced during a chimpanzee hunt). The playback protocol simulates a Colobus monkey alarm calling once for a period of about 5 seconds. The hunt alarm may additionally simulate a hunt already in progress, which the focal individuals can then decide to move towards, monitor, or ignore and continue with their original activity. This action could be coordinated with their partner in the dyad- requiring attention towards, communication with, and monitoring of their partner- or could be enacted independently. How the two individuals direct their attention, change their general behaviour and communicate with each other during the response time after playback is therefore the focus of the experiment.

5.1.4 Predictions

It is predicted that chimpanzees will recognise the different alarm-calls of Colobus monkeys and react with different levels of interest, as indicated by number and duration of looks at the different alarm calls. This prediction is based on similar abilities of inter-species alarm recognition displayed in monkey and bird species (Rainey *et al.*, 2004; Seyfarth & Cheney, 1990; Zuberbühler, 2000). Number and total duration of looks during a response time are measured separately as they may be recording slightly different aspects of attention. Duration of looks may be considered to represent actual monitoring of an object, whereas number of looks is also associated with the frequency of looking at other objects in the same response time.

The chimpanzees' reaction to hearing a Colobus alarm from a hunt is the most poignant aspect of this experiment for looking at socially motivated communication and coordination. Chimpanzee dyads are expected to pay more attention to the vocal response of Colobus monkeys to hunting than to eagles because the hunted alarm

indicates a hunt that is already in progress. This is an occasion of interest to the chimpanzee either if they want to join in, or are simply interested in the outcome of the supposed hunt. If the individuals are interested in a hunt, hearing the playback may result in a change of general behaviour from resting or feeding to travelling in the direction of the playback (depending on their motivation to engage in hunting activity or obtain meat at that time). They are also expected to pay more attention to each other, particularly monitoring the other's behaviour more and potentially vocalising to coordinate the timing of their response. This social aspect could be influenced by the relative dominance positions of the dyad, as those lower down in the hierarchy might be more likely to monitor and follow the behaviour of the more dominant individuals (Altmann, 1967; Chance, 1967).

Vocalisation production is a key variable that is analysed in order to assess coordination of joint responses in the dyad to the Colobus hunt alarm. It is predicted that individuals will vocalise more, especially using the bark vocalisation (Crockford & Boesch, 2003), in response to the Colobus hunt alarm than the Colobus eagle alarm.

Some aspects of looking behaviour associated with producing vocal signals may also help to infer whether calls are given to a specific individual with the intent of altering their behaviour. Table 5.1, taken from Schel et al. (2013b), summarises criteria used to assess intentionality of signals from work with great ape gestures. This thesis will assess criteria used to infer intentionality from the experimental data where possible. However, it does not seek to give a definitive answer about intentionality in terms of mental states (as discussed in chapter 1), as the thesis aims to remain neutral on the subject of animals' 'thoughts' or 'beliefs'.³⁸ The analyses instead provide evidence comparative with other recent studies on flexible signal production in chimpanzees (Hobaiter & Byrne, 2011; Schel *et al.*, 2013b). The reader can then, if they choose, make their own inferences about intentionality in signal production from the evidence presented.

³⁸ Especially as the data presented include only two experiments with dyads of chimpanzees where coordination of joint action and communication associated with this action were observed in response to the playback.

Table 5.1. The range of criteria used in great ape gesture studies used to infer intentionality of communication, from Schel et al. (2013b).

Criteria	Explanation
Social use	The signal is directed at a recipient. This can be assessed at various levels: 1. Presence/absence audience effect: the signal is only produced in the presence of a recipient. 2. Composition of audience: the signal is only produced in the presence of certain recipients (e.g., kin, dominants, friends) 3. Behaviour of audience: signal production is contingent on the behaviour of the recipient
Sensitivity to attentional state of recipient*	Visual signals are only produced in the field of view of recipients. If signaller does not have a recipient's visual attention, tactile or auditory signals should be produced. This can also be considered a level (3) audience effect.
Manipulation of attentional state of recipient*	Before a visual signal is produced, attention-getting behaviours are directed towards a recipient who is not visually attending to the signaller.
Audience checking and gaze alternation	Signaller monitors the audience and visually orients towards the recipient before producing a signal. If a third entity is involved, gaze alternation may occur between recipients and this entity.
Persistence or elaboration	Goal-directed signalling shown by repetition of the same signal (persistence), or production of different signals (elaboration) until the desired goal is met.

*indicates applicable only to visual signals and therefore not relevant for vocal production.
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‘Audience checking and gaze alternation’ and ‘persistence’ are relevant criteria for this study. As per Schel et al. (2013b) and Hobaiter and Byrne (2011), we can assess audience checking by coding the looking behaviour of the focal in the five seconds before a new vocalisation. If they look towards their partner, in the direction of the playback, or the direction of other out-of-sight individuals (applicable for loud vocalisations which can be heard over larger distances), this indicates an awareness of this potential recipient prior to calling. Gaze alternation was also assessed, as per Schel et al. (2013b) from Leavens and Hopkins (1998), by coding a change in gaze from their partner to the playback, or vice versa. If this occurred in the 3 seconds either side of call production, it could indicate that the individual may have been calling about an external object (the playback) and was checking the behaviour and attentional state of the receiver (Leavens & Hopkins, 1998).

The playback experiment carried out for this study with wild chimpanzees is now presented, where the vocalisations and behavioural responses of an affiliative pair of chimpanzees was filmed after the playback of Colobus alarm calls for different predators. In a repeated-measures paradigm, the different predator alarms were played to the same dyads. The video data were coded and analysed (1) for differences in attention to different Colobus alarm types, to see if chimpanzees recognise different monkey alarms, and (2) for variation in the direction of attention, vocal responses, social

interactions and overall behavioural changes in the chimpanzee dyads in response to the Colobus hunt alarm stimuli compared to control alarm stimuli. The second set of analyses were designed to try and elucidate whether chimpanzees responded with joint action to Colobus hunt alarms, whether this joint action was associated with any communication, and whether this communication could be said to coordinate the action, either through a shared motivation or inferred intentionality.

5.2 Methods

5.2.1 Stimuli

Playback stimuli were created using Adobe Audition 3.0 (Adobe Systems Incorporated) by A. M. Schel from recordings of Colobus monkeys taken during a previous experiment in the Budongo Forest Reserve (Schel *et al.*, 2009) and alarms given to chimpanzee hunts collected by A.M. Schel or C. Crockford with a Sennheiser ME66 microphone and Marantz PMD-670 digital recorder. In order to make the stimuli as natural and true to the different contexts of production as possible, alarm roars were only used as stimuli that were recorded as a response to the original predators, i.e. in response to leopard calls, eagle calls, and to chimpanzees during a hunt. The stimuli were edited using Raven Pro 1.2 (Bioacoustics, 2004) to equalise the amplitude, to remove confounding or unusual noises (such as those from human observers or other animals), and also to fade-in and fade-out of the vocalisation, thus avoiding abrupt changes in background noise. Sounds were saved and played as uncompressed .WAV files.

Colobus alarms given in response to chimpanzees are relatively rare in the Budongo Forest (Schel & Zuberbuhler, 2009). In addition, most recordings consisted of vocalisations produced by multiple callers and confounding calls from the hunting chimpanzees and their movements. As a result, it was only possible to create three different playback stimuli from all recordings of Colobus roars given to hunting chimpanzees. These three recordings sounded natural and were of comparable length to the leopard and eagle alarms (mean playback duration 5.23s s.d.±1.21s). The decision was made to use this smaller number of high-quality stimuli repeatedly than to use a larger number of sub-standard recordings for each experiment, as per Schel *et al.* (2010). The three different stimulus types (relating to each predator group) were assigned randomly to test the experimental dyads. Examples of each alarm type are given below (Figure 5.1).

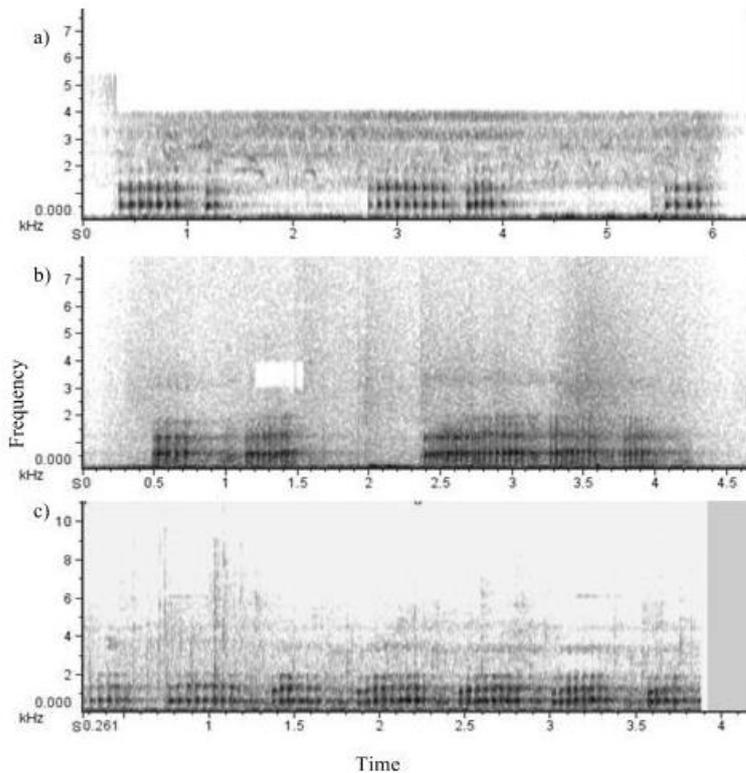


Figure 5.1. Samples of playback stimuli used by CM in experiments to determine responses of chimpanzee dyads to Colobus alarms, represented as spectrograms for: a) alarm roar sequence given in response to a leopard vocalisation; b) alarm roar sequence given during a chimpanzee hunt; c) alarm roar sequence given in response to an eagle vocalisation. Samples provided by A.M. Schel and were recorded in the Budongo Forest Reserve, Uganda.

All playback stimuli were sound-tested in the field to ensure they were of appropriate amplitude, sounded natural, and to assess the maximum range they could be heard by other individuals. The nine stimuli were all broadcast with a Nagra dsm speaker/amplifier from distances of between 25-45m in an area at the edge of the chimpanzees' range when no individuals were nearby, both along an open pathway and through denser forest to assess the exact distance and volume each vocalisation would be played at to make sure they sounded the same. The speaker was carried in a backpack similar to those worn daily by field assistants, with a hole cut over the amplifier so the stimulus could be played from 1.5m height on a person's back and then be easily walked away from the site without drawing attention to the equipment (Schel *et al.*, 2013a;

Slocombe, Townsend, & Zuberbühler, 2009). The sound files were labelled with the correct speaker settings so that they showed on the display screen of the 2BG Apple iPod Nano (Apple Incorporated), and the iPod itself kept at maximum volume. The maximum distance any of the calls could be heard from was 170m, although calls were quiet and indistinct at 100m.

5.2.2 Playback procedure

Playback experiments were carried out by a team of four observers. Four trials were carried out from 22/10/2011-18/11/2011, and another eight trials were carried out from 07/07/2012-20/09/2012. BCFS has strict guidelines for carrying out playback experiments with the Sonso community, so playbacks could only be conducted during these periods when no other experiments were being carried out. This led to an average of three experiments conducted per month during a three and a half month period. This is also representative of the natural encounter rate of experimental conditions, as on only one occasion was the experiment not conducted when the right conditions were encountered (due to a problem with the video recording equipment).

A further experiment was conducted on 29/09/2013 with P. Fedurek (PW) as the team leader and main observer, and attempts to conduct further trials are on-going. All members of the team carried remote radios (Motorola GP340) to maintain contact. Two of the team (CM and JK) carried video cameras (Panasonic SD90) fitted with in-line microphones (Sennheiser MKE400) to focal and record the two subject individuals; one (SM) carried the playback speaker attached via the microphone input to the iPod containing the playback stimuli; one (JC/BK) served as a scout and circled the area patrolling for signs of other chimpanzees or Colobus monkeys.

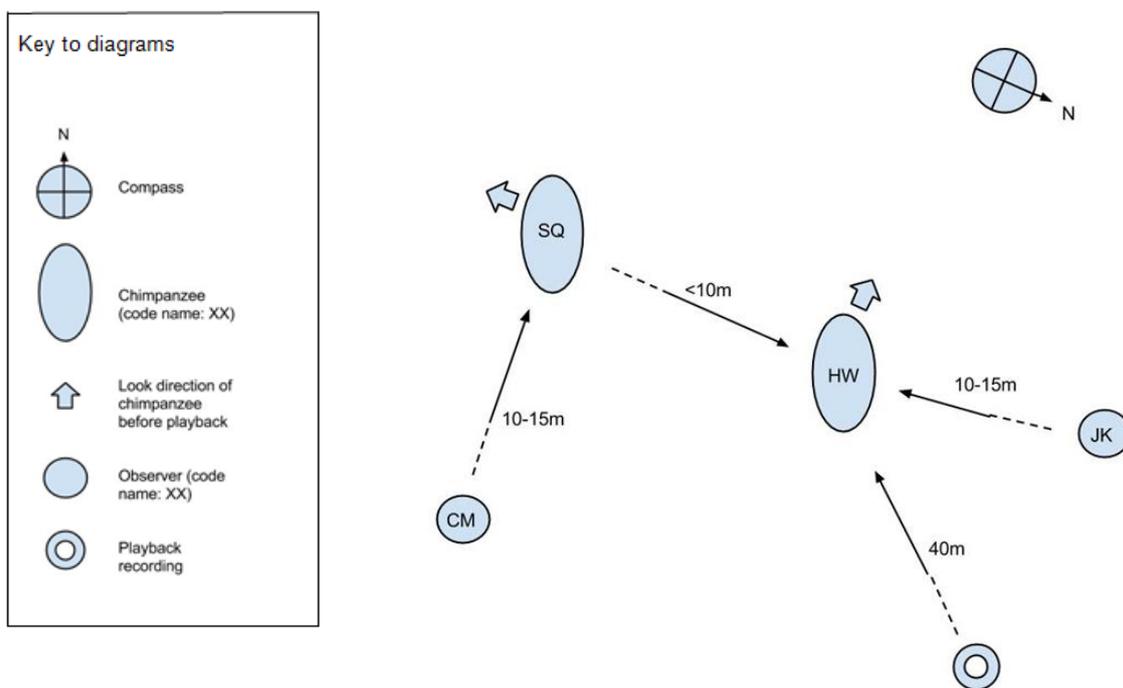
In order to set up the experiment, each observer spread out in the forest looking for specific test subject dyads³⁹ to move away from other chimpanzees, keeping the team

³⁹ Dyads were determined using the CIA measure of affiliation presented in chapter 2 (table 2.2).

leader (CM) informed of all sightings and locations which were recorded to gain a picture of the community's movements as a whole. Target dyads were decided at the start of the day by prioritising males with the greatest time since the last experiment they encountered, and each dyad had a randomly assigned order of presentation of the three playback alarm types. When a dyad was found alone, the team all agreed on suitability of location, the whereabouts of other chimpanzees and of other Colobus groups before an experiment was initiated. The two test subjects had to be within 10m of each other and no more than 3m above the ground if in trees, be able to see each other but be out of sight of all other chimpanzees, and be either feeding or resting (see figure 5.2).

There was a minimum time period of 10 days between playbacks of the Colobus hunt alarm calls (naturally occurring hunting rate from my data was 10 hunts in 99 days of observation of the main community party, September 2010 - August 2011). Steps were taken to limit the number of non-subject chimpanzees within 170m of the playback by having a fourth observer patrol the area to minimise risk of over-exposure. Extra care was taken to ensure that any individual which had already heard the playback stimulus was more than 170m away (the maximum distance playbacks would be heard from), and if this was unclear then the experiment was not carried out. Field assistants also walked a 50m radius around the playback site to ensure that no actual Colobus monkeys were close to the site and could be distressed, as well as to try to prevent initiation of an actual hunt which would otherwise have been unlikely to occur. However, when possible, the Colobus alarm was played back from the general direction where monkeys had been heard previously, to try and make the experimental situation more realistic for the chimpanzees. Observers also made sure that the speaker was not placed in a direction from which it would be impossible for other members of the chimpanzee group to be, for example if the experimental dyad had just left all other males in the group in a specific tree only 20 minutes previously. No unusual behaviour was observed from chimpanzees or monkeys after any of the playback experiments, and no real Colobus hunts were initiated.

To carry out the experiment, SM carried the speaker 35-40m from the test pair, preferably in the general direction of known Colobus monkey groups⁴⁰. SM whistled and main observers CM and JK whistled back to confirm distance. The scout (JC/BK) then circled around the site and checked nearby fruiting trees to confirm absence of other individuals while the playback stimulus was prepared by SM and CM confirmed with other field assistants in the forest the location of other chimpanzee parties using walkie-talkies. Observers found a vantage point from which they could see the focal animal's face and where they were at right-angles to the playback and partner's position (for example see figure 5.2; all experiment set-ups are displayed in appendix 3).⁴¹ The main observers (JK and CM) then each began filming an individual of the pair, making commentary on the video. Commentary included: the direction the test subject was facing; the direction and distance to the observers, to the playback speaker and to each other; direction and distance of any Colobus monkey vocalisations; test subject's general behaviour, looks (direction and what was in that direction), vocalisations, self-directed behaviour, social interactions, and movements.



⁴⁰ This helps to make the playback set-up more realistic for the chimpanzees.

⁴¹ This was to make coding of looks from video data more reliable.

Figure 5.2. Example of playback experimental set-up with chimpanzee focals SQ and HW. Observers CM and JK video and sound recorded a focal male each, the third experimenter (SM) carried the playback speaker, and the scout (BK/JC) circled around the entire area to search for other chimpanzees and monkeys within a 100m radius.

When the experimental pair had been filmed resting or feeding in the same place for five minutes, CM radio called SM to play the stimulus from the speaker and CM and JK continued filming for 10 minutes after playback. After playback, SM turned off the speaker and slowly circled around to re-join the main observers. After 10 minutes, the subject chimpanzees and the rest of the group continued to be monitored by experienced observers (5-8 years as field assistants) for the remainder of the day (up to 16:30), looking for changes in their general behaviour and social interactions.

5.2.3 Observer training

All observers taking part in the study spent two days training in the experiment procedure and practising video commentary after playback. The protocol was practised at the edge of the forest where no chimpanzees were around, and repeated until no errors were made and everyone was familiar with the set-up. The scout was timed walking the perimeter in different areas of the forest to give an idea of how much time this would take in different vegetation. In areas of dense undergrowth, the Sonso grid system (paths crossing north to south and east to west every 100m) was used and GPS tracks were checked to ensure the minimum radius was observed when circling around the experiment.

In order to ensure that commentary on the looking behaviour of the focal chimpanzees after playback was accurate, all observers (observer 1 in figure 5.2: CM JK and PW) underwent the following training with the experimenter and an assistant (observer 2). 20 objects (tree trunks and branches) were chosen in the forest under differing visibility conditions and distances (from 2-20m at all angles around observer 2). Observer 2, was asked (by the experimenter, who was using a compass) to look at a randomised range of

angles between 0° and 90° away from each specified object (with head direction in-line with eye-direction). Observer 1, who was being trained in commentary on looking behaviour, was asked each time to judge whether the observer 2 was looking at the specified object or not. Looking at the object was defined as looking less than 30° either side of the object (see figure 5.3). Assessment of attention using head direction is similar to Genty et al. (2009), although the training used here allowed a slightly narrower visual field (30° as opposed to 45°) to be used. Percentage accuracy was then determined. The observer was only considered to have completed the training when this percentage accuracy was greater than 80%. Main observers who commented on the videos (CM and JK) completed this training with 85 and 95% accuracy respectively.

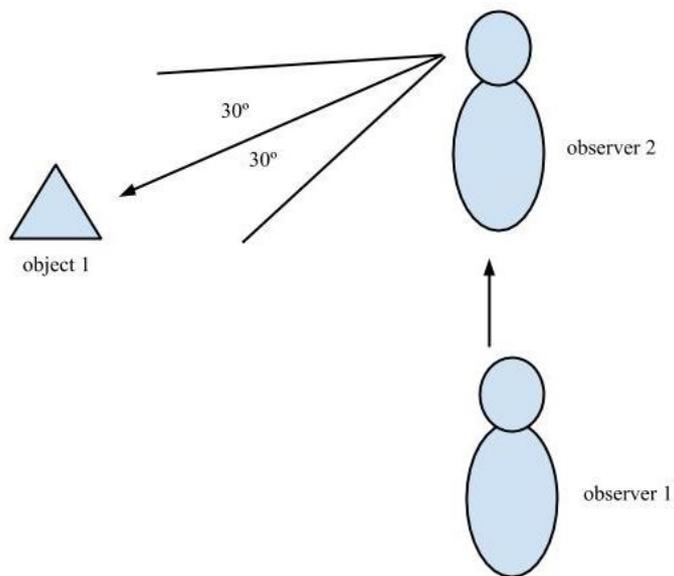


Figure 5.3. Observer training in assessing look direction from head direction: observer 2 is told by the experimenter what angle to look at away from object 1. Observer 1 then judges whether observer 2 is looking at the specified object or not ($\pm 30^\circ$). The experimenter repeats this process, telling observer 2 what angle to look at away from a second object, until 20 objects are assessed by observer 1.

5.2.4 Video coding and analyses

Video recording were downloaded using an Apple MacBook Pro using the iMovie (version 9.0, Apple Incorporated) into .mov format (48kHz, 16-bit Stereo uncompressed). Clips were then analysed by CM on Adobe Premiere Pro CS4, version 4.2.1 (Adobe Systems Incorporated) starting from the onset of playback and recording looks, vocalisations and behaviour frame by frame on an excel spreadsheet (Microsoft Excel 2010), moving forward at a frame rate of 25 frames/s (Hauser, 1998). Where a direct view of the subject was obscured in the video footage (due to fast movements and foliage obstruction), vocal commentary was used to score behaviour, although these instances were marked in the analyses and were added to analyses separately.

Coding notes included the time when video commentary was in synchrony with the other observer recording the partner chimpanzee, the time code when the playback started, and the direction the focal individual is facing. Initially videos were coded for: the observer; the test subject ID, their partner ID, and the distance between them; the direction the test subject was facing; the direction of the playback speaker; the direction of the partner test subject; and the direction of the human observers (as shown in figure 5.2). The video coder then examined the first 30s time period after playback began and recorded as events any changes in: general behaviour (resting, feeding, travelling, social behaviour); looks (direction, what was in that direction, and start/end time); vocalisations (type and start/end time); and social interactions (grooming, touching, play, aggression/submission displays- see appendix 2.3). This process was repeated for the 30s time period prior to playback, which provided a baseline of looking behaviour against which the behaviour after playback could be compared. Total number of looks and total duration of looks at the playback, partner, human observers and out-of-sight individuals relative to the pre-playback baseline was then calculated (minus the equivalent values from the baseline period) to include in the analyses. Notes also included the direction and distance of any Colobus monkey vocalisations, and movements of any other chimpanzees which may have joined the party (see appendix 2.3).

Look direction was determined from head direction when the focal animal's face and eyes were not clearly visible in the video recording for several reasons: because head direction is thought to coincide with gaze direction in apes; it is useful when eye-tracking equipment is not appropriate; and it has been shown to be the most salient indicator of attention for chimpanzees in laboratory experiments (Genty *et al.*, 2009; Povinelli, Eddy, Hobson, & Tomasello, 1996; Schel *et al.*, 2013b; Tomasello, Hare, Lehmann, & Call, 2007).

Four males were out-of-sight of the observer for different sections of the response time during Colobus hunt alarm trials (due to their travelling response), so only the exact times they were visible were used across their trials so that equal time periods were compared per individual and all three stimulus alarm types had the same total response time analysed. A new 'look' event was defined as occurring only when the subject was visible again, and if the individual looked in a different direction compared to the last visible recording.

The coding data were further analysed to show whether individuals looked at their partner in the five seconds prior to vocalisation or not, and whether or not a vocalisation was produced in the three second period either side of a gaze alternation from the partner or other individuals to the playback (or vice versa) (Schel *et al.*, 2013b).

5.3 Results

After presenting the results of the reliability test for coding the experiments, the results from comparison of chimpanzee attention differences between different Colobus alarm stimuli are analysed. The Colobus hunt alarm trials are then analysed in detail, comparing behaviour and vocal responses of dyads with matched samples from the Colobus eagle alarm trials (which serve as a control). Finally, the looking and vocal behaviour of dyads are explored in more detail when there is a joint response of the experimental pair in the direction of the Colobus hunt alarm.

5.3.1 Reliability of coding

A quarter of the trails (6/20 individual videos of experiments) were chosen using the random number function in Excel (Microsoft Inc.) to be re-analysed by a secondary coder. The secondary coder (KM) was naïve to the experimental aims and predicted outcomes, was blind to the trial number or stimulus type used, and was unfamiliar with the social relationships between chimpanzees involved in the experiments. A Pearson correlation test showed strong agreement between the two coders' assessment of number of looks from the focal towards the playback, their partner, the observer and towards other individuals: $N = 24$, $r = 0.89$, $p = 0.000$, $\alpha = 0.01$. A Pearson test between the duration of looks recorded by the two coders also showed a significant correlation between the coders' results ($N = 24$, $r = 0.86$, $p = 0.000$, $\alpha = 0.01$).

5.3.2 Attention responses to different Colobus alarm calls

Four male chimpanzee dyads were all tested with Colobus eagle and hunt alarms, yielding a total of 16 individual responses. Two of the four dyads were also tested with the Colobus leopard alarm stimulus, giving an additional four individual responses (see table 5.2).

Table 5.2. List of playback experiments carried out, showing: the date and time of the playback; main observer's initials; stimulus used; male dyad identities; the distance between them; and the dyad's travel and vocal response.

Date	Time	Observer	Playback	ID 1	ID 2	Distance (m) between dyad	Joint travel response	Joint bark response
26/10/2011	12:00	CM	hunt 1	ZL	ZD	9	no	no
31/10/2011	10:45	CM	hunt 2	SQ	HW	7	no	no
1/11/2011	10:30	CM	hunt 3	FD	FK	10	yes	yes
11/7/2012	8:30	CM	leopard 1	NK	MS	10	no	no
21/7/2012	15:30	CM	eagle 3	ZD	ZL	10	no	no
1/8/2012	13:00	CM	hunt 2	NK	MS	4	yes	yes
14/8/2012	11:30	CM	eagle 1	FD	FK	1	no	no
26/8/2012	11:40	CM	leopard 3	ZL	ZD	5	no	no
1/9/2012	7:40	CM	eagle 3	MS	NK	10	no	no
29/8/2013	13:44	PW	eagle 1	HW	SQ	1	no	no

In order to investigate the whether chimpanzee recognise different Colobus alarms, the vocal and looking responses of chimpanzees were only compared between Colobus eagle alarm and Colobus hunt alarm trials, as only two trials with Colobus leopard alarms were carried out. First, the looking responses of the eight individuals were compared across the trials for the first 30 seconds after playback. Looking responses were analysed for each individual rather than combining responses for dyads. This was done because it does not make sense to average the results of trials across the dyads - each male within the dyad had different looking responses to the playback - even though individual responses in the same experiment were not strictly independent samples.

The number of looks towards the playback was higher in response to Colobus hunt alarms than to Colobus eagle alarms (see figure 5.4). A Wilcoxon signed-ranks test was used to compare the matched samples of looks for each individual between trials and revealed a significant difference between look responses towards the playback for Colobus hunt and Colobus eagle alarms (hunt median = 3.00, IQR = 1.00; eagle median = 1.00, IQR = 1.00; $Z = -2.598$, $N_{\text{males}} = 8$, $p_{\text{exact}} = 0.008$). Whilst using the exact probability can help minimise the chance of getting false positives, it is also noted that the individuals in each dyad are not independent of each other, and so a larger sample size from further experiments is needed to confirm significance of results.

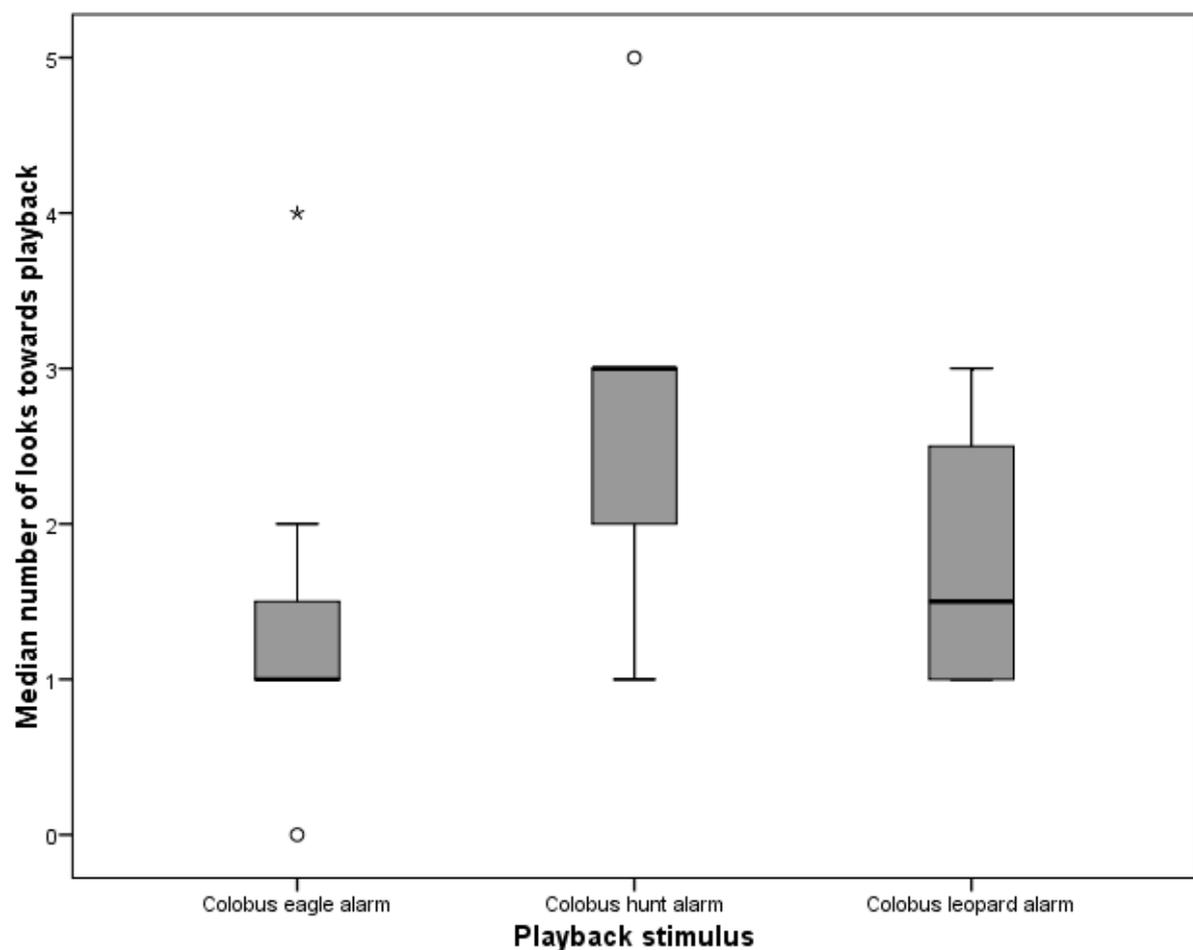


Figure 5.4. The mean number of looks towards the playback during the 30s response time to Colobus eagle alarms and Colobus hunt alarms, $N_{\text{males}} = 8$ (and for comparison, Colobus leopard alarms, $N_{\text{males}} = 4$).

Look duration, which was measured as well as looking events, shows the same response pattern between trials. Individuals looked longer in the direction of the playback stimulus for Colobus hunt alarms than Colobus eagle alarms, (see figure 5.5). The difference between the look duration for Colobus hunt and Colobus eagle alarms was, however, non-significant (hunt median = 10.93, IQR = 4.34; eagle median = 2.72, IQR = 2.53; $Z = -1.680$, $N_{\text{males}} = 8$, $p_{\text{exact}} = 0.109$).

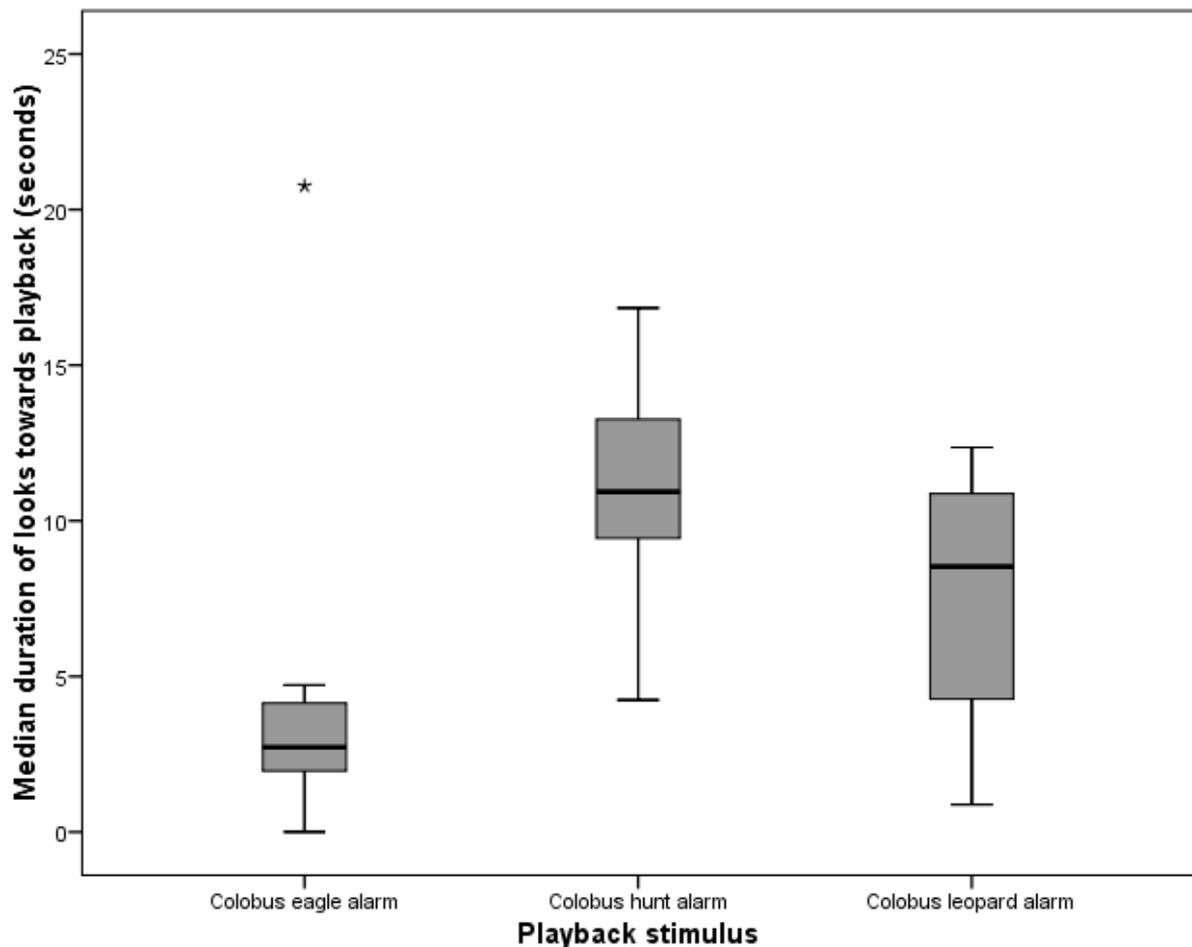


Figure 5.5. The mean duration of looks towards the playback during the 30s response time to Colobus eagle alarms and Colobus hunt alarms, $N_{\text{males}} = 8$ (and for comparison, Colobus leopard alarms, $N_{\text{males}} = 4$).

5.3.3 Attention to other chimpanzees during *Colobus* hunt alarm trials

There was a significant difference between number of looks towards individuals that were out-of-sight at the start of the playback experiment between *Colobus* hunt and *Colobus* eagle alarms (hunt median = 1.00, IQR = 3.00; eagle median = 0.50, IQR = 1.00; $Z = -2.264$, $N_{\text{males}} = 8$, $p_{\text{exact}} = 0.031$). The males also looked for a longer duration towards other individuals which were out-of-sight when the playback experiment commenced (hunt median = 1.40, IQR = 2.39; eagle median = 0.38, IQR = 3.63; $Z = -2.201$, $N_{\text{males}} = 8$, $p_{\text{exact}} = 0.031$).

The pattern of looking responses from individuals towards their partner after the playback of different *Colobus* alarms shows double the median number of looks after the *Colobus* hunt alarm than the *Colobus* eagle alarm (see figure 5.6). However, this difference was not significant using a repeated measures statistical test (hunt median = 1.00, IQR = 2.50; eagle median = 0.50, IQR = 1.00; $Z = -1.342$, $N_{\text{males}} = 8$, $p_{\text{exact}} = 0.500$).

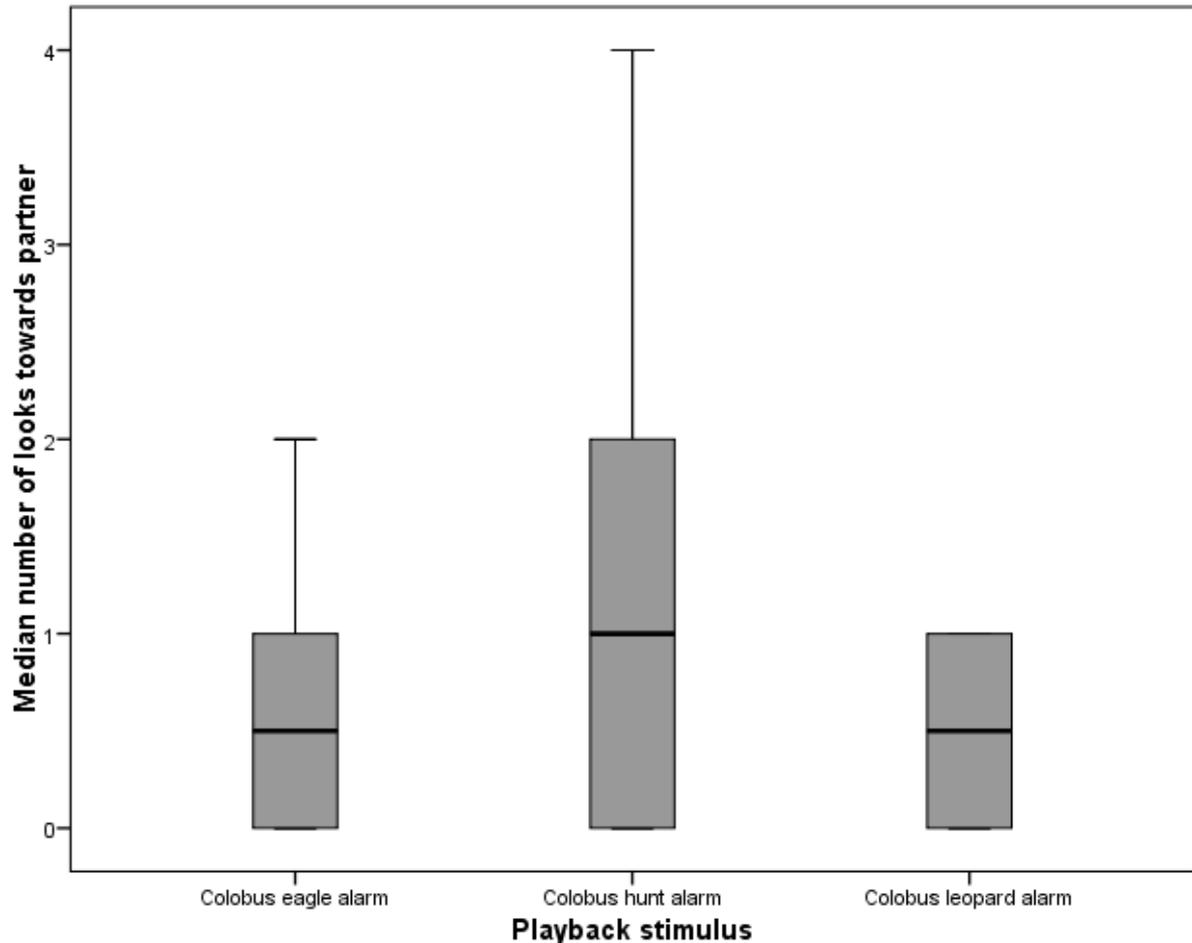


Figure 5.6. The mean number of looks towards dyad partner during the 30s response time to Colobus eagle, chimpanzee hunt and leopard alarm.

The dominance relationship between dyads also had no significant effect on number of looks or look duration towards their partner (Mann-Whitney U test comparing average number of looks between dominant and subordinate partners: $N = 4,4$, $T = 7.000$, $p = 1.00$; comparing look duration: $N = 4,4$, $T = 6.000$, $p_{\text{exact}} = 0.657$), although the sample size of only four in each group means these statistics lack statistical power and further experiments are recommended to analyse effects of dominance relationships on responses to Colobus alarm playbacks.

5.3.4 Vocalisations and joint responses to Colobus hunt alarm

Two of the four Colobus hunt alarm trials resulted in the production of loud bark vocalisations from both individuals in the dyad prior to joint travelling behaviour. The sample size (N = 4) is too small to perform statistical comparisons of differences in joint response between the trials. However, it is important to note that the only two trials which resulted in a joint response (a change in general behaviour from resting or feeding to travelling together in in proximity) came from the Colobus hunt alarm playback experiments, and no joint movement was recorded in response to any other Colobus alarm type (see table 5.2).

5.3.5 Looking behaviour associated with vocalisation during joint responses

Different elements of vocalisation production during the 30s response time to Colobus alarm playbacks are displayed below in table 5.3. All barks in response to Colobus hunt alarms (except NK who was not visible while he was vocalising) gave looks towards their partner in the five seconds prior to calling, and gaze alternation in the three seconds either side of calling. However, the sample size of vocalisations from other stimulus trials is much too small to allow comparison of this potential ‘audience checking’ behaviour (one of the possible indicators of intentionality in call production).

Table 5.3. Call production by focal individuals in response to Colobus hunt alarm playbacks and whether calls were preceded within five seconds (<5s) by a look towards their partner or towards other out-of-sight individuals, or whether there was gaze alternation between their partner and the playback within three seconds (<3s) before or after calling. NK moved behind some vegetation while vocalising in the last Colobus hunt alarm playback experiment, so looks could not be coded for the final trial (displayed as N/A in the table).

Focal ID	Call type	Number of calls	Duration of calls	Partner looks <5s	Look at others <5s	Gaze alternation <3s before or after
FD	bark	2	2.40	yes	no	yes
FK	bark	1	0.12	yes	yes	yes
MS	bark	8	4.80	yes	no	yes
NK	bark	7	5.16	N/A	N/A	N/A

5.4 Discussion

First I will discuss the evidence that chimpanzees can recognise the different Colobus alarm calls indicated by differences in attention shown by looking behaviour. I will then look at the Colobus hunt alarm trials and, comparing behaviour and vocal responses of dyads with matches sample from the Colobus eagle alarm trials (which serve as a control). Finally, I will discuss what the results can reveal about communication and coordination of joint action when there is a joint response of dyads towards the Colobus hunt alarm.

5.4.1 Response to different Colobus alarm calls

The results show that individuals paid more attention to the Colobus hunt alarm than the Colobus eagle alarm, shown by higher rates of looking and duration of looks at the stimulus. The difference in number of looks between trials was statistically significant, although a possible effect of pseudoreplication from using individuals from the same dyads as independent samples is acknowledged and a repetition of trials is suggested with additional dyads to confirm results.⁴² The trend in difference of attentional response to Colobus leopard and eagles alarms also requires replication by further trials. However, initial results from these experiments indicate that chimpanzees do recognise the different Colobus alarm calls as different signals (displayed in figures 5.4 and 5.5).

The patterns of looking behaviour at the playback and their partner were interesting, as there was almost no difference between an individual looking at their partner for the Colobus leopard and eagle alarms. This would be expected if both alarms held no socially-relevant signals and individuals do not expect their partner to change their activity and do not monitor them. Leopards have not been seen in Budongo for the chimpanzees' lifetimes, and so they should not show any social and/or defensive response to the Colobus leopard alarm as seen at other field sites (Klailova *et al.*, 2013). The sample size was very small here (only 2 trials with four individuals), but only one

⁴² Additional trials are currently being attempted with the same chimpanzee community by Pawel Fedurek in the Budongo Forest.

male, MS, showed a fear (whimper) and social (moving to sit next to NK) response to the Colobus leopard alarm. It is unclear why MS reacted in this way and his partner did not, but it should be noted that the trial was the earliest in the day that an experiment was conducted, and an overcast sky made it very dark under the forest canopy- a factor which has been shown to influence other monkey species' responses to alarm playbacks (*pers. comm.* K. Zuberbühler).

5.4.2 *Colobus hunt alarm trials and joint responses*

Half of the trials with the Colobus hunt alarm elicited a vocal response of bark vocalisations from both of the males in the experiment. These same trials resulted in a change of general behaviour and an initiation of joint movement (whilst in proximity) in the direction of the playback. These joint responses were not observed for any other predator alarm trials conducted. Additional trials are needed to confirm the difference in joint action response to Colobus eagle and hunt alarms, but results indicate that bark vocalisations are associated with the initiation of joint activity, which could be interpreted as joint hunting activity as the context of the joint action was after hearing a Colobus hunt alarm. There were no vocalisations produced during subsequent movements, indicating that (for two trials and for the short observation time before subjects moved out-of-sight) vocalisations were not produced during joint movements and therefore that there was no subsequent coordination of joint action using communication after initiation. Further trials are needed to test this observation.

Further trials would also allow comparison of looks and behaviour *within* the Colobus hunt alarm trials, between dyads when they react with vocalisations and movement towards the hunting alarm as opposed to not changing their general behaviour or vocalising. Such a comparison might reveal what behaviour or environmental factors (for example vegetation or canopy type) are associated with moving towards the playback as a joint response, i.e. factors influencing a dyad's 'motivation to hunt'.

5.4.3 Looking behaviour associated with vocalisation during joint responses

Number and duration of looks from a subject towards their partner was not significantly higher in response to Colobus hunt alarms than Colobus eagle alarms, and neither were the measures different depending on the dominance relationship of partners in a dyad. These results seem to suggest that visual monitoring of their partner's response was not higher when the Colobus hunt alarm stimulus indicated that a socially relevant event was occurring (a group hunt). It should also be considered that two of the Colobus hunt alarm playbacks induced joint movement responses within the thirty-second response observation period. This means that the same problem discussed in chapter 3 on joint travel is encountered, whereby individuals may be monitoring an individual's movements and actions by ear rather than watching them, and there is no way to tell this from observations alone.

Number and durations of looks from a subject in the direction of other out-of-sight individuals (whose position was known to the chimpanzees from calling behaviour or recent travel movements) was significantly higher in response to Colobus hunt alarms than Colobus eagle alarms, which might be expected if the bark were being used to recruit other out-of-sight individuals to join in with the joint action towards the Colobus hunt alarm. This may also explain why number of looks towards a subject's partner was not higher in response to the Colobus hunt alarm, if the loud bark vocalisation was being broadcast to attract other individuals to the hunt rather than their partner who was always within 10m distance in the experiment. These few results seem therefore to coincide with data on barks from the previous chapter, indicating that production was associated with initiators of a hunt and with high overall motivation to hunt. However, they also further imply that barks are directed at other individuals to recruit them to hunt, which was not indicated in the previous chapter (although this is mere speculation as such inferences are based on joint response of dyads from only two experiments).

5.4.4 Indicators used to infer intentionality

The design of the experiment described in the present study (repeated design) meant that only dyads with high levels of affiliation were repeated in the different conditions, so the presence and composition of the audience remains the same and the criteria ‘social use’ cannot be manipulated. In future studies, the experiment could be repeated with dyads of different levels of affiliation. The likelihood of encountering two males who rarely associate both alone and within 10m of each other, however, is such that it would take a lot more time to complete all the trials.

The loud bark vocalisations associated with hunting (Crockford & Boesch, 2003) and general behaviour changes to travel responses were only given to the Colobus hunt alarm. The small sample size makes it difficult to establish whether this response is coordinated with their partner. All barks were preceded by a look towards the partner in the previous 5 seconds, and some included gaze-alternation. However, such ‘audience-checking’ behaviour by itself is an inconclusive indicator of whether there was an intended recipient of the signal, as there are many other reasons one individual may be monitoring their partner after hearing a Colobus hunt alarm. Furthermore, the potential indicators of intentionality in signal production described in table 5.1 should only be considered as a whole group. By themselves, they do not offer enough evidence to support making inferences about intentionality in signal production. They were considered here as an example of how video observations of experiments could be used to infer intentionality and to offer a template for analyses of future experiments.

5.4.5 Conclusions

In summary, the data suggests that Sonso males respond differently to cues from another species’ alarm calls by showing increased interest in the call when it indicates something relevant to them (i.e. that a hunt is occurring, whereas an eagle alarm is not relevant), and potentially an increased interest in their social partner’s behaviour when the call is relevant to them (i.e. whether to change behaviour or do nothing). There are no claims made about the beliefs of the chimpanzees with regards to the Colobus alarms

or their intentions when they bark and move together towards the hunting alarm, other than that dyads appear to have a higher interest in the Colobus hunt alarm and this motivates joint movement towards that stimulus and vocalisation production the same way in both members of the dyad. Further trials currently being conducted by PW in Sonso should provide increased statistical power to draw firmer conclusions.

The one example of the trial where FD and FK both barked, then other individuals joined from further away and they all moved in the direction of the hunting alarm playback, could indicate that the vocalisations increased the probability that other individuals would join the callers (i.e. recruiting). Repeated trials would show whether this was a 'one-off' result or not. The hunting alarm experiment with NK and MS did not result in any other males joining their movements towards the playback direction after they vocalised; however, as all other males appeared to be located at least 200m beyond the playback position, the social environment of the dyad was quite different. This highlights a major difficulty with carrying out playback experiments with wild chimpanzees when it comes to the interpretation of results. A long-term plan involving collaborating researchers repeating experiments using the same methodologies can help with identifying and categorising consistent differences between trials, allowing for an increased measure of control during analyses.

That being the said, the striking difference in behaviour and vocal response to two of the hunting alarm experiments- both resulting in all individuals moving towards the direction of the playback- suggests that they were motivated to join a hunt already in progress. It should be noted, of course, that even if this response was observed from all four hunt alarm playbacks, no actual hunting behaviour was subsequently observed, even after encountering real Colobus groups in the forest later in the day. It is therefore difficult to say unequivocally whether their actions specifically represent a motivation to hunt, and that the vocalisations represent some form of coordination of their action towards this shared goal of hunting.

These final conclusions are made: that dyads were more interested in the Colobus hunt alarm vocalisation than in the control eagle alarm vocalisations; that, at the very least,

individuals with an active response to the Colobus hunt alarm moved to investigate the area of the forest from which the vocalisation emanated; and that their actions were socially motivated – as evidenced by joint production of bark vocalisations and travelling in the same direction alongside other individuals. These results support the idea that group hunting is a joint action with a shared goal, but not necessarily that individuals are mutually responsive through looking behaviour, although monitoring of a partner's actions through auditory signals may render such visual monitoring unnecessary (as with the joint travel behaviour observations). The coordination of group hunting behaviour in wild chimpanzees is therefore of very real interest to those wanting to compare the coordinating signals of humans' nearest genetic relatives during naturally-occurring joint actions, which has the potential to shed light on the evolution of human joint cooperative activities and communicative abilities utilised during the coordination of such activities.

Chapter 6. Overall Discussion

6.1 Aims of study

The overall aim of this study was to investigate joint actions in wild chimpanzees and how they are coordinated, with a focus on vocal communication. Joint actions are an interesting area for investigation due to the close genetic relatedness of chimpanzees with humans, which gives the potential for comparisons in behaviour to reveal something of the evolutionary origins of a trait and a likely last-common-ancestor (Laland & Brown, 2011). The focus of this research was on communication and cognitive processes during joint actions, and these traits are unlikely to have a specific traceable gene, being instead heavily influenced by the developmental environment of the organism (Slocombe *et al.*, 2010). However, that the results may serve to reveal areas ripe for further investigation aimed at tracing evolutionary origins of traits is certainly a possibility.

A framework for investigating joint actions in natural chimpanzee behaviour was presented, based on Bratman's definition of a joint cooperative action as one in which participants are: a) mutually responsive; b) share a goal; and c) coordinate their actions to reach that goal. The two categories of naturally occurring joint behaviour that were deemed suitable for investigating coordination and communication in this study were joint travel and group hunting. Joint travel was investigated in small groups where local coordinating behaviour and communication could be discerned between specific signallers and receivers, as opposed to the long-distance coordination of sub-group travel movements within the whole community. Group hunting was investigated in two ways: firstly through observations of individuals' behaviour and communications during naturally occurring hunts, and; secondly with a playback experiment that aimed to simulate a hunt by playing the alarm call of a Colobus monkey recorded during a chimpanzee hunt.

Communication that might coordinate action was looked for in these naturally occurring joint activities. Communication included signalling behaviour (vocalisations), looks and

other behaviour such as pausing, which could be considered to coordinate joint actions. Coordination of joint action was considered when there was evidence that a behaviour increased the probability of initiation or recruitment to carry out joint action, or in the case of hunting, communication associated with different hunting strategies towards the same goal. The results of these investigations will now be summarised, followed by some overall conclusions.

6.2 Joint travel

Communication associated with joint travel was investigated using three data sources to offer more comprehensive details of small-group travel behaviour in Sonso chimpanzees than a previous study (Gruber & Zuberbühler, 2013). There was no evidence for a vocalisation type that is systematically associated with general travelling behaviour, the initiation of travel with other individuals (from analysing a predeparture period), or recruitment of others to engage in joint travel on a local level. Video data provided the most detailed and reliable evidence of the initial stages of travelling from resting or feeding behaviour. There was no difference between whether a hoo vocalisation was produced when an individual was alone compared to when they were with a potential travel partner. This suggests that the call was not being produced as a signal directed at another individual to coordinate travel. There was no association found between vocal production, pausing or looking at a partner and the partner's subsequent following behaviour, indicating that none of these potential signals could be considered as recruiting signals. It was concluded from the results that, contrary to a previous studies' findings (Gruber & Zuberbühler, 2013), local coordination of joint travel in Sonso chimpanzees may have been generally achieved without specific signal production. In these instances, joint travel would not have fulfilled Bratman's requirement that participants in a joint cooperative activity are mutually responsive or coordinating their action towards the shared goal of travelling together (although it remains possible that individuals could be mutually responsive by monitoring another chimpanzee's movements in the forest through auditory cues).

These data presented in chapter 3 do not rule out the possibility that certain environmental or social factors, such as visibility, vegetation type, location within territory and general position relative to other individuals might be affecting the production of signals that coordinate actions before travelling or change the likelihood of a caller being followed. Such questions could be assessed in future studies by including vegetation type, GPS location data and whole-group location data as variables in analyses. It is also possible that more subtle signals other than vocalisations (for example as-yet-unknown gestures, or combinations of gestures and calls) are being used to locally coordinate travel movements, which would require further investigation from a greater sample of video recordings of individuals' travel departures.

It is still possible that joint travel in male chimpanzees may be coordinated on a global scale and entirely in the auditory arena, as potential signals used to coordinate long-range subgroup movement patterns were found, although not directly tested for. Male pant-hoots included as part of displays were produced more during travel than during other activities, and pant-hoots were produced during the predeparture period at a rate higher than each male's individual calling rate, supporting previous studies which implicate pant-hoots and drumming as long-distance coordinating signals (Mitani & Nishida, 1993). Pant-hoots are a loud vocalisation that can be heard for hundreds of metres and so are more suited for the coordination of subgroup travel within the whole community.

Further data on the subsequent travelling behaviour of subgroups after calling, including the relative positions of all individuals in the group and their social relationship with the caller, are needed to explore the association of pant-hoots with travel coordination in male chimpanzees. However, the extent to which long-distance coordination of subgroup travel patterns can be theoretically considered as a joint cooperative activity is debatable. For example, although it may technically fulfil the criteria for being mutually responsive (if they reply to each other), having a shared goal (for example moving from different places to the same location at the same time) and coordinating that action (through mutual adjustment of movement patterns depending on the other's location), the behaviour would move away from Bratman's original impetus to define cooperative

activities where individuals are doing something *together*, and thus the extent to which the action is shared is diminished (Bratman, 1992). As discussed in the opening chapter on background information, the shared goal of a joint action in wild chimpanzees can only be assumed from their observed behaviour, and so the goal of widely-dispersed groups travelling at the same time would need to be very obvious *before* they reached the location for the groups to be considered as ‘travelling together’ and communication occurring during that travel to be considered as coordinating (the theoretical assumption used in the local travel behaviour observed in chapter 3).

6.3 Group hunting

Coordination of group hunting behaviour was investigated by analysing descriptions of hunts from my data as well as those from the long-term database. Bark vocalisations were associated with group hunting more than other vocalisations, as has been found in a previous study from Taï (Crockford & Boesch, 2003). Barks were more likely to be given by those initiating the hunt and were produced flexibly depending on affiliative relationships with other hunters. The data analysed indicate that the bark vocalisation may have some role in the coordination of group hunts by affecting the initiation of hunts, and this is associated with a higher motivation to engage in joint hunting activity. A potential theory is that a high motivation to hunt and the presence of other affiliative hunters may result in a convergence of physiological changes in hunting individuals which is associated with bark production.

There was no evidence that vocalisations produced during the hunt were associated with the individual’s hunting strategy, suggesting that barks do not directly coordinate the different hunting strategies used during a group hunt. The absence of evidence for coordinating hunting strategies does not necessarily mean such communication is not occurring, as observations recorded during hunts represent only a fraction of individuals’ behaviour that was occurring, especially in larger hunting groups. For comparison, the data from the experiment could not elucidate this matter, as the experiment did not lead to an actual hunt but only provided the cue that a hunt was

already occurring. It is therefore still possible that more directed vocal coordination occurs when the chimpanzees reach the monkeys and view the canopy where their prey is moving – it is at this time when individuals’ strategies could be planned, as is suggested to occur by Boesch (2005), and further evidence, possibly from video recordings of hunts using directional microphones from many different camera angles, may help to elucidate this matter.

Barks were not associated with the potential recruitment of out-of-sight affiliated individuals who were not already hunting, although it is suggested that playback experiments of chimpanzee barks recorded during hunting are needed to confirm this result. The experimental paradigm presented in chapter 5 offers a design that may be used for such experiments using chimpanzee barks as a stimulus instead of Colobus alarm calls. The increase in bark production seen when an individual is hunting with close affiliates supports the theory that the motivation towards joint action in hunting behaviour is socially affected and associated with a flexibility in vocal production.

Playback experiments were suggested to investigate the role of bark vocalisations in the initiation of joint action and coordination of movement in the context of group hunting. These experiments were carried out in Budongo and presented in chapter 6.

6.4 Hunting playback experiment

A novel field experiment was presented which used the alarm calls of the chimpanzees’ prey species - the Colobus monkey - to explore coordination of joint action between chimpanzee dyads in response to the call. Alarm calls produced by the monkeys when they were being hunted by chimpanzees and in response to an eagle stimulus were played back to dyads of affiliated males and their vocal, looking and general behaviour responses recorded.

First of all, individual chimpanzees were shown to recognise the different Colobus alarm calls, as indicated by a difference in level of attention towards the different calls.

This is important because the different alarm calls are expected to vary in their relevance to chimpanzees - in particular the Colobus hunt alarm which was used to simulate a Colobus hunt in progress to the subjects of the experiment.

The joint vocalising and travel response of chimpanzee dyads when they responded with a change in general behaviour to the Colobus hunt alarm playback indicated that a convergence of motivation and behaviour had occurred. This is the most parsimonious explanation from evidence on vocalisations described from natural hunts, as barks given by initiators (i.e. those most heavily invested in hunting) suggest they are produced when in a highly excited emotional state. The actions and barks of initiators may in turn excite receivers and motivate them to hunt as well, as the evidence that barks were produced with larger party sizes and with greater affiliation with other hunting individuals suggests, through a process similar to response facilitation (Byrne, 1994). Individuals, it seems, are more likely to join in a group hunt when more individuals are already hunting, and barks may facilitate this process by bringing party members into similar physiological states (as seen in crossbills which increase vocalisation as a group to encourage flock travel; Cornelius *et al.*, 2010).

The playback experiments were recommended to be repeated with different chimpanzee dyads of varying affiliative relationships in future studies. The long-term nature of such a study is acknowledged, as the experiments were challenging to conduct in natural settings in the field compared to studies in captivity. However, the benefits of using a naturally occurring paradigm for joint action to investigate coordination of joint action are considered to outweigh this cost, as group hunting is likely the most frequently occurring joint activity in chimpanzees where an external joint goal is clearly visible (as discussed in the introduction chapter).

6.5 Overall conclusions

The two naturally-occurring joint activities investigated in this study provided both unexpected and interesting results on the communication involved in potential joint cooperative activities. In the context of joint travel, there was no vocalisation found that coordinated the initiation of travel or recruitment of other individuals to join in travelling behaviour on a local level within small parties, despite a recent previous study indicating the hoo vocalisation as a coordinating travel signal. This indicates that joint travel, in general, is not a joint cooperative activity towards a shared goal that is coordinated with specific signals, but instead may be coordinated by individual responses to another's movements (or cues to movement). The idea that long-distance pant-hoot vocalisations and displays have the potential to coordinate sub-group movements over larger distances was supported and research suggested into how loud vocalisations predict the travelling behaviour of small parties of chimpanzees within the community as a whole. However, these signals may not relate directly to joint action, if the motivation of individuals coordinating travel is not to achieve the shared goal of travelling together. The second joint activity, group hunting, was therefore investigated through observations and an experiment in order to examine communication that might coordinate joint actions towards a more obvious shared goal that is recognisable from observed joint behaviour towards that goal.

An overall picture was created of chimpanzee coordination of joint action in naturally observed hunts where vocal signals were produced by those individuals highly motivated to hunt. This was shown as the bark vocalisations were associated with initiators of hunts, were produced more when there was a larger number of hunters and when those hunters are more affiliated with the caller. It was not clear from the evidence whether barks increased the probability of a group hunt being initiated, a question which may require playback experiments of bark vocalisations to answer. The data from naturally occurring hunts, therefore, did not provide conclusive evidence that vocal signals were being used to coordinate joint hunting activity. However, bark vocalisations were singled out as a potential coordinating signal worthy of further

investigation – a process which was started with the playback experiment presented in this study.

Initial results from the playback experiments indicated that chimpanzee males in the Budongo Forest recognise the hunt alarm of Colobus monkeys as being different to other Colobus alarm calls. They sometimes respond to the Colobus hunt alarm with barks and joint action in the direction of the call, although this reaction was not consistently observed as it is expected that a host of environmental and social factors may influence the initiations of hunting behaviour. When a joint reaction was observed, the barks were produced at the same time prior to moving in proximity by both individuals in the experiments, supporting the idea that barks produced by chimpanzees in the hunting context represent a shared motivation towards a joint action with a shared goal. In spite of this, it is not yet clear how the vocalisation may be coordinating the joint response, as a long-term study repeating the experiments with many different chimpanzees is needed to compare signals produced with looking and following behaviour. A large data set may also help to elucidate the social use (with individuals of varying affiliation levels) of communication to coordinate the joint response, for example by clarifying whether bark production *before* hunting behaviour commences is flexibly produced depending on the presence of specific individuals, whether it consistently elicits a joining response in that individual (either vocal response, increased proximity, or both), and ultimately, whether the signal initiates group hunting behaviour and recruitment of other out-of-sight individuals to join a hunt.

Overall, the experiments offer a strong paradigm within which to investigate the initial joint action responses in group hunting chimpanzees. The context of group hunting has an obvious shared goal where the behaviour of individuals acting together towards that goal is not easily confused with other behaviour, individuals have to be mutually away of each other's actions in order to follow the same prey, and there is a specific candidate signal, the bark vocalisation, that is associated with group hunts and their initiation, which may also be involved in coordinating the hunt. Chimpanzee group hunting is also comparable with early hominid hunting behaviour which is known to have occurred in groups, although obvious differences include the use of weapons to hunt in humans and

the hunting of larger prey (Boesch & Boesch, 1989; Churchill, 1993). These differences are significant when considering the evolution of coordinating communication, as the coordination of hunting larger and more dangerous prey (e.g. mammoths compared to monkeys) would likely require more precise communication to reduce risk and ensure success where the actual killing of the prey requires a coordinated attack of more than one hunter. Such group hunts differ from chimpanzee group hunts where only one individual was seen to physically attack a monkey at a time.

In my opinion, much of the apparent 'coordination' of joint action seen in chimpanzees travelling and hunting together at the same time can actually be coordinated by individuals reacting in predictable ways to simple learned behavioural cues about a social partner's movements. It is not impossible, but may simply be rare, that signals, such as contact hoo vocalisations which gain the attention of others, are used within an environment and sequence of behaviour that impact individuals' local travel coordination. The same may also be true of the bark produced in the hunting context.

Barks produced in group hunts may simply represent a growing motivation to hunt in a party of individuals. This is different to having a shared goal with a coordinated plan of action, as was suggested for human joint cooperative activities; however, it is equally easy to apply this explanation of simple coordination to much of human joint action where a literal plan has not been discussed prior to action. The comparison is difficult to take further as it requires every instance of human joint action to be accompanied by data on the mental states of the actors- a requirement that cannot be applied to animals. It is significant that there is some communication specific to the hunting context in wild chimpanzees and that it appears to have some coordinating function, whatever the mechanism, of initiating group hunts; unfortunately it is as yet impossible to ask whether this represents a plan of action on the part of the caller. The lack of evidence for a signal specific to individual strategies during a hunt suggests that a precursor to complex inferential language is not present in the bark of hunting chimpanzees, but simple behaviour methods for monitoring others and coordinating actions may be common to both species, as is a flexibility in response to differing social environments.

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Appendix 1: Table displaying Sonso chimpanzee community ID codes, sex, age, offspring and focal time (where individual was in-sight of the observer and close enough to hear all vocalisations).

ID code	Sex	Age (on 1/9/2012)	Offspring (sex,age)	In-sight focal time (hours)
AN	F	22		
BC	F	36	BG (F, 8)	0.27
FD	M	18		12.31
FK	M	13		25.98
FL	F	33	FA (F, 6)	
GL	F	36	GN (F, 16), GR (F, 6)	
HT	F	34	HL (F, 11), HY (F, 8), HR (F, 5)	10.50
HW	M	19		14.62
JN	F	28	JT (F, 13), JS (M, 6)	11.20
JL	F	22	JB (M, 1)	
KG	F	36	KE (F, 14), KI (F, 9), KP (M, 4)	
KL	F	33	BH (F, 18), KM (F, 12), KC (M, 6)	10.90
KT	M	19		22.19
KU	F	33	KN (F, 14), KS (M, 9), KH (F, 4)	10.80
KW	F	31	KR (F, 11), KB (F, 5)	11.38
KY	F	29	KA (F, 14), KX (F, 5)	17.66
KZ	M	17		21.22
MK	F	32	MI (F, 5)	14.70
ML	F	37	MN (F, 9), MB (M, 3)	0.72
MS	M	21		23.30
NB	F	50	NT (F, 9)	13.00
NK	M	30		26.94
OK	F	16		
PS	M	14		15.43
RH	F	47	RM (F, 10), RF (F, 5)	10.90
RS	F	15		1.45
SE	F	41	SK (M, 6)	
SM	M	19		13.47
SQ	M	21		19.41
TJ	F	28	TP (F, 13), TM (F, 8), TW (F, 1)	
WL	F	31		4.48
ZD	M	11		
ZF	M	30		20.33
ZG	M	15		3.99
ZL	M	17		13.04
ZM	F	44	(Died, with ZK, on 6/5/2011)	

Appendix 2: Data labels used for recording behaviour from focal follows and video recordings of individuals.

2.1 Table showing data labels used when coding pauses from travel videos

Data label	Description	Data label	Description
Date and time	Time noted to the nearest second	Pauses (>5<30s)	Number of pauses in travel before focal travels for longer than 30s
Focal ID		1st pause vocals	Number and type of vocalisations from focal to ID2 in first pause of 5-30s
Start location	Tree <i>or</i> on ground	1st pause looks	Number of looks from focal to ID2 in 5s before travel
Infant contact (yes/no)	Whether infant was already in contact with focal before travel	1st pause vocals ID2	Number and type of vocalisations from ID2 to focal in 5s before travel
ID2	ID of potential travel partner	30s final travel period vocals	Number and type of vocalisations from focal to ID2 in first 30s of final travel period >30s
ID2 distance (m)	Distance of ID2 from focal at start of focal's travel initiation	30s final travel period looks	Number of looks from focal to in first 30s of final travel period >30s
5s pre-travel vocals	Number and type of vocalisations from focal to ID2 in 5s before travel	30s final travel period vocals ID2	Number and type of vocalisations from ID2 to focal in first 30s of final travel period >30s
5s pre-travel looks	Number of looks from focal to ID2 in 5s before travel	30s final travel period ID2 distance	Distance of ID2 from focal at start of focal's final travel period >30s
5s pre-travel vocals ID2	Number and type of vocalisations from ID2 to focal in 5s before travel	Follow = 0	No follow behaviour (of less than 45° divergent from the focal animal's travel direction for at least 10m)
30s initial travel period vocals	Number and type of vocalisations from focal to ID2 in first travel period <30s	Follow = 1	ID2 follows in same direction as focal and <15m behind
30s initial travel period looks	Number of looks from focal to ID2 in first travel period <30s	Follow = 2	Focal follows in same direction as ID2 and <15m behind
30s initial travel period vocals ID2	Number and type of vocalisations from ID2 to focal in first travel period <30s	Notes	Including location on grid system, other individuals known <100m, other gestural behaviour

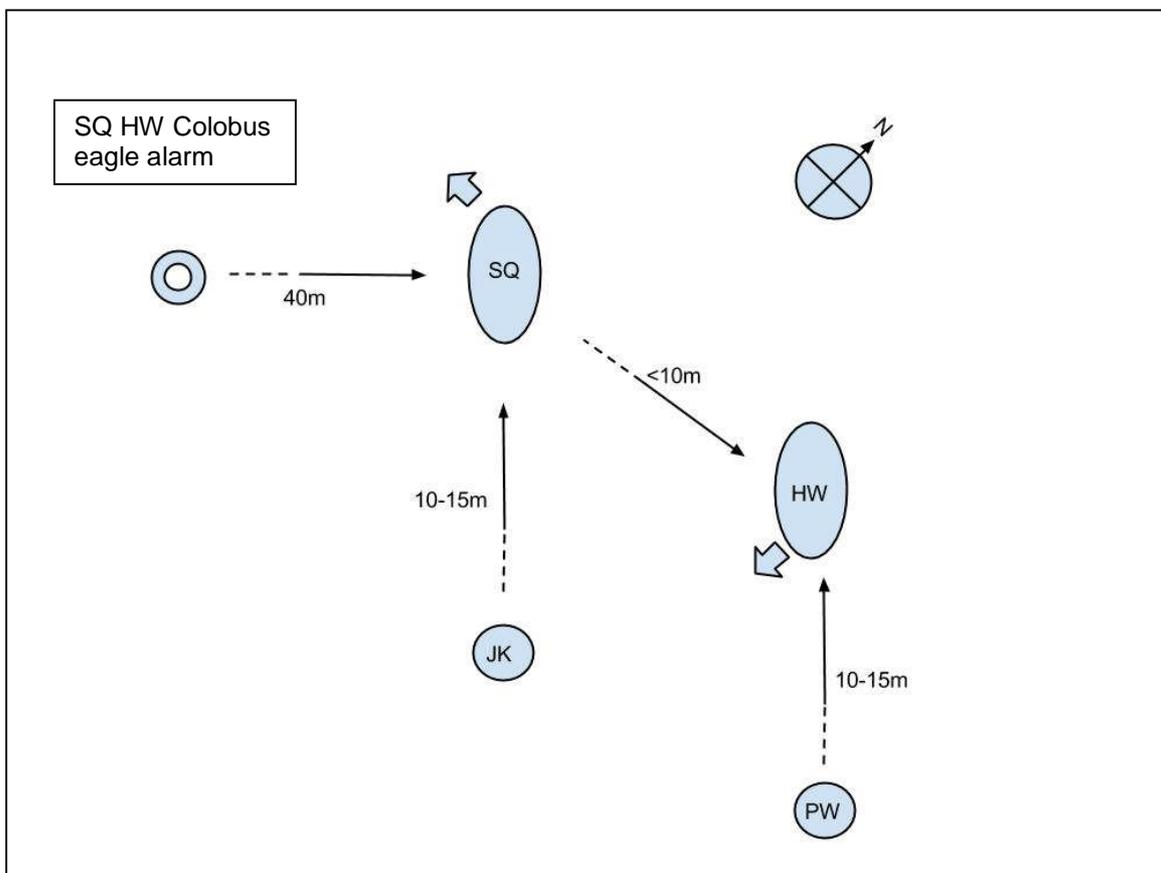
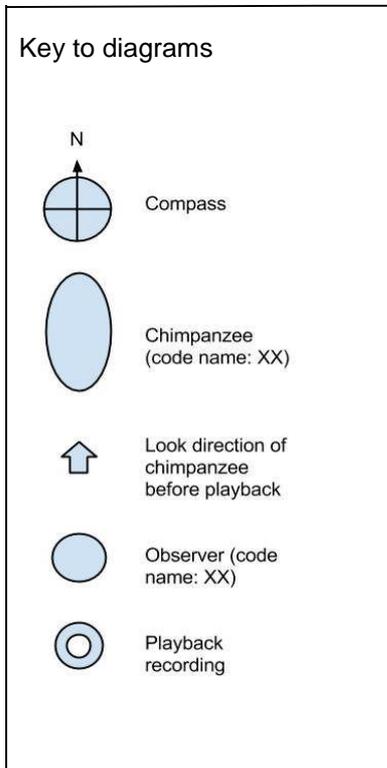
2.2 Table Focal data and behaviour definitions

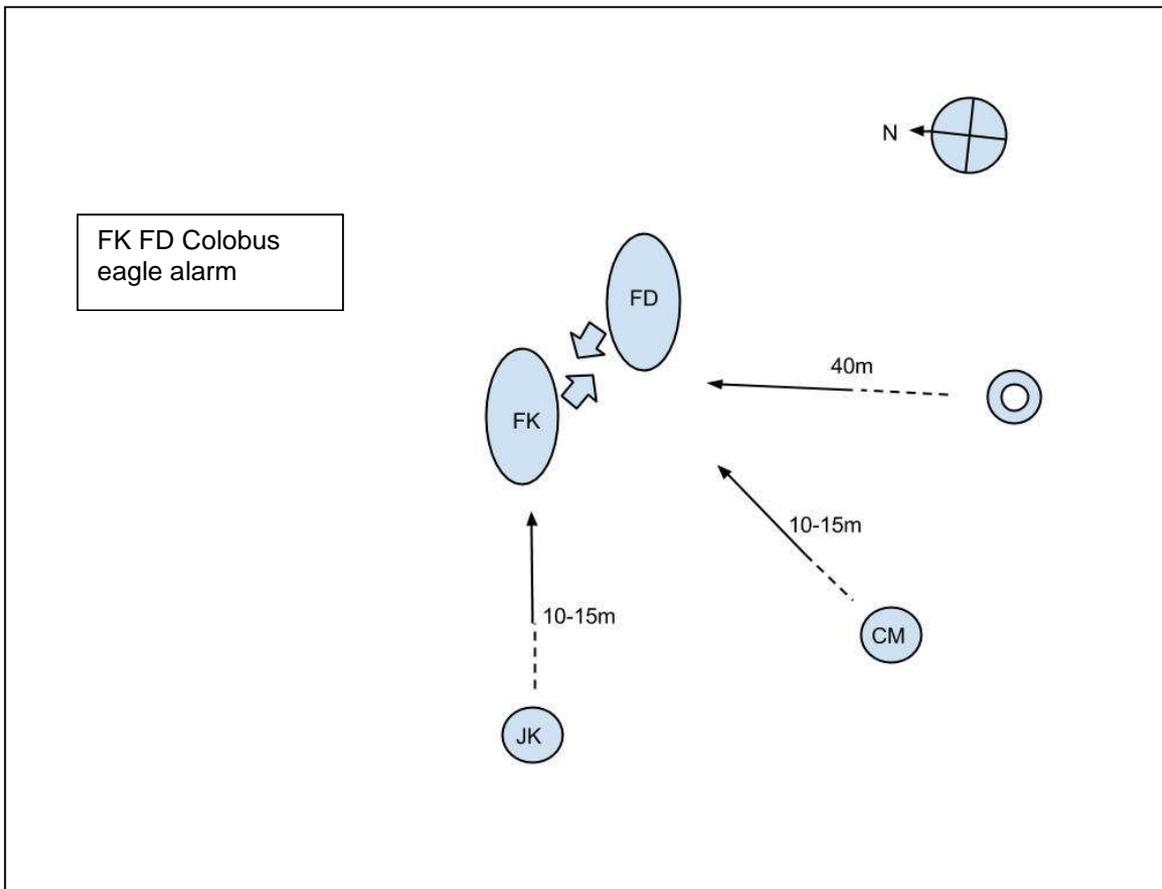
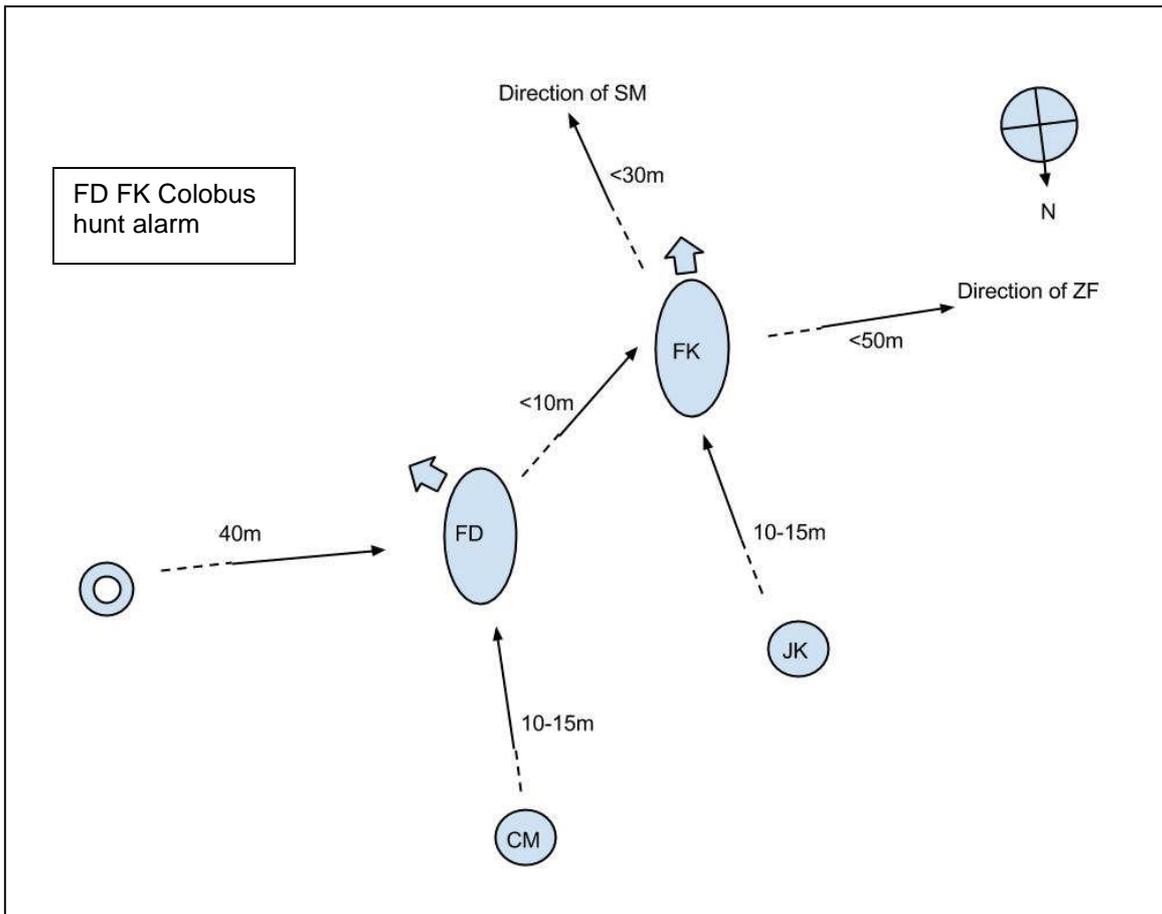
Data label	Description	Behaviour	Definition
Date and time	Time stamp recording date and time to nearest second	Resting	Sitting or lying down, eyes closed or open, for >5s
Focal ID		Feeding	Foraging or manipulating food item/chewing for >5s
Location	Tree (>3m height)/on ground/on path/on log or branch <3m height	Travelling	Walking or running through trees or on ground for >5s away from original location
General activity	Resting/feeding/travelling/social-behaviour/self-grooming	Social-grooming	Inspecting, scratching or running fingers through hair of social partner, including picking out parasites with fingers or teeth
ID2	ID of social partner/s	Social- physical aggression	Includes, wrestling, lunge, hit, slap, grab, bite, throw, and claw
ID2 distance (m) and behaviour	Distance of ID2 from focal and notes on any vocals or behaviour from ID2	Social- sex	Mounting/penetrating ID2, sometimes with copulation screams
Vocalisation produced by focal	Type of vocalisation from list table 3.1	Social- display	Aggressive behaviour without any clear and identifiable recipient. May include pilo-erection, and such behaviours as beating on or moving inanimate objects, stomping, slapping, swaying, hooting, chest-beat, or running
Social behaviour	Grooming/physical aggression/sex/displays/solicitation/submission/play	Social-solicitation	Branch-shaking, leaf clipping (stripping bit off a leaf with teeth), reaching (stretching arm out) to social partner
30s initial travel period vocals	Number and type of vocalisations from focal to ID2 in first travel period <30s	Social-submission	Crouching, bobbing, fleeing, avoiding, fear grimacing, bared teeth towards social partner
30s initial travel period looks	Number of looks from focal to ID2 in first travel period <30s	Social- play	Fighting or chasing with partner whilst making 'play face'/'laughing' vocalisation
30s initial travel period vocals ID2	Number and type of vocalisations from ID2 to focal in first travel period <30s	Self-directed behaviour	Inspecting, grooming, scratching own fur
Nearest neighbours	ID of individuals within 0, 2, 5, 10 and 10+m at time of event recorded	Notes	Comments (including location, food type eaten, other community encounters, and other behaviour and gestural behaviour such as kiss-touching lips- or embracing)

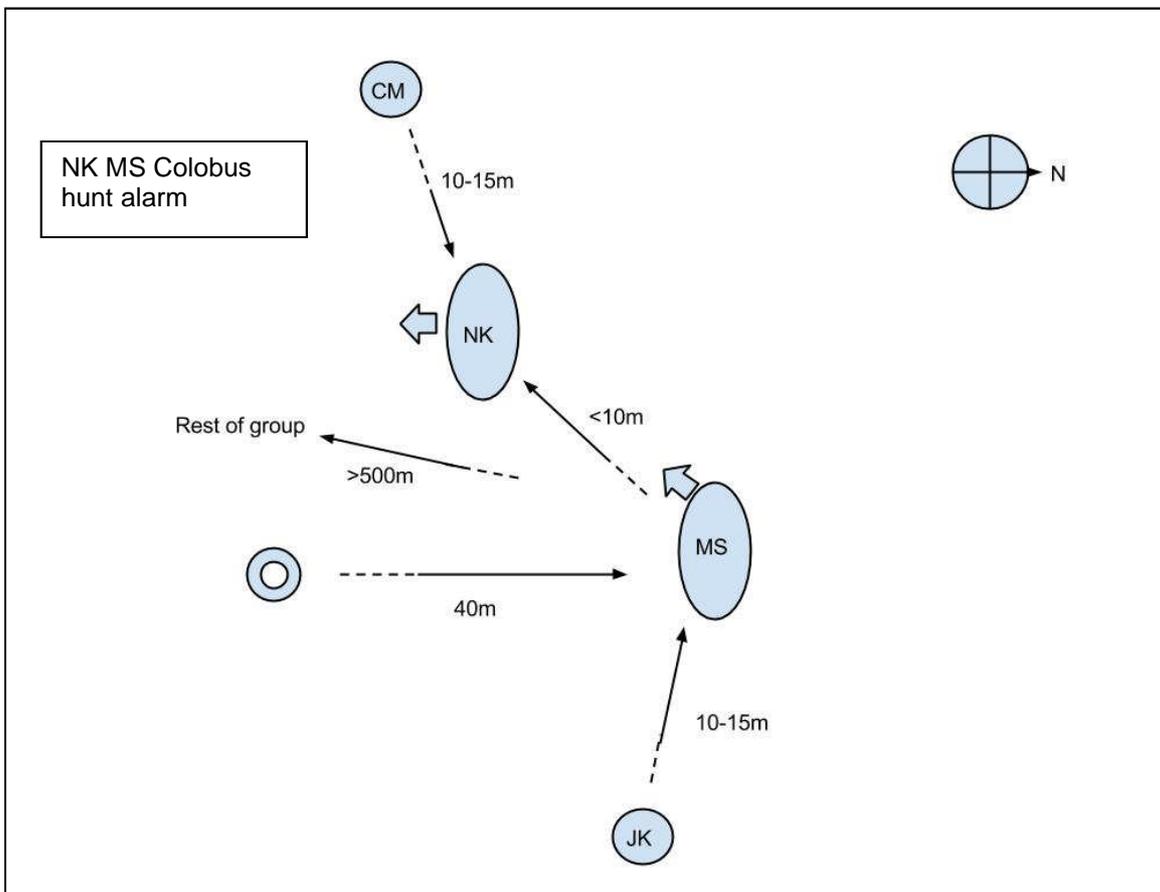
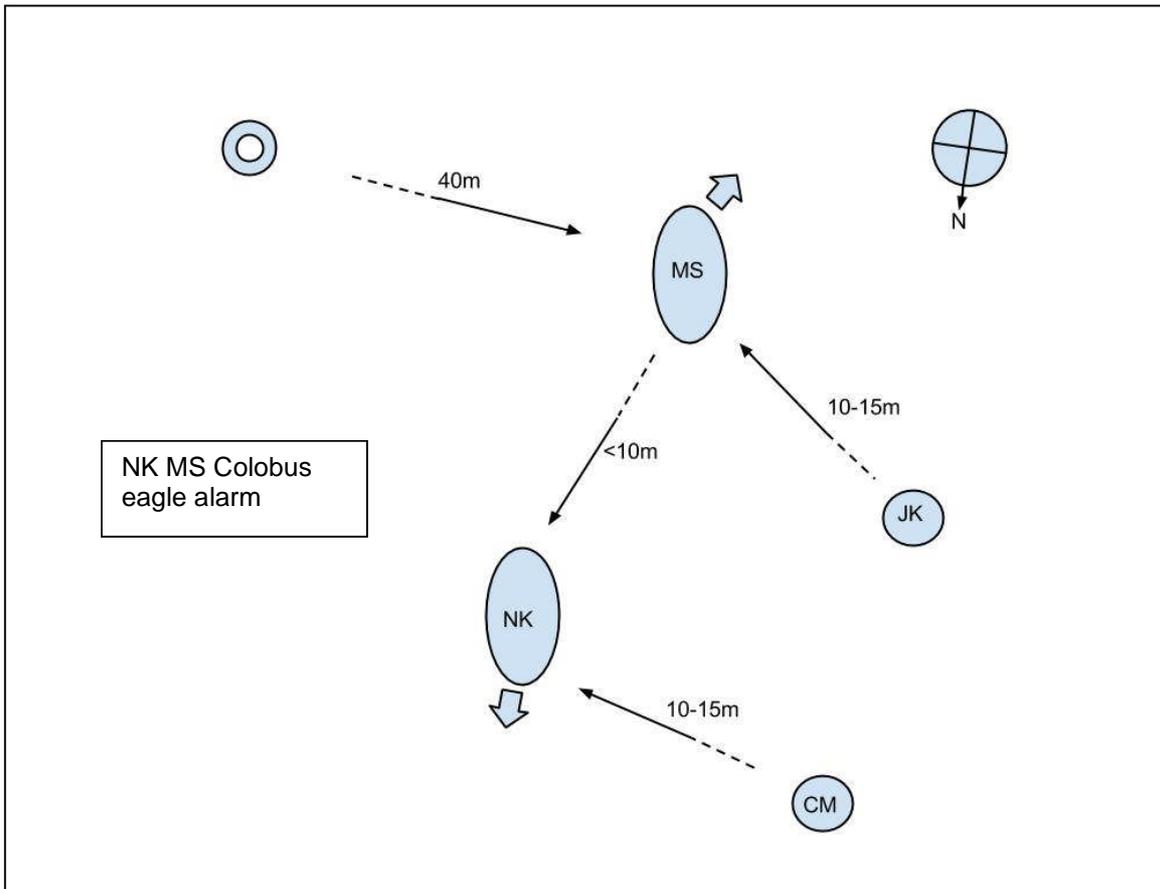
2.3 Playback experiment coding table.

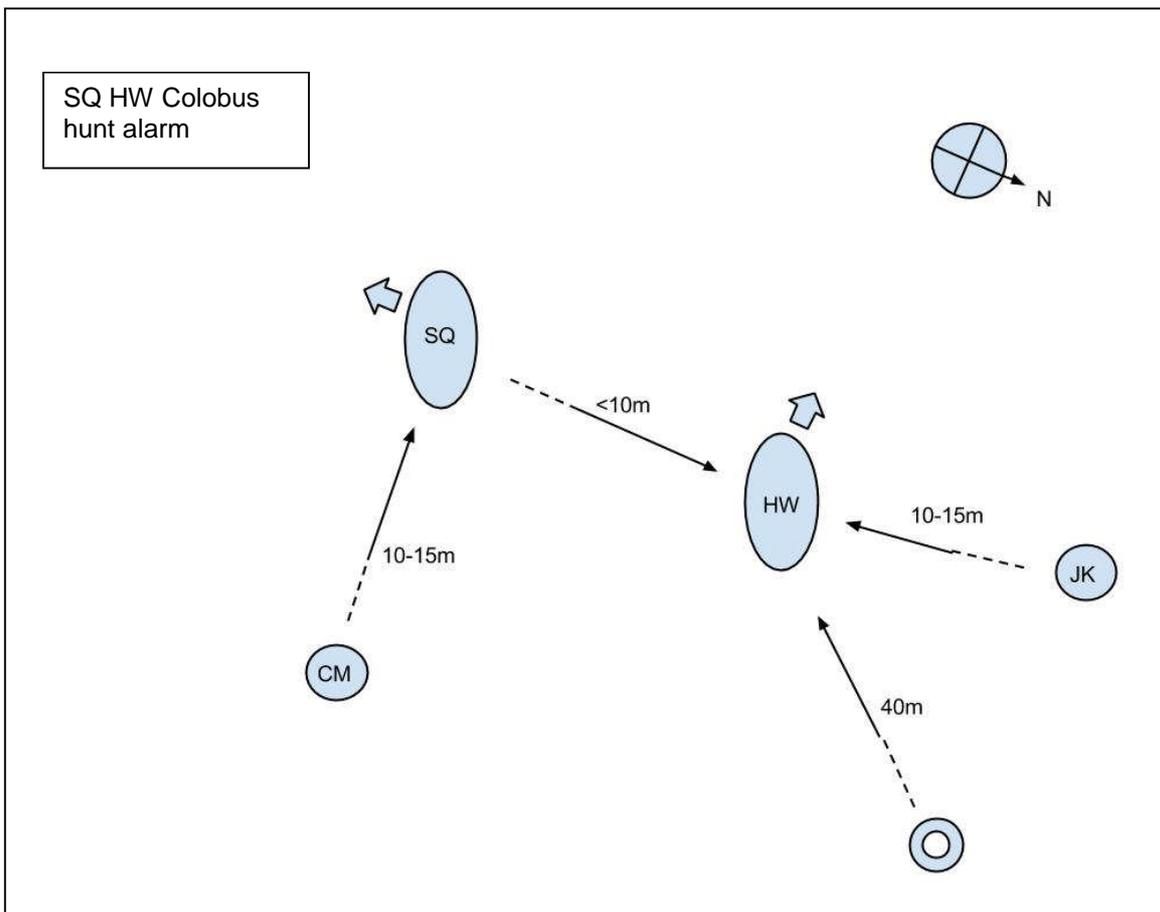
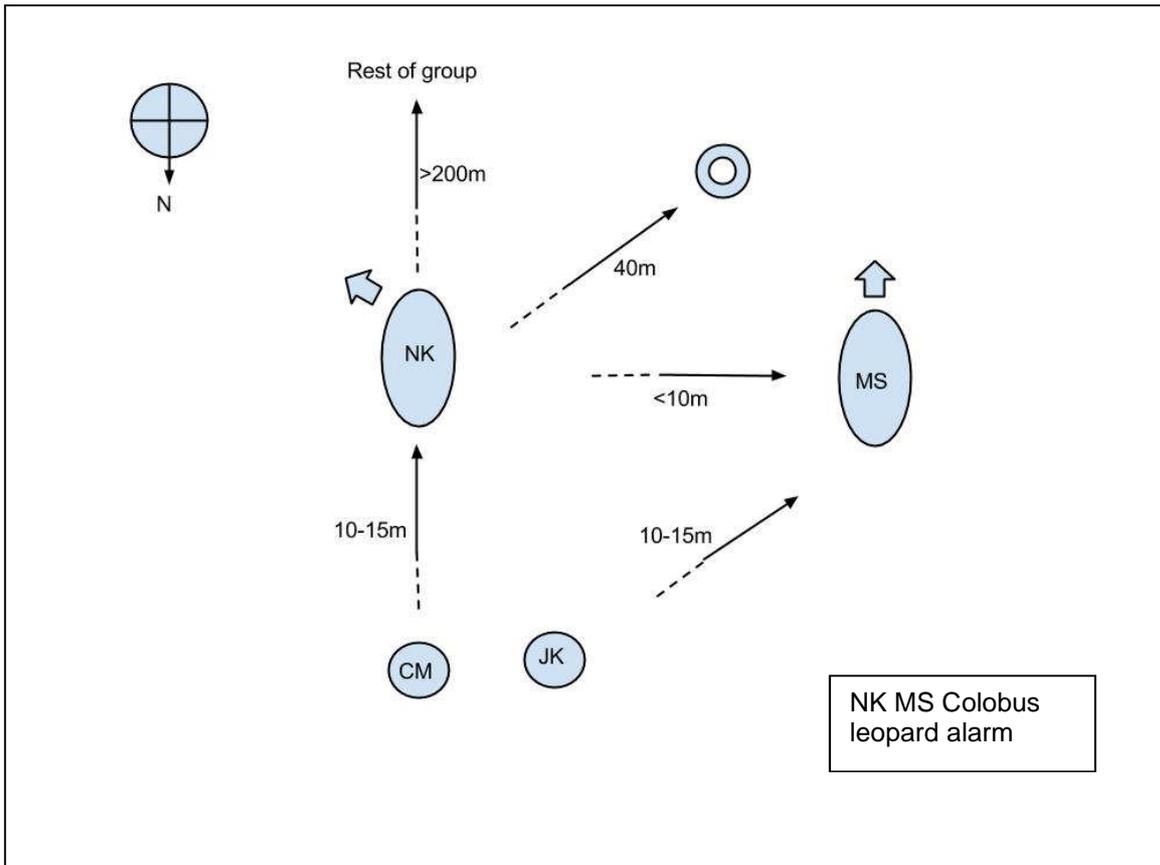
Data label	Description
Observer ID	
Date and time	Time recorded to nearest 0.04s (from video frame rate 25 frames/s)
Focal subject ID	
Partner ID	
Start location	Tree (including species and height of both partners from ground)/ on ground
Distance between subjects (m)	Distance of partner from focal subject at start of experiment
General behaviour	Resting/feeding/travelling/social/self-grooming (see appendix 2.2)
Look direction	Direction of subject's look, or head direction if eyes not visible (to nearest 15° on NSEW system). See Chapter 5 section 5.2.3 for description of observer training in assessing look direction
Playback look	Look at playback start = 1, end = 2
Partner look	Partner look start = 1, end = 2
Observer look	Look towards either human observer start = 1, end = 2
Out-of-sight individual look	Look in direction of known location of out-of-sight individuals <200m distance start = 1, end = 2
Vocalisation	Vocalisation type produced by focal subject
Vocalisation start end	Vocalisation start = 1, end = 2
Other behaviour	Notes on any gestural behaviour observed
Coding	Coding from video or commentary
Notes	Including location on grid system and environment, other individuals known <100m and their direction/location, direction/location of any Colobus monkey vocalisations or other chimpanzee vocalisations

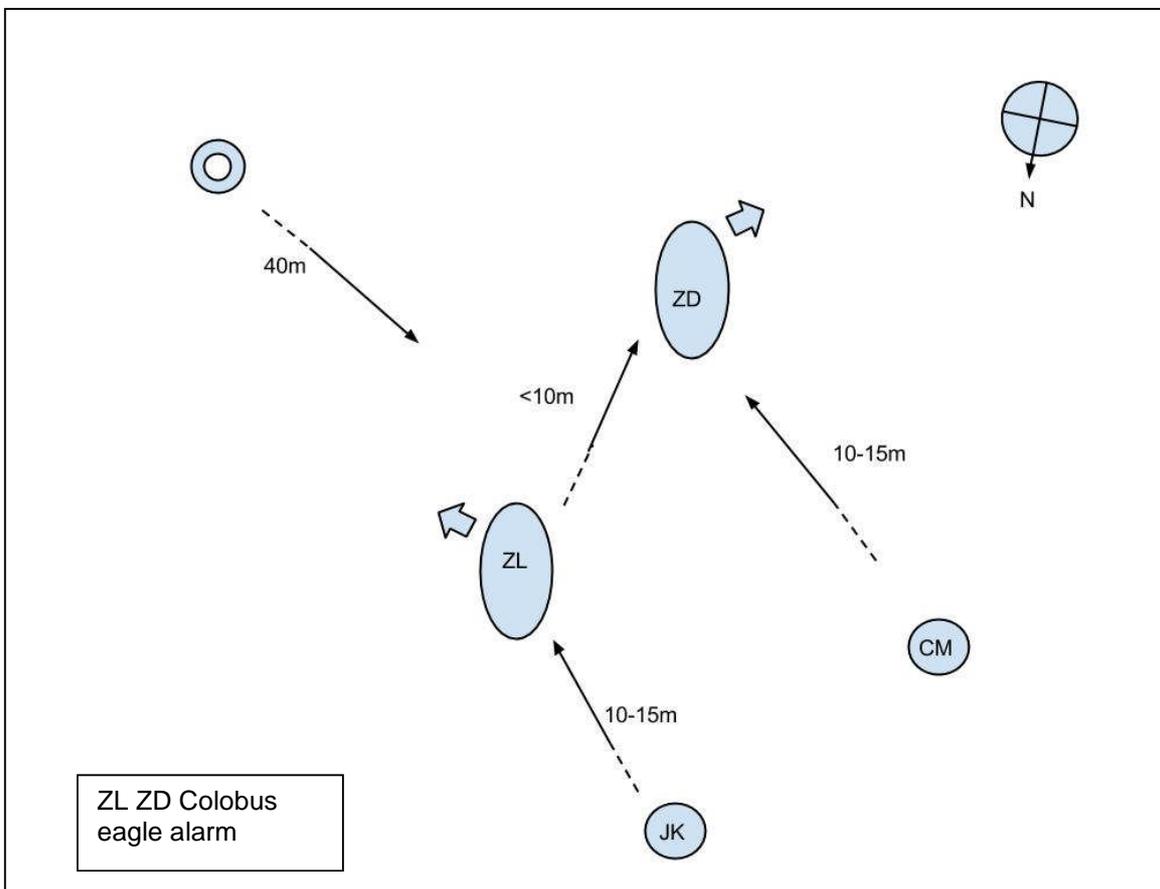
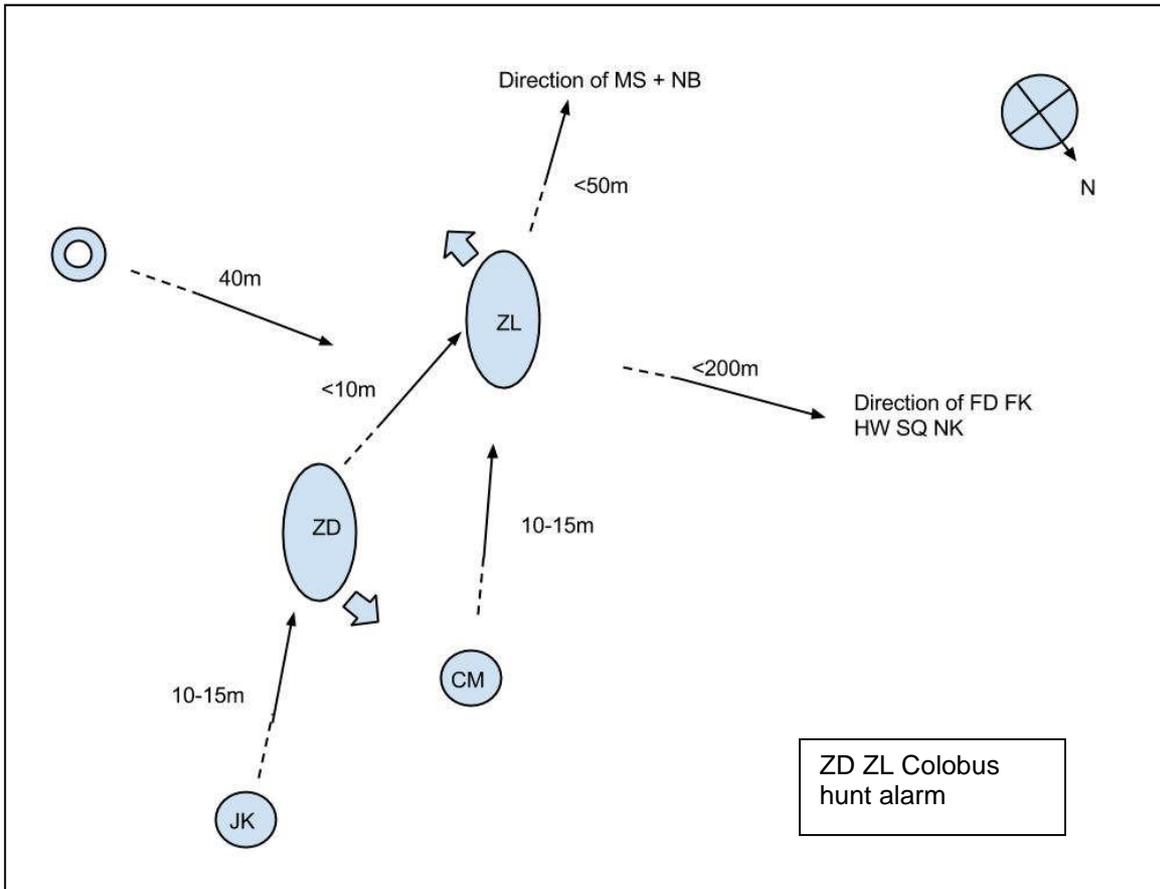
Appendix 3: Playback experiment video coding diagrams displaying experiment set-up and initial look direction of the chimpanzee upon playback of the stimulus.

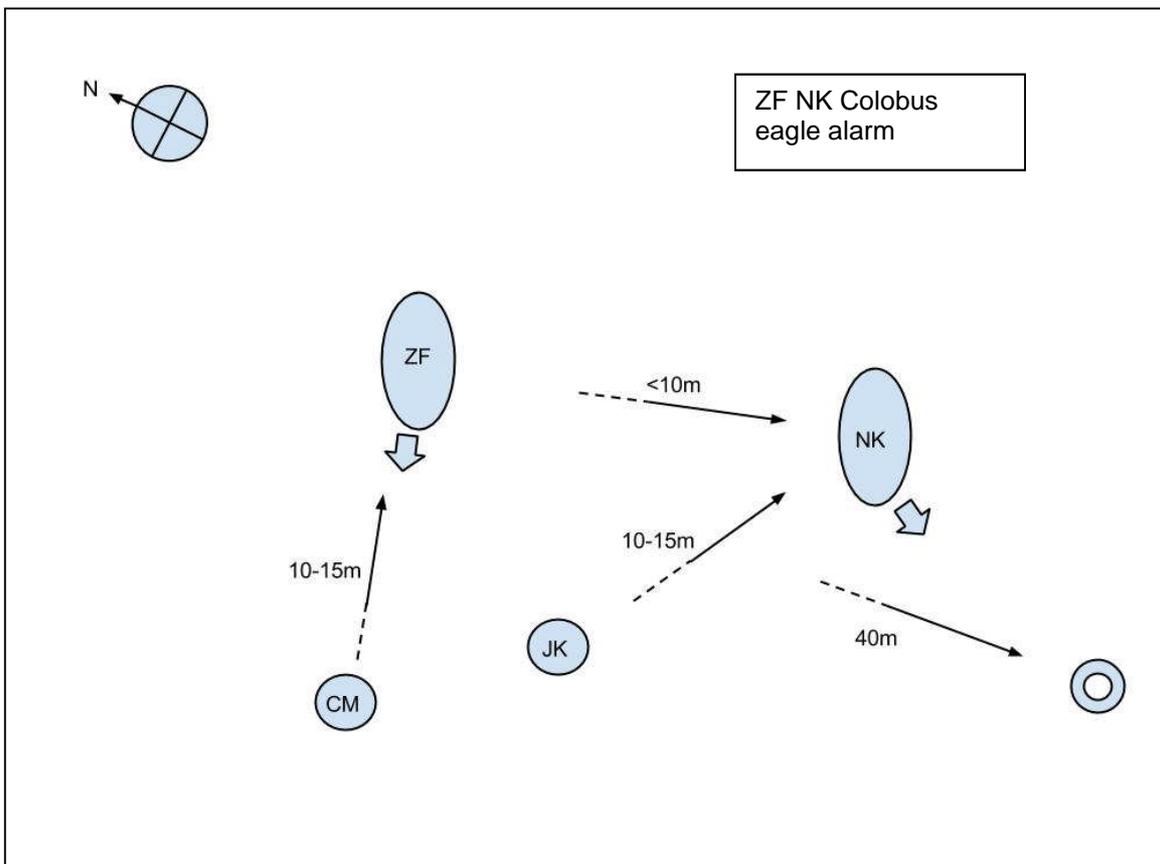
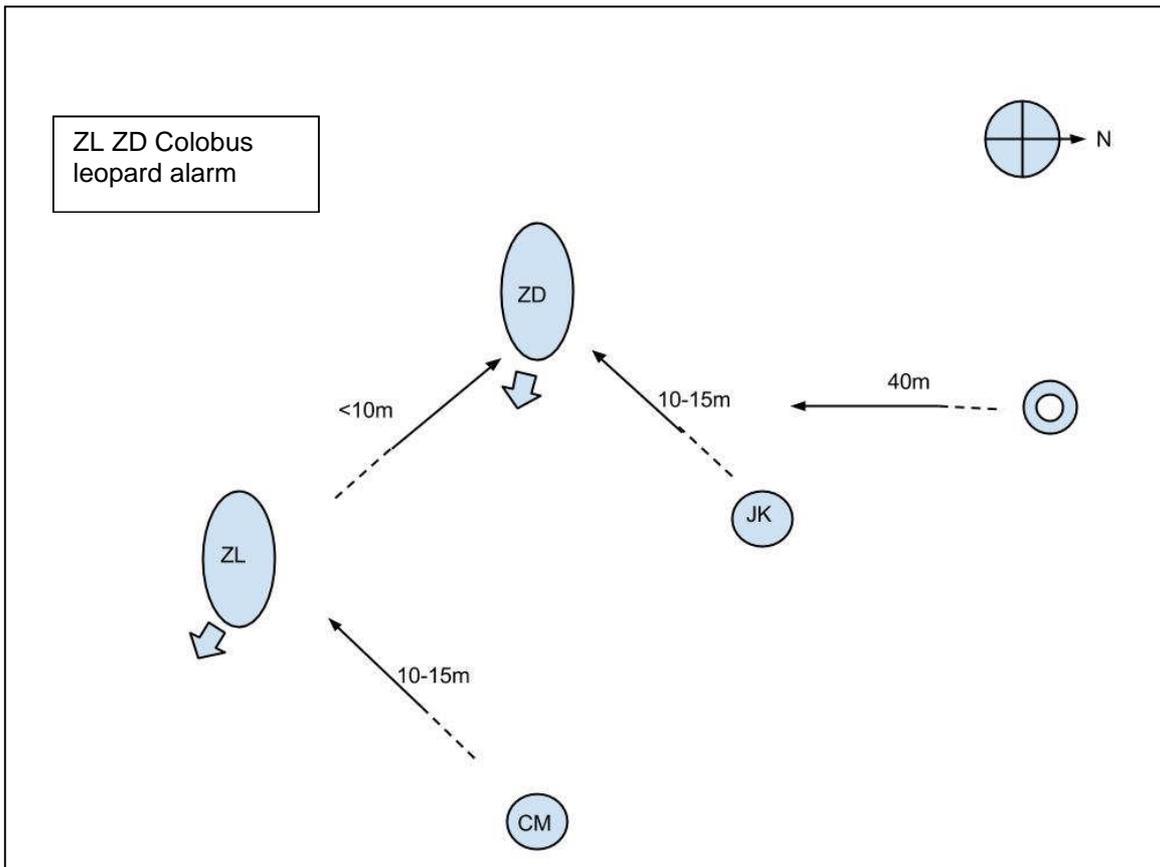












Appendix 4: Research approval from the Ugandan Wildlife Authority (UWA). Direct application for permission from the Ugandan National Authority (NFA) is not currently required (<http://www.nfa.org.ug>).



UGANDA WILDLIFE AUTHORITY
PLOT 7 KIRA ROAD KAMWOKYA
P O Box 3530, Kampala Uganda

Our Ref: UWA/FOD/33/02

19th November 2009

Mullins Caroline
32, Ravenswood Ave
Crowthorn, Berks
RG45 ^Ay
UK

RE: RESEARCH APPROVAL

I am in receipt of your application letter dated 12th October 2009 seeking to carry out research on "**levels of intentionality in the communication of wild chimpanzees (*pan troglodytes*) of the Budongo Forest**".

I am glad to inform you that your research application has been approved for you to carry out the research with effect from 1st January, 2010 to 11th November, 2011. You will be expected to submit a progress report by June 2010 and a final report by September 2012 to the Monitoring and Research Unit of the Uganda Wildlife Authority. Should you be unable to work within these dates, please notify us in writing. Please note that, any researcher failing to submit reports at the appropriate time will either not be allowed to continue with the research or in the case of the final report, will not be allowed to come back to wildlife protected areas to do further research.

You will be required to pay non-refundable research application fee of US\$ 20 and a refundable report deposit fee of US\$ 300 to Uganda Wildlife Authority in accordance with UWA Monitoring and Research Policy.

You are required by law to seek approval from the Uganda National Council for Science and Technology (UNCST). By copy of this letter, UNCST is dully informed that your research has been approved by UWA.

Since your research will be conducted in the forest reserves, you will be required to seek clearance from National Forest Authority.

Conserving for generations

Sincerely,


Anying Pamela

For: **EXECUTIVE DIRECTOR**

c.c: Executive Secretary, Uganda National Council for Science and Technology
c.c: Executive Director, National Forest Authority
c.c: Director, Budongo Conservation Field Station

Tel: 041 4355000 Fax: 041 4346291 E-Mail uwa@uwa.or.ug Website: www.uwa.or.ug

Appendix 5: Ethical approval from the University of St Andrews School of Psychology Ethics Committee to conduct playback experiments (requirement for fieldwork introduced in 2011).



University of St Andrews
School of Psychology Ethics Committee

17 May 2012

Project Title:	Coordination in wild chimpanzees: A playback experiment
Researcher' Name:	Caroline Mullins
Supervisor:	Professor Klaus Zuberbuhler

Thank you for submitting your application which was considered at the Psychology School Ethics Committee meeting on the 16th May 2012. The following documents were reviewed:

1. Animal Ethics Form 16/05/2012

The School of Psychology Ethics Committee approves this study from an ethical point of view.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (published in *Animal Behaviour*, 2003, 65, 249-255, <http://www.sciencedirect.com/>) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Prof. K. Zuberbuhler (Supervisor)
School Ethics Committee
Dr Tamara Lawson (Home Office Liaison Officer)

Appendix 6: Ugandan National Council for Science and Technology (UNCST) approval for research. (NB: Approval for the study was received from the Ugandan National Council for Science and Technology. Despite repeatedly emailing, telephoning and visiting the UNCST office in person throughout the study period, approval from the President's office (a new requirement where security information about the researcher is reviewed for clearance) was never received. Approval for the playback study was obtained from UNCST under an amendment to the permission for playback studies submitted by A.M. Schel.)

2/17/2014 Research approval, UNCST Ref. NS 277 - Outlook Web App, light version

Microsoft Outlook Web App Type here to search Entire Mailbox Options Sign out

Mail Calendar Contacts Deleted Items (1322) Drafts (48) Inbox (184) Junk E-Mail Sent Items

Click to view all folders

APE Soc (1) experiment spam-folder (21) Manage Folders...

Research approval, UNCST Ref. NS 277
Leahtabo [leahtabo@yahoo.com]

Sent: 12 January 2010 06:15
To: Caroline Mullins

Dear Ms. Mullins,

Re: Levels of intentionality in the communication of wild chimpanzees of Budongo Forest, Uganda

This is to notify you that the Uganda National Council for Science and Technology (UNCST) approved the above protocol on 6th January 2010. The approval is subject to the following conditions:

1. Payment of the research administration and clearance fee of 300 US Dollars.
Payment is made to Standard Chartered Bank Speke Road Branch; the account title is UNCST and the account number is 8705611811400. If however you wish to pay in Uganda shillings, the account number is 0105610632101. If you intend to wire the research fees, the swift code is SCBLUGKA. Note that bank charges will entirely be the researcher's responsibility.
2. Obtaining of clearance to the study districts from the Research Secretariat, Office of the President;
The process of obtaining clearance from the Research Secretariat, Office of the President is handled by UNCST on behalf of the researcher.

Note that this notification does not give you authorization to start the research. Once we obtain feedback from Office of the President, you will receive a formal approval letter to start the research.

https://animal-st-andrews.ac.uk/owa/?se=Item&IPM.Note&id=RgAAAA2HF%2bzqCP8QrcjwXwfr369vCulMM6dC9fz60y48CCKIAAAASZGBAACul... 1/2

2/17/2014

Research approval, UNCST Ref. NS 277 - Outlook Web App, light version

Yours sincerely,

Leah Nawegulo

Science Officer (Research Management)

for: Executive Secretary

UGANDA NATIONAL COUNCIL FOR SCIENCE AND TECHNOLOGY

"And the peace of God, which passeth all understanding, shall keep your hearts and minds through Christ Jesus" Philippians 4: 7

Connected to Microsoft Exchange

