GESTURAL COMMUNICATION IN WILD CHIMPANZEES

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Gestural communication in wild chimpanzees

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Abstract

Great ape gesture is an elaborate, flexible system of intentional communication. It has been suggested that human language originated in gesture, thus, the gestural communication of great apes is of great interest for questions on the origin of language. To date, systematic studies of great ape gesture have been limited to restricted captive settings, supplemented by the study of a few specific gestures in wild populations. To address questions about gestural communication from an evolutionary perspective it is necessary to extend the systematic study of gesture into a wild ape population. I therefore undertook a 22-month study of gesture in the wild Sonso chimpanzee community in Budongo, Uganda.

Sonso chimpanzees employ a large repertoire of species-typical gestures in intentional communication; a proportion of this repertoire appears to be ape-typical, as would be expected with a biologically given trait. Chimpanzees can acquire new behavioural patterns through imitation; however, this apparently does not represent a significant means of acquiring gestures. Gesturing was employed regularly in an intentional manner from the end of the first year, and was used by chimpanzees of all ages to communicate across a range of contexts, including the evolutionarily urgent context of consortship. Immature chimpanzees used a wide range of gestures, which they combined into rapid sequences. With maturity, use of the repertoire was ‘tuned’ to focus on the most effective gestures, which were then used individually. Despite the evidence for referential pointing in captive chimpanzees, there was little evidence for the regular use of it in wild chimpanzees. Gestures were used to communicate a range of imperative requests that regulated social behaviour. Chimpanzee gestures vary from the ambiguous to the highly specific in meaning; and, while gestures were used flexibly, they tended to be associated with a single dominant meaning.

Acknowledgements

"*I may not have gone where I intended to go, but I think I have ended up where I needed to be.*" (Douglas Adams, 1988).

As isolated as life in the field can be, none of it is possible, or as enjoyable, without the support and guidance of the many people who are around us in spirit if not in body. I'd like to thank my family who instilled in me not just the value of chasing your dreams but the invaluable belief that there was always a way to do so, the colleagues who became friends, and the friends who patiently found out more than they ever wanted to know about great ape gesture, and my supervisor, without whose guidance, patience, and humour none of this would ever have made it out of the tangled forest and onto these pages.

There are many moments in the forest which will stay with me; a not inconsiderable number of them involve being led through muddy swamps on endlessly wet days via what seemed to be every fire-ant colony in the forest, just to hear the chimps playing in deep undergrowth where I couldn't film them; for the 5th time that week, for the 3rd week that month. On the other hand, there were those wonderful days when suddenly the whole community joins you, and you spent the day watching their lives unfold; the barely perceived displacements that signify a critical sea change in the social hierarchy, the first stumbling steps of a tiny infant who trips over only to be caught by the massive alpha male and gently bounced on his broad chest, the manic energy of a hunt, the days when I wish I had 5 pairs of arms and 10 sets of eyes just to collect half the observations. But, as amazing as the days of big drama are, those that stick with me are the quiet moments in the green and gold where you realize why some people spend their lives in the field.

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Chapter 1. Introduction

1.1 Man the linguist?

Following Darwin's break-through in understanding our shared ancestry with modern great apes, we humans have continuously sought to define new ways to differentiate our own species from that of the rest of the animal kingdom. Initially we became 'man the tool maker' but Goodall's observation in the 1960s of a male chimpanzee stripping the leaves from a stem and using it to dip for ants, led Louis Leakey to write to her: 'Now we must redefine tool, redefine Man, or accept chimpanzees as human' (qtd. Goodall, 1998). Since then we have strenuously resisted the third option (accepting chimpanzees as humans, or perhaps more correctly accepting humans as a third species of chimpanzee (Diamond, 1991)), in favour of either redefining tool, or, more commonly, redefining Man. Our new 'unique' trait became language: the complex, flexible and universally human system of communication.

Whether or not language is unique to humans is not an easy question to address, and how and when it developed have been the subject of intense debate (Hewes, 1973, Dunbar, 1998, Pinker, 2000, Knight et al., 2000, Hauser et al., 2002, Corballis, 2002). We have learned much about the lives of our early hominid ancestors through the painstaking excavation of tools, bones, artefacts and other fossilized remains: where they lived, what they ate, even what they looked like. We can estimate the dates of different types of stone tools and trace the evolution of their design (Renfrew and Bahn, 2000), in a similar fashion we can trace the early origins of art and ornamentation (Bolus and Conard, 2001), we can even extrapolate information about religion and beliefs from burial traditions (Bowler et al., 1970, Bowler and Thorne, 1976); language, however, doesn't fossilize, making it impossible to directly trace its development in the evolutionary lineage.

It has been suggested that the entire system of language is uniquely human and stems from a single genetic mutation (Chomsky, 2007), however, this is considered extremely implausible (Dawkins, 1996) and while the expression of language may be a very recent evolutionary event, it is likely that this ability was scaffolded upon a foundation of existing cognitive competencies (Enard et al., 2002, Armstrong et al., 1994). Thus, one approach to developing theories of where and how human language evolved is to study the cognitive skills demonstrated in the communication of our closest relatives: the great apes.

1.2 Primate communication

Although reports on gestural communication date back to the first field studies of chimpanzees in the 1960s (Van Lawick-Goodall, 1967, Goodall, 1968, Plooij, 1978, Plooij, 1984), vocalizations—superficially more similar to language—appeared the logical starting place for research into primate communication, with the development of technology permitting the detailed analysis of sound and the use of playback in field experiments. This bias towards vocal communication seemed to be validated by the findings on the informational content of referential alarm calls in monkeys (e.g. Seyfarth and Cheney, 1980a, Cheney and Seyfarth, 1990), and the finding of some signs of meaning changes when calls are combined (Seyfarth et al., 2005, Arnold and Zuberbühler, 2006, Arnold and Zuberbühler, 2008). However, work of this kind also demonstrated that, unlike language, primate vocalizations are unlearned, at least in their form. Furthermore, while primates hearing conspecific calls are able to extract a wide range of information from them, it is less clear that signallers produce these calls with the intention of communicating this information to others (Rendall et al., 2009). The most highly referential calls are the ‘alarm calls’ produced to give warning of potential predators and the focused nature of their use makes it difficult to establish the flexibility of calling in general. Perhaps most crucially for anthropology, while this work has now been repeated in a range of monkey species (Vervets: Seyfarth and Cheney, 1980b; Diana monkeys: Zuberbühler, 2000; Black-and-white colobus: Schel et al., 2009), to date there is little evidence that apes have similarly referential vocalizations (although see: Slocombe and Zuberbühler, 2005) and, nearly 50 years after Goodall started the systematic investigation of wild chimpanzee behaviour, little has been found to challenge her claim that that the ‘production of sound in the absence of the appropriate emotional state seems to be an almost impossible task for a chimpanzee' (Goodall, 1986 p.125), so that it is unlikely that human language evolved from a system based upon these types of vocalizations.

In parallel with the work on the communication of wild primates, a group of studies examined the extent to which captive apes could be taught language. The seminal study by Hayes and Hayes described their observations of a young female chimpanzee, Viki. Adopted and raised 'as nearly as possible like a human child' from birth (Hayes and Hayes, 1951), Viki's development showed many parallels with that of human children; however, critically, she failed to acquire speech. Even following the instigation of an intensive speech-training program at 5-months old, by the time she reached 3-years old she had only acquired three poorly vocalized 'words' (mama, papa, cup), and by 6-years old had added only a single extra 'word' (up) (Hayes and Hayes, 1951, Hayes and Nissan, 1971). This failure to add to her vocal repertoire led the authors to described language as 'the one field of behaviour in which we have thus far been able to find a large, clear-cut, and important superiority of man over chimpanzee' (Hayes and Hayes, 1951).

In contrast to their relatively limited control of vocalization, great apes display great manual dexterity and have a large range of movements available in the shoulder, elbow and wrist (Tanner and Byrne, 1999). This bias, together with reports on the use of gestural communication in wild chimpanzees (Goodall, 1968), led Gardner and Gardner to revisit the idea of language training with an ape, but using gesture rather than speech. The Gardners adopted the female chimpanzee Washoe at around 1-year old and reared her within an environment where all communication was conducted with American Sign Language (ASL). The results were dramatic: Washoe quickly acquired a large reliable repertoire of ASL signs (30 within 22-months; 133 over her life time), and, at an early stage, started to combine them spontaneously (Gardner and Gardner, 1969, Gardner et al., 1989). She went on to use these signs towards other chimpanzees, including her adopted son Loulis, who himself acquired a rich vocabulary of signs directly from his mother and other ASL trained chimpanzees (the researchers carefully avoided signing in his presence) (Fouts et al., 1989).

The capacity to acquire a large repertoire of ASL gestures and to use them in a meaningful fashion has now been demonstrated in both gorillas (Patterson, 1978, Patterson et al., 1988), and orang-utans (Miles, 1990). Bonobos have shown a similar capacity to acquire and use a large number of signs when employing a keyboard of lexigrams, and appear to be able to combine them in a meaningful fashion (Savage-Rumbaugh et al., 1985, Savage-Rumbaugh et al., 1986). Thus, the evidence that great apes can be taught to communicate with gesture but not speech, along with the evidence that the vocalizations of great apes are largely fixed and under emotional control, suggests that a system of gestural communication, rather than vocalizations, may have provided the platform for the development of human language.

1.3 Gestural origin theory

The theory that human language may have its roots in gestural communication has been around since at least the 18th Century, when the sensationist philosopher Bonnot de Condillac described language as developing from the 'language of action' (Bonnot de Condillac, 1714-1780/2002). However, the shift in scientific focus towards the role that gesture takes in primate communication led to a revival of the gestural origin theory in the seminal article by Hewes (Hewes, 1973). Building upon the work of Hewes, the gestural origin theory was further developed, notably by Armstrong and colleagues (Armstrong et al., 1994, Armstrong et al., 1995), and most recently by Corballis, (Corballis, 2002, Corballis, 2003) whose position can be summarized as follows.

Given the relatively fixed nature of vocalizations, and the evidence for a rich detailed repertoire of gestures in wild apes, it is likely that the common ancestor of humans and great apes had a similar bias towards gesture in flexible intentional communication. This bias may have originated as a result of the manual flexibility developed while living as an arboreal primate, and which, on descent from the trees, could have been exapted into a manual gestural system of communication. The bipedalism in the human line would have provided further opportunities for manual communication. Gestures involve movements of the face as well as the hands, and while vocalizations may have originally functioned as ‘emotional accompaniments’ to gestures, the increasing involvement of forelimbs in other activities such as manufacture may have promoted a shift towards the involvement of the face in communication. It could even be argued that there is a continuous transition from manual gestures of the fingers and hands, to vocal gestures of the tongue and larynx. Certainly there appears to have been a strong selective pressure towards the development of the vocal tract, as this occurred despite the fact that the modifications that enable speech also leave humans particularly vulnerable to choking. Indirect evidence for the gestural theory of origin is provided by the fact that these modifications did not occur until relatively late in the genus *Homo*, suggesting that communication before this point was dependent on manual gesture. The shift to autonomous speech may have only occurred as recently as 50,000 years ago, freeing the hands for use in manufacture, and facilitating teaching; both of which may have been advantageous in the migration into new environments (Corballis, 2002, Corballis, 2003).

While a well-developed argument, this sort of evolutionary theorising inevitably relies on rather sweeping interpretation of very patchy data and can thus be difficult to defend against alternative interpretations (the 2003 Corballis article is followed by 37 published peer commentaries, the majority of which, if not seriously critical, offer alternative explanations for major points in the theory (Corballis, 2003)). However, a parallel body of research in the field of neuroscience also supports a gestural theory of origin. For example: Broca’s area, traditionally considered the ‘seat of language’ in the brain, appears to be intimately connected with fine arm and hand movements (Kimura and Archibald, 1974, Fadiga et al., 2006), and the homologue of Broca’s area in the monkey brain (region F5) is involved in controlling physical gesture rather than vocalization (Rizzolatti and Arbib, 1998). A recent study of chimpanzee gesture found a right-hand preference when gesturing to other chimpanzees, but not in other, non-communicative actions. It has been suggested that this mean that, like human language, chimpanzee gesture is left lateralized in the brain (Meyuerditchian et al., 2010), although this logic is considered controversial, as the correlation between handedness and language lateralization is not straightforward (see: McManus, 2002).

Thus, because of the natural human tendency to understand the development of language as our 'unique' trait, there has been considerable interest in the development and nature of gesture, both in our own species, and in those with whom we most recently shared a common ancestry. Of course modern great apes have undergone their own evolution in the period following the divergence of the human line, and it would be inappropriate to treat them as a simple model for ancestral human behaviour (Lovejoy, 2009). Nevertheless, in better understanding the gestural communication of modern chimpanzees we may be able to identify shared cognitive capacities that likely existed in our most recent common ancestor, and from this address the question of whether or not there are truly unique capacities that would justify the distinction between the Genera *Homo* and *Pan.*

1.4 Great ape gestural communication

One of the first descriptions of great ape gesture dates to 1935, when the Russian psychologist Nadezhda Nikolaevna Ladygina-Kohts described the natural facial expressions and hand gestures of the young captive chimpanzee Joni (Ladygina-Kohts, 1935/2002). However, it was Goodall, in her pioneering work at Gombe in the 1960's, who first highlighted that, in contrast to the affect laden vocal repertoire, it was the rich repertoire of chimpanzee gestures that might be used to communicate information (Goodall, 1968, Van Lawick-Goodall, 1972). Plooij developed these observations, and noted several features of chimpanzee gesture that appeared to demonstrate the basic traits of human language (Plooij, 1978). He reported that, in addition to parallels in the development of infant chimpanzee gesturing and infant human speech, the regular combination of gesture types and the use of the same gesture forms in different contexts suggests 'openness, which is one of the most characteristic design features of human language' (Plooij, 1978, p.130). Although there has been no systematic study of gestural communication in wild apes, more recent studies have paid attention to a few specific gestures, such as the grooming hand-clasp (McGrew et al., 2001), directed scratching (Pika and Mitani, 2006), and leaf-clipping (Nishida, 1980, Matsumoto-Oda and Tomonaga, 2005), which have been used to demonstrate interesting inter-group differences.

Tomasello instigated the first systematic examination of the nature and development of gesturing in a captive group of chimpanzees in a series of studies over a period of 9-years (Tomasello et al., 1985, Tomasello et al., 1989, Tomasello et al., 1994). More recently this has been extended to include bonobos (Pika et al., 2005b), gorillas (Pika et al., 2003, Pika, 2007, Genty et al., 2009, Genty and Byrne, 2010), orang-utans (Liebal et al., 2006, Cartmill and Byrne, 2007, Cartmill, 2009) and siamangs (Liebal et al., 2004b). Their work focused on the development of gestural communication within individuals and has provided the most compelling evidence for the intentionality and flexibility of gestural communication.

In parallel, Tanner and Byrne provided a longitudinal account of the gestural repertoire of gorillas at the San Francisco zoo. They showed a specialized gestural repertoire, within which even greater flexibility was shown: iconic reference, indicating desired movement paths; some level of intentional deception, by hiding of play-face; and both triadic and collaborative social interaction, in object-related play (Tanner and Byrne, 1993, Tanner and Byrne, 1996, Byrne and Tanner, 2006, Tanner and Byrne, 2010). More recent work on gorilla and orang-utan gesture has started to address the question of the function of gesturing, presenting evidence that great ape gestural communication is used to convey imperative requests that modulate social interaction (Genty et al., 2009, Cartmill and Byrne, 2010).

One of the most familiar examples of human gesture is in pointing. Pointing requires the cognitive ability to direct another individual’s attention to an external object: a triadic, rather than simply dyadic, interaction. If the triadic communication occurs in the pursuit of a shared goal, this is categorised as collaborative interaction. These more complex triadic and collaborative social interactions have been argued to be uniquely human (Tomasello et al., 2005). For this reason, particular attention has been paid to questions of whether great apes point, and if so, under what circumstances? (Call and Tomasello, 1994, Povinelli and Davis, 1994, Leavens et al., 1996, Povinelli et al., 1997, Leavens and Hopkins, 1998, Leavens and Hopkins, 1999, Leavens et al., 2004, Leavens et al., 2005a, Tomasello, 2005, Gómez, 2007).

1.5 So what is a gesture?

At this point it's worth pausing briefly to discuss what exactly is meant by a gesture, and which features distinguish them from primate vocal communication. A wide range of definitions exist within the gesture literature, from studies with a specific focus on the movements of the hands, wrists, and fingers (Pollick and de Waal, 2007, Pollick et al., 2007), to studies which include facial expressions, patterns of locomotion, and even postures (King, 2004, Tomasello et al., 1989).

To be defined as a gesture, a movement should not be physically effective in achieving the goal of the communication; otherwise it is simply an action (Cullen, 1972). For example, Pollick and DeWaal require that a gesture 'visibly lacks the mechanical force to bring about the reaction shown by the recipient' (Pollick and de Waal, 2007, p.8185). Furthermore, as described earlier, one of the critical distinctions between the gestural and vocal communication of great apes is the intentional nature of gestural communication. Not all bodily movements are intentionally communicative, and there is disagreement between studies as to which movements should be included as gestures. For example: after picking up a plate I may furrow my brow and open my mouth in shock, and from this you might well extract the information that the plate was hot; but this is quite distinct from my deliberately choosing to gesture in order to warn you that it is. Similarly, in great apes there is evidence that facial expressions are more automatic and under less voluntary control than manual gestures. A young female gorilla was repeatedly observed to hide her, apparently involuntary, 'play-face' expression by using her hands to cover it (Tanner and Byrne, 1993). Nevertheless, some studies continue to include facial-expressions as intentional gestures (e.g. pout-face: Tomasello et al., 1994).

As well as in the intent to communicate, rather than achieve their aim by mechanical effective means, another key difference between gesture and vocal communications is in their flexibility. Unlike the stimulus driven nature of primate vocalizations, the flexibility of gestures is demonstrated in the use of individual gestures for multiple purposes, and multiple gestures for a single purpose. Plooij first identified the flexible nature of gesture, describing the use of individual gestures in multiple contexts (Plooij, 1978). Appropriate choice of modality of an individual gesture represents a further expression of flexibility, along with showing some recognition of the importance of another's attentional state. Tomasello et al. found that juvenile chimpanzees used visual play signals when the recipient was in a position to receive them, and tactile or auditory gestures when the intended recipient's attention was diverted elsewhere (Tomasello and Call, 1994). This 'audience effect' has now been replicated in several species (orang-utans: Liebal et al., 2006; gorillas: Tanner and Byrne, 1996, Pika et al., 2003, Genty et al., 2009; siamangs: Liebal et al., 2004b).

1.6 How do great apes acquire their gestures?

In their work with the Gombe community in Tanzania, Goodall and Plooij provided the earliest descriptions of the acquisition of gestures by young chimpanzees (Van Lawick-Goodall, 1972, Plooij, 1978). Plooij suggested that gestures are acquired as an infant gains awareness of the 'signal value' of his actions and starts to use them to deliberately engender his mother's interaction; with maturity these actions are then produced in a ritualized form. He also described the acquisition of at least one gesture, 'lies on back and reaches' (a play invitation) as arising through a process of 'social negotiation', whereby the older partner develops the gesture through a process of trial and error in response to the infant's behaviour (Plooij, 1978). Plooij's description of the conventionalization of action into gesture inspired the now dominant theory for the acquisition of gestures: Ontogenetic Ritualization. Developed by Tomasello and Call ontogenetic ritualization proposes that gestures are ritualized from full, instrumental actions into a symbolic, shorthand gestures (Tomasello et al., 1985). Current studies still use the language of 'conventionalization' (Pollick and de Waal, 2007); however, a recent study of gorilla gesture from several captive groups has suggested that the flexible use of a large species-typical repertoire is a more appropriate explanation (Genty et al., 2009).

The anthropologist King has adopted a different approach to the study of communication, and suggests that gestures are mutually constructed through the 'co-regulation' of behaviour (King, 2004). While this seems initially similar to the ritualization of action into gesture in ontogenetic ritualization, they differ in the dynamic two-way nature of co-regulation as opposed to the creation of fixed one-way gestures through ritualization.

Although several studies have now examined the capacity for captive apes to acquire novel gestures through imitation (Hayes and Hayes, 1952, Custance et al., 1995, Byrne and Tanner, 2006), this is not considered to represent a significant means by which they acquire gestures within their natural communication (Tomasello et al., 1989, Tomasello et al., 1994). Indeed, the frequently imperfect nature of the imitations led Byrne and Tanner to suggest that these cases may reflect the facilitation of rare actions in the large existing repertoire. By looking back over 11-years of data, they were able to demonstrate that this was in fact the case (Byrne and Tanner, 2006).

1.7 How do great apes use their gestures?

Tanner and Byrne describe the intentional use of *iconic* gestures in a pair of captive gorillas (Tanner and Byrne, 1996). It has been argued that these actions could be seen as ritualized forms of incipient action (Pika et al., 2005a), although the gorilla actions were not incomplete versions of any full, instrumental act, and can therefore be considered iconic. The use of iconic gestures may represent a critical stage in the development of an arbitrary symbolic system of communication such as language (Tanner and Byrne, 1996); however, current evidence for the capacity appears to be limited, even amongst captive apes (although see: Savage-Rumbaugh et al., 1977). Thus, while the potential to develop iconic gesture may be present in great ape communication, the regular use of iconic gestures does not appear to develop under natural circumstances.

The possible subdivision of gestures into different types, such as ritualized, iconic, or species-typical, makes the analysis of gestural sequences particularly interesting, as the possibility is opened for intentional combinations. For example: the combination of a meaningless but loud 'attention getting' gesture, followed by a meaningful silent informative gesture, as suggested by Tomasello & Call (1994), however, to date there is little evidence to suggest that this occurs. These authors described a specific case where an individual used an ‘attention getter + facial expression’ combination, but otherwise concluded that multiple gesture communications were being used to achieve the same aim as the individual gestures when used separately (Tomasello et al., 1994). This interpretation was supported by the work of Liebal et al. who again found no evidence that captive chimpanzees use ‘attention getters + informative gesture’ combinations (Liebal et al., 2004a), and that of Genty et al. (2009) who found no evidence for a category of purely attention getting gestures.

Although there appears to be little evidence for the combination of different types of gesture, the use of gesture sequences is common to the gestural communication of all great apes (Liebal et al., 2004a, Pollick and de Waal, 2007, Cartmill, 2009, Genty and Byrne, 2010). Liebal et al. provided the first quantitative analysis of sequences in chimpanzee gesturing, concluding that they were produced in a post-hoc fashion after the recipients failed to react to the first gesture. Tanner did find some evidence for the use of multiple gesture communications to convey more than simply re-emphasis of a single message between two captive gorillas (Tanner, 2004). However, Genty & Byrne failed to find a similar effect when looking at the gestural communication of several groups. They also failed to find any support for the hypothesis that sequences result from failure to receive a response, and instead suggest that they function as a form of ongoing dynamic modification of the interaction (Genty and Byrne, 2010).

1.8 When do great apes use their gestures?

Play is the behavioural context within which the largest proportion and greatest variety of gesturing occurs in captivity (Tomasello et al., 1985, Tomasello et al., 1994, Tomasello and Call, 1997, Pika et al., 2005b, Genty et al., 2009). Play is also the main context within which gestural sequences occur (Tanner, 2004, Genty and Byrne, 2010). As compared with the contexts of feeding, sexual behaviour, or agonism, during play any misinterpretation of a conspecific's communicatory intentions would have relatively less impact on individual fitness. This allows greater opportunity for flexibility and experimentation in forms of communication; as play behaviour may include mock forms of fighting, sex, infant care, etc., the breadth of context may also result in greater need for specificity in gestural communication. However, the focus on captive groups may have exaggerated the dominance of play. Individuals in captivity spend less time in foraging and feeding (Celli et al., 2003), and immature individuals are more likely to have peers of their own age close by, thus the captive environment may promote play activity and by association the use of gestural communication by immature chimpanzees.

While gesturing occurs across all age groups, there appears to be a consistent peak among subadults in the volume and variety of gestures produced in captive ape populations. In contrast there is a dearth of information on adult gesture in captivity, predominantly because of the low level of gestural communication displayed in captive adults (Tomasello et al., 1994, Tomasello and Call, 1997). However, this could be because zoos are unable to present relevant opportunities for the use of gesture by adults. Certain contexts, which may promote the use of gesture in adult chimpanzees, are simply not available in captivity. For wild chimpanzees, patrolling the boundary between territories increases the chance of coming into lethal contact with individuals from other groups, and sequestering a sexually receptive female on consortship away from the other males within the group can result in aggressive attack from more dominant individuals who would normally enjoy the majority of sexual access. In both cases there may be a strong selective pressure towards discreet forms of communication. Within the dense secondary rainforests of Africa, where visibility can be highly restricted, a silent gesture can be easily limited to its intended recipients, unlike a vocalization. Thus, in a wild population, there may be contexts that promote the use of gestural communication in adult chimpanzees.

1.9 Aims of this study

To date the studies of gestural communication in great apes have either adopted a systematic approach with small captive groups, or a focused approach on the use of single gestures in the wild. However, small captive groups are not simply scale models of natural ape populations. Natural chimpanzee communities are large multi-male, multi-female groups, in which individuals and mother-offspring family units often travel in small parties, exploiting a large forest territory by fission-fusion ranging. In contrast, the constraints of captivity include small group sizes, unnatural group composition (such as one-male, multi-female chimpanzee groups), small enclosures with limited environmental variation and the risk of human influence, all of which restrict the extent to which we can employ findings from captivity when considering questions about the communicative and cognitive abilities of chimpanzees from an evolutionary perspective. As well as the potential effect of the captive environment on behaviour, most captive studies are based on short periods of intensive observation (Tomasello et al., 1985, Liebal et al., 2004a, Pika et al., 2005b), with even longitudinal work conducted as a series of brief snap-shots (Tomasello et al., 1994). This method limits the range of behaviour recorded from the already small sample sizes available, and is thus vulnerable to exaggerating apparent variation between individuals, groups or time periods, making it less suitable for addressing questions of species behaviour.

To address questions about the nature of great ape gesture from the evolutionary perspective it is critical to undertake the systematic study of gestural communication in a wild population, living within a natural social and physical environment. In this study I aimed to address this need directly with a 22-month study of the wild Sonso chimpanzee community in the Budongo forest in Uganda.

I aimed to establish a complete repertoire of intentional gesture in the Sonso community, and to examine gesturing across the full range of age groups, and behavioural contexts available in a natural population. In doing so I hope to address questions about whether or not the gesturing of wild chimpanzees supports the acquisition of gesture through ontogenetic ritualization, or the new view of a species-typical repertoire, and to determine to what extent gesturing occurs within evolutionarily urgent contexts, or contexts that might promote the use of silent communication. Through a quantitative analysis of gestural sequences I hope to explore when and where sequences of gestures are used, and the motivation for the combination of gestures.

I aim to examine what a natural population of chimpanzees uses gestural communication for, including whether or not there is evidence for the use of referential gestures. In doing this I hope to provide insight into the cognitive capacities demonstrated in the natural gestural communication of a great ape.

Chapter 2. General Methodology

2.1 Study site

The Budongo Forest Reserve lies in the western Rift Valley in Northwestern Uganda (1°35' – 1°55'N, 31°18'-31°42' E) at a mean altitude of 1050m. Running adjacent to Lake Albert and extending up into the large Murchison Falls National Park, the 793km^2 Reserve contains a total 482km^2 of continuous medium altitude semi-deciduous forest cover (Eggeling, 1947).

2.1.1 The Budongo Forest

A rich source of hardwood, the first sawmills were established in Budongo in 1926 and quickly grew to be among the largest in East Africa, with the large Budongo Sawmills Company producing upwards of 600 tons of sawn timber per month (Reynolds, 2005). Much of this was exported to Europe (the floor of the Royal Albert Hall is Budongo *Cynometra* (Ironwood)). As a result the forest today is predominantly secondary forest growth; although all legal logging has halted, illegal logging continues, and only a handful of old-growth trees remain in the northern tip contained by the Murchison Falls National Park. From a research perspective, the dense secondary growth frequently restricts ground visibility to less than 6m, and increases the challenge of locating and following specific individuals.

2.1.2 Budongo primates

The Budongo forest supports two species of prosimian: potto (*Periodicticus potto*) and bushbaby (*galago* spp. unconfirmed); four species of monkey: baboon (*Papio anubis*), black and white colobus (*Colobus guereza*), blue monkey (*Cercopithecus mitis stuhlmanni*), and redtail monkey (*Cercopithecus ascanius schmidti*); and one species of great ape: chimpanzee (*Pan troglodytes*).

Recently estimated to include 584 individuals (Plumtree et al., 2003), the chimpanzee population is divided into a number of communities, one of which, the Sonso community (which takes its name from the old sawmill site at the heart of their home range) has been habituated to observation. Other communities are referred to in terms of the location of their territory relative to the Sonso community, for example: the Eastern, or the Northern community.

2.1.3 The Budongo Conservation Field Station

The first observations of chimpanzee behaviour in Budongo took place in 1962 when Vernon and Frankie Reynolds conducted an 8-month observational study of un-habituated chimpanzees (Reynolds and Reynolds, 1965). These initial observations were followed by a 6-month study of social structure in 1966 (Sugiyama, 1968), but the intense political turmoil that engulfed Uganda over the next two decades meant that, while Tanzanian sites such as Gombe and Mahale became established research centres, Budongo fell back into obscurity and, surrounded by villages whose populations had swelled with refugees from the war, the forest became a rich resource for poachers and hunters. When Professor Reynolds was able to return in 1990, it was clear that the forest, and the communities of chimpanzees that it supported, were under serious threat. This time it was possible to set up a long-term research base within the forest, and over the years this developed into the Budongo Forest Project, now known as the Budongo Conservation Field Station (BCFS).

20-years later, the field station is a well-established, and internationally renown research centre. Set up in a clearing approximately 3km inside the forest on the site of the old Sonso sawmill are sleeping quarters, a kitchen, office, and even a library and laboratory. A permanent Ugandan staff either lives on site, or commutes in daily from villages bordering the forest; this includes 8 highly trained chimpanzee field-assistants, 3 of whom have been with the project from its earliest days. As well as the research side, BCFS has an education team that works in local villages and schools explaining the importance of conserving the forest as a resource for the future. One of the key conservation programs employs ex-hunters as snare-removers. The team works to clear the forest of the illegal traps that can kill or maim the chimpanzees and, in return, as well as providing a stable income, BCFS supports a pig breeding program so that an alternative source of meat is available to the local communities.

A 100m x 100m grid system of cut trails is well established over approximately 6km^2 surrounding the research centre, and covers the core area of the Sonso chimpanzee community territory. The community's use of areas within the territory varies between years and seasons. Recent incursions by the neighbouring Eastern community into the central areas of established Sonso territory appears to have displaced the core area slightly and the community may spend days and even weeks away from the main grid system.

2.1.4 Long term BCFS data-collection

As well as collaborating with visiting researchers on a wide range of research programs, field-assistants collect data for the long-term project records on a daily basis. These include: chimpanzee party composition, ranging, and the form, frequency and duration of behaviours such as vocalization, grooming, feeding, copulation and physical aggression (Zuberbühler and Reynolds, 2005).

2.2 The Sonso chimpanzee community

At the start of data collection in October 2007, the Sonso study community of chimpanzees consisted of 81 named individuals. A full list of names and ages is provided in Appendix 1, along with mother-offspring family trees that indicate paternity where this was known. Site rules stipulate that researchers maintain a distance of 3 meters from chimpanzees, and make no responses to any chimpanzee behaviour directed towards them. However, while researchers obey this rule the chimpanzees do not necessarily do so, particularly those immature individuals who were born to habituated females and who have always been exposed to the presence of researchers. As the site took the decision not to habituate individuals to observation using food, we are generally treated as slightly odd, occasionally inconvenient obstacles that are better off ignored. There are several exceptions; for example the young male Zig who, as the result of a bad snare injury is quite underdeveloped, but who has learned that he can very successfully terminate a challenge from his larger peers by sitting down next to us. Nevertheless, in general, the Sonso community provides an excellent opportunity for close observation of natural chimpanzee behaviour.

Female chimpanzees have a smaller range than males, generally located within the male chimpanzee community territory (Wrangham, 1979). As a result adult Sonso females are conventionally distinguished as *core*, *peripheral* or *rare* on the basis of their regular range and, to a lesser extent, their likelihood of being found in a social group with other Sonso chimpanzees (female status is listed in Appendix 1). *Core* females spend the majority of their time within the central area of the community territory; *peripheral* females spend the majority of their time in areas bordering (and sometimes overlapping) the territory of other communities. *Peripheral* females are still encountered on a regular basis (normally seen at least once per month with no prolonged absences) and are thus distinguished from *rare* females about whom very little range information is known and who may be absent for months or even years, sporadically rejoining the community for a few weeks or months before disappearing again. These *rare* females appear to be members of more than one community, however, in the cases where they are seen repeatedly over several years and can readily be recognised they are assigned a Sonso name and letter code. On at least 2 occasions un-named females have 'immigrated' to Sonso accompanied by almost mature male offspring. This extremely unusual situation has suggested the possibility that these females (and their sons) were originally rare or peripheral Sonso members who have returned after a long absence; and that this status as previous group members, with a possible Sonso paternity, would account for the acceptance of the males into the Sonso hierarchy.

2.2.1 Age and age groups

The definition of developmental categories in the chimpanzee literature tends to employ chronological age, only resorting to physical and behavioural characteristics (e.g. adult males = 'testicular development complete, face black, dominates females and challenges males' (Reynolds, 2005, p.36)) where chronological data is unavailable. While physical and behavioural characteristics are perhaps more appropriate for describing development they rely on a subjective assessment, which may vary between observers, particularly those at different sites where methods of researcher training and observation techniques may differ considerably. Although division by chronological age is, to a certain degree, quite arbitrary (today you are an infant, tomorrow on your 5th birthday you will be a juvenile – irrespective of any apparent development in your physiology or behaviour), it does allow for a consistent method of assigning age group.

At Sonso we are in the fortunate position of knowing the year, and frequently the month of birth for the majority of juvenile individuals. Age was recorded in years for all individuals, and for individuals under 5-years old an estimate in months was also recorded. Outside of detailed developmental analyses, individuals were assigned to one of 4 basic age groups:

1. Infant (<5years)
2. Juvenile (5-9years)
3. Sub-adult (female: 10-14years, male: 10-15years)
4. Adult (female: >15years, male: >16years).

Using these categories, the initial distribution was 32 adults (7 males and 25 females), 16 sub-adults (10 males and 6 females), 15 juveniles (6 males and 9 females) and 18 infants (3 males and 15 females). Over the course of the 22-month study there were 10 deaths or long-term disappearances, 6 immigrations and 5 births, leaving the final total at 82.

2.3 Training

In gestural analyses, the quality of observational data depends heavily on the extent to which the observer has been able to distinguish gestures from other, locomotor and non-communicative behaviour, and whether they are able to record evidence of any intention behind the gesturing. In preparation for this project I spent the first 8 months of my Ph.D. working within an existing project looking at gestural communication in Western Lowland Gorillas (*Gorilla gorilla gorilla*), part of the EU-funded Referential Communication project at St Andrews. I worked within the team to identify individual gestures in high quality video footage obtained from one field site and a number of captive groups, cutting observation footage of social interaction to relevant segments of gestural communication and coding these within a specifically developed database. I then isolated subsets of data and coded them in terms of context, degree of recipient attention, gestural modality (silent, audible, contact), length and form of gestural communications, and the outcome of these interactions. This process was entirely representative of the analyses that were needed for the data collected in my own study, and therefore provided an excellent period of training and development of the skills required. Furthermore, in 2005 I conducted a separate project on forest-based ecology in the savannah baboon (*Papio cynocephalus anubis*) at the Budongo Conservation Field Station. This provided the opportunity to develop a methodology specifically suited to the site facilities and surrounding terrain, promoting accurate and efficient data collection in the current study.

2.4 Procedure for data collection

My methodology for data collection is based on the protocol used in the E.U. Referential Communication project on gorilla gestural communication at St Andrews. These methods are consistent with those established throughout the recent literature (Genty et al. 2009, Pika et al. 2003-5, Tanner & Byrne 1993-6, Tomasello et al. 1985-97).

Observations were made on all chimpanzees within the Sonso community during three field periods between October 2007 and August 2009 (Oct 07-Mar 08; Jun 08-Jan 09; May 09-Aug 09). Primary data were recorded between 7.30am and 4.30pm, on a schedule of 3 days on, 1 day off, 3 days on, 2 days off. Casual observations outside these times were also used in the final analyses. Because members of the Budongo Forest Project follow individuals of the habituated group daily, locating chimpanzees did not normally present difficulties; however, location of specific individuals could be problematic, particularly for peripheral group members who may not be seen for weeks. The combination of low visibility and varied levels of habituation among individuals thus limited opportunities to capture clear video footage of social interactions. I therefore used a *focal behaviour* sampling approach (Altmann, 1974), and maintained a record of the frequency with which a particular individual was observed; where I had to choose which of several social interactions to film, I targeted individuals previously sampled infrequently.

An initial phase of 4-weeks at the outset of the first 4-month study period was used in order to familiarize myself with the chimpanzee individuals and to begin to establish the gestural repertoire. This initial period was also used to familiarize my field assistant with the equipment and techniques for identifying the target intentional gestures, for example 'response waiting' as defined by Tomasello et al. (1985) and below in section 2.5.5. Subsequent field time was spent recording observations on an *ad libitum* basis.

All social interactions that were judged to have any potential for gestural communication were recorded on miniDV tape using a Sony Handycam (DCR–HC-55). Essentially, this meant any circumstance where more than one chimpanzee was present and not occupied in a solitary activity, such as self-grooming or sleep. Previous studies have found the highest frequency and variety of intentional gesture use to be in the context of play (Genty et al., 2009, Tomasello et al., 1994), so where several social interactions were taking place I gave recording preference to those involving play. Solitary play was also recorded when no social interactions were in progress.

2.5 Analysis

The digital videotapes were transferred to an Apple MacbookPro computer, and scanned to locate episodes that involved gestural communication; these were edited out into discrete clips using iMovie, and labelled for analysis and categorisation in a Filemaker Pro 7.0v3 database (see Appendix 2. for an example Filemaker coding sheet). The coding of footage from the first field period took place on my return to St Andrews, however, as I became familiar with the procedure I was able to code the majority of footage while in the field and most gesture cases were analysed within 2-3weeks of collection. In order to avoid any inconsistency due to my increased experience in coding, at the end of the final field period I re-coded the first 10 tapes collected (filmed over the first 2-months of data collection).

2.5.1 Location of gesture cases within footage

120 hours of behaviour with the potential for gesture was filmed and then cut into clips; at this stage footage containing nothing of interest, or only very badly obscured behaviour was eliminated. This created a database of 5724 clips containing 62.7 hours of footage.

These clips were coded for the following basic descriptive data: date, individual(s) present, situational context(s), clip length, and any other notes of general interest (e.g. this behaviour follows an inter-community interaction). They were also filtered to distinguish cases of intentional gesture that were suitable for detailed coding (Yes/No). Cases of gestural communication where the start of the communication was missed, where the behaviour became obscured by foliage or where the gestures were not accompanied by the required indications of intentional communication (see section 2.5.5) were separated out at this stage. 1864 clips (total footage time: 23.8hrs) contained cases of intentional gestural communication that were suitable for the detailed coding of intentional gesture use described below.

2.5.2 Measuring gesturing time

From the process of cutting the footage described above, it was possible to calculate both the total amount of footage; and, separately, the total amount of footage containing coded cases of intentional gesture. Through this procedure, I could distinguish between footage in which an individual was recorded as present, and footage in which they actively participated in gestural communication: this measure of active participation was termed their *gesturing time*. In the case where the cut and thrust of communication goes back and forth between two individuals, both individuals were considered to be actively gesturing throughout the clip; whereas, when a signaller gestures to an incommunicative recipient only the signaller was credited with being actively gesturing.

2.5.3 Statistical analysis

In cases where a choice of behaviour was available to film I targeted individuals previously sampled infrequently; however, it was not possible to collect equivalent quantities of data from all individuals. In order to remove any possible effect of pseudo-replication, data were converted to means for each individual. Furthermore, only individuals with 5 or more cases contributing to their individual mean were included in analyses.

Statistical analyses were carried out in SPSS v11, with $\alpha=0.05$ required for significance. Means are given ± Standard Deviation, throughout. Data were all examined for appropriateness for parametric statistics and where necessary transformations applied and the data re-tested. Where no appropriate transformations were possible non-parametric alternatives were used. Specifically this included testing for skewness and homogeneity of variance in the data set.

For skewness, Z values over 1.96 or under -1.96 were considered to be positively or negatively skewed. In the case of positive skew a transformation of either $\sqrt{(x)}$, or, where the data set include negative percentage values $\sqrt{(x+101)}$, was applied. In the case of negative skew I used the transformation: $\sqrt{((x_{max}+1)-x)}$, where x_{max}=the highest value within the data set. Transformed data were then retested for skewness, if Z values remained outside of the appropriate bounds for parametric statistics, non-parametric alternatives were used. Where parametric statistics were calculated from transformed data these cases are clearly labelled, for example: data transformed to correct for positive skew with $\sqrt{(x)}$: one-way ANOVA $f_{1,72}=0.51$, $p=0.48$. Homogeneity of variances was checked using Levene's test. Where Levene's statistic showed the assumption of homogeneity was not applicable, the alternative test which did not require homogenous data was used and clearly labelled e.g. $\text{t-test}_{\text{unequal variances}}$ $t=3.33$; $\text{ANOVA}_{\text{Brown-Forsythe}}$ $f=0.777$).

Where planned comparisons could be made, standard t-tests or their non-parametric equivalents were used, with Bonferroni correction if the number of planned comparisons equalled or exceeded the number of experimental conditions. In the case of unplanned, post hoc tests I used Tukey's HSD in the case of equal sample sizes, or the equivalent Games-Howell test where sample sizes varied between conditions or where the requirement for homogeneity of variance was violated.

2.5.4 Defining gestures

Gestures were defined as discrete, mechanically ineffective physical movements, observed during periods of intentional communication. These movements included body movements and movements of the limbs and head, but not facial expressions or static body postures. With contact gestures, it was sometimes difficult for an observer to distinguish whether an action was mechanically effective in achieving its aim or communicating a gestural request for it, in such cases, I erred on the side of caution.

During the course of the study a visiting film crew included a trained specialist in tree climbing. This gave me the unique opportunity to climb up into the canopy and obtain a more chimpanzee like perspective of this environment. This proved extremely valuable in determining which actions were necessary for normal locomotion, and which may be cases of gestural communication. For example: branches that looked small from the ground, turned out to be extremely stiff and difficult to move. In response to this, movements that might previously have been categorized as possible gestures, due to their apparently exaggerated nature, were re-considered as potentially effective actions.

A large number of the Sonso chimpanzees suffer from injuries caused by snare traps, left in the forest by bush-meat hunters from local villages. In some particularly severe cases the tendons within the hand or foot are permanently severed causing partial or full paralysis. The range of movements for individual chimpanzees was well known and data from individuals unable to, for example, extend the fingers fully, were discarded from the appropriate analyses.

2.5.5 Measures of intentional communication

Where one or more of the following accompanied gesture use, I took it that the gestures were used in intentional communication:

Audience checking: The signaller shows signs of being aware of the potential recipients and their state of attention, e.g. turning to look at the recipient before gesturing.

Response waiting: The signaller pauses at the end of the communication and maintains some visual contact.

Persistence: The production of further gestures, after response waiting and in the absence of a response that in other cases is taken as satisfactory. (In certain circumstances, such persistence might be impossible, for example where an adult carries an infant away; these cases are marked as unable to persist, rather than no persistence.)

Where a string of gestures, separated by less than 1second, is followed by response waiting, I attributed the intentional aspect to every one of the gestures within the string (see Analysis: Describing the structure of gestural communication, below). Insisting that each instance of gesture use must be within intentional communication is of course conservative; the procedure forced me to discard many cases that may have been intentional communication. However, where previous researchers have made a similar stipulation (Call and Tomasello, 2007, Genty et al., 2009), they have nonetheless found abundant gestures to analyse.

2.5.6 Classifying gestures by modality

I categorized gestures according to modality used. Visual, audible and tactile have often been used as categories in the past ((Tomasello et al., 1985) (Pika, 2007) (Genty et al., 2009)), but these terms make presumptions about the recipient. Thus, as all gestures are visible and it is the lack of any audible component that distinguishes some distal gestures from other, ‘audible’ ones; I prefer the term ‘silent’. Similarly I use the term ‘contact’ rather than tactile, in order to recognize the active intent of the action.

Classification of gestures as silent or audible was not always straightforward. In a dense forest environment, whether or not a gesture happens to make a noise may be a matter of circumstance. Shaking a sapling, for instance, might be intended as a visual display, but sometimes leaves rattle audibly; in the dry season, the quantity of dry leaves makes almost all movements audible. I classified gestures as audible only where they were made audible by their intrinsic features. However, I also noted whether a 'silent' gesture, or some element of the signaller's behaviour at the time of gesturing, made any noise, so that I could identify cases where the recipient was likely made aware of the signaller's presence, even though their intentional gesture was a silent one. Similarly, vocalization at the time of gesturing was recorded.

2.5.7 Measuring repertoires

Captive studies usually distinguish between idiosyncratic gestures that form part of only one individual's repertoire and those that are used by more than one individual within a social group, forming the group repertoire. The community of chimpanzees at Budongo was much larger than any chimpanzee group yet studied in captivity, which gave me the opportunity for a finer classification. In particular, I considered the possibility that a gesture might be used within a matriline yet not generally within the social group. I therefore distinguished an intermediate level of usage, where gestures were used by several members of a matriline.

For categorization as part of an individual's repertoire, I required a gesture to be recorded used at least twice by that individual; idiosyncratic gestures were those only recorded in one individual's repertoire and never observed in any other individual. For categorisation as part of a matrilineal repertoire, I required a gesture to be included in more than one individual's repertoire from the same maternal family line; 'matrisyncratic' gestures would be those only ever observed in individuals of a single matriline. Where a gesture was used by more than one individual, not in the same matriline, I classed it as part of the group repertoire. Note that these definitions are conservative in identification of idiosyncrasy and 'matrisyncrasy': it only takes one counter-example to disconfirm apparent cases of these kinds of local usage. The inevitable corollary is that the set of gestures in a matrilineal or group repertoire may include gestures in fact used regularly only by a small subset of those categories.

2.5.8 Describing the structure of the gestural communication

As with many forms of real-life communication, the use of gesture is not necessarily a straightforward matter of taking turns: gestures by two individuals may overlap in time, and each participant may gesture in a sequence that may or may not include pauses for response waiting. In order to describe this potential complexity, I broke down chimpanzee gesturing into discrete structural phases. To describe them, I borrow familiar terms from linguistics, but with no intent to imply anything beyond a superficial structural similarity that acts as an *aide memoire*. I distinguish:

G-clause: a chimpanzee gives one or more gestures without interspersed pauses of more than 1s

G-sentence: a chimpanzee gives two or more G-clauses in succession, separated by pauses of >1s of response waiting; during these pauses, the apparent recipient may make non-gestural responses, but does not gesture itself.

G-dialog: a series of G-clauses or G-sentences are given in turn between two or more individuals.

Each individual gesture was then coded for structural position within G-clause, G-sentence and G-dialog (e.g. 1/3, 1/1, 2/2).

As gestures can overlap within a G-clause, aspects of the communication such as response waiting and persistence were recorded at the level of the G-clause rather than the individual gestures. A full list of variables coded at the level of the G-clause and the individual gesture is provided in Table 1.

Table 1: List of all variables coded by gesture and G-clause. All variables coded for each case of gesture along with their definitions and possible values. As explained in the section on describing the structure of the communication, certain variables were coded at the level of the individual gesture, and some at the level of the G-clause.

Variables coded per G-Clause	**Variable**	**Definition**	**Possible values**
	Signaller	Individual performing the gesture	Name from list of Sonso group members
	Directedness	Is gesture directed to another individual	Yes or No
	Recipient	Individual to whom the gesture is directed	Name from list of Sonso group members
	Gaze before	This identifies if the signaller is capable of having seen the attentional state of the recipient prior to gesturing, this includes both the deliberate action of looking at the recipient, and the circumstantial situation where the recipient is already in view	Yes No Unknown
	Situational context*	Mutually exclusive and selected from the adjacent list	Affiliation, Agonism, Patrol, Consortship, Feeding, Grooming, Resting, Sexual (including mating and inspections), Solitary Play, Social Play, Travelling or Unknown
	Function*	Mutually exclusive and selected from the adjacent list	Climb on, Climb on you, Follow, Give affiliation, Give object, Give sexual attention, Groom me, Groom you, Position, Direct attention, Move closer, Move away, Play start, Play continue, Play change (chase-contact), Play change (contact-chase), Stop behaviour
	Response waiting	Signaller pauses and maintains some visual contact	Yes, No, Unknown
	Recipient's response	Mutually exclusive and selected from the adjacent list	**A gesture:** from the complete gesture list (see Table 4) **Another reaction:** non-gestural behaviour from the list of functions **None**

Table 1 continued (part 2)

	Variable	**Definition**	**Possible values**
Per G-clause (cont.)	Persistence	Does the signaller continue to gesture	Yes, No, Unable
	Position in G-sentence	Position of G-clause in G-sentence	e.g. 1/1 = single G-clause 3/4 = 3rd G-clause in a 4 clause G-sentence
	Position in G-dialog	Position of G-sentence in G-dialog	e.g. 1/1 = single G-clause or G-sentence with no gestural response 1/2 = 1st G-clause/G-sentence followed by a gestural response from recipient
Variables coded per individual gesture	Gesture	Type of gesture used	From complete list of gestures in Table 4
	Mode	Modality of the gesture	Silent, Audible, Contact
	Audible	Is the gesture or any accompanying behaviour by the signaller audible	Yes, No, Vocalizes
	Body part signaller	The body part primarily used by the signaller in the act of gesturing	Head, Mouth, Teeth, Face, Back, Body, Bottom, Front, Left arm, Left hand, Left knuckles, Left fingers, Left fist, Left leg, Left foot, Right arm, Right hand, Right knuckles, Right fingers, Right fist, Right leg, Right foot, Both arms, Both hands, Both knuckles, Both fingers, Both fists, Both legs, Both feet, Swelling, Testes
	Body part recipient	The body part of the recipient primarily touched in contact gestures	As Body part signaller
	Object used	Object used during the act of gesturing	This is described on an individual case basis. For example, a branch during an object-shake gesture
	Position in G-clause	Position in total number of gestures in G-clause	e.g. 1/2 = 1st gesture in 2 gesture G-clause 3/4 = 3rd gesture in 4 gesture G-clause

Notification * indicates that the full definitions are available in specific method sections

2.5.9 The function and success of gestural communication

I consider the meaning, or instrumental function (hereafter function) of a communication to be defined by the behaviour that appears to satisfy the gestural communication, i.e. the one that immediately precedes the cessation of communication. Persistence in communication was considered to imply the failure of an earlier G-clause, leading to the production of a new G-clause with the same function; hence, the function of a gestural communication was assigned at the level of the G-sentence. For a detailed definition of functions see Chapter 10.

Success and partial success

As discussed above, if following the recipient's behavioural response the signaller persisted in the production of further G-clauses, this was considered to represent the failure of the previous G-clause to bring about the desired behavioural response. Thus, where a recipient response appears to satisfy the gestural communication, the communication immediately preceding it is considered to be *successful*. However, there were cases where a behavioural response was given which did not satisfy the signaller, but was congruent with a subsequent behaviour that did. For example: a signaller gestures towards an inattentive recipient, the recipient looks round and moves towards the signaller but stops short of reaching them, the signaller gestures again and the recipient then moves to play with the signaller after which the signaller stops gesturing. In this case both the first and second G-clauses would be assigned the function of play-start, as this is the behaviour that leads to the cessation of communication. However, while the first G-clause did not fulfil the function completely, the behavioural response was congruent with the function, as opposed to the recipient walking away, or making no response. In the case where a function could be assigned to a G-sentence, behaviours that followed initial G-clauses, and were congruent with the behaviour that satisfied the final G-clause, were considered to be *partially successful* responses. All behaviours considered to be a partially successful response to a particular function are described in Table 2.

Table 2: Partially successful responses by the recipient. Definition of behavioural responses by the recipient considered to be congruent with the function of the communication and scored as partially successful responses.

Function	**Behavioural responses congruent with function (partially successful)**
Climb on	Recipient pays attention or approaches but fails to climb on
Climb on you	Recipient pays attention, approaches or partially positions to allow climb on but insufficiently to allow successful climb on (e.g. recipient crouches down but not low enough to allow climb on)
Follow	Recipient pays attention, moves closer or follows for under 1m
Give affiliation	Recipient pays attention or moves closer
Give object	Recipient pays attention or moves closer
Give sexual attention	Recipient pays attention or moves closer
Groom me	Recipient pays attention or moves closer
Groom you	Recipient pays attention or moves closer
Position	Recipient pays attention or moves but fails to hold position
Direct attention	Recipient pays attention or moves closer
Move closer	Recipient pays attention or moves closer but under 1m
Move away	Recipient pays attention or moves away but under 1m
Play start	Recipient pays attention or moves closer
Play continue	Recipient pays attention or moves closer
Play change: chase-contact	Recipient pays attention
Play change: contact-chase	Recipient pays attention
Stop behaviour	Recipient pays attention or pauses behaviour but resumes immediately (<3 second pause).

2.5.10 Time limits on recipient responses

Previous studies of great-ape gestural communication have employed pre-defined time constraints in defining behaviour as being a response to a gestural communication. For example: Leibal et al. require that the behaviour be produced within 5 seconds of the gestural communication to be considered a response to it (Liebal et al., 2004a).

During the initial period 4-week period of familiarisation with the subjects and gestural repertoire, I noted that time to respond varied considerably and was at times extensive (>20seconds). For example: in situations where two requests for grooming are produced almost simultaneously between similarly ranked males, long periods of response waiting may ensue, due to the social posturing involved in an individual not being the first to 'concede' their own request in favour of the other individual's. Thus, it seemed that the imposition of an arbitrary time-constraint would be inappropriate for the accurate description of the communicative behaviour. Rather than imposing in advance a time within which a behaviour was considered to be given as a response to a prior communication, I took intermediate behaviour directed towards the recipient (for example: audience checking, or holding the position of a body part presented for grooming), and the absence of either non-directed behaviour (such as self-grooming) or behaviour directed towards another individual to indicate that response waiting was ongoing. I considered any change in behaviour produced while response waiting was ongoing to be a response to the previous communication.

2.6 Reliability of the coding

The analysis of great-ape gesture requires extensive training, gestures occur extremely quickly and accurate coding depends on the observation of, at times, subtle changes in behaviour. This is rendered particularly difficult when coding from footage collected in a forest environment where high-contrast low-light conditions and dense foliage frequently result in sub-optimal filming conditions. As a now highly experienced coder, familiar with all the study subjects; 1-hour of footage containing gestural communication may still take me between 6-10 hours to code depending on the complexity of the interactions. The availability of experienced coders, and thus the opportunities for testing inter-observer reliability, was therefore highly restricted; for this reason I focused on the variables associated with identifying gesture type and intentionality.

An experienced gestural coder from the EU Referential Communication study, Emilie Genty (EG), re-coded a subset of the gestures. The method for coding gesture followed here was highly similar to that with which EG was already familiar; however the great-ape species studied varied in being chimpanzee, not gorilla. EG re-coded footage containing 50 gestures (approximately 1% of the data set) on the four variables: directedness, gaze before, attentional state of the recipient, and gesture type. Although the procedure for coding these four variables was identical to the one with which EG was familiar, the possible values differed in places (e.g. the gesture types within the repertoire). EG was provided with a modified Filemaker data sheet containing drop-down lists that restricted possible options to the values defined above. In addition to this EG was provided with full definitions of all four variables and their possible values.

2.6.1 Results of inter-observer coding

Table 3 reports the high levels of agreement achieved between the two coders across a range of variables.

Table 3: Levels of inter-observer reliability. Percentage agreement between the two coders on each of the four variables.

	Directedness	Gaze before	Attentional state of recipient	Gesture
Percentage agreement (%)	75.7	91.9	70.2	89.2

The inter-observer reliability of the coding of gestures was tested more rigorously; taking into account the likelihood the agreement occurred by chance (Cohen's Kappa, K= 0.86). This confirmed that an excellent level of inter-coder agreement has been achieved.

Chapter 3. How do chimpanzees acquire their gestural repertoire? Is there still a case for ontogenetic ritualization.

3.1 Introduction

‘*Gradually…. the infant learns to respond to the gestural, postural, or auditory equivalents of his mother’s early signals.*’ pp149 (Van Lawick-Goodall, 1973)

The acquisition of gestures by chimpanzees: is there a case for Ontogenetic Ritualization?

There are several theories that seek to explain the acquisition of gesture by great apes: do they acquire them through social learning? (Van Lawick-Goodall, 1972) Do signallers have an individual repertoire, or are the signals mutually constructed with the recipient? (King, 2004) Are they born with a species-typical repertoire? (Genty et al., 2009). To date, the most dominant theory is that of Ontogenetic Ritualization, developed by Tomasello and Call in 1985 and which, with little change, is still widely accepted today (Tomasello and Call, 2007, Pika, 2007, Pollick and de Waal, 2007).

The development of Ontogenetic Ritualization Theory.

Plooij originally suggested that infant chimpanzees progress from ‘unintentionally eliciting’ actions from their mothers, to deliberately doing so, as they gain awareness of the social effect that their behaviour has. He described how the characteristic posture that infants adopt when being tickled, was, over time, used as a gesture to request a tickling session (Plooij, 1978). These descriptions prompted Tomasello and Call to undertake the first systematic examination of the nature and development of gesturing in a captive group of chimpanzees.

Over a period of 9-years the authors recorded a series of three snapshots of the intentional gestural communication of immature individuals within the captive Yerkes group (Tomasello et al., 1985, Tomasello et al., 1989, Tomasello et al., 1994). In order to identify intentional cases of gestural communication they focused on those accompanied by indicators of a communicative goal such as the signaller waiting for a response, or alternating its gaze between the goal object and the recipient (Tomasello et al., 1985).

They reported large differences in the gestural repertoires of individuals within the group, between the repertoires of immature and mature individuals at any one time, and between the repertoires of different cohorts of immature individuals over time (Tomasello et al., 1985, Tomasello et al., 1989, Tomasello et al., 1994). These high levels of variability led the authors to state that it is ‘unlikely that particular gestures are transmitted across generations genetically’, and instead they concluded that the acquisition of most gestures is most ‘easily explained by a direct conventionalization process’ with any overlap in gestural repertoires the result of common behavioural repertoires from which the gestures were ritualized (Tomasello et al., 1985).

This ‘direct conventionalization’ process was initially explained as the ‘very subtle ritualizations (incipient movements) of important social behaviours’ (Tomasello et al., 1985, p.179) and was subsequently expanded into their theory of Ontogenetic Ritualization (OR). OR is comprised of 4 stages:

- Individual A performs behaviour X (not a communicative signal);
- Individual B consistently reacts by doing Y;
- Subsequently B anticipates A’s performance of X, on the basis of its initial step, by performing Y; and
- Subsequently, A anticipates B’s anticipation and produces the initial step in a ritualized form (waiting for a response) in order *to* elicit Y.

(Tomasello and Call, 2007, p.6)

In other words if Jack repeatedly grabs an object from Jill, and Jill’s reaction is to repeatedly give it to him, then Jill starts to anticipate Jack’s desire for the object from the early *intention movements* of his grabbing action, for example: the reaching part. Jill then starts to give Jack the object in response to him reaching for it. Subsequently, Jack realises that Jill gives him the object in response to him simply reaching for it, and starts to produce just the reach movement in order to communicate his desire for the object. At this stage the reach movement functions as a communicative signal to indicate Jack's desire for the object: a reach gesture.

Any of Jack's actions can be ritualized into a gesture in this manner, as long as they predict his subsequent behaviour with enough consistency to allow Jill to anticipate it. Thus, if Jack repeats the ritualization process with 5 other individuals it may result in 5 different gestures, as the process must be started from a full effective action with each new recipient. Importantly, there is also no *understanding* of Jack's desire by Jill; she is simply *anticipating* a subsequent action by him. Thus the ritualization process only occurs in one direction, if Jill wants to take an object from Jack she could not simply produce a reach gesture as it has no meaning in that direction. Instead they would have to re-start the process of ritualization from action to gesture in the other direction: from Jill to Jack. The process of OR therefore leads to gestural repertoires characterised by high levels of both idiosyncratic and one-way gestures (gestures used by A to B, but never vice versa); just as Tomasello and his colleagues reported (Tomasello et al., 1989, Tomasello et al., 1994).

The high levels of idiosyncrasy led the authors to rule biological inheritance as a major means by which gestures are acquired (Tomasello et al., 1985). They do discuss the case for imitation, either in the form of second-person imitation (where an individual learns the gesture through having received it in a previous communication) or third-person imitation (where an individual learns the gesture after observing it being used by others). Again though, they argue that, while their observational method makes it hard to distinguish between the different forms of social learning, neither form of imitation can account for idiosyncratic gestures (as there is no model from which to imitate them), and only third-person imitation could account for the presence of one-way gestures. Thus, they conclude that direct conventionalization through OR is the most likely means by which chimpanzees acquire their gestural repertoire (Tomasello et al., 1989).

One of my initial concerns about the use of idiosyncratic gestures to justify eliminating other possible theories for the acquisition of gestures is that Tomasello and Call have a rather idiosyncratic definition of idiosyncrasy. For a gesture to be defined as idiosyncratic they only require that a gesture be used by a single individual, *within a single study period*. So, for example, they describe the gesture 'Head-grab' as idiosyncratic despite the fact that in 1983 it is recorded in Georgia's repertoire, and in 1991 it is recorded in Rhett's repertoire (Tomasello et al., 1994). This method risks mis-categorising rare gestures, only used occasionally, as idiosyncratic, exaggerating the apparent variability in the data, a particular risk with short-term studies of small groups. The presence of one-way gestures as evidence for ritualization is also subject to the same problem of sample size. Some level of one-way usage occurs in all systems of communication, differences in age, sex, and social status inevitably lead to some level of asymmetry, thus, it is not clear what level of one-way usage would provide support for OR.

Attention-getters: what are they?

One source of empirical weakness in the theory of OR is that all studies of great ape gesture include the intentional use of gestures whose physical form is incompatible with having been ritualized from an effective action (for example: drumming, pirouetting). Thus, additional categories of gesture become necessary: one of these is the suggested sub-category of 'attention-getters'. First referred to in the 1989 paper (Tomasello et al., 1989), they are described as gestures that have no intrinsic meaning, functioning only to draw the recipient's attention to an accompanying signal (either an unlearned expression/posture, or another meaningful gesture).

'The meaning of an attention getter most often derives not from the signal itself or from the surrounding context but rather from some accompanying behaviour. The ontogenetic ritualization of attention getters may also be somewhat different, as the initial behavior (e.g. slapping the ground) is not abbreviated/ritualized during learning in the same way as intention movements.' (Tomasello and Call, 2007, pp.10-11)

Thus, still considered intentional ontogenetically (presumably rather than phylogenetically) ritualized gestures, it is the recipient's response, rather than the physical form of the gesture, which is ritualized in some manner, although how this process might occur is never addressed. They are considered to be distinct from the 'intention-movement' gestures in several ways. For example, as they have no intrinsic meaning they are ‘context free and occur quite widely across contexts’ (Tomasello and Call, 2007, p.10) as opposed to intention-movements which are used in a limited range of contexts.

A second point of difference concerns the flexible use of different modes of gesture to accommodate the recipient’s ability to receive the communication. Tomasello and Call first demonstrated that chimpanzees tend to employ silent gestures to an attentive recipient able to see the communication, and audible or contact gestures to inattentive recipients (Tomasello et al., 1994). They then contrast the use of intention-movements and attention-getters, arguing that while intention-movements have an intrinsic meaning, attention-getters function only to attract an inattentive recipient’s attention, which is then drawn to some accompanying involuntary display of mood such as a play-face expression, or a penile erection (Tomasello and Call, 2007). I question whether or not this assumption is correct. If the displays of mood are involuntary, they should accompany all communication within the appropriate context. For example, an involuntary penile erection is by definition not something that is under voluntary control, and should therefore be present throughout communication; whether or not this is in the form of an intention movement or an attention-getter. If this is the case, then there is no justification for the argument that an audible or contact based attention-getter functions solely to draw attention to the involuntary signal any more than an intention-movement would. Instead they may both represent the intentional use of an appropriate and communicative gesture selected in order to accommodate the ability of the recipient to perceive it. Any accompanying involuntary display may well contribute to the general context of the communication but isn’t necessarily the only meaningful component.

In addition, somewhat surprisingly, no data is provided as the basis for this differentiation between attention-getters and intention-movements, and no distinction is drawn between the two categories of gesture in the analyses of gestural communication (Tomasello et al., 1989, Tomasello et al., 1994). In fact, in a later paper with Liebal, Tomasello and Call found no evidence for the use of an attention-getter + meaningful communication combination, instead finding that signallers chose to locomote into a position where the recipient could perceive the communication (Liebal et al., 2004a).

The category of attention-getters also fails to account for the intentional use of silent gestures that have no plausible origin in an effective action. For example the widespread use of the head bob or wrist-bend gesture, reported in all three studies (Tomasello et al., 1994). It is possible that these gestures are acquired through imitation, but an alternative explanation would be that these represent intentional species-typical gestures. A recent study of intentional gestural communication in several gorilla groups found no justification for the division of the repertoire into separate categories of ontogenetically ritualized intention-movements and other intentional gestures. These authors also examined idiosyncrasy of gestures across three captive groups, the result was that gesture types initially classified as idiosyncratic in the first group were, as more groups were included, then reported in other individuals, until only a single case idiosyncratic gesture type remained –used by a partially human-reared female to a human keeper. These authors suggest that gorilla gestural communication is founded upon a large single class of intentional species-typical gestures (Genty et al., 2009).

Are there any species-typical gestures in OR theory?

The question of species-typical gestures is largely glossed over in the work on OR, the authors do refer to ‘non-intentional’ postures and facial expressions (despite including one facial expression in their list of intentional gestures – pout face (Tomasello et al., 1994)), but make no mention of the common species-typical gestures such as chimpanzee drumming. The first mention of the possibly intentional use of species-typical gestures is in a small footnote to the 1989 paper where Tomasello and Call refer to the possible use of an unlearned Fixed Action Pattern (FAP) in an intentional manner. They suggest that with the appropriate cognitive capacities individuals may, with experience, learn to use unlearned (so presumably biologically-inherited) behaviours in specific contexts and at appropriate times. They cite De Waal’s 1982 report of hiding a fear-grimace (de Waal, 1982), a classic example of an automatic emotion driven *facial-expression*, the communication of which was controlled by a voluntary manual action. However, the authors are in fact proposing use of a FAP as a possible explanation for the universal form across chimpanzee groups of the *manual* ‘wrist-bend’ gesture (Tomasello et al., 1989).

In the 1994 study they acknowledge that most of the overlap in individual repertoires occurs in play gestures. They suggest that any of these ‘species-typical’ gestures are still acquired through OR and are the result of similarities in the social experiences of individuals, as this would predict that similar behaviours are conventionalized into similar gesture types (Tomasello et al., 1994). However, it is worth noting that Tomasello and Call found that the greatest frequency, variety and flexibility of gesture use were recorded in the context of play (Tomasello et al., 1994). Thus, the issue of overlap in play repertoires may represent a more serious problem for OR than the authors acknowledge. Later in a summary of their work they appear to make a further concession towards the possible occurrence of some level of intentional use of species-typical gestures by referring to gestures as being on a scale of voluntary control ‘depending on the extent to which the ritualization process occurred during phylogeny or ontogeny’ (Tomasello and Call, 2007, p.8).

Is OR relevant to wild chimpanzee gesture?

As Tomasello and Call note, their studies are based on a small group of captive chimpanzees in a socially atypical situation (at one stage a human-devised harem with one male and several females). The majority of the data comes from only a few months of observation on very few individuals. For example, in their developmental analyses, they frequently only have one or two individuals within each age category (Tomasello et al., 1985, Tomasello et al., 1989). Although this allows them to provide extremely detailed notes on the behaviour and gesture of specific individuals at a specific time, it is not necessarily appropriate to use the same data to draw general conclusions about species typical behaviour. Nevertheless, the authors state that ‘it is presumably the case that the most basic developmental and learning processes involved in the communicatory signalling of chimpanzees…. are the same in all reasonably normal social settings.’ (Tomasello et al., 1989, p.49).

Natural chimpanzee communities are large multi-male, multi-female groups, the Sonso community, for example, contains 81 named individuals. As discussed above, the acquisition of gestures through OR does not lead to an understanding of the signal. Thus, each gesture must be ritualized anew with each recipient, and for an individual to acquire every intentional gesture in its repertoire by ritualization would require a great number of repeated dyadic reactions. While this may seem plausible in very small stable groups with a limited repertoire, I would question whether or not it is realistic to assume that the same process could underpin the acquisition of gesture in large fission-fusion community.

Given the recent compelling evidence for the intentional use of a large species-typical repertoire in gorilla gestural communication (Genty et al., 2009), my aim in this first chapter is to describe the intentional repertoire of gesture in the wild Sonso community, and to address the question of whether or not the data from a wild population better supports the predictions of OR, or the new view of a single class of species-typical gesture.

As several studies have found no justification for a category of pure 'attention-getter' gestures (Liebal et al., 2004a, Genty et al., 2009), and given the doubts discussed above, I did not find it useful to make this distinction from intention-movements. Instead, I chose to follow Genty et al. in taking all gestures that had a physical form incompatible with a ritualized origin to be presumably species-typical (ST), as this follows our understanding of the majority of species studied (Genty et al., 2009). OR makes a number of easily testable predictions, namely that:

1. Gestures acquired through OR differ in being more flexible than those that are ST
2. Gestures acquired through OR differ from those that are ST in being used with sensitivity to the audience's state of attention
3. OR leads to the widespread occurrence of idiosyncratic and one-way gestures
4. The physical form of intention-movement gestures acquired through OR must be a ritualized form of the early movements of the effective action.

The results have been broken down into appropriate sections in order to deal with each of the predictions in turn. Section 3.3.3 compares and contrasts the use of 'potentially-ritualized' gestures with those provisionally classed as species-typical. The section 3.3.4 deals with a comparison of the physical form of 2 potentially-ritualized gestures and those of the actions from which they were presumably ritualized. In a final section (3.3.5), I assess any evidence for overlap of gestural repertoires between the several groups of chimpanzee and between the species of great ape, as would be predicted if the majority of gestures were species-typical.

3.2 Specific method

3.2.1 One-way gestures

I define one-way gestures as any gesture type recorded as produced by an individual, but never recorded as received by that individual. Due to the differences in size and social status, some level of one-way usage is expected irrespective of the means by which the repertoire is acquired, particularly when only one period in any individual's ontogeny is recorded.

3.2.2 Distinguishing ontogenetically ritualized from species typical gestures

Ontogenetic ritualization requires that the physical form of the gesture be ritualized from the incipient movements of an effective action, in the course of dyadic interactions during individual ontogeny (Tomasello and Call, 2007). I treated all gestures that could reasonably be described as the incipient movements of an effective action as 'potentially-ritualized'. A typical example, as described in the introduction, is the Reach gesture, used when begging, which might have become ritualized from the (originally effective) action of taking the desired object directly. The reaching movement might often have been the first part of the action sequence, terminating in a mechanically effective grasp. Only where a gesture could not reasonably have originated in an intention movement, or the early part of a sequence of action that could have achieved the same goal, did I treat the gesture as 'species-typical'. Note that this classification is asymmetric: potentially-ritualized gestures might in fact be part of the chimpanzee's natural repertoire; species-typical gestures could not be derived from ritualization during ontogeny.

If this classification is appropriate, and even if not every one of my attributions is correct, then I would expect a characteristic difference in communicative attributes to emerge. Thus, gestures learned by ritualization during dyadic interactions, compared to species-typical displays, might be expected to be: used more flexibly; more obviously used deliberately and under voluntary control (indeed, the stipulation of intentional use might have removed all species-typical displays); I examined the data for evidence relevant to these predictions.

In addition, if a gesture has been ritualized from an originally effective action or an intention movement towards that action, it should sometimes retain a trace of its ontogeny in its physical form. In particular, I would expect consistency in the manner in which the movements of gesture and original action are performed: the direction of movement, the orientation of the hand, and so forth. If, on the other hand, the identification between communicative gesture and its supposed pre-ritualization origin is spurious, I would expect no such consistency. In order to examine this prediction, I analyzed the physical movements in which two potentially-ritualized gestures were conducted, comparing them to the actions from which they might have ritualized. These were the 'Begging-reach' gesture, i.e. a 'reach' gesture given with the apparent goal of acquiring a desired object, compared to the 'take' action; and the 'directed push' gesture, used to indicate a desired position during grooming, compared to the 'position' action. I chose these gestures not only because they were sufficiently common in my corpus to allow analysis, but also because they are particularly obvious candidates for explanation by ontogenetic ritualization.

Begging-reach gestures and actions of taking were described using three categories: palm orientation (Vertical, Up or Down), position of fingers (Curled or Extended), and the part of the hand presented first to the recipient (Front of fingers, Back of fingers, Wrist or Hand). Directed push gestures and actions of positioning were categorised according to the part of the hand used to perform the movement (Front of fingers, Back of finger, Palm, Knuckles or Back of Hand). Only individuals with four or more examples in each category were analysed.

3.2.3 Audience effect

To examine the possibility that gesture modality (i.e. silent, audible, tactile) might be chosen with respect to the recipient's state of attention, I calculated the variations in choice of silent, audible or contact gestures, according to the attentional state of the audience. I examined only the first gesture in each sequence, and individuals with fewer than 5 gestures in each category were excluded from this analysis. For each individual, I first calculated the proportions of its entire gesture usage that involved silent, audible or contact gestures. Then, I selected from that individual's data two subsets: cases where the apparent target audience was attending (that is, making eye-contact with the signaller or moving its head to track movement of the signaller); and cases where the signaller was out of view of the apparent target audience. For these subsets, I again calculated the proportion of gesture use that involved silent, audible and contact gestures. I then calculated the percentage deviation in the variation in use of each mode of gesture for each subset of audience attention state. Thus, if the proportion of silent gesture in the overall corpus was α, and the proportion of silent gestures when eye-contact had been made was β, the deviation would be $(\beta/\alpha -1)*100$. Deviations, which could be positive or negative, were used to indicate active adjustment towards the attentional state of the recipient.

3.3 Results

During 266 days of observation I recorded 111 hours of chimpanzee behaviour with the potential for gestural communication. Other researchers working with the same community kindly contributed a further 19 hours of video, giving a total 120 hours of footage. This produced a data set of 4397 intentional gestures; many other gestures were excluded because they failed to meet one or more of the requirements for intentional gesture use.

3.3.1 Repertoire

In total, I identified 115 different gesture types; however many of these were basic variations on a single type (for example grab 1-handed, grab-2-handed). Where there was no reason to think that these small structural differences had any possible communicative significance, I lumped categories to give an eventual set of 66 distinct gesture types (see Table 4), 5 of which were recorded less than 3 times during the study. Of the 66 gesture types, 29 (43.9%) could plausibly be classed as potentially ritualized (PR), leaving 37 gestures that could only be seen as species-typical displays (ST). Examining the cumulative frequency of gesture types, recorded as used by any member of the chimpanzee community, shows that this figure has reached asymptote (Figure 1); further observation is therefore unlikely to contribute many further gesture types.

Individual repertoire size varied considerably (n=62, range: 1-41, mean=10.0 ±8.9). Age classes differed significantly from each other in the average size of repertoire ($\text{ANOVA}_{\text{Brown-Forsythe}}$ $f_{3,35.8}=4.62$, p=0.008; see Figure 2). The juvenile age group evidenced the largest individual repertoires (n=14, range 1-35, mean=15.14 ±11.89), followed by sub-adults (n=17, range 1-23, mean=9.76 ±7.54), infants (n=14, range: 1-23, mean=7.86 ±7.18), and finally adults with the smallest individual repertoires (n=29, range: 1-17, mean=5.10 ±4.64). The difference between juvenile and adult repertoires was significant (Post-hoc Games-Howell: mean difference=10.04, p=0.037).

There are several reasons for thinking these measured repertoires underestimate the true sizes of gestural repertoires, however. For individuals, if the criterion for repertoire membership were relaxed to include gestures used only once, estimated repertoire sizes would almost double (1:1.81 ±0.67). Moreover, repertoire size was closely correlated with the active gesture time recorded for that individual (Pearson's correlation r=0.94, n=68, p<0.0001; active time gesturing, n=68, range: 0.27-160.28, mean=29.67 ±36.34min; see Figure 1). Similarly for age category differences, the size of the repertoire was closely correlated to the quantity of active gesture time recorded within the age group (using fine division of age classes: n=7, Pearson's correlation r=0.97, p<0.0001; note also the large overlap in size ranges, Figure 2). Looking at it another way, the number of individuals in whose repertoire a gesture type was recorded was strongly correlated with the overall frequency of the gesture type (Pearson's correlation r=0.89, n=66, p=0.0001). Thus, measured individual repertoires, and the variation between gesture types in how widely they were used, appear to be determined largely by sample sizes.

To investigate what individual repertoires might reach if data collection were to continue indefinitely, I examined the accumulation of the largest individual repertoire, that of Night, female, 4-years old at start of data collection, over the study:

her repertoire appears close to asymptote at 41, but included a further 10 types of gesture recorded on single occasions.

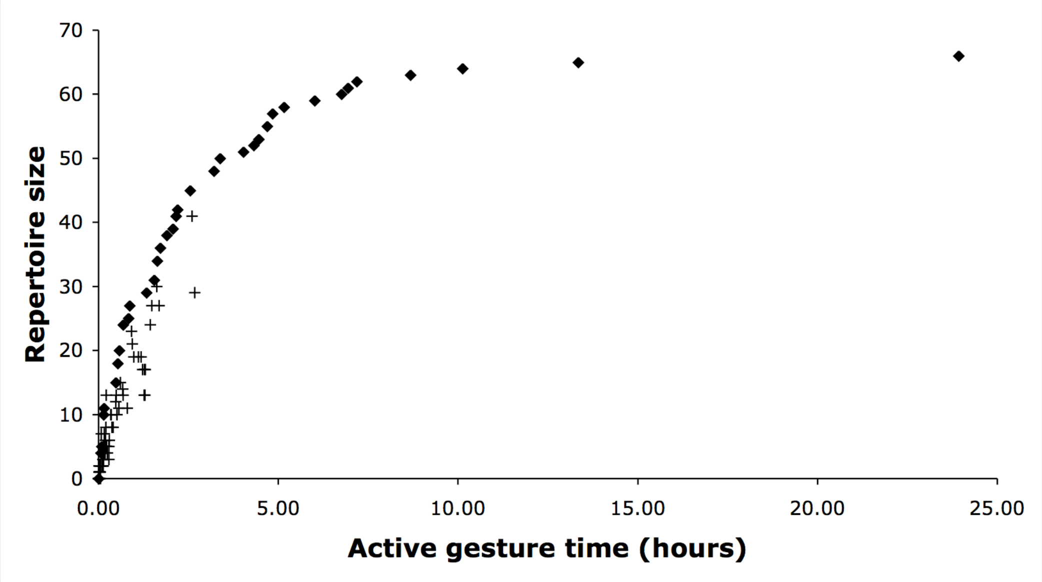

Figure 1: Cumulative record of Sonso group repertoire against group active gesture time; plotted along with individual repertoire size against individual active gesture time. The cumulative number of gesture types recorded is plotted against the cumulative active gesture time collected for the Sonso community as a whole. Asymptote appears to have been reached at approximately 15hours of active gesture time; this corresponds to approximately 150 days of field observation time (represented by black diamonds). On the same axis individual repertoire size is plotted against individual active gesture time (represented by crosses).

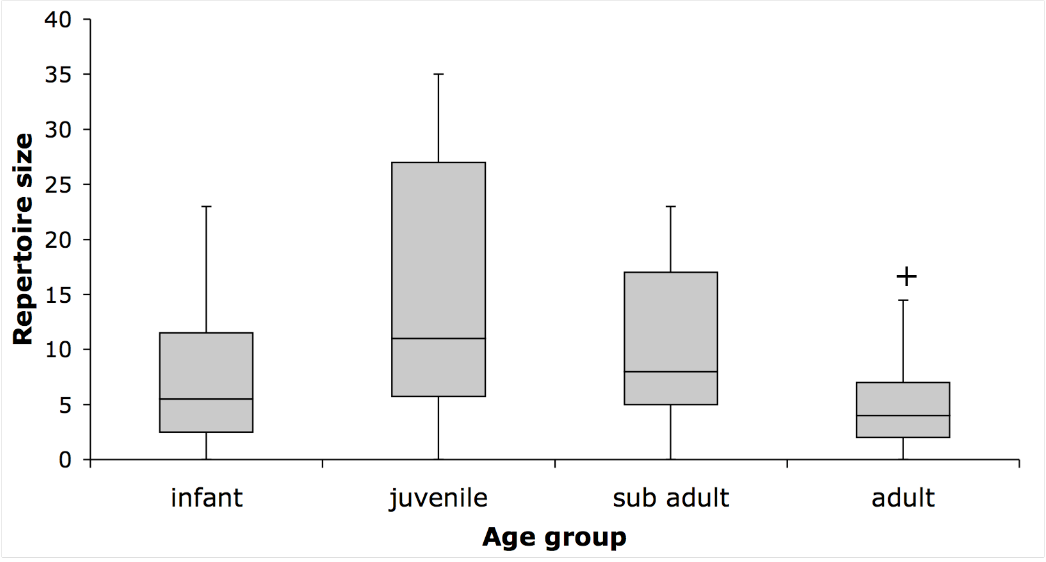

Figure 2: Age distribution of chimpanzee repertoire size. Box plot of age-group repertoire size showing mean, s.d. range and outliers.

Table 4. The chimpanzee gestural repertoire. The repertoire of the Sonso chimpanzees is compared with that of other chimpanzee groups, and two other species of great ape. *Italics*: indicates the actions was not specified as a gesture, but was nevertheless reported to occur. Notification * indicates gesture observed at the Delta Regional Primate Research Center in a study of courtship gestures (Tutin & McGrew 1973). Notification PR and ST indicates gesture was defined as Potentially Ritualized or Species-Typical respectively.

Gesture type **PR/ST**	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe[1] (*Pan*) wild**	**Mahale[2] (*Pan)* wild**	**Yerkes[3] (*Pan*) captive**	***Gorilla*[4] wild & captive+**	***Pongo*[5] captive**
Arm raise PR	Raise arm and/or hand vertically in the air	Arm raise; Arms raise	Arm raise	Raise arm	Arm raise *	Arm raise; Arms raise	Raise arm; Arms up
Arm shake ST	Small repeated back and forth motion of the arm	Arm shake; Arms shake; Arm shake on; Arm shake with object	-	-	-	Arm shake; Arms shake; Arm shake on; Arms shake on; Arm shake with object; Arm shake; Arms shake with object	-
Arm swing PR	Large back and forth movement of the arm held below the shoulder	Arm swing; Arms swing; Arm swing direction; Arms swing under; Arm swing with object	-	-	Swing	Arm swing; Arms swing; Arms swing under; Arm swing with object; Arm swing	-
Arm wave PR	Large repeated back and forth movement of the arm raised above the shoulder	Arm wave; Arms wave with object	Bipedal arm waving	-	Arm wave	Arm wave; Arms wave; Straw wave	Wave
Beckon PR	Hand is moved in an upwards sweep from the elbow or wrist towards signaller	Beckon	Beckoning	-	Finger curl; Beckon	-	Beckon
Big Loud scratch ST	Loud exaggerated scratching movement on the signaller's own body	Big loud scratch	Self scratch	Self scratch	-	-	Long body scratch

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[1] Goodall, J. 1968, 1986; Plooij, F. 1984
[2] Nishida et al. 1979-1999
[3] Tomasello et al. 1989, 1994, Pollick & De Waal 2007
[4] Genty et al. 2009, Tanner & Byrne 1996-2010
[5] Cartmill, E. 2008, Cartmill & Byrne 2010

Table 4 continued (part 2)

Gesture type	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe (*Pan*) wild**	**Mahale (*Pan*) wild**	**Yerkes (*Pan*) captive**	***Gorilla* wild & captive+**	***Pongo* captive**
Bite PR	Recipient's body is held between the teeth of the signaller	Bite	Mouthing/ Gnawing; Open mouth kiss; Submissive kissing	Open mouth kiss; Mouth	-	Bite	Bite, Mouthing
Bow ST	Signaller bends forward from the waist while standing	Bow	Bowing	Bow	-	Bow; Bow-extend; Bow-extend aerial	
Clap ST	Both palms moved towards each other and are brought together with an audible contact	Clap hands on	-	-	Hand clap; Clap hands	Clap; Feet clap	Clap
Dangle PR	To hang from one or both arms from a branch above another individual, this is audible as there is normally significant disturbance of the canopy	Dangle; Dangle with feet shake	*Dangle*	*Dangle*	-	Rope spinning; Rope swinging	Dangle; Swing
Directed push PR	A light short non-effective push that indicates a direction of desired movement, immediately followed by the recipient moving as indicated	Directed push	Pull towards; Hand leading	Pull face to face	Direct-hand	Positioning	Turn head
Drum belly ST	(Mahale) 'Slapped his belly with his right hand to make drum-like sounds'	-	-	Drum belly	-	Body drum	-
Drum object (palms) ST	Short hard audible contact of alternate palms against an object	Drum object (palms)	Drum	Slap ground	-	Drum object (palms); Drum object (fists)	-
Drum other ST	As 'Drum object (palms)' but contact is with recipient's body	Drum other	-	-	-	Drum other	-
Embrace PR	Signaller wraps both arms around the recipient and maintains physical contact	Embrace	Embracing; Mounting embrace	Embrace full; Mount	-	Embrace	Embrace

Table 4 continued (part 3)

Gesture type	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe (*Pan*) wild**	**Mahale (*Pan*) wild**	**Yerkes (*Pan*) captive**	***Gorilla* wild & captive+**	***Pongo* captive**
Feet shake ST	Repeated back and forth movement of feet from the ankles	Feet shake; Legs shake	-	-	-	Feet shake; Feet shake with object	-
Foot present PR	Sole of the foot is presented to the recipient	Foot present; Foot present with directed movement	-	-	-	-	-
Gallop ST	An exaggerated running movement where the contact of the hands and feet is deliberately audible	Gallop; Gallop (stiff)	*Gallop*	*Gallop*	-	Gallop; Stiff gallop; Gallop with object	-
Grab PR	The hand is firmly closed over part of the recipient's body	Grab 1-handed; Grab 2-handed; Grad and hold; Grab intention	Grab; Hair pulling; Hands around head	Grab	Head-grab; Face grab	Grab 1-handed; Grab 2-handed	Grab; Grasp; Restrain; Air grab
Grab-pull PR	As 'Grab' but closed hand contact is maintained and a force exerted to move the recipient from their current position	Grab-pull; Grab-pull 2-handed	Hand in neck	Pull	Lead; Pull head	Grab-pull; Grab-pull 2-handed	Pull; Pull hair; Pull away
Hand fling PR	Rapid movement of the hand or arm in the direction of the recipient	Arm fling; Hand fling	Arm threat; Hitting away	Flap; Raise arm quickly	*	-	Shoo
Hand on PR	Palm of the hand is placed on the recipient, contact lasts for more the 2 seconds	Hand on; Hands on	-	-	Arm on	Hand on; Hands on	Cover
Hand shake ST	Repeated back and forth movement of hand from the wrist	Hand shake; Hands shake	*Hand shake*		Shake wrist		
Head butt PR	Head is briefly and firmly pushed into the body of the recipient	Head butt	-	-	-	Head on	-

Table 4 continued (part 4)

Gesture type	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe (*Pan*) wild**	**Mahale (*Pan)* wild**	**Yerkes (*Pan*) captive**	***Gorilla* wild & captive+**	***Pongo* captive**
Head nod ST	Repeated back and forth movement of the head	Head nod; Head shake	Head tipping	Bob; Tip head	Head bob	Head nod; Head shake; Head shake with object	Chin up/nod
Head stand ST	Signaller bends forward and places head on the ground	Head stand	-	-	-	-	Head stand
Hide face ST	Face is hidden by the hands and/or arms	Hide face	-	-	-	Hide playface	-
Hit with object PR	An object is brought into short hard contact with the body of the recipient	Hit with object	-	Club	-	Hit with object	-
Jump ST	While bipedal both feet leave the ground simultaneously, accompanied by horizontal displacement through the air	Jump	-	Bipedal jump	-	Jump	-
Kick PR	Foot is brought into short hard contact with the recipient's body in a movement from the hip with a horizontal element (for vertical see Stomp other ritualised)	Kick	Kick	Kick; Kick backward	-	Kick	-
Knock object ST	Back of the hand or knuckles are brought into short hard audible contact with an object	Knock object	-	Rap	Rap knuckles	Knock; Knock object	-
Leaf clipping ST	Strips are torn from a leaf (or leaves) held in the hand using the teeth; produces a conspicuous sound	Leaf clipping	-	Clip leaf	-	-	-
Leg swing ST	Large back and forth movement of the leg from the hip	Leg swing; Legs swing; Leg swing with object	-	-	-	Leg swing	-

Table 4 continued (part 5)

Gesture type	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe (*Pan*) wild**	**Mahale (*Pan)* wild**	**Yerkes (*Pan*) captive**	***Gorilla* wild & captive+**	***Pongo* captive**
Look ST	Signaller holds an eye-contact position with the recipient – minimum duration 2 seconds	Look	Wait; Putting face close	Look back; Wait; Peer	Look back	Look; Peering	Look back; Peer
Mouth stroke PR	Signallers palm and fingers and repeatedly run over the mouth area of the recipient	Mouth stroke	-	-	Rub chin; Beg with hand	-	-
Object in mouth approach ST	Signaller approaches recipient while carrying an object in the mouth (e.g. a small branch)	Object in mouth approach	-	-	-	-	-
Object move PR	Object is displace in one direction, contact is maintained through movement	Object move; Object move 2-handed	Branch dragging; Scrub	Sway vegetation; Dance bipedal; Push backwards; Drag branch; Rake/scratch dead leaves; Lift rock	Push barrel	Move object, 2-handed; Push object	Drag object
Object shake ST	Repeated back and forth movement of an object	Object shake; Object shake 2-handed	Branch shaking; Shake detached branch; Branching	Flail; Shake branch; Rinse	*	Shake object	Shake object
Pirouette ST	Signaller turns around their bodies vertical axis while also displacing along the ground	Pirouette	*Pirouette*	*Pirouette*	-	Pirouette; Pirouette with object	-
Poke ST	Firm, brief push of one of more fingers into the recipient's body	Poke; Poke (multiple)	Tickling and poking	Poke	Poke at; Hard touch; Poke	Poke	Poke
Pounce ST	Signaller displaces through the air to land quadrapedally on the body of the recipient	Pounce	-	-	-	Pounce	-

Table 4 continued (part 6)

Gesture type	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe (*Pan*) wild**	**Mahale (*Pan*) wild**	**Yerkes (*Pan*) captive**	***Gorilla* wild & captive+**	***Pongo* captive**
Present climb on me PR	Arm or leg is extended to young recipient in order to facilitate them climbing onto the signallers body (normally mother to infant)	Present climb on me	Flexed knees; Leg bending; Lowering back	-	-	-	-
Present grooming PR	Body is moved to deliberately expose an area to the recipients attention which is immediately followed by grooming of the area	Present grooming	Present for (solicit) grooming	Solicit grooming; Lean forward; Lie with back to another; Lower; Raise leg; Turn face downwards	Back-offer; Belly offer	-	Present body part
Present sexual PR	Signaller approaches recipient backwards, exposing the swelling or anus to the recipients face (normally female to male, but sometimes a submissive gesture from male to male)	Present sexual	Present	Present with limbs flexed	*	Present rear	Present genitals
Pull through stem ST	(Mahale) 'Pull the leafy branch of a shrub or a clump of grass stems through the hand by a rapid upwards movement of the forearm, then the stem is immediately released. Produces a conspicuous sound'	-	-	Pull through stem	-	-	-
Punch object/ground ST	Movement of whole arm, with short hard audible contact of closed fist to an object or the ground	Punch object/ground; Punch object/ground 2-handed	-	Thump	-	Punch object	-
Punch other PR	As 'Punch object/ground' but contact is with recipient's body	Punch other; Punch other (multiple)	-	Hit	Wrist hit	Punch other	-

Table 4 continued (part 7)

Gesture type	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe (*Pan*) wild**	**Mahale (*Pan)* wild**	**Yerkes (*Pan*) captive**	***Gorilla* wild & captive+**	***Pongo* captive**
Push PR	Palm in contact with recipient's body and force is exerted in attempt to displace recipient	Push 1-handed; Push 2-handed	-	Push	Back push	Push, 1-handed; Push 2-handed	Push
Reach PR	Arm extended to the recipient with hand in an open, palm upwards position (no contact)	Reach	Begging with hand; Extend hand; Holding hand towards another; Reach hand; Wrist bending	Beg with hand; Extend hand; Extend leg; Offer arm	Hand beg; Wrist offer; Point; Wrist mouth; Leg offer; Bent wrist; Reach out	Reach; Beg; Stretch out hand	Reach
Roll over PR	The signaller rolls onto their back exposing their stomach, normally accompanied by repeated movements of the arms and/or legs	Roll over	Lie down on back	-	-	-	Roll on back
Rump rub ST	Push/rub rump against the body/swelling of recipient	Rump rub (body); Rump rub (swelling)	Rump turn	-	*	-	-
Shake hands ST	Signaller grasps recipient's hand in their own hand and then makes small repeated back and forth movements from the wrist	Shake hands	Hand holding/shaking	Hold hand	-	-	Hold hands
Side roulade ST	Body is rotated around the head-feet axis while lying on the ground with horizontal displacement along the ground	Side roulade	-	-	-	Side roulade; Side roulade with object	-

Table 4 continued (part 8)

Gesture type	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe (*Pan*) wild**	**Mahale (*Pan*) wild**	**Yerkes (*Pan*) captive**	***Gorilla* wild & captive+**	***Pongo* captive**
Slap object ST	Movement of the arm from the shoulder with hard short contact of the palm of the hand to an object	Slap object 1-handed; Slap object 1-handed (multiple); Slap object 2-handed; Slap object (multiple)	Slap ground; Flap; Flapping	Slap (in Slap-stamp)	Ground slap	Slap object, 1-handed; Slap object 2-handed; Slap surface	Hit ground/object
Slap object with object ST	As 'Slap object' but the hand holds an object which is brought into contact with another object (e.g. a branch is slapped against a tree)	Slap object with object 1-handed; Slap object with object 2-handed	Banging	Club ground	Ground slap	-	-
Slap other PR	As 'Slap object' but the palm is brought into contact with the recipient's body	Slap other 1-handed; Slap other 1-handed (multiple); Slap other 2-handed; Slap other 2-handed (multiple)	Slapping, Hit	Slap; Club another	Poke at	Slap other; Slap other 2-handed, Hit	Hit; Simultaneous hit
Somersault ST	Signaller's body is curled into a compact position on the ground, and rolled forwards so the feet are brought over the head and returned to sitting position	Somersault	*Somersault*	*Somersault*	-	Somersault; Somersault with object	Somersault, Back roll
Spit water ST	(Yerkes) Subject spits water at other to invite play	-	-	-	Spit water	-	-
Stomp ST	Sole of the foot is lifted vertically and brought into a short hard audible contact with the surface being stood upon (e.g. ground or a branch)	Stomp single; Stomp single on object; Stomp multiple; Stomp multiple on object	Stamping	Stamp; Heel kicking	Foot stomp; Stomp	Stomp ritualized; Stomp object ritualized; Multiple stomp; Multiple stomp on object, Foot beat	-

Table 4 continued (part 9)

Gesture type	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe (*Pan*) wild**	**Mahale (*Pan)* wild**	**Yerkes (*Pan*) captive**	***Gorilla* wild & captive+**	***Pongo* captive**
Stomp other ST	As 'Stomp' but contact is made with recipient	Stomp single on other; Stomp single on other; Stomp multiple on other	Stamping	Stamp; Heel kicking	Foot stomp	Stomp ritualized; Multiple stomp	
Stomp 2-feet ST	As 'Stomp single' but both feet used, normally alternately	Stomp 2-feet; Stomp 2-feet on object; Stomp multiple 2-feet; Stomp multiple 2-feet on object	Jumping; Stamping; Heel kicking	Leap bipedal on spot; Drum	Foot stomp	Stomp, 2-feet; Stomp 2-feet object; Multiple stomp 2-feet; Multiple stomp; 2-feet on object	-
Stomp 2-feet other ST	As 'Stomp 2-feet' but contact is made with recipient	Stomp 2-feet on other; Stomp multiple 2-feet on other	Jumping; Stamping; Heel kicking; Stamping on the back		Foot stomp	Stomp, 2-feet	
Tandem walk ST	Subject positions arm over the body of the recipient and both walk forward while maintaining position	Tandem walk	Arm round	Embrace half	Arm neck, Hunch over	Tandem walk	Tandem walk
Tap object PR	Movement of the arm from the wrist or elbow, with firm short contact of the fingers to the object (single/multiple)	Tap object; Tapping object	-	-	-	Tapping object	-
Tap other PR	As 'Tap object' but contact is with recipient's body	Tap other; Tapping other	Dabbing; Patting	Pat; Dab	Dab	Tapping other; Tap other	Tap
Throw object ST	Object is moved and released so that there is displacement through the air after moment of release	Throw object	Aimed throwing	Lift and drop; Drop branch; Throw at	Throw stuff; Ball throw; Throw aimed	Throw object; Throw threat	-

Table 4 continued (part 10)

Gesture type	**Definition (Sonso unless specified otherwise)**	**Group gestures within category**					
		Sonso (*Pan*) wild	**Gombe (*Pan*) wild**	**Mahale (*Pan*) wild**	**Yerkes (*Pan*) captive**	***Gorilla* wild & captive+**	***Pongo* captive**
Touch other PR	Light contact of the palm and/or fingers on the body of the recipient, contact under 2 seconds	Touch other	Touch; Hold genitals	Touch; Light touch Stroke; Hold genitals	Touch-side, Gentle touch	Touch; Stroking	Touch; Brush
Walk (stiff) ST	Walk quadrapedally with a slow exaggerated movement	Walk (stiff)	*Play walk*	-	-	Stiff walk; Stiff 3-feet walk	-
Water splash ST	Hand is moved vigorously through the water so that there is audible displacement of the water	Water splash	-	*Hit water*	-	Water splash	-

3.3.2 Distribution of measures of intentionality: Response waiting and Persistence

Only behaviours accompanied by some measure of intentional communication were considered as possible cases of gesture, therefore both response waiting and persistence were already selected for within the data set; however, it was possible to check for variation in their distribution. Measures of intentionality were recorded at the level of the G-clause and a total of 3422 separate G-clauses were recorded during the study. Response waiting followed 65.23% ±12.97 of G-clauses (individuals with 5 or more G-clauses, n=56).

Persistence was observed following the failure (n=41, mean frequency =48.02% ±20.43), and partial failure (n=23, mean frequency =71.31% ±15.97) of the communication’s function (see Figure 3). The level of persistence when the goal was partially achieved was significantly higher than when the goal had completely failed to be met (Independent t-test: t= 4.76, df=62, p<0.0001, see Figure 3).

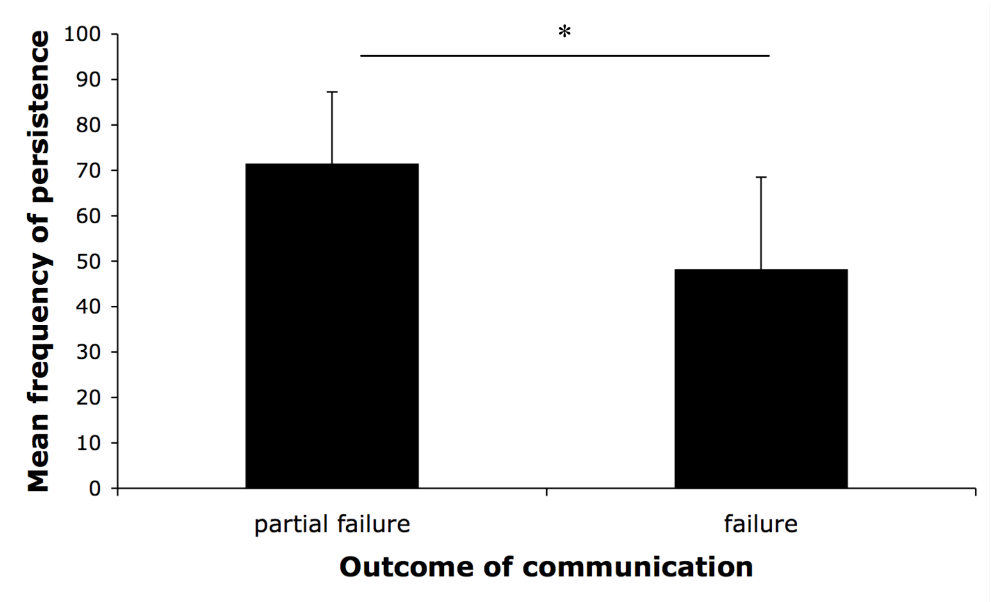


Figure 3: The frequency of persistence following failure of the communication. The mean frequency with which individuals produced an additional G-clause following the partial failure or failure of a previous G-clause. Notification * represents $p<0.0001$

3.3.3 Do potentially-ritualized gestures differ from other gestures in signs of intentional usage?

Of the 66 gesture types, 29 (43.9%) could be classed as potentially-ritualized (PR), leaving 37 gestures that I classed as species-typical displays (ST). Of the PR gestures the majority were contact gestures (51.7%), while the majority of ST gestures were audible (43.2%), see Table 5.

Table 5: Distribution of repertoire across modes. The frequency of gesture types by mode and classification as PR or ST.

	Silent (%)	**Audible (%)**	**Contact (%)**	**Total**
Potentially-ritualized	11 (37.9)	3 (10.3)	15 (51.7)	29
Species-typical	14 (37.8)	16 (43.2)	7 (18.9)	37

Flexibility

Following Call & Tomasello (2007) and Genty et al. (2009), I used the range of situational contexts in which each gesture was recorded to estimate its flexibility. Both PR and ST gestures were produced in several contexts. Although the spread was slightly higher for PR gestures (1-9) than ST gestures (1-7), there was no significant difference in flexibility (gestures with 3 or more recorded examples: n=61, Chi-square χ^2=13.76, df=8, p=0.09; see Figure 4).

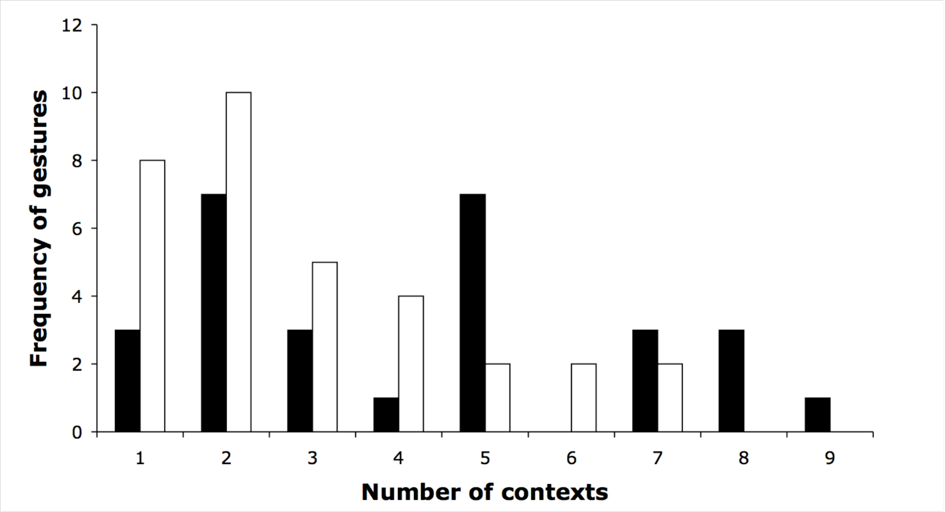


Figure 4: Context specificity of gestures. The frequency of gestures is plotted against the number of contexts in which they occur. White bars represent species-typical gestures, black bars represent potentially-ritualized ones.

Adjustment for audience

As verification of the audiences attention state was measured at the level of the G-clause (i.e. a rapid sequence of gestures separated by <1sec), I limited the data set to consider only gestures used singly or as the first gesture in a G-clause, leaving 3410 gestures for analysis.

From this subset I examined whether for gesture use in general, there was evidence that the audience's attentional state was taken into account. To show any such effect I calculated the variation in choice of silent, audible and contact gestures, according to the attentional state of the audience (Figure 5). The choice of different modes of gesture varied significantly with the recipient's attention state (n=225, ANOVA $f_{5,219}$=50.70, p<0.0001). Specifically, silent gesture use increased when the recipient was attending and decreased when they were out of sight (attending: n=40 mean=14.5 ±37.0; out of sight n=35 mean=-64.9 ±36.7; planned t-test t=-9.31, df=73, p<0.0001), and contact gesture use decreased when the recipient was attending and increased when they were out of sight (attending: n=40 mean=-26.9 ±41.3; out of sight: n=35 mean=49.7 ±67.5; planned t-test t=6.02, df=73, p<0.0001). There was no variation in the use of audible gestures (attending: n=40 mean=7.7 ±42.8; out of sight: n=35 mean=4.5 ±54.0; planned t-test t=-0.29, df=73, p=0.776).

I then repeated this exercise for the use of PR and ST gestures separately, for each individual, and examined whether, for each modality, the variation in use differed significantly between PR and ST gestures, and between recipient attentional state. Thus, in this comparison, every individual provided a total of 12 measures of variation of use (PR, silent, attending; PR, silent, out of view; ST, silent, attending; ST, silent, out of view; etc.). Separate 2x2 between-subjects ANOVAs (or an equivalent non-parametric alternative) were used to examine each mode of gesture (silent, audible, contact) for any effect of categorization, as PR or ST, or attention state on the variation in use of the mode of gesture.

For each mode of gesture there was a significant effect for audience attentional state, but no difference in the use of gestures designated as PR or ST, or interactions between the gesture category and the audience's attentional state. For silent gestures (ANOVA n=78, f=0.039, df=3,74, p=0.843), attentional state was significant (f=25.32, df=1,77, p<0.0001), gesture category was not (f=0.053, df=1,77, p=0.819). For audible gestures, the data were still positively skewed following transformation so non-parametric statistics were applied. Attentional state was significant (Kruskal-Wallis Test Chi^2=34.34, df=1, p<0.0001), whereas gesture category was not (Kruskal-Wallis Test Chi^2=0.015, df=1, p=0.904). For contact gestures (ANOVA n=78, f=0.062, df=3,74, p=0.803, data transformed to correct for positive skew), attentional state was significant (f=36.57, df=1,77, p<0.0001), gesture category was not (f=0.080, df=1,77, p=0.778).

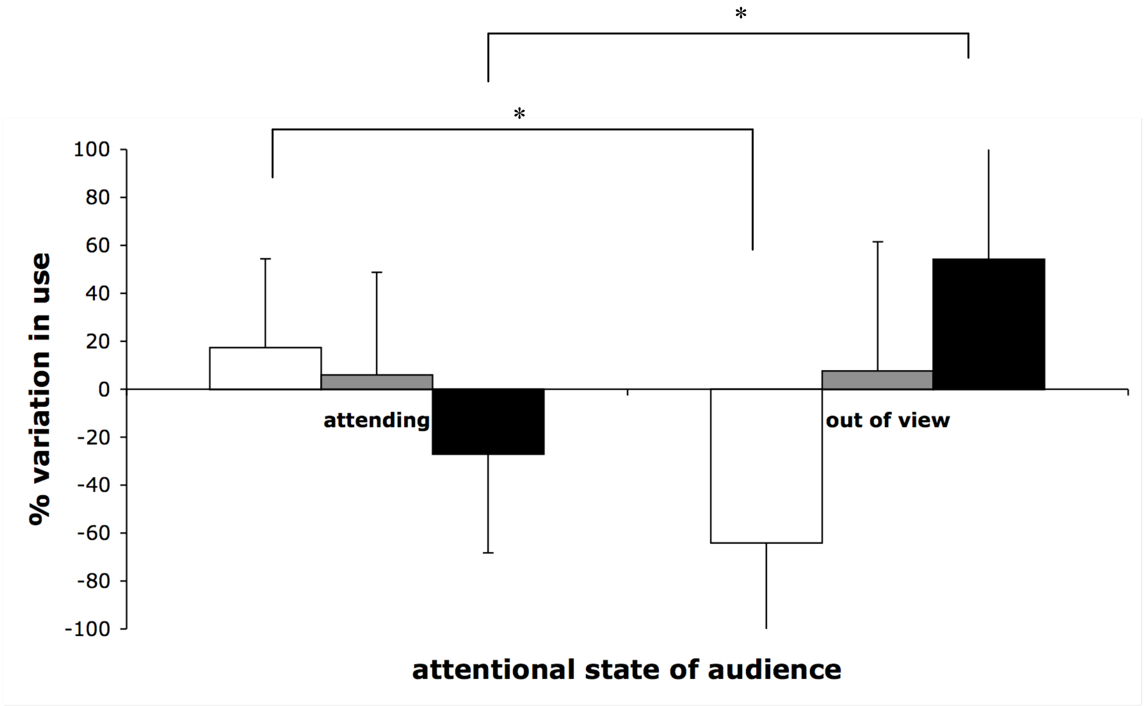


Figure 5: Variation in use of gesture modes with recipient's state of attention. Notification * represents variation ($p<0.0001$) in the choice of silent, audible, or contact gestures; according to the attentional state of the target audience by posthoc Games-Howell test. White bars represent silent gesture, grey bars represent audible gestures and black bars contact ones.

Idiosyncratic gestures

I found no evidence for any idiosyncratic gestures in wild chimpanzees. All of the 61 gestures recorded 3 or more times were used by more than one individual. Seven gestures were found in only one individual's repertoire; that is, each was recorded at least twice for those individuals. However, all those 7 gestures were recorded as used by other individuals on single occasions. Nor was there any evidence for 'matrisyncratic' gestures. Again, seven gestures formed part of the repertoires of only one matriline; but, again, all 7 were also used on single occasions by individuals outside of the matriline.

One-way gestures

Of the five individuals with the largest repertoires, a mean 17.8% ±5.0 (range 7-12 gestures) of the individual repertoires were one-way gestures (those recorded as produced but not recorded as received by that individual). These individuals were recorded as producing 25.4% ±12.8 more cases of gesture (range 21-119 cases) than they received.

Four of these five individuals were also in the group of five individuals who received the most cases of gesture. The fifth individual was an adult female Zimba, who received very high levels of gesture following her involvement in two consortship events. She received 303 cases of gesture, and produced only 13. Only a single one-way gesture was recorded in her repertoire: Present-sexual, which would not normally be directed towards an adult female.

3.3.4 Does the physical form of potentially ritualized gestures accord with ontogeny by ritualization from an effective action?

I examined two gestures, Begging-reach and Directed push, comparing their physical form with that of the effective actions (taking an object, and physically positioning, respectively) from which they might plausibly have been ritualized.

For the gesture Begging-reach, I compared 68 taking actions with 163 Begging-reach gestures, for the orientation of the palm, position of the fingers and which part of the hand was presented first (see Figure 6). The 3 possible palm orientations differed significantly in frequency between the Begging-reach gesture and the action of taking (3x2 between subjects ANOVA $f_{2,48}$=16.90, p=0.01). Specifically, from 3 planned t-tests between gesture and action for the 3 palm positions: the Begging-reach gesture was usually performed with the palm held vertically (gesture: n=12 mean=45.5 ±26.0; action: n=6 mean=2.4 ±5.8; planned t-test t_{16}=3.96, p=0.001), whereas the take action was usually performed with the palm held down (gesture: n=12 mean=14.0 ±16.1; action: n=6 mean=62.9 ±24.7; planned t-test t_{16}=5.09, p=0.001). There was no difference in the frequency with which the up position was used (gesture: n=12 mean=38.4 ±25.6; action: n=6 mean=24.8 ±29.5;

planned t-test t_{16}=1.01, p=0.135). The use of the curled or extended finger position also differed significantly between Begging-reach-and take (2x2 between subjects ANOVA $f_{1,32}$=4.19, p=0.049). However, from 2 planned t-tests between gesture and action for the 2 finger positions, the difference in the frequency with which the fingers were held in an extended position only approached significance (gesture: n=12 mean=46.1 ±30.5; action: n=6 mean=20.6 ±18.6; planned t-test t_{16}=1.87, p=0.079) and there was no difference in the frequency with which they were held in the curled position (gesture: n=12 mean=51.8 ±32.8; action: n=6 mean=69.5 ±30.5; planned t-test t_{16}=1.10, p=0.290). Finally, the part of the hand presented first did not differ between begging reach and take (2x4 between subjects Kruskal-Wallis H=0.05 df=1, p=0.826), with the front of the fingers predominantly used in both the Begging-reach gesture (n=12 mean=84.6 ±20.3) and take actions (n=6 mean=71.0 ±27.5).

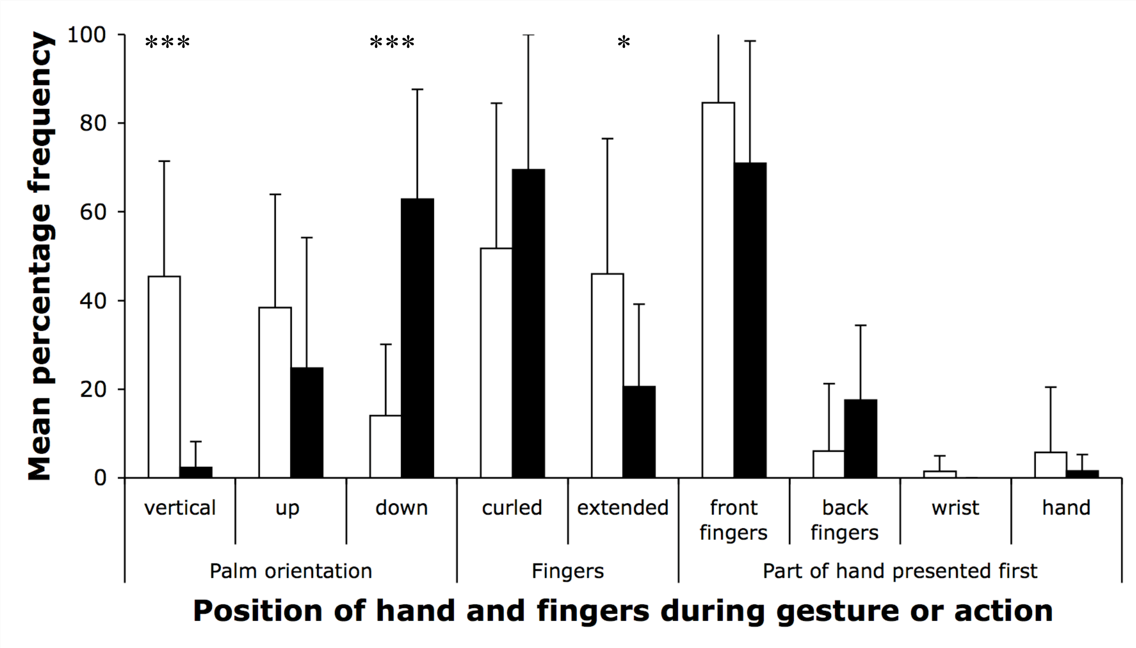


Figure 6: Comparison of the physical form of Reach gestures with Take actions. Notification *, *** represents variation in the frequency with which the different parts of the hand are used to perform either the reach gesture or take action by planned t-tests (respectively <0.1, <0.001). White bars represent reach gestures; black bars represent take actions.

For the Directed push gesture, I compared 130 positioning actions with 127 Directed push gestures, for the part of the hand used to perform the movement (see Figure 7). The part of the hand used differed significantly between the Directed push gesture and the positioning action (2x5 between-subjects ANOVA $f_{4,60}=12.22$, $p<0.0001$). Specifically from 5 planned t-tests, the palm was used significantly more often to perform the action rather than the gesture (gesture: n=7 mean=2.6 ±4.9; action: n=7 mean =49.5 ±18.7; planned t-test $t_{12}=6.37$, $p<0.0001$); whereas the back of the fingers was used to perform the gesture rather than the action (gesture: n=7 mean=24.1 ±19.2; action: n=7 mean=6.4 ±9.5; planned t-test $t_{12}=2.24$, $p=0.045$). Although, the front of the fingers was predominantly used to perform the gesture (n=7 mean=62.8 ±26.8), the difference in frequency with the action (n=7 mean=37.7 ±22.7) only approached significance (planned t-test $t_{12}=1.91$, $p=0.081$). The knuckles and back of the hand were used rarely in either gestures (n=7, knuckles: mean=3.5 ±5.9; back of hand: mean =6.2 ±9.6) or actions (n=7 knuckles: mean=5.4 ±9.2; back of hand: mean=1.1 ±2.9), and there was no difference in the frequency with which either was used (knuckles: planned t-test $t_{12}=0.45$, $p=0.663$; back-of-hand: planned t-test $t_{12}=1.35$, $p=0.202$).

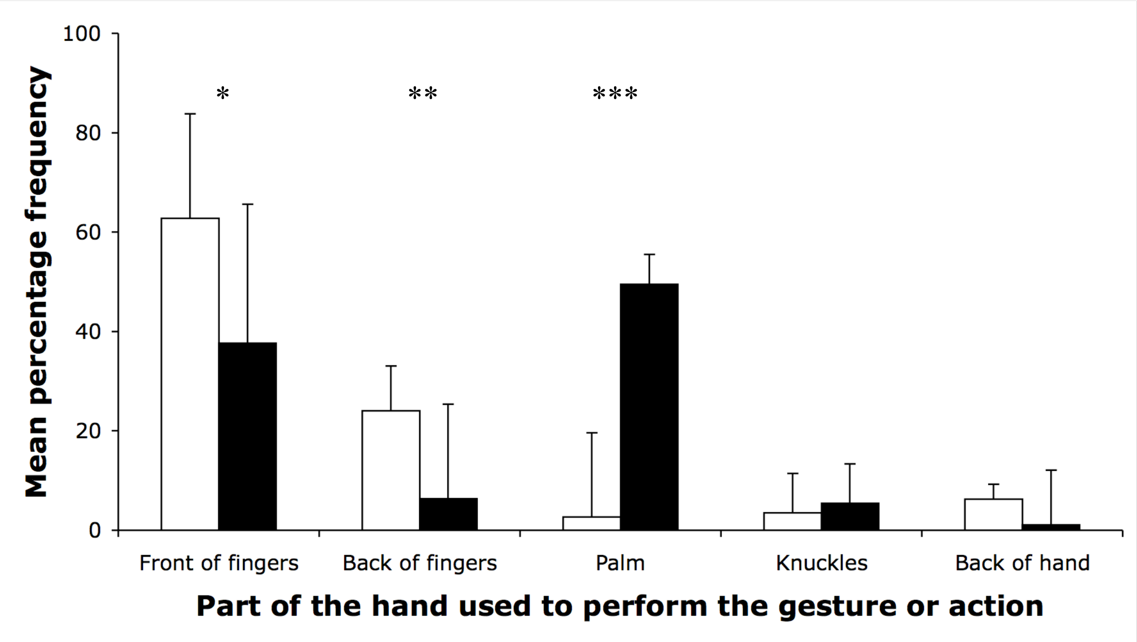


Figure 7: Comparison of the physical form of Directed push gestures with Position actions. Notification *, **, *** represents variation in the frequency with which the different parts of the hand are used to perform either the directed push gesture or position action by planned t-tests (respectively <0.1, <0.05, <0.001). White bars represent directed push gestures; black bars represent position actions.

3.3.5 Does the gestural repertoire of Sonso chimpanzees match that at other sites?

Having found no evidence of any functional difference between gestures that might plausibly have been ritualized and those that must be species typical, or evidence of idiosyncratic use, I considered instead the possibility that the entire gestural repertoire was species-typical. For chimpanzee gestures that are species-typical, it may be that they have a more ancient origin in the great ape lineage, so I also considered the possibility of 'family-typical' gestures, occurring in more than one great ape species.

I compared the repertoire of 66 Sonso chimpanzee gesture types with that recorded in three other chimpanzee populations (using studies of gesture at Gombe, Mahale, and the captive Yerkes group, with additional data from a captive study that did not focus on gesture in particular), and gorilla and orang-utan repertoires from published studies of gesture (see Table 4). I excluded behaviour that was not considered to be gesturing by my definition (e.g. static postures, such as crouching, treated as a gesture at Gombe; facial expressions, such as pout face, treated as a gesture at Yerkes; and effective actions, such as 'begging' with the mouth, treated as a gesture at Gombe and Yerkes). Repertoire overlap was examined in two ways: how many of gestures recorded in other chimpanzee studies (or great ape species) were recorded in the current study of one Ugandan chimpanzee community; and how many of the Sonso chimpanzees' gestures have been recorded in other chimpanzee studies (or great ape species). In the case of the comparison with the gorilla repertoire, I used the finer detail specifications of gestures at Sonso (115), as the gorilla study used a more detailed level of categorization.

Most gestures, previously recorded in chimpanzees at other sites in Africa or in captivity, were also recorded at Sonso in the present study (Gombe: 100%, 56 out of 56; Mahale: 97%, 59 out of 61; Yerkes, captive: 97%, 29 out of 30). Moreover, a considerable number of gestures in the repertoire recorded for the gorilla and orang-utan were also found in this study of Sonso chimpanzees (gorilla: 60%, 72 out of 121; orang-utan: 84%, 43 out of 51). Twenty-two gestures were recorded from all three great ape genera. Looking at the question from the other perspective, 47 of the 66 gestures recorded at Sonso have also been recorded in other chimpanzee gestural studies. In addition, a further 7 of the Sonso gestures have been seen in other chimpanzee studies, although they were not treated as gestures. Of the 12 Sonso gestures not recorded in other chimpanzee gesture studies, 10 have been recorded in other great ape species (9 in *Gorilla*, 1 in *Pongo*). Only two gestures (Object in mouth approach, Foot present) were uniquely noted at Sonso.

3.4 Discussion

In this study I define a gesture as a case of *intentional* communication, and require that each instance be accompanied by evidence that the signaller was paying attention to the audience prior to gesturing, was waiting for a response to their communication, and, if necessary, persisted in further communication if no response was forthcoming or if it failed to meet the goal of their communication.

Despite this strict definition I found ample cases for analysis, and was able to demonstrate that, as has been shown in captivity, Sonso chimpanzees employ gestures flexibly across multiple contexts, and individuals actively adjust the mode of their gestures in order to accommodate the attentional state of their target audience. Thus, silent gestures were used significantly more often when the recipient was already paying attention to the signaller and therefore able to see the gesture, than when the signaller was out of sight. In contrast, contact gestures were more likely to be used when the signaller was out of sight than when the recipient was paying attention to them.

Sonso chimpanzees were also more likely to persist in further attempts to communicate following partial success rather than where the communication failed completely. This replicates the recent finding in captive orang-utans (Cartmill and Byrne, 2007), and suggests that, as with the orang-utans, the chimpanzees may be deriving some form of positive reinforcement from the partial success of the goal, which encourages them to persist in the attempt to communicate.

As discussed in the introduction there are a number of reasons to question the dominant theory for the acquisition of gesture: Ontogenetic Ritualization, and recent work in gorilla gestural communication suggests that, instead, gestural communication may be founded on a large, flexible species-typical repertoire (Genty et al., 2009). In this chapter I followed Genty et al. in dividing the repertoire of intentional gestures in to two subsets: one containing those gestures whose physical form was compatible with an ontogenetically ritualized origin, and one containing those where I could see no plausible effective action from which they could have been ritualized. In doing this I could find no characteristic differences between the sets. Both were used across a similarly broad range of contexts and both were adjusted to accommodate the target audience's state of attention in an equal manner.

Gestures whose physical form excludes them from categorization as potentially ritualized from effective actions are not necessarily required to be species-typical, they could, for example, be acquired through social learning. However, a species-typical theory of acquisition provided the most parsimonious explanation for their acquisition and, as there was no evidence to suggest that more complex social learning mechanisms were necessary, the species-typical theory was sufficient to account for the acquisition of the repertoire.

Critically for the suggested category of attention-getters, audible gestures were the only mode not to show a significant adjustment to the recipient's attentional state. In fact when the two sets (PR and ST) were examined separately, in both cases there was a small decrease in the use of audible gestures towards inattentive recipients. As both attentive and inattentive recipients can receive audible gestural communications, this is still consistent with their intentional use; however, it does clearly show that the ST set of audible gestures (which would be classed by Tomasello as attention-getters as they were not incipient-action gestures) were *not* being used solely to acquire the attention of inattentive recipients and therefore can certainly not be described as attention-getters.

In essence it is incorrect to assume that just because a gesture *can* attract attention that this limits it to *only* attracting attention. King argues that audible gestures such as chest-beating and leaf-clipping are not clearly adjusted to the actions of the partner to the same degree as other gestures (King, 2004). However, I would argue that this is exactly what would be expected of audible gestures, as their meaning can be communicated to a target audience irrespective of their state of attention. Impressively, the effect of adjustment to the audience's state of attention in silent and contact gestures was so strong that it remained significant within the ST set despite the fact that the majority of gestures in this subset were audible and therefore not used in a targeted fashion.

While Tomasello and Call use the variability in the gestural repertoire to rule out alternative hypotheses such as a species-typical origin, or second-person imitation, they don't test whether or not there is any evidence *for* the theory that 'intention-movement' gestures are being ritualized from effective actions. Here I attempted to test the prediction that the physical form of the ritualized gesture should match the physical form of the action it is ritualized from. Two gestures appeared to be clear candidates for ritualization from effective actions: the Begging-reach (from a taking action), and the Directed push (from the physical act of repositioning another individual). However, a detailed analysis of their physical form showed several significant differences from that of the actions. The part of the hand used to perform the movement, the orientation of the palm, even whether the fingers were curled or extended, differed between gesture and action.

As would be intuitively expected the Begging-reach gesture tended to occur with the fingers extended and the palm in an open vertical position, while in contrast, taking actions were conducted with the palm down and the fingers frequently curled. The more defensive position of the take action, which shelters the vulnerable palm while in the vicinity of sharp canine teeth, is entirely suitable for the potentially risky action of simply taking food from another individual. Any one who has observed chimpanzees feeding can easily recall the highly vocal and frequently physical altercations that arise over access to regularly available foods such as fruit, let alone highly desirable foods such as meat. However, while the more defensive taking action hand position is quite logical, it is not consistent with a possible physical origin from which the Begging-reach gesture could have been ritualized. This makes it impossible to describe the Begging-reach as an intention-movement of the Take action.

The same was true of the physical form of the Directed push gestures and Position actions. The Position action is frequently performed with the palm of the hand, which is consistent with the normal physically effective grip-action; however, the palm is almost never used during Directed push gestures. Instead the Directed push is usually performed with the fingers, and includes the frequent use of the back of the fingers: particularly difficult to ascribe to an effective-action origin.

Perhaps most critically for the question of an ontogenetically ritualized or species-typical origin, there was no evidence for any idiosyncratic gesture use. All gestures were used by at least two individuals, although occasionally at very low frequencies. I also found no evidence for the presence of gestures types that were specific to matrilines. While a number of idiosyncratic gestures have been described in captivity, some of these examples are extremely difficult to accept as having been ontogenetically ritualized. The Disco-Arm shake observed in a gorilla (Genty et al., 2009) or the finger-curl or spit-water as described in chimpanzees (Tomasello et al., 1989) are all gestures where it is difficult to conceive of any effective action from which they could be ritualized. Captive apes have one importance source for imitation outside of their own species: us. Observation of either visitors or carers would provide extensive opportunity for potential imitation. Alternatively, it is possible that these gestures are rare species-typical actions that would be observed more widely with further observation. Critically in wild apes an external source of imitation such as humans, is predominantly absent; so any evidence for idiosyncratic gesture use would have indeed strengthened the case for OR. However as we found no evidence for idiosyncratic gesture use, there was no support for a ritualization-based theory of acquisition.

One-way gestures were the exception rather than the rule. For those individuals with the largest repertoires, one-way gestures accounted for less than 18% of the repertoire. These same individuals were observed to produce approximately 25% more gesture cases than they received, given the evidence that the size of an individual’s repertoire is predicted by the quantity of gesture cases, I would expect that the proportion of one-way gestures would decrease with additional observation of gestures received by these individuals. As discussion in the introduction, the presence of one-way gesture types would be expected in any natural system of communication because of the inherent imbalances in the size, sex and power of different individuals. For example, the 'present-climb on me' gesture would never be produced by an infant who is far to small to carry anyone, or received by an adult who is far too large to be carried. However, those adults currently producing the gesture may have received it when they were themselves infants, thus, while it would not be recorded as received by them, it may not be truly one-way. While ontogenetic ritualization does not make specific predictions about the level of one-way gesture forms in the repertoire, the creation of two-way gestures requires that the repeated dyadic interactions necessary to ritualize a gesture from an action happen twice as opposed to only once, suggesting that one-way gesture should be the norm. Thus, a small proportion of one-way gestures, as found in the Sonso community, are more compatible with a species-typical theory of gestural acquisition.

While this represents the first comprehensive study of gestural communication in a wild chimpanzee population, it was possible to construct the approximate repertoires of two other wild chimpanzee populations (Gombe and Mahale) using the detailed ethograms recorded by other researchers. Naturally the size of the repertoire depends to a certain extent on the level of detail with which individual gestures are defined, and different studies can be classed as either lumpers or splitters. However, using a similar level of categorization, the repertoires of the three wild populations are very similar: Sonso 66 (using the broader level of categorization comparable to the other chimpanzee sites; using a finer level of categorization the repertoire was 115); Gombe 61 (Goodall, 1968, Goodall, 1986, Plooij, 1984), and Mahale 69 (Nishida et al., 1999). In contrast the repertoire of the captive Yerkes group was only approximately half this at 33 gestures (Tomasello et al., 1985, Tomasello et al., 1994), as additional gestures have been added with each new study (Call and Tomasello, 2007, Pollick and de Waal, 2007) this suggests that the repertoire has yet to reach asymptote.

The smaller repertoire reported from Yerkes may be the result of the relatively shorter quantity of observation time. Both the Gombe and Mahale communities have been the subject of rigorous study for over 40-years, and the repertoire of the Sonso community only neared asymptote following a 2-year study with 266 days of observation time specifically focused on gestural communication. Even at this stage no individual repertoire had reached asymptote. I therefore strongly caution against the premature assignation of a gesture as being either absent from any one individual or group's repertoire, or as idiosyncratic, following shorter study periods.

From an OR perspective there is no straightforward concept of an individual repertoire of gesture types, as each gesture is specific to the recipient with which it was ritualized. Thus, an individual who uses a grab gesture in interactions with three different recipients actually has three different gestures within their repertoire. This dramatically increases the number of ritualizations necessary to acquire even a relatively limited repertoire. In the case of the Sonso chimpanzees, with an available repertoire of 66 gesture types, to ritualize these with even half of the 81 individuals within the Sonso community would require 2,640 separate cases of ritualization. Naturally given the fission-fusion nature of chimpanzee social interactions, the number of regularly available social partners may be quite small. To take a real example: Night, the 5-year old female with the largest individual repertoire, was observed to use 51 different gesture types in gestural communications with 32 different recipients. This amounted to 196 different 'gesture + recipient' combinations; each one of which she would have had to ritualize from a fully effective action. Furthermore, Sonso chimpanzees regularly produced the same gesture types from the gestural repertoire they used to communicate within their own species, when gesturing towards other species, including baboons, bush pigs, and field researchers. Clearly no process of ontogenetic ritualization took place in these situations.

Much of the evidence for OR was founded upon the high levels of variability reported in individual repertoires. At Sonso the largest individual repertoire included 41 of the possible 66 gestures types (with a further 10 observed on single occasions). Across the group I found that the size of an individual's repertoire was closely predicted by the quantity of gesturing recorded for it, suggesting that most individual repertoires were yet to reach asymptote. In fact when plotted on the same axis, individual repertoires fall along, or close to, the curve of the cumulative repertoire for the group as a whole. Thus, I suggest that individual repertoires are likely to have been under-reported, and that many of the idiosyncratic gestures described in captivity are in fact simply part of the larger species repertoire.

The repertoire of different age groups did vary: as in captivity the peak was found in the juvenile age group with a decline into the sub-adult and adult categories. However, once again repertoire size was closely predicted by the quantity of gesturing recorded for that age group. The most significant source of variation may, then, be less in fixed age-group repertoires, than in the sheer amount of gesture used by chimpanzees of different ages.

If, as the data suggests, chimpanzee gestural communication is based upon a species-typical repertoire, I would expect that repertoires of different groups should, as well as being the same size (once asymptote is reached), contain the same gesture types. This is in fact the case, with almost all of the gestures recorded at Gombe (56 of 56, 100%), Mahale (59 of 61, 97%) or Yerkes (29 of 30, 97%) present in the Sonso repertoire, including gestures described as rare or idiosyncratic elsewhere. Only 3 potentially group specific gestures were found: Spit water (Yerkes), Drum Belly (Mahale) and, Pull through stem (Mahale). The Drum belly gesture is regularly observed in gorilla gesturing (Genty et al., 2009), and the Pull through stem is based upon a common food processing action (the 'strip up') reported both in other chimpanzee groups (Byrne and Stokes, 2002), and in gorillas (Byrne and Byrne, 1993), leaving only Spit water as a possibly group specific 'gesture' from the captive Yerkes group. As Spit water cannot be described as ritualized from an effective action, it cannot provide support for an ontogenetically ritualized theory of acquisition.

Conversely over 70% of all gestures reported at Sonso were described at other sites. This suggests that the Sonso repertoire is actually somewhat larger and that the others have yet to reach asymptote, but I would expect this overlap to increase with further observation. This is consistent with the observation that there were no idiosyncratic gestures described at Sonso and, that the inclusion of a gesture in any individual's repertoire could be predicted by the number of cases of that gesture.

Impressively, when we compare the Sonso repertoire to that described for gorilla and orang-utans then there is still a significant overlap: 60% in gorilla and 80% in orang-utan. Rather than a simply species-typical repertoire it appears that there is a large ‘family-typical’ great ape repertoire. When comparing the Sonso chimpanzee repertoire with the published gorilla repertoire (121) at the same level of categorization, the Sonso repertoire (115) is still slightly smaller, and unlike the gorilla repertoire had appeared to near asymptote, suggesting that gorillas may have a larger gestural repertoire than chimpanzees, and orang-utans (at 51) a slightly smaller repertoire.

3.4.1 Summary

The data from the gestural communication of the Sonso chimpanzees supports the theory that the majority of chimpanzee gestural communication is in fact founded upon a large, flexible, *species-typical* repertoire. I find no support for ontogenetic ritualization, and although, like imitation, this may occur on occasion, it cannot be described as the major process by which chimpanzees acquire their intentional gestures.

Chapter 4. The ontogeny of gestural communication in wild chimpanzees

4.1 Introduction

Age categories: where to draw the line?

In captivity detailed information on individual age is usually readily available; however, as noted in Chapter 3 the group-size is often very small, reducing the scope of the findings to individual rather than species ontogeny. Natural communities have much larger group-sizes, however, in early studies demographic data was often extremely limited, and the difficulties of locating and identifying individuals made accurately describing infant development extremely challenging. Thanks to the consistent long-term observation of several wild populations, more detailed individual information on natural groups is now available, and it has become possible to examine early ontogeny in more detail. For example, recent work at Gombe revealed a sex difference in the rate of learning by focusing on the development of infants under 5-years old (Lonsdorf et al., 2004).

In any study of ontogeny it is critical that not only are age categories clearly defined, but that the boundaries of each age group distinguish periods that describe salient variations in development. In her work at Gombe, Goodall describes the 4 basic categories of: infant, juvenile, sub-adult and adult (Goodall, 1968), also employed other sites (Taï (Boesch and Boesch-Achermann, 2000), Budongo (Reynolds, 2005)). However, in an early analysis of mother-offspring relationships, Goodall actually distinguishes 5 different categories of immature individuals: *infant 1* (0-6months); *infant 2* (6months to 2years); *infant 3* (2years to 3/3½years); *juvenile* (3/3½ - 6/7years) and *adolescence* (6/7 – 11/13years) (Van Lawick-Goodall, 1967). In later work these were largely combined, but more detailed distinctions were drawn in the sub-adult and adult periods: *infancy* 0-5y, *childhood* 5-7y, *early adolescence*: male 8-12y, female 8-10y, *late adolescence*: male 13-15y, female 11-13/14y, *maturity*: young adult males 16-20y, prime adult males 21-26y, middle age males 27-33y, females 14/15-33y, and finally *old age* 33y-death (Goodall, 1986). These distinctions then allow the separation of younger adults, for example: a 16-year old nulliparous female, that may have recently immigrated to a new group; and older adults, such as a 50-year old male patriarch, who has lived many years in one community. However, at the other end of the spectrum we have returned to a lumped 'infant' category, which combines individuals from birth up to 5-years old. At this period in their life, as the youngest offspring (female chimpanzee inter-birth intervals being approximately 5-years in the wild (Goodall, 1986)), the infants are constantly cared for and carried by their mother. They share their mother's nest overnight, still regularly nurse, and rarely stray far from her side. Once they reach 5-years old they are defined as juveniles. At this stage they are normally weaned or in the process of being weaned; and starting to gain more independence, sleeping and occasionally travelling alone, although usually still in the close vicinity of their mother. Thus, the separation of infants and juveniles at around 5-years old, defines clearly distinct periods in a young chimpanzee's life history; and yet at the same time it allows for no distinction to be drawn between the behaviour of individuals at 4-days old and at 4-years old. So where do we draw the line?

I found that the most useful approach was to vary the level of distinction I make with the question I aim to address. Outside of specific analyses of ontogeny I refer to individuals in terms of the four basic categories; however, where I aim to examine the development of gestural communication with age I draw more detailed distinctions between individuals (see Table 6).

Table 6: Definition of age groups. Definition of the detailed age groups in years/months and their broad age group equivalent.

Broad age group	**Detailed age group**	**Chronological age (inclusive)**
Infant	Baby	0.0 – 0.11years
Infant	Younger infant	1.0 – 2.11years
Infant	Older infant	3.0 – 4.11years
Juvenile	Juvenile	5.0 – 9.11years
Sub-adult	Sub-adult	10.0 – 14.11years (female), 10.0 – 15.11years (male)
Adult	Young adult	15.0 – 25.11years (female), 16.0 – 25.11years (male)
Adult	Mature adult	>25.0 years

The development of gestural communication

Studies to date have focused on the gestural communication of juvenile apes ((Tomasello et al., 1985) (Tomasello et al., 1989) (Tomasello et al., 1994) (Povinelli et al., 1997) (Pika et al., 2005b) (Pika, 2007)), with very little attention paid to either the onset of gesture in young infants or the development of gestural communication beyond the juvenile stage.

In an early report of mother-infant interaction in the Gombe community, Goodall states that all adult gestures are present by the second year of life (Van Lawick-Goodall, 1967); Plooij provides a more detailed description of early infant development at Gombe, in which he records the onset of gestural communication at 9-months old where begging is accompanied by both response waiting and gaze-alternation; this is followed by gesture use in play and grooming at around 11-months old (Plooij, 1978, Plooij, 1984). These brief descriptions from Gombe were followed by the first systematic observations of gestural communication in a longitudinal-study of the captive Yerkes group by Tomasello et al. ((Tomasello et al., 1985) (Tomasello et al., 1989) (Tomasello et al., 1994)). Here snapshots of the gestural communication of immature individuals within the group were taken on three points between 1983 and 1991, allowing for comparisons between both age groups and cohorts. Tomasello et al. initially describe the gestural communication of 'five infant and juvenile chimpanzees' (all individuals under 5-years old) although when presenting the results they only make the distinction between juvenile and adult individuals (Tomasello et al., 1985). The gestural communication of these same (and two additional) 'juvenile' individuals is described several years later when they are all between 5 and 8-years old (Tomasello et al., 1989). In the final study, the gestural communication of a new generation of 'infants and juveniles' (again all under 5-years old) is described (Tomasello et al., 1994). The somewhat inconsistent use of undefined infant/juvenile age category labels is initially confusing; however, because of the very small number of individuals in these studies in practice the authors describe much of the variation on an individual case by case basis; occasionally combining individual data by age in years. They report early attempts at gestural communication in individuals from 1-year old, and more clearly intentional communication from 2-years old where gestures started to be accompanied by response waiting, and (later at 3-years old) gaze-alternation (Tomasello et al., 1985). They also report that the flexibility of gestures (measured in terms of the number of contexts in which individual gestures are produced) increases with the signaller's age.

However, even when the data from all three studies were pooled by age, there were never more than 3 immature individuals able to contribute to any one year-group (more usually only 1 or 2); and observation times were relatively short (10-15hrs per week; studies of 6, 3, and 3-months respectively). As discussed in Chapter 3, short observation time and limited study-group size may result in artificially high reports of individual variability, masking evidence for species-typical behaviour. This effect seriously limits the power of the study to draw conclusions about anything more than individual development.

Thus, descriptions of early chimpanzee gestural communication are restricted to either brief comment on more general observations of wild behaviour, or detailed study on a limited number of captive individuals for a short time. To address these shortcomings in the literature I aimed to apply the systematic approach to the study of gesture in long-term observations of a natural community, and thus provide a more comprehensive basis for the description of species ontogeny of gestural communication.

At the start of data collection in 2007 the Sonso community contained 32 adult, 16 sub-adult, 15 juvenile and 18 infant chimpanzees, with a further 5 individuals born over the course of the fieldwork. Furthermore I was in the extremely fortunate position that, after 20-years of continuous study, the exact year, and in many cases month, of birth is known for all immature individuals. I took advantage of the large group size and detailed individual information available for the Sonso community to describe the development of gestural communication in greater depth.

4.2 Specific method

4.2.1 Age group repertoire

The age group repertoire was compiled by pooling data from all individuals within the age group at the time of gesturing (see Table 6 for definition of age groups). This represented the only feasible method as, due to the focal behaviour protocol, different individuals contributed different quantities of data, and with the long-term nature of the study (>2-years) some individuals contribute data to more than one age group. Gestures observed on 2 or more occasions within the age group are included in the age group repertoire.

4.3 Results

4.3.1 Repertoire

Gestural communication was recorded from chimpanzees of all age groups; the youngest examples were from the 4-month old female Marion (accompanied by audience checking and persistence), and the 5-month old female Kathy (accompanied by audience checking and response waiting), who were both observed to gesture to their mothers. In total, 26 cases of intentional gestural communication were recorded from baby chimpanzees (0-11months) (see Table 7). The repertoire at this age included with just 4 types of gesture (Dangle, Grab, Object-move, and Reach), although this included all 3 modalities (silent, audible and contact). An additional 4 types of gesture were seen on only single occasions.

By 1-2years old the use of gestural communication was far more prolific, with over 500 cases in the 9 individuals and a repertoire of 33 gesture types (9 further gestures seen on single occasions). Relatively few gestures were recorded from 3-4year old chimpanzees (139 cases, repertoire =22), despite there being 7 individuals within this category; however, there was relatively little *gesturing time* recorded from these individuals. This low value of gesturing time may be due to the fact that 4 of the 7 individuals were only briefly recorded within this age group, as they spent the majority of the study time in either the 1-2year or 5-9year old categories; restricting the opportunities to regularly record gesturing from 3-4year old chimpanzees to only 3 individuals. As in captivity, both the repertoire and the number of gestures appeared to peak in juvenile chimpanzees (5-9years) with 52 types of gesture and over 1600 cases recorded (from 15 individuals). After this the repertoires of sub-adult (46), young-adult (18) and mature-adult chimpanzees (34) were all smaller.

Table 7: The distribution of repertoire and time variables across detailed age groups. A summary of the data for each age group.

Age group	Age (inclusive)	No. of individuals	Total video (hrs)	Mean individual gesturing time (hrs)	No. gesture cases	Repertoire size	Ratio of gestures cases : repertoire size
Baby	0-11m	5	8.26	0.03 (±0.02)	26	4	6.50
Younger infant	1-2.11y	9	17.61	0.36 (±0.49)	551	33	16.70
Older infant	3-4.11y	7	15.68	0.13 (±0.17)	139	22	6.32
Juvenile	5-9.11y	15	53.44	0.77 (±0.87)	1618	52	31.12
Sub-adult	10-14.11y (female) 10-15.11y (male)	17	38.05	0.44 (±0.43)	862	46	18.74
Young adult	15-25.11y (female) 16-25.11y (male)	10	10.60	0.14 (±0.10)	170	18	9.44
Mature adult	>25y	20	55.46	0.33 (±0.45)	977	34	28.74

Individual repertoire size is highly correlated with quantity of gesturing time (n=68, Pearson's correlation r=0.94, p<0.0001, see Chapter 3). A similar pattern emerges when we consider the data by age group, for example: older infant and young adult chimpanzees both have near identical quantities of gesturing time recorded per individual, and both have a similar number of gesture cases and repertoire size. Analysing the relationship between gesturing time and repertoire size by age group confirms that, again, the two are nearly perfectly correlated (n=7, Pearson's correlation r=0.94, p=0.0002).

Considered from another perspective, if we plot the repertoire size against total number of gesture cases for each age group, the variables are almost perfectly correlated (n=7, Pearson's correlation r=0.91, p=0.0007) (see Figure 8).

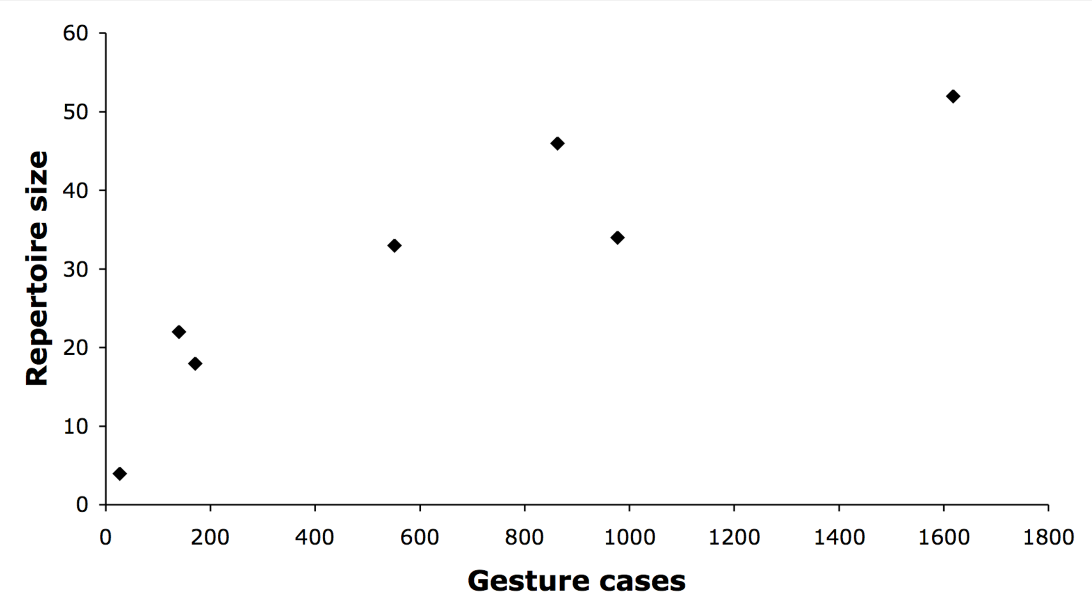


Figure 8: Age group repertoire size against number of cases of gesture. The number of gesture types within an age group repertoire is plotted against the number of cases of gesture in that age group

The three age groups with the smallest repertoires (0-11m; 3-4y and 15/16-25y) have the lowest ratios of number of gestures to repertoire size recorded (see Table 7). The near perfect correlations of repertoire-size with both gesturing time and total cases of gesture, suggests that the variation in age group repertoire size is due to a sampling artefact, rather than any true difference between, for example, juvenile and adult chimpanzee repertoires.

4.3.2 The use of modes of gesture across age groups

There appears to be no age trend for the use of any one mode of gesture over another with silent, audible and contact gestures present at the earliest stages of gestural communication (n=66, Chi square χ^2=3.16, df=12, p=0.994) (see Figure 9).

There was significant overlap of the repertoire across age groups; only 5 of the 66 gesture types were observed within a single age class: Clap, Head butt, Hide face, Stiff walk and Water-splash. All five were rare gestures observed on 5 or fewer occasions.

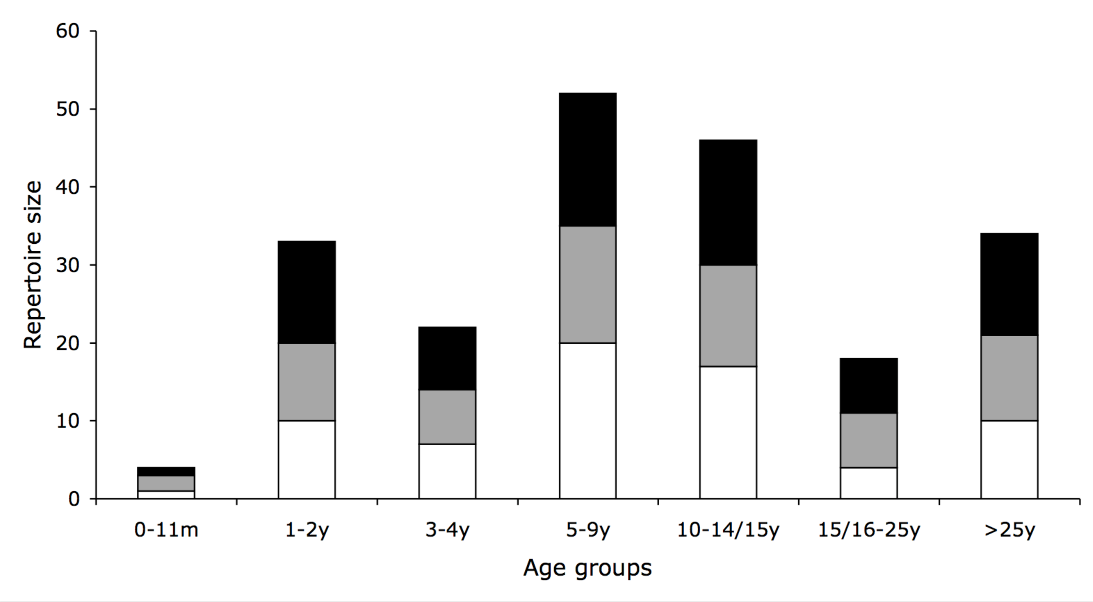


Figure 9: Modes of gesture recorded in detailed age group repertoires. The repertoire size of age groups is described with the proportion of the different modes of gesture detailed. White sections represent silent gestures; grey sections audible gestures and black sections contact gestures

Only one gesture was recorded in the adult repertoire (younger 15/16-25years, and mature >25years), but never seen in immature individuals (0-9years): Present climb-on, although it was observed in sub-adult individuals. In contrast 14 gestures were recorded in immature repertoires but never seen in adults (12 of these 14 were seen at least once in sub-adult individuals). The number of age-group repertoires in which a gesture was recorded as present (2 or more cases) was correlated with the number of cases of the gesture (Pearson's correlation: $n=66$, $r=0.73$, $p<0.0001$).

Moreover, gestures normally recorded within the context of sexual behaviour, were observed in young females extremely unlikely to have any personal experience of sexual behaviour (unlike infant males, that were observed to engage in sexual behaviour such as inspection and copulation attempts). For example: the Present-sexual gesture is recorded in Sonso female chimpanzees as young as 3-years old (Honey), and in 5-years old males (Kasigwa and Zak). Similarly leaf-clipping, which is commonly observed in Sonso adult male gestural communications when soliciting for copulation to oestrus females, was observed in male and female chimpanzees as young as 6-years old in the context of play.

4.3.3 Quantity of time spent actively gesturing

While filming I seldom had to choose between two potential gesture situations; the difficulties of filming in a dense secondary forest made it more likely that we would have to wait hours for a suitable case. The mean individual gesturing time can thus be used as a proxy for the total quantity of gestural communication produced by an individual or age group.

The mean individual gesturing time of baby chimpanzees (0-11months) was extremely small, only around 2min (see Table 7). The peak in mean individual gesturing time was recorded in juvenile chimpanzees (individual mean =0.77hrs ±0.87); however the standard deviations were extremely large in all age groups (Table 7); and I found no significant difference between age groups in the quantity of individual gesturing time (all age groups: n= 89, Kruskal Wallis H=11.50, df=6, p=0.074; excluding baby chimpanzees: n=84, Kruskal Wallis H=6.55, df=5, p=0.256).

Although I was able to record gesture use in baby chimpanzees (under 1-year old), this was in a very limited form from a handful of cases. The resulting low volume of data collected means that baby chimpanzees under 1-year old have been excluded from the analyses in the remainder of this chapter.

4.3.4 Is there age variation in the recorded measures of intentionality and flexibility?

Is response waiting used more by some age groups?

I used response waiting following communication as one of the measures to identify possible cases of intentional communication. As the data set was restricted to cases of intentional gesture, all gesture cases are accompanied by some measure of intentional communication, thus response waiting was to a degree already selected for; however, the frequency with which individuals of different ages employ response waiting behaviour may vary.

I found no significant difference in the distribution of response waiting across age groups (individuals with 5 or more gestures: younger infant (1-2y): n=7, mean=57.03% ±8.17; older infant (3-4y): n=5, mean=73.66% ±19.09; juvenile (5-9y): n=12, mean=67.93% ±12.80; sub-adult (10-14/15y): n=15, mean=63.17% ±12.69; young adult (15/16-25y): n=7, mean=68.46% ±14.34; mature adult (>25y): n=18, mean=68.31% ±16.63) (n=64, one-way ANOVA: $f_{5,58}=1.13$, p=0.354)
group mean = 66.23% ±14.37.

Do signallers of some age groups take the attentional state of the recipient into account more often?

In this analysis I examined whether or not adjustment to the attentional state of the recipient was equally present in all age groups. As the division into age groups substantially reduced the number of individuals within each data set, it was not possible to use the same statistical analysis as in Chapter 3. By calculating individual means for all subjects with 3 or more cases per category (rather than the 5 or more used as a standard throughout) it was possible to construct Figure 10, which breaks-down by age group the percentage deviation in the use of each mode of gesture for each attentional state category (for a detailed definition of the method see Chapter 3, specific methods). This percentage deviation illustrates the extent to which the chimpanzees within an age group adjust their use of a mode of gesture with reference to the recipient's ability to receive the communication.

From this we see that even the youngest 1-2year old chimpanzees appear to vary their use of gesture appropriately to the audiences attention state. Across all age groups, as expected, silent gestures were consistently used more in situations when there was eye-contact with the recipient than when the recipient was out of sight. Contact gestures were used more in situations where the recipient was out of sight, and audible gestures show no clear pattern of use.

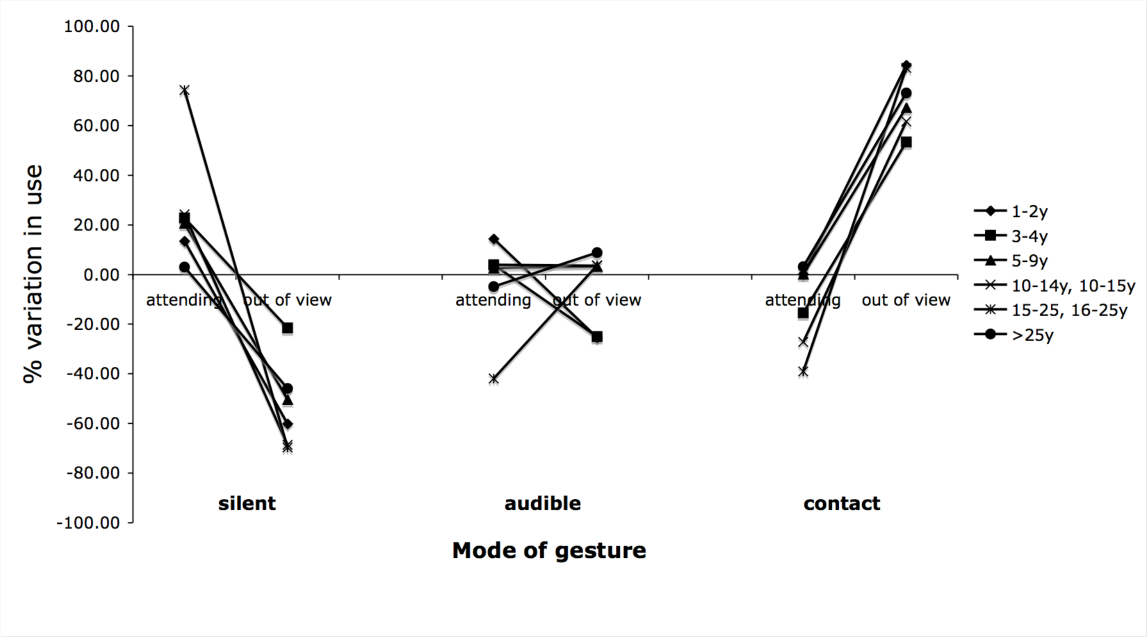


Figure 10: Variation in use of gesture modes with recipient's attentional states by detailed age group

In a similar fashion to the analysis of Chapter 3, for each mode of gesture (silent, audible, contact), I compared the variation in mean frequency of use towards recipients that were attending or out of view, between age groups. I found no significant interaction between age group and recipient's attentional state in any mode of gesture (silent: n=97, data transformed to correct for positive skew with √(x+101): ANOVA $f_{5,97}=1.13$, $p=0.354$; audible: n=97 ANOVA $f_{5,97}=0.74$, $p=0.596$; contact: n=97, data transformed to correct for positive skew with √(x+101): ANOVA $f_{5,97}=0.22$, $p=0.952$). Nor was there a main effect of age group on the variation in use of any mode of gesture (silent: n=97, data transformed to correct for positive skew with √(x+101): ANOVA $f_{5,97}=0.60$, $p=0.702$; audible: n=97 ANOVA $f_{5,97}=0.32$, $p=0.900$; contact: n=97, data transformed to correct for positive skew with √(x+101): ANOVA $f_{5,97}=0.04$, $p=0.999$).

As in the gesture corpus as a whole (see Chapter 3), I found a main effect of the recipient's state of attention on the use of silent (n=97, data transformed to correct for positive skew with √(x+101): ANOVA $f_{1,97}=39.19$, $p<0.0001$) and contact (n=97, data transformed to correct for positive skew with √(x+101): ANOVA $f_{1,97}=22.24$, $p<0.0001$) but not audible gestures (n=97, ANOVA $f_{1,97}=0.02$, $p=0.903$).

A detailed look at the flexible use of leaf clipping

Leaf clipping behaviour has been well documented in the wild chimpanzee literature ((Boesch, 1995, Nishida, 1987, Reynolds, 2005) (Sugiyama, 1981) (Watts, 2007) (Whiten et al., 1999)) and is of particular interest because it has been suggested that consistent group specific variations in its occurrence and the context of its use can be used as evidence for cultural traits in chimpanzees (Whiten et al., 1999) (McGrew, 2010).

At Sonso the gesture is described by the highly experienced field-assistants as being a courtship gesture: exclusively used by males towards oestrus females when soliciting for copulation, as is found at Mahale. However, during the 18-months of my observation time at Sonso, 9 of the total 40 cases of intentional use I saw were in non-sexual contexts (22.5%), 7 of which were produced by 3 different female chimpanzees (Rachel, Rose and Karo). Table 8 describes the detailed use of the gesture in terms of the context, signaller and recipient.

The monthly frequency at Sonso (2.22 cases per month) is lower than that reported at Taï (between 30.66-45.70; (Boesch, 1995)). However, the dataset at Sonso is restricted to clearly intentional cases of gesture; this strict definition excludes cases where the recipient was unclear or out of sight and is likely to under-estimate the actual frequency of use. In addition, the majority of adult females at Sonso during the study period had un-weaned infants and had not yet recommenced regular oestrus cycles. The lack of available parous, oestrus females may explain both the overall low frequency of this gesture for courtship, along with the relatively high proportion of cases produced by males in the courtship of nulliparous sub-adult females (26/31); and the high frequency of use by young or sub-adult males (29/31).

One case was recorded in *travelling* from a young sub-adult female; she had been waiting and repeatedly gesturing for some time at the foot of the tree where her mother and younger sister were still resting in a day-nest, thus it might also be appropriate to categorize this as produced in *frustration*. The recipients eventually moved down the tree and the family moved off together.

Table 8: Use of leaf-clipping across contexts and age-sex categories. Recipients of leaf clipping are detailed in the context section. Notations are defined as follows: yi=younger infant, oi=older infant, j=juvenile, sa=sub-adult, ya=young adult, ma= mature adult; ♀=female, ♂=male; for example: young adult female = ya♀

	Context of use and recipient (age group and sex)			
Signaller (age in years)	**Play**	**Courtship**	**Travelling**	**Total**
Mature adult male				
Nick (26)		3 (sa♀)		3
Young adult male				
Musa (17)		2 (ma♀)		2
Sub-adult male				
Hawa (15)		3 (sa♀)		3
Kato (15)		10 (sa♀, ya♀, ma♀)		10
Kwezi (13)		5 (sa♀, ma♀)		5
Pascal (10)		1 (sa♀)		1
Zalu (13)		4 (sa♀)		4
Zig (11)	1 (j♂)	3 (sa♀, ya♀)		4
Sub-adult female				
Rachel (10)	1 (j♂)			1
Rose (11)			1 (ma♀)	1
Juvenile female				
Karo (7)	5 (yi♂, j♀, ma♀)			5
Juvenile male				
Kasigwa (6)	1 (j♂)			1

The remaining 8 cases were produced in *play*, to a mixture of male and female recipients of all age groups (infant-adult). During courtship the gesture was only produced towards appropriate recipients (sub-adult and adult females); similarly during play the majority (7/8) of cases were directed towards chimpanzees aged 9-years and under. There were no cases of its use in play between adult, or sub-adult chimpanzees; the single case of its use in play to an adult was between a juvenile female and her mother. Interestingly, the one individual who was observed to use the gesture in the contexts of both play and courtship (sub-adult male Zig) varied the use; so that in play it was directed towards a juvenile, and in courtship to sub-adult and young adult females.

4.4 Discussion

Intentional gestural communication, including audience checking, persistence and response waiting, was used by individuals as young as 4-months old; however, these cases were extremely rare and, although I would expect the number of cases and the repertoire to increase with further observation, the regular use of gesture appears to emerge from 1-year old. It is possible that early cases of gesture use were missed due to the difficulties of observing the behaviour of very young chimpanzees; baby chimpanzees are not only rare in themselves (I was extremely fortunate in being on site during the birth of 5 new additions to the Sonso community), but they are also extremely difficult to observe. Females with a new infant often absent themselves from the community for weeks or sometimes months; and even very well habituated Sonso females were highly protective of their infants, placing themselves between the infant and any curious observers. However, the large increase in cases observed in 1-2year old chimpanzees, strongly suggests that, while occasional early gesture use may exist as early as 4-5months old, the onset of regular use occurs at around 12months. At this age, infant chimpanzees showed levels of response waiting equivalent to that of adult individuals, and appropriately varied their use of different modes of gesture with the recipient's state of attention. Once again I find that total repertoire size and cases of gesture are tightly correlated to gesturing time, so that with further observation, I would expect the differences in repertoire size between groups to diminish.

These results correspond to those reported in the Gombe community, where the onset of intentional gesture is reported at 9-12months (Plooij, 1978) and 'most if not all of the gestures used by adult chimpanzees during individual interactions appear' by 1-2 years old (Van Lawick-Goodall, 1967); but is earlier than that described from captivity by Tomasello et al. who report the emergence of response waiting in captive chimpanzees from 2-years and fully intentional use of gesture at 3-years old (Tomasello et al., 1985). This may represent, as Tomasello notes, either a true earlier onset of intentional communication in wild chimpanzees, perhaps as a result of variations in their social and physical environment; or, individual differences due to the very small sample sizes previously available. Plooij only reports a couple of observations, and Tomsello et al. had a single individual in their year 2 group. Here I am able to use data from five 0-11month olds, nine 1-2year olds, and seven 3-4year olds: providing a much more detailed description.

There is evidence that baby chimpanzees start to vary their vocal responses to specific stimuli from around 2-3months old (Plooij, 1984); however, the first cases of gestural communication were not recorded until 4-5months old. This corresponds to the onset of early attempts to walk and climb (Van Lawick-Goodall, 1967, Plooij, 1984). Gesture and locomotion require fine motor control and spatial awareness; and the prerequisite development of these skills may impede the earlier emergence of gestural communication. Additionally, it is only with the onset of independent locomotion that the infant chimpanzee can free up his limbs for gesturing. Prior to this, hands and feet are occupied with the job of clinging onto the mother, limiting the opportunity for their use in gestural communication.

Gesturing time can be considered a proxy for the extent to which gestural communication is employed; and, while this appeared to peak in the juvenile period, individual differences were extremely large. Thus, there was no significant variation in the extent to which gestural communication was employed by any one age group. Furthermore, of the total repertoire of 66 gesture types, only 5 rarely observed gestures were recorded as age-group specific. The very low level of age-group specific gestures, along with the regular use by infants of gestures usually associated with mature sexual behaviour, such as ‘present-sexual’ (also reported in infants by (Plooij, 1984)) and ‘leaf-clipping’, argues against the theory that gestures are acquired through experience. Instead the large degree of overlap, along with the evidence that any variation in repertoire size is an artefact of the methodology, rather than a result of true difference between age groups; supports the case for a species-typical repertoire.

Leaf-clipping varies between sites in both the manner and frequency of its use; it has been recorded in the contexts of frustration and play at Boussou (Sugiyama, 1981); as a means to attract attention at Kibale (Watts, 2007) and as a common courtship gesture at Mahale (Nishida et al., 1999), but appears to be near-absent in Gombe chimpanzees (2 cases, (Nishida, 1987)). One of the most interesting reports of this behaviour describes an apparent change in the group's use of the gesture over time in the Taï forest chimpanzees. Here, leaf clipping, which had been restricted almost exclusively to male drumming displays, with occasional examples from cases of sexual frustration; was suddenly produced by chimpanzees of all ages and both sexes while resting on the ground (Boesch, 1995).

At Sonso, leaf-clipping was regularly used as a courtship communication between older individuals, and in play communication towards and from young individuals. One case was recorded in the travelling context, although the specific manner of its use could also have been interpreted as frustration. Where an individual was observed to leaf-clip to both younger and older individuals, the signaller varied its use to appropriately match the recipient. Thus, leaf clipping was used flexibly across contexts, but in a targeted fashion with respect to the age of the recipient.

It is not clear to what extent these new observations of the use of leaf-clipping during contexts outside of courtship represent a genuine change in the range of functions for which leaf-clipping is used within the Sonso community, as was suggested at Taï (Boesch, 1995). Or, whether or not they represent the first observations of an existing but more rarely used function following the first systematic study of gesture at Sonso. Although individual gesture types are used flexibly for a range of functions, they tend to be associated with one, or perhaps two, dominant functions (Genty and Byrne, 2009). Thus, just as there may be variations between groups in the extent to which any one gesture-type within the species-typical repertoire is employed; the variation between groups in use of leaf-clipping for different functions may be better described as a group-specific preference for one function from a range of species-typical functions. This model then accounts for the variation in the dominant function of leaf-clipping between groups, the occasional observation of leaf-clipping for alternative functions within a group, and over time, changes in a group's dominant, or 'preferred' function.

4.4.1 Summary

Sonso chimpanzees regularly employ gestural communication in a fully intentional manner from 12-months old. There is little evidence to support age group specific gesture types, or the cumulative acquisition of gesture types with age; instead the findings support the use of a species-typical repertoire in a flexible manner throughout ontogeny. There are no consistent differences in the extent to which gestural communication is employed at different stages of development; however for an analysis of the use of gesture in different contexts by different age groups see Chapter 7. In addition to the flexible use of gesture with regards to the recipient's state of attention, there is evidence that the function of at least one gesture, leaf-clipping, is adjusted to accommodate the recipient's age.

Chapter 5. Why combine gestures? The form and function of sequences

5.1 Introduction

Gestural communication is not simply a case of gesture → response; gestures may be combined into long strings, within which gestures may overlap, be interspersed with bouts of response waiting, and may be exchanged back and forth between individuals. Very little quantitative research has been conducted on the use of gesture sequences: Tomasello et al. describe the use of gesture combinations in their early work on the development of gesture, and suggest the potentially syntactical use of ‘attention getter + communicative gesture’ combinations (Tomasello et al., 1989, Tomasello et al., 1994); but provide no detailed analysis. Liebal et al. conducted the first quantitative analysis of gesture sequences in 2004, with the captive chimpanzee group at Yerkes (Liebal et al., 2004a). They describe a range of sequence lengths from 2 to 39 gestures, with 2-gesture combinations accounting for the majority of sequence use. Approximately one third of gestures were produced as part of sequences, the majority of which were recorded from the context of play. A large proportion of sequences (particularly the longer forms) were simple repetitions of the same gesture type. Despite a detailed analysis, they found no evidence for the ‘attention getter + signal’ combination proposed in the earlier work; and instead suggest that the sequences are produced as ‘post hoc responses to an unresponsive recipient,’ which, they argue, explains the high number of single gesture-type repetitions, as opposed to the addition of a second, more efficient gesture type (Liebal et al., 2004a).

This research was followed by the only other quantitative analysis of gestural sequences in great apes: a study of captive gorilla gesture by Genty and Byrne (Genty and Byrne, 2009). These authors again found no evidence for a syntax arising from the combination of differing categories of gesture, and report little evidence that combination of gestures resulted in any major deviation from the function (or meaning) of the individual component gestures. In cases where a change in function did occur this tended to be towards the secondary or tertiary function of the component gestures, rather than some other previously unrelated function.

However, in contrast to Liebal et al., they found no support for the suggestion that sequences of gestures were produced in response to the failure of single gesture communications; or, that repetitions of the same gesture type served as a more emphatic alternative. Instead they describe the use of gestural sequences as a form of ongoing modification of the behavioural interaction, drawing the analogy with controlling the forward motion 'of a heavy wheelbarrow, with continuous slight adjustments of force in different directions in order to keep the forward progress' (Genty & Byrne 2009, p.239).

Initially the findings from both studies seem incompatible; however, as Genty & Byrne point out, this almost certainly stems from a difference in the way in which they define separate sequences of gestures. Genty & Byrne focus on rapidly made sequences, with gestures produced after response waiting considered to be an entirely new communication (Genty and Byrne, 2009). This definition, I think, provides a problem for their explanation of sequences as ongoing behavioural modification. Although play behaviour provides a rapid and dynamic environment for social interaction, where modification of the behaviour may well be necessary, they require that there are no pauses of >1sec between gestures in order to consider them part of the same sequence. I question whether or not it is realistic to assume that regulation of the play behaviour alone could motivate the production of new gestures less than one second after a previous communication? There would be, by definition, no waiting for a response from the recipient; thus it is difficult to accept variation in recipient behaviour as the major motivation in the production of further gestures.

In contrast, Liebal et al. include as part of the same sequence a gesture produced up to 5 seconds after a former gesture, and do not appear to distinguish between sequences where the gestures were 'combined in a pre-meditated fashion' and those where gestures are separated by response waiting, and/or a recipient response (Liebal et al., 2004a). This method may be problematic when seeking to understand the motivation behind the production of gesture sequences. The motivation to produce further gestures after a period of response waiting, and possibly a response by the recipient, may be influenced by the recipient's behaviour; in contrast, the 'premeditated' decision to produce two or more gestures in rapid sequence without pause can not be influenced by the recipient's behaviour, as there would be no opportunity to verify the recipient's response, and so some other factor must motivate the production of the additional gesture(s).

Thus, in order to accurately describe the complexity of gestural communication it is necessary to differentiate between combinations of gestures produced together without pause, and additional gestures produced following response-waiting behaviour. Furthermore, it is useful to distinguish cases where a gesture or sequence of gestures is produced in response to a gestural communication. To describe this more complex hierarchical structure I borrowed 3 familiar terms from linguistics, but with no intent to imply anything beyond a superficial structural similarity that acts as an aide memoir. As described in the general method I distinguish:

G-clause: a chimpanzee gives one or more gestures without interspersed pauses of more than 1s.

G-sentence: a chimpanzee gives two or more G-clauses in succession, separated by pauses of >1s of response waiting; during these pauses, the apparent recipient may make non-gestural responses, but does not gesture itself.

G-dialog: a series of G-clauses or G-sentences are given in turn between two or more individuals.

All G-clauses within a G-sentence are defined as produced for the same functional goal. G-clauses can consist of either a single gesture or a *rapid sequence* of gestures: 'g' or 'ggg'; however, all G-sentences are constructed from multiple G-clauses: 'ggg + g + gg' (the alternative is a single G-clause used in isolation: 'ggg'). A new G-clause produced after a bout of response waiting is considered part of the same communicative attempt (the G-sentence) towards the same functional goal, but is at the same time a distinct structural element from the previous G-clause.

Genty and Byrne restricted their analyses to what I would define as a rapid sequence within a G-clause. In contrast, Liebal et al. appear to lump both G-clauses and G-sentences into a single category of gesture 'sequences'.

Here I examine the use of G-clauses and G-sentences separately; I aim to test the hypothesis that the use of G-sentences is associated with the failure of earlier G-clauses, and to try to address the question of what motivates the production of rapid sequences within G-clauses.

5.2 Results part I: The form of gesture sequences

5.2.1 The use of G-clauses, G-sentences and G-dialogs

Over 70% of gestures (3125/4397) were produced within some form of sequence. The 4397 gestures recorded during the study formed a total 3422 G-clauses. The majority of G-clauses contained only a single gesture (2699/3422, 78.9%) i.e. were single gestures followed by response-waiting, but up to 11 consecutive gestures were recorded in rapid sequence within a single G-clause, and 1698 gestures (38.6%) were part of rapid sequences.

38.3% of G-clauses (1312/3422), were contained within 504 G-sentences (2 or more G-clauses), containing up to 14 G-clauses separated by response waiting (range =2:14, modal value =2).

Both single G-clauses and G-sentences were alternated between the initial signaller and the recipient to form 269 G-dialogs constructed from between 2 to 8 communications (either a G-clause or a G-sentence) given in turn (mode =2-units, i.e. A to B and B to A; number of 2-unit G-dialogs=222).

5.2.2 Was there any variation in the use of gesture sequences across contexts?

G-clauses: single gestures and rapid sequences

The majority of rapid sequences were produced within *play* (n=34, mean frequency =63.4% ±34.7); followed by *agonism* (n=34, mean frequency =10.5%

±16.3), (see Figure 11). *Play* also contained the majority of single gesture G-clauses (n=56, mean frequency =40.0% ±33.5); followed in this case by *grooming* (n=56, mean frequency =19.9% ±20.8).

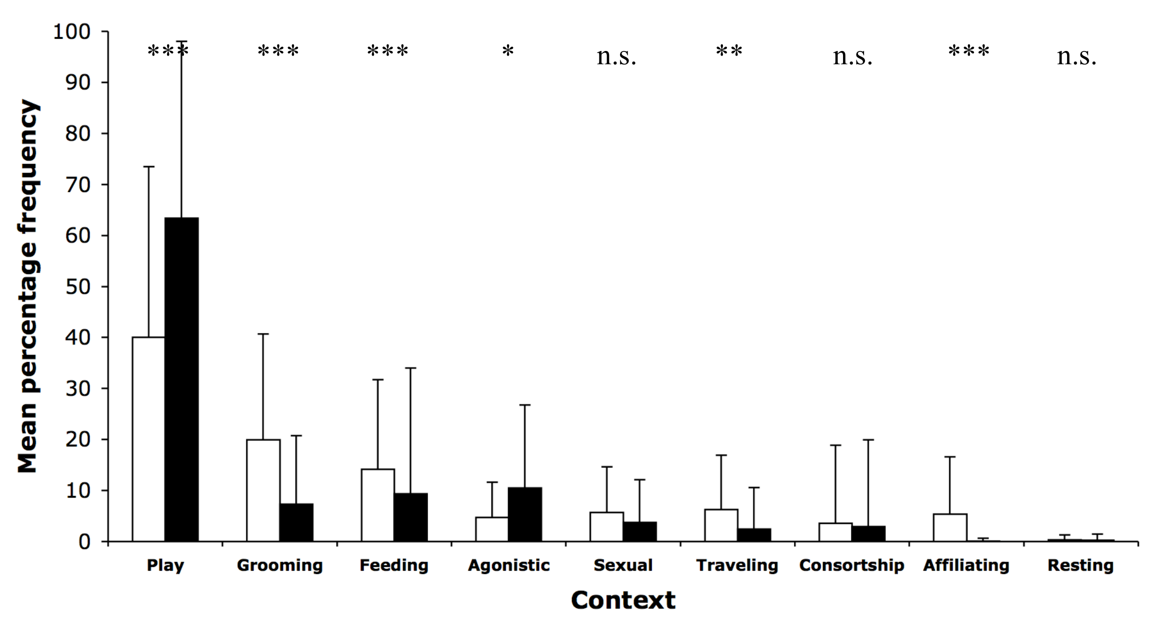


Figure 11: Mean proportion of single gesture or rapid sequence G-clauses across contexts. White bars represent single gestures; black bars represent rapid sequences. Notifications *, **,*** and n.s. refer to p< 0.05, 0.01, 0.001 and p>0.05 respectively.

In both *play* and *agonism* the proportion of rapid sequences was higher than the proportion of single gestures (Wilcoxon signed ranks tests, n=34: *agonism* Z=-2.43, p=0.015; *play* Z=-3.31, p=0.001). Across the 7 other contexts, the proportion of rapid sequences was either equivalent to that of single gestures: (Wilcoxon signed ranks tests, n=34: *consortship* Z=-0.45, p=0.655; *resting* Z=-1.40, p=0.161; *sexual* Z=-0.72, p=0.469); or lower than that of single gestures: (Wilcoxon signed ranks tests, n=34: *affiliating* Z=-4.20, p<0.0001; *feeding* Z=-3.291, p=0.001; *grooming* Z=-3.23, p=0.001; *travelling* Z=-2.82, p=0.005).

Individual G-clauses and G-sentences

As with single gesture and rapid sequence G-clauses described above, individual G-clauses and multiple G-clause G-sentences were predominantly found in *play* (single G-clauses: n =69, mean frequency =39.9% ±36.5; G-sentences: n =55, mean frequency =53.5% ±36.1), see Figure 12.

However, unlike G-clauses, the proportion of G-sentences used in any one context was never higher than that of single G-clauses, only equal or smaller.

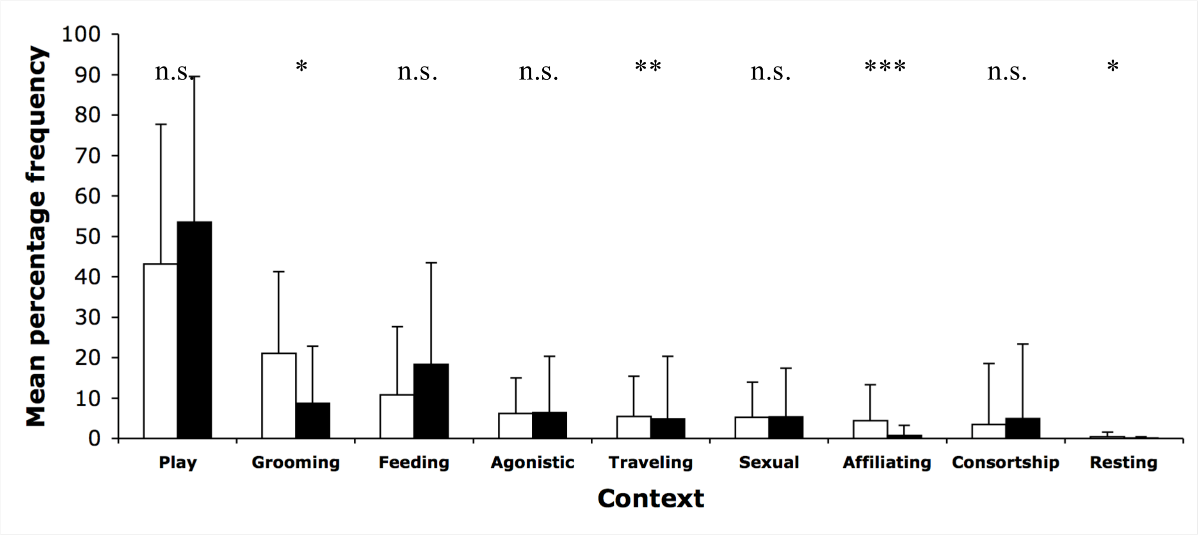


Figure 12: Mean proportion of single G-clause communications compared to that of G-sentences across contexts. White bars represent single gesture G-clauses; black bars represent multiple gesture G-clauses. Notifications *, **,*** and n.s. refer to p< 0.05, 0.01, 0.001 and p>0.05 respectively.

A larger proportion of single G-clauses were found in *affiliation, grooming, resting* and *travelling* (Wilcoxon signed ranks tests, n=37: *affiliation* Z=-3.60, p<0.0001; *grooming* Z=-2.52, p=0.012; *resting* Z=-2.09, p=0.037; *travelling* Z=-2.59, p=0.010). There was no difference in the proportions in the remaining contexts (Wilcoxon signed ranks tests, n=37: *agonism* Z=-1.00, p=0.316; *consortship* Z=-0.37, p=0.715; *feeding* Z=-1.88, p=0.061; *play* Z=-0.84, p=0.401; *sexual* Z=-0.22, p=0.823).

5.2.3 Does the use of gesture sequences vary with signaller age?

G-clauses: rapid sequence use

The mean frequency with which rapid sequences were used decreased significantly with increasing age. (Mean frequency of the use of rapid sequences –

younger infant (1-2y): n=5, x=48.5% ±10.0; older infant (2-3y): n=9, x=45.7% ±15.9; juveniles (5-9y): n=13, x=38.4% ±13.8; sub-adult (10-14/15y): n=15, x=25.9% ±15.5; young-adult (15/16-25y): n=7, x=23.2% ±24.6; and mature-adult (>25y): n=16, x=15.7% ±17.5), (one-way ANOVA$_{\text{Brown-Forsythe}}$ $f_{5,59}$=6.14, p<0.0001). Post hoc Games-Howell tests show a significant difference between baby (mean difference=32.77, p=0.002), infant (mean difference=30.03, p=0.004) and juvenile chimpanzees (mean difference=22.70, p=0.007) when compared with mature-adult chimpanzees; and between baby and sub-adult chimpanzees (mean difference=22.58, p=0.028), see Figure 13.

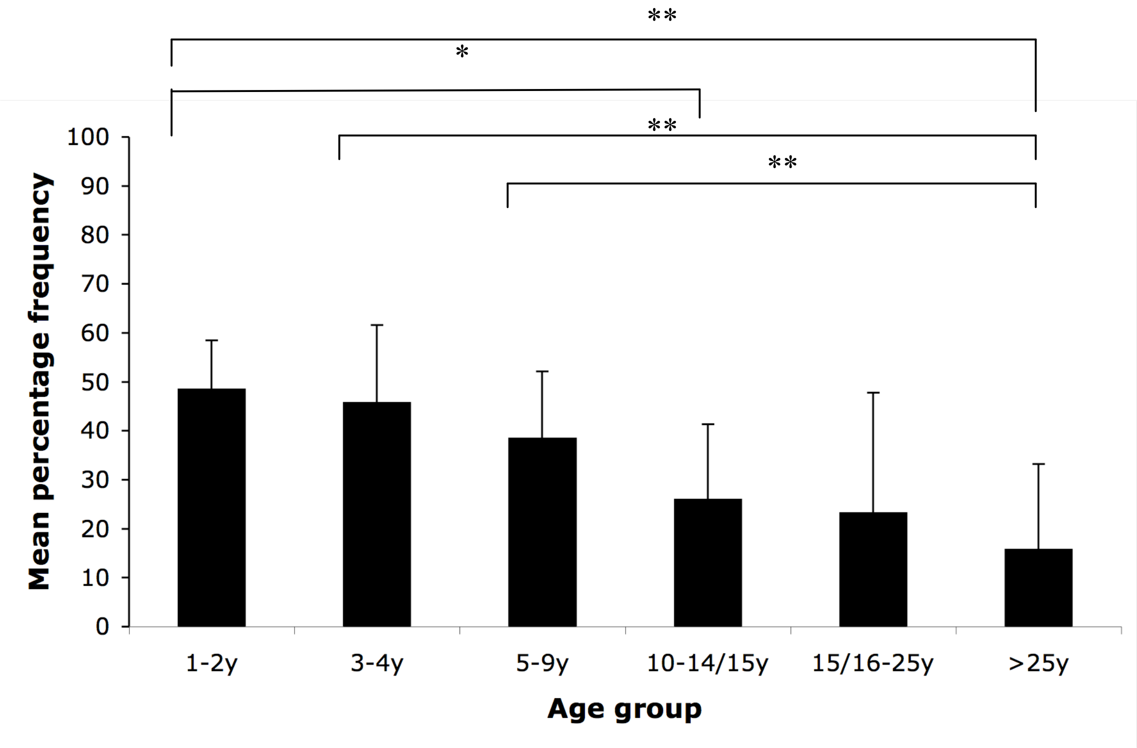


Figure 13: Distribution of rapid sequence use across age groups. The percentage frequency with which individuals within an age group produced rapid sequences. Notifications * and ** refer to p<0.05 and 0.01 respectively.

G-sentence use

The distribution of the frequency with which G-sentences (multiple G-clauses) are used by different age groups is described in Figure 14. Use varies significantly with the age of the signaller (Mean frequency of the use of G-sentences – younger infant (1-2y): n=5, x=38.9% ±5.9; older infant (3-4y): n=9, x=47.9% ±23.3; juveniles

(5-9y): n=13, x=39.1% ±19.3; sub-adult (10-14/15y): n=15, x=25.3% ±15.8; young-adult (15/16-25y): n=7, x=14.2% ±13.1; and mature-adult (>25y): n=16, x=31.2% ±20.7), (one-way ANOVA $f_{5,59}$=3.47, p=0.008)).

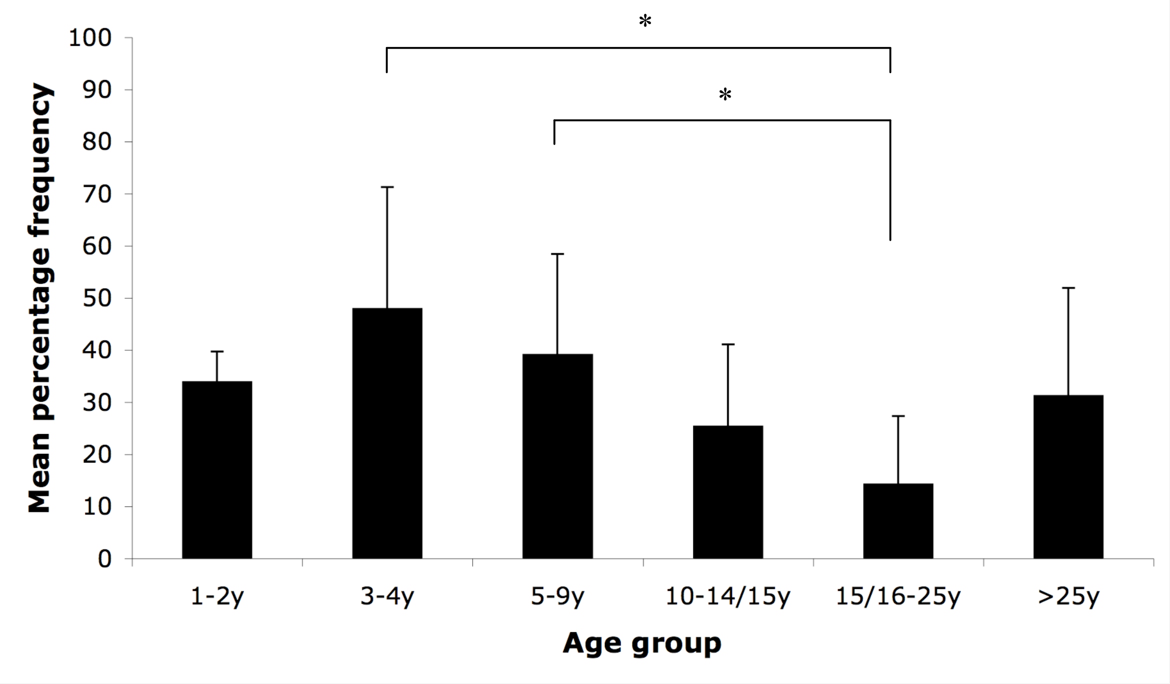


Figure 14: Distribution of G-sentence use across age groups. The percentage frequency with which individuals within an age group produced G-sentences (multiple G-clauses). Notification * refers to p<0.05.

Across age groups the use of G-sentences decreases with increasing age; there appeared to be a slight variation from this in the case of younger infant (1-2year olds) and mature adult (>25year old) chimpanzees; however, neither case varied significantly from the other age groups. Post hoc Games-Howell tests show significant differences between older infant (3-4y) (mean difference=33.7, p=0.028), and juvenile (5-9y) chimpanzees (mean difference=24.9, p=0.033) when compared with young-adult (15/16-25y) chimpanzees.

5.3 Results part II: The function of gesture sequences

5.3.1 The function of G-sentences

Chimpanzees persist in the production of new gestures following the complete, or partial, failure of the original communication (see Figure 3). The mean success of gestural communication varies between age groups (n=63, one-way ANOVA: $f_{5,57}$=5.603, p<0.0001); with a significant difference between the success of juvenile (n=13, mean frequency =43.03% ±12.66) and mature adult communications (n=16, mean frequency =63.78% ±16.47) (post-hoc Games-Howell: mean difference =20.74, p=0.008) see Figure 15. The lowest rate of success was recorded from older infant chimpanzee communication (mean frequency =30.40% ±18.04; however, only a small number of individuals met the requirements to contribute to the group mean (n=5) and the difference with mature adults only approached significance (post-hoc Games-Howell: mean difference =33.38, p=0.065).

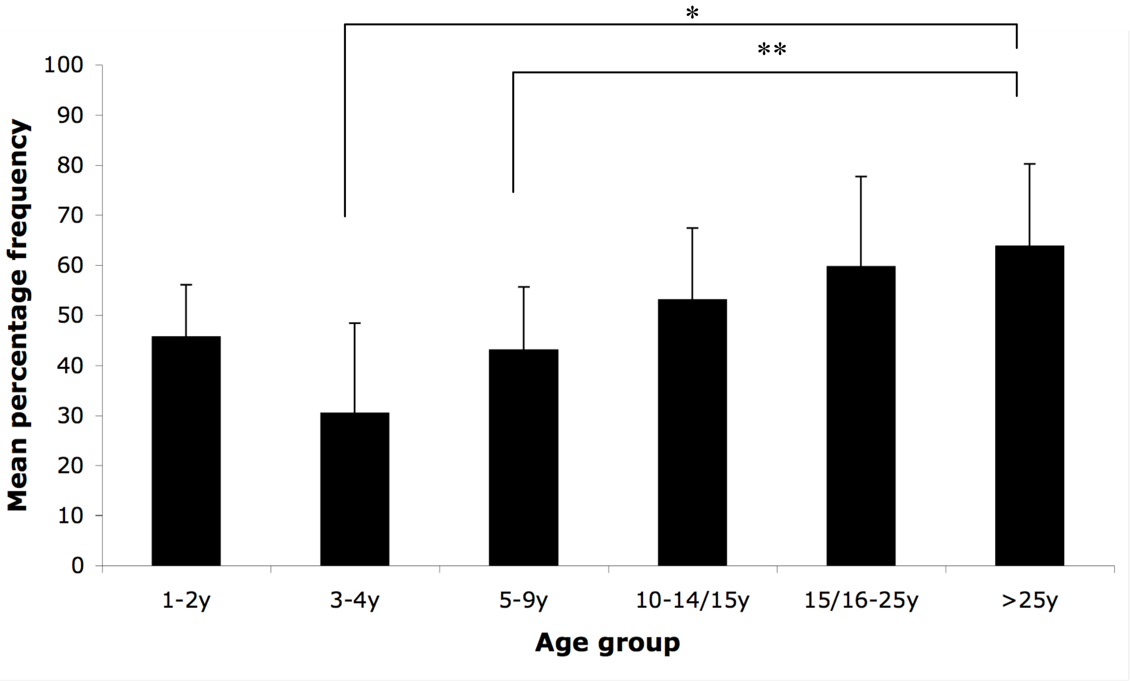


Figure 15: Mean frequency of successful communication across age groups. The percentage frequency with which a G-clause produced a successful behavioural response across age groups. Notifications * and ** refer to p<0.1 and 0.01 respectively.

The pattern of success across age groups almost exactly mirrors the pattern of the use of G-sentences (see Figure 14), with an overall trend of increasingly successful G-clauses, and decreasing use of G-sentences. As with the frequency in the use of G-sentences, baby chimpanzees appear to deviate slightly from the trend; however, once again this was not in a significant fashion. Across age groups, there is a very good correlation between the use of G-sentences and success (Pearson's correlation: n=6, r=0.82, p-0.013).

Thus, the production of G-sentences is a direct result of persistence following the failure of an earlier G-clause. If all initial G-clauses were successful there would be no G-sentences, as there would be no need to persist in the communication.

5.3.2 The function of G-clauses

As gestures within a G-clause are produced without intermittent response waiting, it is improbable that rapid sequences are produced in response to recipient behaviour; I therefore considered a number of factors associated with signaller behaviour and the inherent properties of the gestures or gesture combinations used.

5.3.2.1 Does the use of rapid sequences increase the likelihood of a successful response?

There was no difference in the mean frequency with which single gesture G-clauses (n=57, mean frequency success =55.2% ±17.3) and 2-gesture rapid sequences were successful (n=28, mean frequency success =51.5% ±22.3); and both were more successful than 3 gesture rapid sequences (n=8, mean frequency success =23.8% ±22.9) (One way ANOVA: $f_{2,90}$=9.166, p<0.0001; Games-Howell post hoc: 1 and 2 gesture G-clauses: mean difference =3.61, p=0.734; 1 and 3 gesture G-clauses: mean difference =31.6, p=0.014; 2 and 3 gesture G-clauses: mean difference =27.8, p=0.028). So rapid sequences were not inherently more successful than single gesture G-clauses, and in the case of 3 gesture G-clauses were actually less successful.

5.3.2.2 Do rapid sequences function as a more emphatic alternative to single gestures?

Liebal et al. (2004) suggest that multiple gestures may provide a more emphatic alternative to single gestures. In this case the 2nd and 3rd G-clauses in a G-sentence would be more likely to contain rapid sequences than the 1st G-clause. 11 individuals produced G-sentences of between 1-3 G-clauses (with 5 or more cases in each category), the frequency with which rapid sequences were used is described in Table 9.

Table 9: Distribution of rapid sequences with position in G-sentence. The percentage frequency with which the 1st, 2nd or 3rd G-clause in a G-sentence contains multiple gestures.

	1st G-clause	**2nd G-clause**	**3rd G-clause**
Mean % frequency of rapid sequences (n=11)	24.62 ± 14.12	22.36 ±12.94	22.56 ±6.82

There was no significant increase in the use of rapid sequences following failure of the 1st G-clause (Friedman test: n=11, χ^2 =0.605, df=2, p=0.739); therefore there is no evidence to suggest that rapid sequences function as a more emphatic alternative to single gestures.

5.3.2.3 Are certain gestures more likely to be combined into rapid sequences?

Table 10 describes the gestures which, when used individually, elicit a successful response at least 70% of the time (high-success gestures) or less than 40% of the time (low-success gestures).

Of the 45 gestures used individually in 5 or more cases, 11 had an individual success rate of over 70% and 7 were successful in under 40% of cases (see Table 10). When we compare the use of high-success gestures with low-success gestures; we find that high-success gestures are more likely than low success gestures to be used individually rather than in rapid sequences (frequency of use in single gesture G-clauses: high-success gestures: n=53, mean =81.44% ±20.05; low-success gestures: n=31, mean =48.82% ±24.77; Mann-Whitney test: n=83, U=463.50, p=0.001).

This suggests that the combination of gestures into rapid sequences is related to the inherent successfulness of the gestures when used individually: low success gestures are more likely to be combined into rapid sequences, high-success gestures are more likely to be used individually.

Table 10: Success rate of gestures used individually. Detailed success rates of gestures with a successful response rate of over 70% and under 40% when used individually as single gestures. Only includes gestures with 5 or more cases. Notification * represents gestures never seen in combination with other gestures.

High success gestures (success rate ≥ 70%)	
Roll over	91.9 ±13.0
Present (climb-on) *	88.3 ±16.2
Present (grooming)	86.6 ±20.5
Embrace	84.7 ±31.4
Directed push	82.3 ±30.5
Hand shake	80.0 ±44.7
Present (sexual)	75.6 ±34.5
Shake hands *	75.0 ±50.0
Slap object with object	75.0 ±35.4
Side roulade	72.0 ±43.8
Big loud scratch	70.3 ±35.8
Low success gestures (success rate ≤ 40%)	
Poke	40.0 ±54.8
Tap other	37.2 ±43.0
Pirouette	35.7 ±47.6
Leg swing	33.3 ±57.7
Arm shake	33.3 ±50.9
Stomp	29.6 ±36.4
Stomp 2-feet	23.8 ±30.5

5.3.2.4 Is there any evidence for increased efficacy of individual gestures through repetition?

Only a small proportion of rapid sequences were simple repetitions of the same gesture (112/721, 15.5%) see Figure 16. I recorded 27 different forms of same gesture repetition, constructed from between 2 and 4 repetitions of 22 different types of gesture (some gestures were seen as both double and triple repetitions, e.g. AA;

and AAA: these were considered to be different forms). The majority of repetitive rapid sequences contained only 2 gestures e.g. AA or BB (22/27).

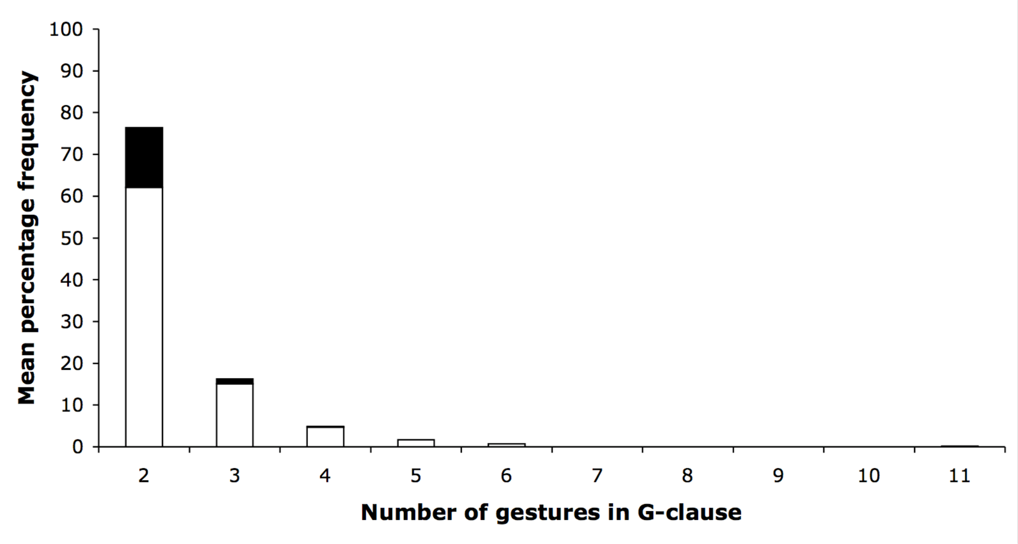


Figure 16: Mean percentage frequency of rapid sequences. The frequency of different lengths of rapid sequences is described as a percentage of the total number of rapid sequences. Black bars represent repetitions of the same gesture type, white bars represent combinations of different gesture types.

It was possible to calculate the success rate of the 22 different types of gesture when used individually. Many of the forms of repetition were only seen on single occasions; however, I found no difference between the success rate of gestures seen individually or as repetitions for either the complete data set (n=21, Paired t-test: t=1.43, df=20, p=0.169); or in the set restricted to gestures in repetition forms seen on more than one occasion (n=12, Paired t-test: t=1.08, df=11, p=0.305); so repetition of a gesture did not act to increase its efficacy.

5.3.2.5 Is there any evidence for meaningful combinations of different gesture types?

Variation in mode within rapid sequences

407 gestures were produced as part of rapid sequences given to inattentive recipients. As would be expected in communication to an inattentive recipient, the majority of gestures used in these communications were either audible (49%) or

contact (41%) gestures, with only 11% silent. Where silent gesture types were used they were produced in combination with audible or contact gestures with one exception: a single 2-gesture rapid sequence composed of exclusively silent gesture types, and which on this occasion were accompanied by other audible behaviour.

Where silent gestures were combined with either audible or contact gestures they were no more likely to be used either before (34.9% ±33.4) or after (65.1% ±33.4) contact or tactile gestures (Individuals with 3 or more cases: n=6, Wilcoxin Signed Ranks Test: Z=-0.94, p=0.344).

Are high-success gestures used at the start of a rapid sequence?

While there is little evidence to suggest that there are audible or contact gestures which function simply to attract attention, it is possible that high-success gestures, which are individually very effective at eliciting a successful response, could be used at the start of a sequence as attention getters. 9 high-success gestures were seen in combination with other gestures (62 rapid sequences, 28 individuals); these were no more likely to be used first (n=56, mean frequency =47.0% ±45.3) as opposed to any other position within the sequence (n=56, mean frequency =53.0% ±45.3) (Paired samples t-test: n=56, t=-0.492, df=55, p=0.625).

5.3.2.6 Was there any evidence that the inclusion of high-success gestures affected the success of rapid sequences?

I tested 517, 2-gesture G-clauses - pairs of gestures in rapid sequence. 81 of these pairs included at least one high-success gesture. Pairs that contained at least one high-success gesture (n=81, mean frequency success = 61.5% ± 42.0) were more likely to be successful than pairs that did not (n=436, mean frequency success = 44.1% ±35.3), (n=118, independent t-test, t=2.42, df=116, p=0.023). There was no difference in the success of pairs that included 1 (n=38, mean frequency success = 62.2% ±41.3), or 2 (n=43, mean frequency success = 60.9% ±43.8) high-success gestures (n=44, independent t-test, t=-0.11, df=42, p=0.915).

5.3.2.7 Is there a variation in the use of high-success gestures across age groups?

As described in Chapter 3, I argue that the total repertoire is species-typical, however, there may be variation in the use of this repertoire. For example, whether or not certain types of gesture account for a large proportion of gesture cases.

There was a significant difference between age groups in the proportion of all gesture cases accounted for by 'high-success' gesture types (data transformed to correct for positive skew with $\sqrt{(x)}$: n=62, one-way ANOVA $f_{5,57}=23.20$, $p<0.0001$) increasing from baby (n=7, mean proportion =2.46% ±3.38) to peak at young adult (n=7, mean proportion=57.09% ±23.47) and mature adult (n=16, mean proportion=54.29% ±26.64), see Fig. 17.

Specifically, posthoc Games Howell tests revealed that younger infants (1-2y) use a smaller proportion of high success gestures than juveniles (5-9y) (mean difference =2.21, p=0.029) sub-adults (10-14/15y) (mean difference =4.10, p<0.0001), young-adults (15/16-25y) (mean difference =6.38, p<0.0001) and mature adults (>25y) (mean difference = 6.10, p<0.0001). Older infants (3-4y) use a smaller proportion than sub-adults (mean difference =3.85, p=0.028), young-adults (mean difference =6.13, p=0.002) and mature-adults (mean difference =5.85, p=0.002); and juveniles use a smaller proportion than younger infants (mean difference =2.21, p=0.029); sub-adults (mean difference =1.89, p=0.031), young-adults (mean difference =4.17, p=0.002) and mature-adults (mean difference =3.89, p<0.0001).

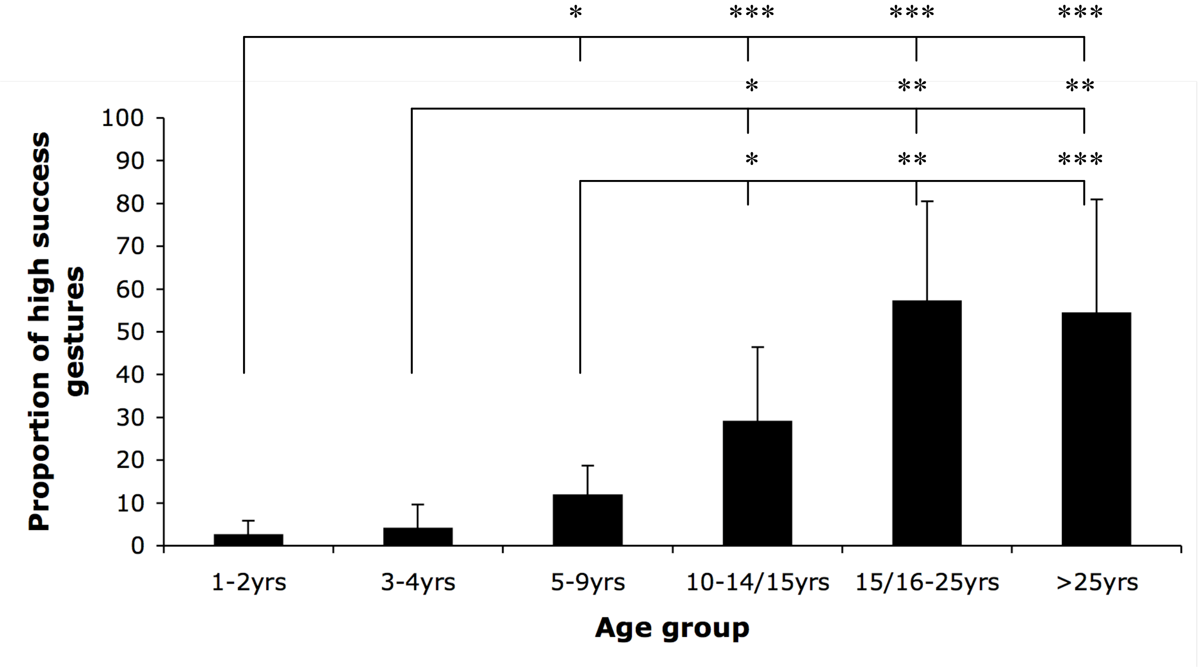


Figure 17. Use of high success gesture types. Variation across age groups in the mean percentage frequency of all gesture use accounted for by gestures defined as ‘high-success’ gesture types. Notifications *, ** and *** refer to p<0.05, 0.01 and 0.0001 respectively in post hoc Games Howell tests.

It is possible that the variation in the successfulness of individual gestures may be due to the individuals using the gestures; so that, for example, if older chimpanzees are inherently more successful in their gestural communications, any gestures that are more frequently used by that age group may appear artificially more successful.

To investigate this possibility, I compare the success rate of individual gestures when employed by young (aged 1-9years) and old (aged 10years and over) chimpanzees. 4 of the 11 high-success gestures described above were either: not observed in one of the two groups, or were observed in fewer than 5 individuals within one of the groups. The rate of success across both age groups for the remaining 7 gestures is described in Table 11. The success rate does falls below 70% on 3 occasions when the gestures were used by young chimpanzees; but there were no significant differences in the success rate of the gestures when used by either younger or older chimpanzees. Therefore there is no evidence to suggest that it is simply the use of these gestures by older chimpanzees that makes them highly successful.

Table 11: Success rate of gestures used individually by young and old chimpanzees. The successfulness of the gesture types when used individually by signallers of different ages. Notification * refers to where the success rate falls to below 70%

	Mean frequency of success as individual gesture		Mann Whitney U (p)
	Young chimpanzees	Older chimpanzees	
Big loud scratch	64.55 ±36.06*	70.27 ±33.56	164.50 (p=0.670)
Directed push	83.80 ±29.64	80.65 ±33.45	110.50 (p=0.810)
Embrace	61.90 ±48.80*	94.44 ±13.61	14.00 (p=0.366)
Hand shake	50.00 ±54.77*	83.33 ±40.82	12.00 (p=0.394)
Present (grooming)	82.45 ±29.76	85.68 ±21.18	188.00 (p=0.692)
Present (sexual)	87.50 ±35.36	71.85 ±36.21	89.50 (p=0.197)
Roll over	89.84 ±14.09	95.00 ±11.18	10.00 (p=0.690)

5.4 Discussion

'I would guess that young and inexperienced chimpanzees have a richer 'vocabulary' of humanoid-like signals than older and more experienced ones and that they are reinforced (perhaps by their companions' obtuseness) into abandoning them for something different' ((Menzel, 1973) p.215).

The division of gesture sequences into G-clauses and G-sentences is critical in understanding the use of combinations in chimpanzee gestural communication. Only once we distinguish gestures produced due to persistence following an earlier failure, can we observe and describe the use of combinations produced for other reasons. Once the separate structural elements of G-clause, and G-sentence are considered in isolation, we see a pattern emerging.

As described in Chapter 3, persistence follows the failure of an earlier gesture to completely fulfil the function of the communication by producing the desired response from the recipient. Older chimpanzees are more likely to produce successful G-clauses, and are therefore less likely to produce G-sentences due to persistence in their attempt to communicate. Although we can explain the production of multiple gestures separated by response-waiting in terms of persistence, this fails to address why there is a variation in the success of the communication across age groups. To tackle this we must consider what factors affect the success of individual G-clauses.

Here I provide a hypothesis that can account not only for the increased success of older chimpanzee communications, but also provides an explanation of why multiple gestures are produced without response-waiting within G-clauses.

The findings for the use of G-clauses can be summarized as follows:

1. Older chimpanzees use fewer rapid sequences in G-clauses
2. There is no evidence that rapid sequences are produced because they are more successful than single gestures, because they represent a more emphatic alternative to single gestures, because they represent a more efficacious alternative to single gestures, or as a result of meaningful combination of gesture types such as attention-getters + information-gestures.
3. Gesture types that are highly successful are more likely to be used individually rather than in rapid sequences.
4. Where at least one high-success gesture is included in a rapid sequence, those rapid sequences are more likely to be successful than those in which they are not included.
5. The successfulness of individual gesture types does not depend on the age of the signaller.
6. Older chimpanzees preferentially employ highly successful gesture types in their gestural communication.

Chimpanzee gestural communication appears to be founded upon a large species-typical repertoire. The variation between age groups in the size of the recorded repertoire can be explained as a sampling artefact, suggesting that the total available repertoire is similar across age groups. In contrast, there is a clear variation between age groups in the *use* of this repertoire. Young chimpanzees have a very large species-typical repertoire available to them; when they produce multiple gestures together within a rapid sequence, rather than simply repeating the same gesture type, they almost always use several different ones, particularly in longer combinations. Their production of multiple gestures together within a rapid sequence may reflect a conservative strategy aimed at reducing error rate given the large range of options available.

However not all gesture types are equally successful, the use of highly successful gesture types would be positively reinforced by an appropriate recipient response. As well as being more successful individually, the inclusion of at least one high-success gesture in a rapid sequence of gestures means that the entire rapid sequence is more likely to be successful, which further reinforces the use of high-success gesture types. With experience, this would lead to the selective use of the most effective gesture types, which can then be employed individually. So that by adulthood over half of all gesture use is restricted to these high-success gesture types, and the use of rapid sequences is greatly diminished. In turn, the more frequent use of successful gesture-types increases the success of the first G-clauses produced, leading to a reduction in the need for persistence following failed communications and thus a reduction in the use of G-sentences.

The perceptual tuning of a large species typical repertoire to distinguish between and reinforce the production of the most useful elements underlies many processes in human cognition. For example: in our ability to hear the range of phonemes in a language (Oyama, 1976, Kuhl et al., 2003); or to distinguish between facial characteristics of our own species (Pascalis et al., 2005), or even ethnicity (Meissner and Brigham, 2001). Thus, in a similar fashion, within the very large species-typical repertoire of chimpanzee gestures may be, with experience, restricted to a reduced repertoire of regularly used, highly successful, gesture types.

This variation in the use of the repertoire may also underlie the variation in repertoire size previously described for the different age groups in captivity (Tomasello et al., 1985). If young juvenile chimpanzees are less selective, they are more likely to produce a large range of gestures within a finite observation time. Where observation times are relatively short this may result in the false impression that juvenile chimpanzees have a larger repertoire, and use types of gesture not employed by adults, as it is only with long-term observation that the rare use of other gestures in adult chimpanzees can be recorded. The presence of a large number of rare or latent gesture types in the adult repertoire also offers an explanation for the imperfect imitation of 'novel' gestures in great apes (Custance et al., 1995, Byrne and Tanner, 2006). As Byrne and Tanner demonstrated, cases of imitation in gesturing may in fact be based on the facilitation of rare behaviours in the extensive gestural repertoire (Byrne and Tanner, 2006).

In a similar fashion, this variation in the use of the repertoire could account for the individual and group variation previously reported (Tomasello et al., 1985, Tomasello et al., 1994, Call and Tomasello, 2007). While a detailed comparative analysis of the repertoire of different groups reveals a near perfect overlap, in practice the 'daily' repertoire of regular use, which accounts for the majority of gestures used, may vary considerably between groups. There is no reason to assume that gestures which are high-success in one group would necessarily be selected for as high-success across all groups; this may lead to a sort of quasi-cultural variation in the mature adult repertoire, reminiscent of the variation between groups of adult humans in the set of phonemes that remain audible when exposed to different languages in childhood. A sort of gestural accent, that could theoretically be used to identify the natal group of an individual chimpanzee from their preferred repertoire in adulthood. In the future it would be extremely interesting to observe whether and to what extent the preferred adult repertoire varies between neighbouring and distant groups; particularly with regards to the effect on the gestural repertoire of female immigrants.

Chapter 6. Imitation

6.1 Introduction

In a wildlife park in France there's a young female gorilla who disco dances. In bouts of intentional gestural communication, she uses a gesture that comes straight out of Saturday Night Fever, rolling her hands around one another in the air (Disco Arm shake, Genty et al. 2009, unpublished data). This gesture is idiosyncratic and only used when gesturing to her human caregivers, never to other gorillas. Clearly this is not a species-typical gesture, nor is it possible to think of any effective action from which it could have been ritualized, so how could she have acquired it? As an idiosyncratic gesture it can't have been socially learned from other individuals in her group; but, as a captive gorilla in a busy wildlife park, who was hand-reared as a young infant, she has had one other regular source of behavioural model: humans.

There are two forms of imitation by which an individual chimpanzee might acquire a gesture: second-person imitation, where an individual imitates gestures that they have received in the past; and third-person imitation, where an individual imitates gestures that they have observed other individuals using. Tomasello et al. discuss the case for the acquisition of gesture through both second and third person imitation (Tomasello et al., 1989); and use the high frequency of one-way gestures and idiosyncratic gestures, that they observed in their group to rule out second-person imitation. They further suggest that the variability in individual repertoires merits a 'conservative approach', which leads them to rule out third-person imitation.

I find no evidence for idiosyncratic gesture use in wild chimpanzees (see Chapter 3), and instead find that the data support a large species typical repertoire, with any observed individual variation a result of experimental methodology rather than originating in the animals themselves. Thus, for different reasons, I agree with these authors that imitation does not play a major part in the acquisition of gesture. However, the compelling nature of observations such as the 'Disco arm shake' suggests that great apes may, on occasion, have the capacity to acquire gestures through imitation. It was not possible within this study to look at the acquisition of gesture through imitation; however, I was able to take advantage of a natural experiment to report on the general capacity for imitative learning in wild chimpanzees.

6.2. Evidence for social learning: observations of imitation in the behaviour of wild chimpanzees

December 7th 2008

The young baby Klaus (2-years old) is watching his sister Kumi (8-years old) groom the old adult male Tinka; she finds a parasite and transfers it to a leaf before carefully inspecting it, peering at it intently. Klaus watches this and then (despite not having groomed anyone) also picks a leaf and closely peers at it for 9 seconds, apparently inspecting it despite there being nothing visible on it.

November 20th 2008

A day of high-octane political wrangling: the alpha male Nick is challenged by an alliance between the beta and gamma males while at the same time the dominant female Nambi is in maximal oestrus swelling and actively soliciting copulations from multiple males. Shortly after 1pm Nambi starts to solicit copulations from several males; Nick initially ignores her advances, but then turns and attacks her physically. She sustains a deep cut to her swelling which bleeds freely. Nambi moves back towards Nick, closely followed by her dependent daughter Night; on the way she picks some leaves and moves up to Nick with them in her mouth. She lies down in front of him appearing to orient herself to deliberately expose her injury to him. She folds the leaves along the central vein so that the hairy underside is exposed and then licks the surface thoroughly; coating it in saliva which she then applies to the wound.

Night watches this behaviour closely; she picks a single leaf and pushes it against the wound, then carefully inspects it. Next she picks a small leaf and licks it briefly before pushing it against the wound; however, she pushes the sharp petiole into the wound and Nambi brushes her hand away. She picks up a leaf Nambi has discarded and carefully licks it but then simply drops it. Nambi continues to use her folded leaves to apply saliva to the wound. At times she bites off the section she's been using and then carefully covers a fresh part of the leaves with saliva and starts to treat the wound again. Night watches carefully for over half and hour and produces *all of the separate elements of Nambi's technique but never combines them to effectively apply saliva to the wound.*

Over a year later, Night was observed to tear off a number of leaves and approach an adult female chimpanzee with a similar deep cut to her swelling apparently with the intention of trying to apply them to the wound (although in this case the un-related female chased her away).

6.3 Evidence for imitation in great apes.

A growing number of species have been reported to show local differences in behavioural traits that appear to be based on cultural transmission (e.g. great apes: van Schaik et al., 2003, McGrew, 1998, Nishida, 1987, Whiten et al., 1999; monkeys: Perry and Manson, 2003, Huffman, 1996, Kawai et al., 1992; whales and dolphins: Rendell and Whitehead, 2001; even coral reef fish: Laland and Hoppit, 2003). The ability to imitate is thought to be critical to the transmission of complex skills and cumulative culture (Tomasello, 1999), and thus, whether imitative learning is within the natural capacity of primates other than humans has been a topic of intense recent interest (Byrne, 2009).

For many the crux of the debate surrounds the claims of culture in the great apes; the complex manual skills involved in tool use (Sanz and Morgan, 2007) and food processing techniques (Corp and Byrne, 2002, van Schaik and Knott, 2001, Byrne and Byrne, 1993), appear ideal candidates for social learning, however to date there is little evidence for how this occurs (Lonsdorf, 2006). Several experimental studies have explored the imitative abilities of chimpanzees in captivity. In these cases the actions are ones that the subject can already do, but learn to employ under a new set of circumstances, this is termed contextual imitation (Tomasello et al., 1993b, Whiten et al., 1996, Horner and Whiten, 2005). This form of learning does not add anything new to the behavioural repertoire, and may be based on relatively simple cognitive mechanisms (Byrne, 2002). Several studies have examined the great ape capacity for imitation of novel gestures (Hayes and Hayes, 1952, Custance et al., 1995, Byrne and Tanner, 2006), however, by examining all cases of naturalistic gesture over a period of 11 years, Byrne and Tanner (2006) were able to show that these cases of 'imitation', may in fact be based on the selection of pre-existing but rare or latent forms from the large natural repertoire.

Detecting imitation in more natural environments is challenging (Custance et al., 1995, Horner and Whiten, 2005, Tomasello et al., 1993b, Whiten et al., 1996). In natural conditions, spontaneous creative behaviours only occur at low frequencies (Bates and Byrne, 2007). The two 'word-pictures' above are classic examples of the sort of one-off anecdotes that regularly crop up following observational based field-studies. What appears to be a clear example of an interesting behaviour, such as ineffectual imitation, is observed and well documented; these single observations are then put on hold pending corroboration from further examples. A number of years later the study ends with no further observations of the behaviour in question, and the records remain in a dusty archive; essentially forgotten, aside from as a short unpublished note in a thesis, or an interesting 'if only I'd seen it again' after-dinner anecdote.

The main obstacle in identifying imitation under natural conditions is that observational methods make it often impossible to identify the original model for imitation. Moreover, if the behaviour is part of the natural species repertoire it remains possible that it would have developed without any social learning. In humans, the clearest observational evidence for imitation comes from the copying of behaviour that has no useful function for the copier, as when right-handed children taught by a left-handed teacher acquire the 'hooked' writing position. At Sonso an unusual set of conditions within the chimpanzee population present a similar set of circumstances under which a number of individuals copied an unnecessary behaviour trait, where the only original model is an individual for whom it is highly functional. I was able to take advantage of this 'natural experiment' and identify imitative learning in a wild population of chimpanzees.

Until recently high levels of hunting within the Sonso community range exposed the chimpanzees to large numbers of snares left in the forest by bush-meat hunters intending to catch dyker or bush-pigs; early efforts to clear the area led to the removal of up to 2000 snares per month by a 4-man team (Reynolds, 2005). As a result one in three of adult Sonso chimpanzees now suffers from permanent injuries caused by snare traps, and several individuals now show idiosyncratic behavioural strategies that compensate their disabilities (food processing techniques: Stokes and Byrne, 2001; walking adaptations: Reynolds, 2005). Adult male Tinka, the most severe case of manual disability, suffers from near-total paralysis of both hands that precludes most normal self-grooming actions (see Figure 19). Apparently in consequence he has developed an efficient but highly idiosyncratic alternative: liana-scratching. His liana-scratch technique consists of grasping a growing liana, pulling it downwards or sideways in order to hold the flexible stem taught, and then rubbing his body back-and-forth against the taut liana (see Figure 18). Imagine using a towel on one's back, except that in this case, rather than the towel moving, the liana is held taut and the body moved relative to it. Presumably as Tinka has no voluntary control of his fingers he uses his toes for the grasping and pulling; at times he increases the tension in the liana with a pull from the second foot, sometimes he uses the back of the hand or foot to manoeuvre the liana before grasping and pulling it taught with a foot.

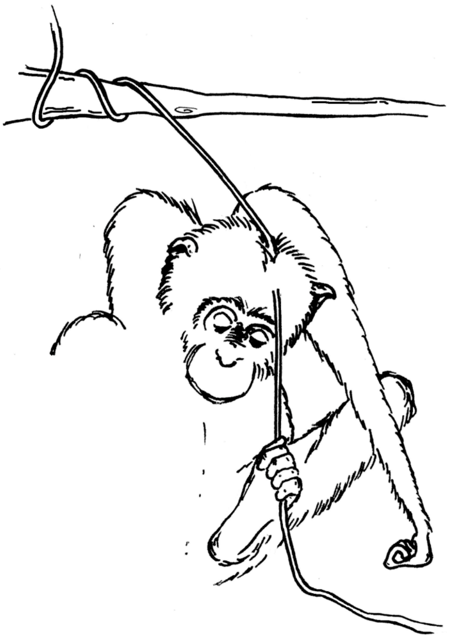


Figure 18: Tinka's liana-scratching technique. He uses his foot to grip and pull the liana downwards and outwards, before rubbing his head against the taut surface.

All of the elements of action within the technique are present in the normal behavioural repertoire of the Sonso chimpanzees: pushing and pulling objects including lianas and rubbing the body against stationary objects such as logs. However, the highly specific procedure of liana-scratch has never been reported in other individuals at Sonso, it is absent from the detailed glossaries of chimpanzee behaviour published from Mahale (Nishida et al., 1999) and Gombe (Goodall, 1986), and from a recent extensive survey of geographic variation in chimpanzee behaviour (Whiten et al., 2001). Thus, this appears to be an original technique developed by the individual Tinka. Here I am able to document the use of Tinka's disability-specific self-grooming technique in a number of healthy individuals, and suggest that the only possible explanation for the acquisition of this behaviour by these individuals is imitation.

6.4 Specific Method

6.4.1 Procedure for collection of liana-scratch data

Observations of climber-scratch behaviour were recorded on an ad hoc basis during data collection for the ongoing project into chimpanzee gestural communication. All examples of behaviour where a climber was used during a self-grooming bout were recorded on miniDV tape using a Sony Handycam (DCR–HC-55). The permanent field-assistants at BCFS collect group composition, ranging and the frequency and duration of behaviours such as grooming onto handheld Workabout Pro computers. All adult and independent sub-adult individuals are recorded individually. Dependent offspring are considered to be a part of the group in which their mother is recorded, because in this chimpanzee community juveniles, including individuals up to 13-years old, travel consistently with their mothers.

6.4.2 Snare injuries in the Sonso community

The Sonso chimpanzee community's range extends to the edge of the forest boundary, and lies adjacent to a number of villages from which local bush-meat hunters regularly enter the forest to lay snares for duiker and other small mammals. Commonly fashioned from wire or nylon, these snares can trap the limbs of passing chimpanzees and are pulled tight across the wrist or ankle as the chimpanzees struggle to remove them. In the case of nylon or grass snares they can be chewed off before permanent damage is caused; however, wire-snares are strong and are rarely broken. If the stake in the ground cannot be broken then the chimpanzee remains trapped and may die of starvation or secondary infection. Where the stake is broken, the wire remains in place around the limb for weeks or months cutting circulation and causing severe nerve and tissue damage. If the individual survives any associated infection then the long-term results can include permanent paralysis, wastage and occasionally amputation of the trapped limb.

Table 12: List of recorded snare injuries in the Sonso community. Notifications f and m represent female and male chimpanzees respectively. *Italics* represent individuals that died before or during study period

Individual	**Snare injury**
Beatrice (adult f)	Right hand amputated
Bob (sub adult m)	*Snare to right hand finger – (missing presumed dead from secondary infection)*
Flora (adult f)	Right hand amputated
Gashom (sub adult m)	*Middle finger amputated (now dead)*
Helen (juvenile f)	Snare to wrist when young, most movement recovered over 3years
Juliet (adult f)	Left hand in permanent fist
Kalema (adult f)	Right hand hooked and wasted
Kana (juvenile f)	Snare marks seen to right ankle but no permanent damage Left wrist snared, movement recovered over 18months
Kasigwa (juvenile m)	Right foot snared, no permanent damage
Kewaya (adult f)	Right hand hooked and wasted
Kigere (adult f)	Right foot amputated
Kwera (adult f)	Snare hand (snare removed by other chimp, no permanent damage)
Monika (juvenile f)	Snare to hand when young, complete recovery
Mukwano (adult f)	Paralysis in several fingers
Nambi (adult f)	Snare to hand, no permanent damage
Nick (adult m)	Snare mark around foot but no restriction to movement
Nora (sub adult f)	Snare to hand when young, no permanent damage
Tinka (adult m)	Both hands hooked and wasted with near-total paralysis
Shida (adult f)	*Left hand amputated, right ankle showed sign of damage (now dead)*
Squibs (sub adult m)	Snare to finger, no permanent damage
Wilma (adult f)	Right hand amputated
Zana (adult f)	*Snare damage to both hands (now dead)*
Zig (sub adult m)	Right hand deformed and wasted

Of the 81 named individuals in the Sonso community, 14 individuals (3 juveniles and 11 adults) have permanent snare related injuries. This represents approximately one third of the adult population. I have observed several cases where a snared individual was fortunate enough to lose the snare before permanent damage was inflicted, and conversely there have been several cases where an otherwise healthy individual simply disappears. Both of these situations suggest that the actual number of individuals trapped by snares may in fact be higher than reported. The limitations of individual chimpanzees with permanent disabilities were well known and a complete list of snare-related injuries is provided in Table 12.

6.4.3 Adult male Tinka

The most marked case of snare injury is Tinka, a mature adult (49±3years) male chimpanzee with severe deformity of both hands (Figure 19). Both Tinka's left and right hand exhibit severe deformities. Most of the muscles of the left wrist are apparently paralysed, which allows the left hand a limited axis of movement, but in its relaxed posture the wrist is hooked and weakened. Digits 1-4 are permanently flexed and incapable of assuming any independent movement although the thumb has retained some function. The right hand exhibits even greater deformity, with complete paralysis of the wrist and voluntary movement impossible (Stokes and Byrne, 2001, Byrne and Stokes, 2002). In addition to his injuries he suffers from a chronic skin infection that causes extensive dry, flaky skin and patchy hair (Reynolds, 2005). This appears to cause him frequent discomfort, exacerbated by the fact that the extremely limited range of movement in his wrists and fingers prevents him from using them to groom or scratch much of his own body in a normal fashion. While he occasionally uses the side of a hand in combination with his lips to groom areas on his chest and arms this technique is very cumbersome and makes it impossible for him to groom his head, back and lower body. Here, where any normal chimpanzee would simply use a combination of scratching and grooming with both hands, Tinka uses his liana-scratch technique.

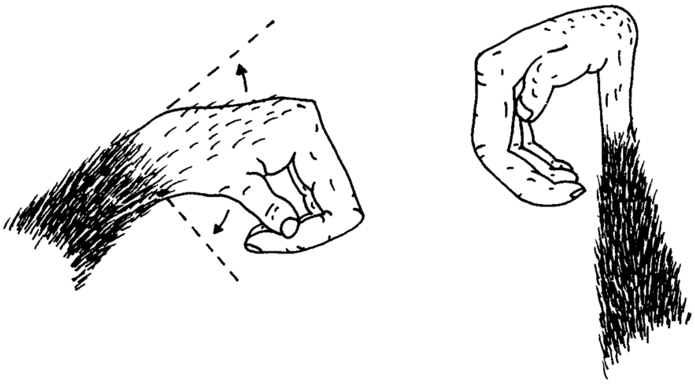


Figure 19: Hand injuries of male chimpanzee, Tinka (Byrne and Stokes, 2002). He suffers from near complete bi-manual paralysis: the fingers of both hands are permanently flexed, and both wrists are effectively paralysed.

In addition to the difficulties he experiences in self-grooming he receives relatively little social grooming from other individuals. When compared to other adult males he ranked 6/7 in terms of the amount of grooming received for the year 2008. The only individual who received less grooming was the young male Squibs who was in the very early stages of establishing himself within the adult hierarchy.

6.4.4 Ranging behaviour of specific individuals

Sonso females include core, peripheral and rare individuals. During the study period 14 parous females were observed on a regular basis: these included 7 core and 7 peripheral individuals (see Appendix 1 for details). One of the core females, Zana, died in 2007 orphaning her immature sons Zalu and Zed, these males retained her core range and where necessary the data of the older brother Zalu was substituted for that of the 'mother' in assigning data on range and time spent with other individuals to the younger brother Zed.

Sonso males spend the majority (80%) of their time in the central core of the community range; consequently, core females and their dependent offspring spend more social time with males than do peripheral females and their offspring. The Sonso community home range is approximately 7 km^2; however, adult males with snare injuries have smaller individual ranges, probably as a result of the increased travel costs resulting from their injuries. Tinka's home range was identified in 2003 as the smallest, with an estimate of only 1-3km^2 and lies entirely in the core area (Newton-Fisher, 2000, Newton-Fisher, 2003a, Newton-Fisher, 2003b).

6.4.5 Analysis of liana-scratch data

Digital videotapes were transferred to an Apple MacbookPro computer; these were edited into discrete clips using iMovie and labelled for analysis and categorisation. Analyses were carried out in SPSS v11, with $\alpha=0.05$ required for significance. Means are given ± Standard Deviation, throughout.

6.4.6 Inter-observer reliability of liana-scratch data

Assessing inter-observer reliability was not straightforward. As the liana-scratch represents a clear and unusual technique, very distinct from normal grooming behaviour, simply including clips of liana scratch in a set of grooming clips would have led to an easy and trivial 100% agreement between the two coders. Instead I presented a second coder (Cristiane Cäsar, CC) with all potential cases of liana-scratch; these included the 21 positive exemplars that I had identified and a number of similar looking manipulations of lianas that I had discarded. CC was made familiar with the behaviours from videos of Tinka's behaviour only, and was unaware of the total number of positive exemplars. Inter-observer agreement in coding material from able-bodied chimpanzees was 'very good' (Cohen's Kappa of 0.85). I also investigated inter-observer reliability for the second measure of how many elements of liana-scratch (of a possible three, grip liana, pull tight, rub body side-to-side) were present in each positive exemplar identified by CC. Here again the agreement between coders was 'very good', with Kappa 0.83.

6.5 Results

6.5.1 Use of the liana-scratch technique by able-bodied individuals

Between October 2007 and August 2009 I recorded video evidence of 21 bouts of liana-scratch (L-S), within self-grooming episodes by 7 able-bodied individuals. All the 7 individuals were healthy and able-bodied, and all were young, age range: 4-13 years: Night (5 yr female; first showed L-S when 4 yr; 4 bouts), Zak

(6 yr male; 5 bouts), Karo (7 yr female; 3 bouts), Kumi (8 yr female; 5 bouts), Zed (8 yr male; 2 bouts), Kana (10 yr female; 1 bout), Bahati (13 yr female, showed L-S when 12yr; 1 bout). None of the bouts occurred within the same party of chimpanzees on the same day. However, on one occasion the juvenile Zed was observed using the L-S technique just after watching Tinka employing it. This was the second observation of Zed employing the L-S technique. On no other occasion was Tinka present within the party when L-S was recorded in an able-bodied individual.

Eighteen of the recorded instances of liana-scratch could be seen clearly; three were partially obscured on the video and were not included in the following analyses. Of these 18, in 13 cases – involving 6 different individuals – the technique closely mirrored that of Tinka: grip liana, pull tight, and rub body part side to side against it. Unlike Tinka, able-bodied individuals normally used a hand rather than a foot to produce the tension in the liana (See Table 13. for details of variation in L-S technique among able-bodied individuals). In the remaining 5 cases, tension in the liana was attained by pushing against it with the back of the hand or wrist, rather than gripping and pulling the liana.

Table 13: Actions use in L-S by able-bodied chimpanzee.
* in these 3 cases Karo added a second grip with the hand so that both hand and foot pulled on the climber

Individual	Liana-scratch technique				
	Tension by pulling		Tension by pushing		Unclear
	Hand	Foot	Hand	Foot	
Bahati (13y. f)	1				
Kana (10y. f)					1
Karo (7yr. f)		3*			
Kumi (8yr. f)	2		3		
Night (5yr. f)	2		2		
Zak (6yr. m)	4				1
Zed (8yr. m)	1				1
	10	**3**	**5**		**3**

6.5.2 Do the able-bodied chimpanzees observed to L-S have the opportunity to regularly observe Tinka's technique?

I used the long-term project records (Zuberbühler and Reynolds, 2005) to investigate the opportunities of able-bodied individuals to observe Tinka's use of the L-S. All able-bodied dependent chimpanzees in the 4-13 year age range were assigned as either core or peripheral on the basis of their mother's home range (as all dependent offspring were reliably found with their mother). I then examined whether or not the home range of these able-bodied individuals overlapped with the home range of Tinka, which lay entirely within the core area. As I recorded significantly more data from core individuals, (core individual video (hrs): n=23 mean =5.82 ±3.07; peripheral individual video (hrs): n=19 mean =1.32 ±0.88; Independent t-test, t=6.18, df=40, p<0.0001), I also interrogated the 6 highly experienced chimpanzee field-assistants employed by the project to ensure all individuals showing the L-S technique had been identified. 2 of these field-assistants have worked with the Sonso community for over 20-years, and several of them have spent time specifically targeting peripheral females for data collection. The field-assistants confirmed that only the 8 individuals (Tinka and 7 young chimpanzees) identified within the study had been observed to employ the liana-scratch technique. I then tested the number of individuals in which L-S was observed, rather than the number of cases of L-S. Use of the L-S by able-bodied chimpanzees was significantly associated with sharing the range area of Tinka (Yates' corrected Chi-square test, one-tailed: among 4-13 year old immatures, n=19, χ^2=4.20, df=1, p=0.02).

Individuals might share the same range, yet not associate with each other in the same foraging parties, and thus lack the opportunity to regularly observe one another's behaviour. However, this was not the case for those individuals showing L-S. During the year 2008, the young chimpanzees that showed liana-scratch were recorded in a group with Tinka during more than twice as many hours as those in whom the behaviour was absent (mother's time with TK: for all mothers of individuals in whom L-S present: n=6, mean =194.8 ±48.1 hrs; for all mothers of individuals in whom L-S absent: n=8, mean=78.3 ±28.3 hrs; t-test: t=5.71, df=12, p=0.01).

6.6 Discussion

The absence of liana-scratch in previous observations at Budongo, and the lack of reports of anything similar at other long-term chimpanzee sites, suggests that liana-scratch is not simply a low-frequency component of the natural chimpanzee repertoire. Liana-scratch does not offer any benefit to able-bodied chimpanzees, which are able to scratch themselves, self-groom, or solicit grooming from others. However, the innovation of the liana-scratch technique by Tinka is not hard to understand. His skin complaint, lack of regular grooming by others, and severe bi-manual disability mean that it allows considerable gains in skin-care and consequent comfort; and the actions which are coordinated to produce the novel pattern are ones that any chimpanzee could do, and are indeed part of the normal repertoire of most Sonso chimpanzees.

The strategies of disabled individuals can be clearly differentiated from the natural repertoire of healthy individuals for whom they have no function; and in the case of highly specific strategies, it is often possible to identify the original model. This makes them an ideal focus in the search to identify clear cases of imitation in wild apes. In the case of Tinka his skin complaint, his inability to self-groom in the normal fashion, and the low levels of social grooming he receives, mean that any additional grooming technique, particularly one that permits access to areas he can not reach, such as the back, head and neck, would be a highly valuable addition to his repertoire. The able-bodied chimpanzees that used liana-scratch were all young, all resident in the same area of the Sonso community as Tinka, and often actually found in parties with him. In contrast, similar-aged chimpanzees in other parts of the community range have never been seen to show this idiosyncratic behaviour. I therefore concluded that observation of Tinka's behaviour was critical for learning the novel behaviour pattern described as liana-scratch.

On one occasion the young juvenile Zed used the liana scratch shortly after watching Tinka employ the technique, however, there were no other cases where two different individuals employed the technique in the same party. Thus, the observations cannot be explained through the facilitation of one individual's behaviour by another's.

Evidence of observational learning – learning by imitation – is sparse in chimpanzees and other great apes, and has been argued to be uniquely human (Tomasello, 1999, Tomasello et al., 1993a). In many cases that superficially suggest imitative learning, the evidence is ambiguous between this and learning by 'emulation', in which it is the physical results rather than the bodily actions that are copied (Tomasello, 1998, Wood, 1989). Chimpanzees and gorillas have been shown to match a demonstrated action in opening a puzzle box, rather than using an equally-effective alternative action (Whiten et al., 1996, Stoinski et al., 2001, see also Bering et al., 2000) (also shown in quail: Zentall, 2004, budgerigars: Heyes and Saggerson, 2002, Richards et al., 2009; pigeons: McGregor et al., 2005; and domestic dogs: Topál et al., 2006). In these cases, however, the actions are ones the subjects can already do. What is learned is not a new action, but the appropriate circumstances to deploy a familiar one; this has been described as 'contextual imitation', rather than the 'production imitation' needed to learn a new behavioural routine (Byrne and Stokes, 2002, Hoppitt and Laland, 2008).

The prevalent limb used by the young chimpanzees to produce the grip and pull elements of the climber-scratch was the hand, rather than a foot as used by Tinka. This implies a degree of rational assessment where aspects of the element that have to be copied (i.e. tighten your digits around the climber to grip) were distinguished from those aspects that were performed through necessity in the case of one individual, but which could be varied to improve the ease or efficiency (i.e. by using fingers rather than toes).

Experiments with chimpanzees and orang-utans have examined gestural imitation, training subjects to match a demonstrated action and then presenting novel actions for the ape to copy (Custance et al., 1995). The subjects do perform actions sufficiently similar to the demonstrated ones to be identified by naïve coders, although the imitations are usually imperfect. However, Byrne & Tanner, in a similar study with a gorilla for whom they had been able to collect gestural repertoire information for over 11-years, were able to demonstrate that all of the 'copies' were in fact rare gestures within the large pre-existing repertoire (Byrne and Tanner, 2006). Thus, in this case and in all others showing gestural imitation, where no long-term records are available, it is possible that observation facilitates the performance of latent actions already in the apes' extensive repertoire, rather than allows new learning. Moreover, all the subjects in these experiments have been at least partly nursery-reared or home-reared, so human enculturation cannot be entirely ruled out (Tomasello et al., 1993b). For these reasons, the conclusion that great apes are incapable of learning by imitation remained strongly defended.

In the cases described here, the subjects are wild chimpanzees and the behaviour performed is novel: a goal-directed sequence of actions that does not normally occur in the chimpanzee repertoire. The 'natural experiment' of the presence of disabled individuals in the population has allowed behavioural strategies to develop that can be clearly differentiated from the natural repertoire of any able-bodied individual, for whom they have no function. Moreover, the disability-specific nature of some of these strategies allows specific individuals to be pinpointed as the only possible models for copying; in this case, Tinka, an individual for whom the liana-scratch strategy is highly functional.

It is not clear why able-bodied chimpanzees should copy this functionless technique. In an anecdotal observation from the Burger's Zoo, Arnheim, de Waal describes how young chimpanzees mimicked the strangely hunched walking style of the adult female Krom: 'the young apes, who think up new games all the time, once had an "ape Krom" craze. For days on end they would walk behind her, single file, all with the same pathetic carriage as Krom' (de Waal, 1982, p.80). My observations differ in that the technique copied was a goal-directed one, which was employed when not with the original model. However, the evidence that chimpanzees are able to learn novel behavioural routines by observation (production imitation), suggests that the functionless fads and mimicry reported elsewhere reflect a natural trait of chimpanzees that may represent a means by which important skills are transmitted culturally.

The cognitive capacity for imitation is directly relevant to the question of how the complex manual skills of tool use and food processing are acquired socially:

chimpanzees are able to learn novel behavioural routines by imitation. In captive apes where the available behavioural models include other species, such as humans, the capacity for imitation may explain the occurrence of rare idiosyncratic gestures within the communicative repertoire.

Chapter 7: The contexts in which wild chimpanzees use gestural communication

7.1 Introduction

The conditions in which captive apes are kept have improved greatly in recent years, with a stronger emphasis on more natural social groups and environmental enrichment (Celli et al., 2003); nevertheless, no captive environment is ever able to replicate the complex physical and social environment of free-living wild apes. The effect of captivity on individual and group behaviour thus limits the extent to which we can generalize descriptions of great ape behaviour from captive observations. This is particularly true when considering behaviour from an evolutionary perspective, as the benefit or cost of a particular behaviour can only be assessed in terms of its ‘environment of evolutionary adaptation.’

Captive studies of gestural communication in great apes have consistently described *play* as the dominant context for gesture use (Tomasello et al., 1994, Liebal et al., 2004a, Pika et al., 2005b, Pika, 2007, Genty et al., 2009). Moreover, the analysis of gestural communication during play has provided some of the best evidence for the use of triadic and collaborative behaviour in great apes (bonobos: Pika and Zuberbühler, 2008; gorillas: Tanner and Byrne, 2010). But is this bias towards play relevant to wild behaviour?

There is no doubt that wild chimpanzees play; Goodall describes social play between all age-sex combinations at Gombe (Goodall, 1986); and at Mahale several studies have now examined specific elements of play (leaf-pile play: Nishida and Wallauer, 2003; group play: Nishida, 2004; pirouettes: Nishida, 2009). However, under natural conditions chimpanzees must spend a considerable proportion of their day in feeding and foraging (from 30-50%), and are less likely to socialize in large parties, particularly when resources are scarce (Doran, 1997). In contrast, captive chimpanzees spend much less of the day in foraging and feeding (Celli et al., 2003), do not have to travel between feeding and sleeping sites, usually have peers of their own age close by, and have limited opportunity for prolonged periods of social isolation. Thus, the captive environment may promote play activity; and this may have contributed to its apparent dominance as a context for gestural communication in captive chimpanzees.

While contexts such as play, feeding or grooming are experienced by both wild and captive chimpanzees, wild chimpanzees encounter contexts rarely or never experienced by captive chimpanzees, some of which may promote the use of gestural communication. Unlike a vocalization, a gesture, in particular a silent one, can be used in a targeted fashion that limits potential recipients to those in view of the gesture, eliminating the chance of other individuals 'eavesdropping' on the communication. Within the dense secondary forest of Budongo, where visibility can be highly restricted, a silent gesture can easily be limited to its intended recipients. The use of silent gestures in this fashion was suggested for a young captive male gorilla in his attempts to interact with a female in the group, while at the same time avoiding advertising these attempts to an older more dominant male (Tanner and Byrne, 1996). However, while this represented a rare and unusual case in captivity (the effect of the 'un-natural' inclusion of 2 male gorillas in the same group), there are a number of contexts in which the benefits of silent communication may promote the use of gesture in wild chimpanzees. Hunting, boundary patrolling and consortship behaviour, all require the limited spread of information to be successful. Encountering a neighboring group while patrolling a territorial boundary can lead to lethal aggression (Goodall, 1986, Boesch and Boesch-Achermann, 2000), exerting a strong selective pressure against unintentionally advertising your own group's location. Similarly, a successful hunt relies upon avoiding alerting potential prey (or at least delaying the alert to an opportune moment). At the risk of anthropomorphising, the powerful image of a stealthy commando holding up his hand to stop his team and then direct them, easily demonstrates the extremely effective way in which silent gestures could be employed to limit communication in environments where the costs of being overheard may be extremely high.

In the following section I examine the use of gestural communication across all the contexts available to wild chimpanzees, with a particular focus on the possible use of gesture in triadic or collaborative interactions during play, and on the use of gesture in contexts that may promote the use of silent communication.

7.2 Specific method

7.2.1. Definition of situational contexts

I defined 10 situational contexts (hereafter: contexts) for the use of gestural communication, recorded at the level of the G-dialog: Affiliation, Agonism (includes display), Consortship, Feeding (includes begging, nursing, drinking), Grooming, Patrolling, Resting, Sexual (includes inspecting and copulating), Social-play (referred to simply as Play), and Travel, see Table 14. As I define gestures as being *observed during periods of intentional communication*, all cases not directed to another individual were excluded from analysis; however, I did maintain a separate record of gesture-like behaviours produced during bouts of Solitary-play. All non-specific references to Play refer only to Social Play.

The varied behaviour of multiple individuals in natural conditions can make it difficult to clearly assign a single context to an interaction. A party of chimpanzees may contain individuals who are feeding, resting, playing, even copulating; some may be engaged in more than one of these activities at once, and communication may occur between individuals engaged in different activities. While coding I define context as the broad situational context, rather than the immediate function, of the communication, so that a gesture produced with the function of affiliation by a female while she is in *consortship*, is categorised within the broader context of *consortship*, not the immediate function of *affiliation*. In order to maintain a consistent approach, I consider context to be the behavioural environment within which the *initiating signaller* produces the communication. For example, in the situation where a mother is resting on the ground and her dependent children play around her; where the infant chimpanzee approaches the mother and initiates a request to play, I consider this communication to occur within *social-play*. However, if the mother, disturbed by the infants' general play, initiates a request to stop the behaviour, I consider this communication to occur within *rest.*

Table 14: Definition of the situational contexts for intentional gesture in wild chimpanzees

Context	Definition
Affiliation	One individual seeks social support or physical contact from another.
Agonism (including display)	One individual seeks to attack or physically displace another. Context includes non-directed social displays such as drumming and branch shaking.
Consortship	Includes individuals engaged in or soliciting for consortship behaviour, see Chapter 8 for a detailed description.
Feeding	Primarily the location, preparation and ingestion of food, but includes all food directed activity such as begging, foraging, nursing, and drinking. Includes hunting behaviour post-patrol i.e. chasing and attack of other species for the purpose of feeding on them.
Grooming	An individual participates in grooming or requests grooming from another
Patrolling	Individuals walk one behind each other in a line while remaining silent and highly vigilant. Includes both boundary and hunting patrol behaviour.
Resting	An individual remains stationary without participating in any self-directed or other-directed physical activity; includes sleeping.
Sexual (including inspection and copulation)	Includes sexual presenting by females in oestrus (non-oestrus females are considered to be seeking affiliation when presenting, as are males). Also includes behaviour relating to the inspection of the female swelling and male-female mounting and copulation from all age groups.
Social Play (referred to as Play throughout)	Two or more individuals engaged in play behaviour, may include both chasing-play and/or contact-play such as wrestling.
Travel	Locomotion from one area to another. Does not include brief locomotion between individuals within a group.

7.2.2 The context repertoire

The data from all individuals observed to gesture within the context is pooled, and gestures observed at least 2 times are included in the context repertoire.

7.2.3 The distribution of repertoire use

While the total observed repertoire may contain a large number of gesture types, the majority of gesture use may be described in terms of only a few gesture types. The correlation between repertoire size and quantity of video described in Chapter 3 suggests that the total repertoires of more rarely filmed contexts are under-reported; however, where a few gestures account for the majority of gesture use, it is unlikely that additional observation would contribute new gestures types that usefully describe the gestural communication within the context. Alternatively, if the distribution of gesture use is more even, then additional observation may contribute further, regularly used, gestures.

I describe the distribution of repertoire use within a context, by comparing the proportion of total gesture use accounted for by the 5 most frequently occurring gestures. From a given repertoire size it is possible to calculate the expected distribution of 5 gestures: for example, if a context repertoire includes 50 gestures with near even distribution of use, any 5 gestures will account for approximately 10% of all gesture use within that context. We can then compare the expected distribution with the observed distribution of the 5 most frequently used (top-5) gestures. If observation shows that the top-5 gestures in a 50-gesture repertoire, account for 60% of all gesture use we can see that the distribution of use is skewed in favour of certain gesture types.

The repertoire of regular use

Within this analysis I refer to the *repertoire of regular use*. To determine this I list the gesture types within a repertoire in rank order of observed frequency, I add together the observed frequency of the top ranked gesture types in order until I reach 70%. This sub-group represents the repertoire of regular use, which accounts for at least 70% of the cases of gestural communication within that context. Two contexts with identical repertoires (all gestures observed on 2 or more occasions) may have very different repertoires of regular use.

7.3 Results

7.3.1 Repertoire

Intentional gesture was flexibly produced across all 10 of the behavioural contexts. Within the Sonso community, *play* was the dominant context for the use of gestural communication, with almost half of all active gesture footage recorded in *play* (46.33%); followed by *feeding* (18.69%), and *grooming* (15.02%). Although there were only very limited opportunities to observe *patrolling*, gestural communication was almost completely absent during this behaviour (see Table 15).

In addition to the most active gesture footage, the greatest number of gestures and largest repertoire of gesture types were also recorded within the context of *play* (see Table 15); however, as with the individual and age-group repertoires described in Chapter 3, both the total number of gestures (n=4353, range= 16:2382, mean =483.7 ±729.8) and the size of repertoire recorded within a context (n=66, range= 1:60, mean =16.0 ±14.7) were strongly correlated to the amount of active gesture footage recorded from that context (total active gesture footage =23.5hrs, mean =2.4hrs ±3.3) (correlation between active gesture footage and number of gestures: Pearson correlation r=0.95, n=10, p<0.001; correlation between active gesture footage and repertoire: Pearson correlation r=0.89, n=10, p<0.001). This finding suggests that the smaller number of gestures and smaller repertoire sizes of other contexts may be a result of a sampling artefact; and therefore, that the variation between contexts would decrease with further observation.

Table 15: Variation in gesturing time, repertoire size and use across contexts. Describes the total quantity of active gesture footage in each context, and the percentage of the total active gesture footage that this represents. Also the total number of cases of gesture, and the size of the repertoire within each context. Finally the percentage of gesture cases accounted for by the 5 most frequently used gesture types. Notification * refers to the case where there were insufficient types of gesture to calculate this variable

Context	**Active gesture footage (hrs)**	**% of total active gesture footage**	**Number of gesture cases**	**Size of repertoire (total observed types)**	**Observed % of gestures accounted for by 5 most frequently used types** (*expected %*)
Affiliation	0.25	1.07	96	10 (15)	82.3 (50.0)
Agonistic	0.45	1.92	212	22 (28)	54.7 (22.7)
Consortship	1.22	5.20	412	14 (21)	81.6 (35.7)
Feeding (includes begging, drinking & nursing)	4.38	18.69	419	21 (31)	69.7 (23.8)
Grooming	3.52	15.02	491	12 (19)	95.3 (41.7)
Patrolling	0.01	0.04	4	1 (3)	*
Play	10.86	46.33	2381	53 (60)	44.9 (9.4)
Resting	1.23	5.25	16	5 (9)	*
Sexual	0.33	1.41	176	9 (15)	89.2 (55.6)
Travelling	1.19	5.08	148	16 (25)	65.5 (31.3)

7.3.2. Does the variation in quantity of gesture recorded from a context depend on the ease with which gesture is coded within that context?

The quantity of gesture recorded from any particular context depends in part on the ease of coding gestures produced in that context. For example: in *grooming*, the individuals involved are usually stationary and it is relatively easy to anticipate the beginning of a communication from preceding behaviour; this makes it easier to film, and then code, the communication. Table 16 describes the percentage of all clips recorded in a context from which it was possible to code gestural communication.

Table 16: Variation in the quantity of clips coded and the gesturing time recorded across contexts

Context	Total number of gesture clips	% coded	Quantity of gesturing time (hrs)
Affiliation	52	63.5	0.25
Agonism	365	26.6	0.45
Consortship	277	41.2	1.22
Feeding (etc.)	804	25.0	4.38
Grooming	893	38.6	3.52
Patrolling	26	11.5	0.01
Play	1729	45.2	10.86
Resting	739	10.6	1.23
Sexual	70	48.6	0.33
Travelling	494	28.1	1.19

There was no correlation between the percentage of codable clips and the quantity of gesturing time recorded within a context (Pearson's correlation r=0.166, n=10, p=0.626). It was therefore not the case that the high quantity of gesture recorded within the contexts of *play*, *feeding* and *grooming* were simply a result of the ease with which gesture was coded in these contexts. The difficulty in coding gestural communication is clearly illustrated by the fact that in 9 out of 10 contexts, over 50% of clips had to be discarded as 'un-codable'.

7.3.3 Is there a difference between age groups in the contexts used for gesture?

When we examine age groups individually we find that *play* is the dominant context from younger infant (1-2y) up to sub-adult (10-14/15y) chimpanzees, but is replaced by other contexts in adult life. In young adults (15/16-25y), *play* is still extremely prominent as a context for gesture use, co-dominant with grooming; in more mature adults (>25y) *play* is surpassed by feeding, grooming and travelling which together account for over 73% of all mature adult gesture use (see table 17). When adult males were considered in isolation *Consortship* represented the dominant context for gesture use, accounting for over 60% of all gesture cases; this will be discussed in detail in Chapter 8.

Table 17: Distribution of gesture use within contexts across detailed age groups
The number of contexts in which gesture use was recorded within the age group, along with the percentage of gesture use recorded within the 3 most frequently observed contexts in that age group.

Category	Age (inclusive)	Number contexts recorded	Top 3 contexts (% of recorded gestures)
Younger infant	1-2y	7	Play (87.5%), Grooming (9.5%), Feeding (1.7%)
Older infant	3-4y	8	Play (52.4%), Agonistic (28.9%), Sex (8.4%)
Juvenile	5-9years	8	Play (72.6%), Feeding (12.3%), Grooming (7.2%)
Sub adult	Male: 10-15years, female: 10-14years	8	Play (38.0%), Grooming (23.2%), Agonistic (12.0%)
Young adult	Male: 16-25years, female: 15-25years	8	Grooming (24.0%), Play (23.6%), Agonistic (10.9%)
Mature adult	>25 years	9	Feeding (32.8%), Grooming (30.3%), Travelling (10.5%)

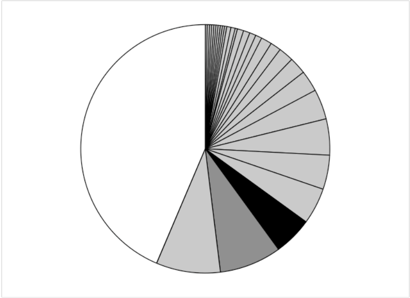
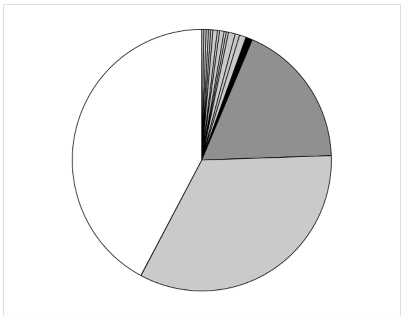
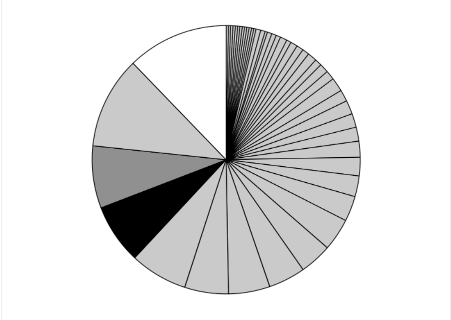
7.3.4. Distribution of gesture use within repertoire

The correlation of repertoire size and gesturing time within a context suggested that variation between contexts in the number of gesture types in the repertoire would reduce with further observation. However, the same sampling artefact did not affect the distribution of use of the repertoire within a context. Thus, in two contexts with equal repertoire size, there may be a variation in the extent to which any one gesture type accounts for a proportional of gesture use. In the following analyses I examined whether or not, and to what extent, there was a variation in the expected and observed frequency of use of gesture types within a context.

Across all contexts the percentage of use accounted for by the 5 most frequently observed gesture types was above that expected by chance (n=8, expected % mean = 33.8 ±15.2, observed % mean =72.9 ±17.4; Paired t-test t=13.57, df=7, p<0.0001, see Table 15). This result indicated that use of the repertoire within contexts was skewed in favour of specific gesture types. In the majority of contexts (6/8), the 5 most frequently observed gesture types accounted for over 65% of all gesture use, despite repertoire size in these cases ranging from 9-21 gestures. In these 6 contexts, where a small number of gesture types account for the majority of gesture cases, further observation would be unlikely to greatly extend the repertoire of regular use.

In the contexts of *agonism* (top-5 gesture types expected=22.7%, observed =54.7% of gesture cases) and *play* (top-5 gesture types expected=9.4%, observed =44.9% of gesture cases) repertoire use was more varied, although it still favoured certain gesture types. The figures in Table 18 show the variation in repertoire distribution within the 3 main contexts for gesture use. The most common 2 gestures accounted for over 50% of all gesture use in *grooming* and *feeding*, but under 20% in *play*.

Table 18: Distribution of repertoire use in the three most frequently observed contexts. The 5 most frequently observed gesture types are listed along with the percentage of gesture use that they account for within that context. The percentage of gesture use accounted for by all of the gesture types within the repertoire is expressed as a pie chart.

5 most frequently used gestures: % of cases (number of cases)		
Feeding (419 cases)	**Grooming** (491 cases)	**Play** (2381 cases)
Reach: 43.7% (183) Directed push: 8.4% (35) Touch other: 7.9% (33) Arm raise: 5.0% (21) Hand on: 4.8% (20) All other gesture types: 17.7% (127)	Big loud scratch: 42.2% (207) Present grooming: 33.4% (164) Directed push: 17.9% (88) Hand on: 1.0% (5) Touch other: 0.8% (4) All other gesture types: 4.7% (23)	Dangle: 12.3% (293) Grab: 18.8% (262) Stomp: 7.5% (179) Slap object: 7.3% (174) Arm swing: 6.8% (161) All other gesture types: 55.1% (1312)
% frequency of gesture use for each gesture type within context repertoire		
		

7.3.5 Does the range of functions, or the flexibility of individual gestures or functions, vary between contexts?

Individual gestures are used flexibly for multiple communicative functions; nevertheless, previous studies have suggested that they tend to be closely associated with a primary, and possibly secondary, function (Genty and Byrne, 2009, Liebal et al., 2004a). Thus, where gestural communication in a particular context is used for a wide range of functions, it may then follow that a wider range of gesture types is regularly employed. The variation between contexts in the use of the repertoire, as described above; may, therefore, be the result of a variation between contexts in the range of functions for which gestural communication is used. For example: in *play*, the regular use of a larger proportion of the repertoire may be the result of a wide range of functions within this context. In contrast, *grooming*, where a small proportion of the repertoire accounts for the majority of gesture use, may be associated with a more restricted set of functions.

Alternatively, there may be a variation in the flexibility of gesture types between contexts. For example, individual gestures in *grooming* may be associated with a large number of functions and, thus, may account for a large proportion of gesture use. Similarly, there may be variation in the number of types of gesture used per function. In this analysis I examine to what extent the range of functions, and the flexibility of individual gesture types varies between contexts.

Individual contexts were associated with a mean 6.00 (±2.11) functions (of a possible 17); *play* communications included the most, with 10 functions (see Table 19); however, there was no significant variation in the total number of functions per context (n=10, Chi-square: χ^2=0.001, df=9, p=0.999).

Table 19: The variation between contexts in the flexibility of gesture use. The total number of functions recorded within the context, along with the mean number of functions per individual gesture type, and the mean number of gesture types per individual function within the context. Notification * represents insufficient cases of gesture to calculate the variable.

Context	**Number of functions**	**Number of functions per gesture type**	**Number of gesture types per function**
Affiliation	7	2.3 ±1.4	2.7 ±2.6
Agonistic	3	1.4 ±0.5	12.7 ±6.0
Consortship	7	1.3 ±0.5	3.7 ±6.8
Feeding	8	2.6 ±1.0	8.1 ±5.0
Grooming	7	2.2 ±0.5	3.9 ±2.5
Patrolling	3	*	*
Play	9	2.4 ±1.1	20.3 ±28.4
Resting	4	*	*
Sexual	5	1.6 ±0.6	3.6 ±4.7
Travelling	7	1.9 ±0.9	3.1 ±2.5

Across contexts individual gestures were associated with a mean 2.13 (±1.03) functions. I find a small but significant difference between contexts in the number of functions per gesture type (one-way ANOVA Brown-Forsyth correction: $f_{7,30}=5.52$, $p<0.0001$). Specifically, that the number of functions per gesture is higher in *feeding* and *play*, than in both *agonism* and *consortship* functions (Games-Howell post-hoc tests, agonistic and feeding: mean difference =1.23, p=0.002; *agonism* and *play*: mean difference =0.98, p<0.0001; *consortship* and *feeding*: mean difference =1.32, p=0.001; *consortship* and *play*: mean difference =1.07, p<0.0001).

Individual functions within a context were associated with a mean 7.5 ±13.4 gesture types. Variation across contexts ranged from a mean 2.7 gestures in affiliation to 20.3 gestures in play; however, the difference between contexts only approached significance (Kruskal Wallis: $Chi^2= 13.02$, df=7 p=0.072).

These findings show that there is no significant variation in the number of functions for which gestural communication is used within a context, but there is a variation between contexts in the flexibility of individual gesture-types: specifically in *feeding* and *play*, gestures are used more flexibly than in *consortship* and *agonism*. Also, there is a variation in the number of gestures used per function: *agonism* and *play* having a particularly large number of gestures per function.

7.3.6 Specific elements of play behaviour in wild chimpanzee gestural communication

Solitary Play

During coding, potential cases of gesture were discarded where it was not possible to clearly identify them as directed; however, cases recorded from bouts of *solitary play* differed in that there was no possibility of then being directed towards another individual. As *solitary play* was only recorded in the absence of potentially intentional communication, these data represent only a limited description.

Nine individuals were recorded in bouts of *solitary play*, 4 infants, 4 juveniles and 1 particularly playful sub-adult female (Nora); from these observations 55 cases of 15 types of gesture-like actions were recorded:
Arm shake (1), Arm swing (6), Dangle (11), Gallop (1), Hand shake (1), Head nod (3), Head stand (7), Object in mouth (2), Object move (3), Object shake (7), Roll over (2), Slap object (1), Stomp (2), Stomp 2-feet (2), Water splash (6).

There were no clear variations between the physical form of these actions and the gesture-types observed in *social play*; instead it was only in the absence of accompanying measure of intentional behaviour and any potential recipient that these could be distinguished from cases of gestural communication.

Was there any evidence for triadic or collaborative play?

Some of the most interesting descriptions of the use of gesture in great ape play involve triadic and collaborative play in captive gorillas (Tanner and Byrne, 2010) and bonobos (Pika and Zuberbühler, 2008); however, to date there have been no similar descriptions in either the chimpanzee literature, or in the literature from wild populations of any great ape.

Although objects were regularly employed in individual solitary play, their use in social play was rarely observed. When this did occur it was usually in the form of tug of war play or in a chase for possession; however, objects were rarely exchanged more than once and there were no examples of gaze or gesture being used to draw attention to the object. Instead the objects appeared to form a part of the play initiation rather than the play itself, and as such there was little evidence for any collaborative or triadic play. Two typical cases are described below.

4th Decemeber 2008. Kasigwa (juvenile male), Zak (juvenile male), Night (juvenile female), Kutu (adult female – mother of Kasigwa)

A large group of chimpanzees are feeding on the fruit of *Desplatsia dewevrei*, these large green fruits have a tough woody outer layer: particularly difficult for young chimpanzees to bite through; so while the adults feed, the younger individuals play with them on the ground. Kasigwa and Zak wrestle with a fruit, Night steals it from them but they continue to play alone and ignore her. She swings over them while holding the fruit and they grab at her, play starts but it doesn't appear to incorporate the fruit in anyway. This play session is characterised by competition to possess the object, but only as an individual goal rather than any shared play. At one stage Kutu (Kasigwa's mother) approaches, takes the fruit and starts to feed on it, but the juveniles continue to wrestle with this event apparently unnoticed. Once she drops it Night takes it back and starts to feed now that it has been opened up, Zak also finds an opened one and starts to feed on a branch a few meters up. At one stage he drops the fruit, Night approaches to look at it, but then climbs up and they play, it is not clear whether or not dropping the fruit was intended to draw Night's attention.

14th July 2009. Karibu (infant female), Klauce (infant male) and Kumi (juvenile female, sister to Klauce)

Karibu knocks a large (hand sized) moth from a branch and starts to play with it on the ground trying to pick it up but appears nervous of its flapping wings. Klauce approaches and starts to try and touch it, he steals it and runs away with his arm stretched behind him, Karibu chases, but when play starts the object is forgotten. Later on Kumi plays with the moth in front of Klauce; he tries to grab at it, but both individuals appear to be motivated by a desire for the object rather than any joint play incorporating it.

A more commonly observed use of objects in social play was the 'Object in mouth' gesture. Here leaves or a stick would be placed in the mouth, occasionally where these were torn off this would produce an audible sound similar to leaf clipping. The signaller would then look over and wait for a response, or would approach slowly until the recipient responded, usually with chasing play. Critically however, the object would usually be dropped and apparently forgotten once play started, the object was a part of the initial gestural communication but not the subsequent play.

In only 2 of the 24 cases of 'object in mouth' gesture use was the object used in any subsequent play:

1. Klauce (infant male) approaches Karibu (infant female) with a stick in his mouth, she takes it and places it in her mouth, after which they play.
2. After Rafia (infant female) uses a stick in an 'object in mouth' gesture, as play starts she and the recipient Faida (infant female) have a brief tug of war over it.

In one interesting example the recipient of an object in mouth gesture responds with an object in mouth gesture of his own. In this case one of the objects is transferred to the hand when play starts but again the play was not focused around the objects.

These findings show no evidence for the use of objects in triadic or collaborative play amongst wild chimpanzees. This variation from the reports concerning bonobos and gorillas may reflect either a species difference, or suggests that triadic interactions are an effect of the captive environment.

7.3.7 The use of gesture in contexts that may promote the use of silent communication.

Consortship

There was extensive use of gesture in *consortship*, with over 412 cases from only 4 consortships. This context alone accounted for over 60% of all adult male gesture use. Given this prolific use in such an interesting and rarely observed context I have devoted the following chapter (8) to a detailed analysis of behaviour and gestural communication in *consortship.*

Boundary and Hunting Patrols

In contrast to *consortship*, there was almost no use of gesture while *patrolling*. While very little *patrolling* was observed (three boundary patrols and four hunting patrols), only four cases of gesture were recorded during any of them. Two of these were requests for affiliation, one a request from an infant to climb-on the mother and be carried, and one a request from a juvenile for play to start. As expected, there were no vocalisations whilst on patrol, and all non-communicative behaviour was notably quiet: to the extent that chimpanzees would turn and stare at even small noises made by stumbling researchers. This suggests that there was a strong selective pressure towards silent behaviour, but that this did not promote the use of silent gestural communication.

Hunting was observed more frequently than actual patrols, predominantly because hunting groups were usually located by the distinctive barks produced after the chase had begun. At Sonso the main prey food are the Black and White Colobus monkeys (*Colobus guereza*). Young colobus are chased through the upper canopy by younger sub-adult and adult males (and occasionally females); here they are occasionally caught, but more frequently knocked to the ground where the dominant older adult males collect and kill them. Despite this apparent division in activities I observed no evidence for the co-ordinated hunting behaviour described at other sites. Adult colobus are sometimes cornered following a slip or fall but even large parties of adult chimpanzees seem extremely wary of them. On one occasion a badly injured adult male colobus was surrounded by 8 chimpanzees, but still held them off and eventually broke through the circle and limped away. The chimpanzees gave a very half-hearted chase, but effectively let this large individual go in favour of a very young much smaller juvenile. On another occasion I was treated to the rather comical spectacle of a large sub-adult chimpanzee trying to pull an injured adult colobus along by its tail, but apparently too afraid to get close enough to kill it. Once an individual was killed the carcass was usually monopolized by the most dominant individual in the group, and other individuals would then beg for scraps.

7.3.8 Gesture use while begging for food

Although there was no use of gesture during hunting, there was extensive use of gestural communication during the period of meat eating following a successful hunt. Of the large number of gestures recorded in the feeding context (419 cases), 63.5% (266 cases) were produced while begging for desirable objects, the majority of these while begging for meat (204 gestures within 110 G-clauses). An individual with a large portion of carcass could take hours to consume the meat, and even once apparently sated (sitting resting with no feeding for periods of >15min), the meat was very closely guarded.

Begging for meat did not represent a particularly effective strategy with only 12 of the 110 G-clauses (10.9%) successful in procuring meat for the signaller. Despite, or perhaps because of this, individuals begging for meat were extremely persistent, stringing together up to 12 G-clauses in long G-sentences (range 1-12, median =1).

After begging, the most commonly recorded functions in the feeding context were: ‘move away’ and ‘move closer’, both equally abundant (54 cases, 12.9% in each case). Gestures with the function ‘move away’ were usually employed to discourage over-active begging. Gestures with the function ‘move-closer’ were produced by mothers towards their offspring or vice versa (1 exception from a sub-adult female to an infant male), during nursing and while feeding on the decaying pith of raphia palms. Raphia pith is reached through a small hole in the base of the dead tree around which there was often some jostling for access and mothers were seen encouraging their offspring to approach the hole.

Was meat used in social bartering?

Females with oestrus swelling were regularly observed to direct ‘present-sexual’ gestures towards males with meat; this usually resulted in inspection behaviour from the male and on several occasions copulation, following which the female was usually permitted to feed from the carcass (although this did not necessarily include being allowed to handle or remove the meat).

The alpha male was repeatedly observed to share large portions of the carcass with the beta male Zefa. One on occasion he was observed to tear off a large piece of carcass and give this to the very low ranking male Tinka. Other cases of true ‘giving’, rather than the more common ‘tolerated pilfering’, were only observed between mothers and their offspring.

7.4 Discussion

Gestural communication was employed in almost all contexts in wild chimpanzee life from *feeding* to *consortship* and *grooming* to *play*; only the contexts of *patrolling* and *resting* were effectively free from gestural communication. As in captivity, *play* represents the dominant context for gesture use in wild chimpanzees. It accounted for almost half of all active gesture footage, and almost 5-times the number of gesture cases of the next most prolific context, *grooming*. Although the large number of cases and the size of the repertoire are sampling artefacts resulting from the large quantity of gesturing time, the sheer quantity of gesturing time is itself revealing. When filming, it was rare to have to chose between two cases of gestural communication; thus, the fact that almost 50% of all gesturing time was recorded in *play* is a fair representation of *play* as the dominant context for gestural communication in wild chimpanzees. *Play* remains the dominant context for the use of gestural communication from infancy up to young adulthood; only in maturity (>25years) was it overtaken by gesturing in feeding, grooming and travel. The dominance of *play* as a context for gestural communication even in sub-adult and young-adult chimpanzees is a striking reflection on the importance of play in chimpanzee behaviour.

While Sonso chimpanzees did not vary the flexibility of their gesturing between contexts in terms of the number of functions for which gestural communication was used, I did find differences in the mean number of gestures per function, and a similar trend in the mean number of functions per gesture. On both of these measures *play* appears to be particularly flexible, employing a broad spread of gesture types towards a large range of functions. Gestures in *play* had the second most functions per gesture type of any context, and conversely the most gesture types per function. Interestingly it may be this high level of flexibility and the use of the full range of the repertoire that has contributed to the perception of *play* as having the 'largest' repertoire of gestures. Within a short-term study, the regular use of a broader range of gestures in *play* would lead observers to report a larger repertoire than that of a context such as *grooming*, where the majority of gesture use is accounted for by three extremely prevalent gesture-types.

After play the main contexts of gesture use were *feeding* (predominantly begging) and *grooming*. The distribution varies slightly across age groups, however *play* remained the primary context for gesture use across immature age groups, and was co-dominant with *grooming* in younger adults. Only in mature adults was it surpassed by the use of gesture in *feeding, grooming* and *travelling*. When adult males were considered in isolation *consortship* represented the dominant context for gesture use (see Chapter 8).

Studies of gesturing in captive gorillas report the frequent use of gesture like actions in non-communicative solitary play, these included the use of idiosyncratic forms that were not seen in communicative contexts (Tanner, 1998, Genty et al., 2009). In contrast, while young Sonso chimpanzees employed gesture like actions during bouts of *solitary play*, these were not common, and no new actions were observed in this context. Thus, the extensive use of 'gestures' in a non-communicative context may be either a feature of gorilla behaviour, or, perhaps more likely, an effect of the captive environment. In small captive groups there may be limited opportunities to interact with peers, and this may promote a richer repertoire of solitary play behaviour.

Triadic or Collaborative Play

I found no evidence for cases of triadic or collaborative play in object related social play. While objects such as leaves, twigs and fruit were regularly incorporated into play-start communications they appeared only to be of relevance to the communication itself, and were normally discarded once play commenced. These were quite different to the lengthy bouts of object exchange described in gorilla play, where individuals went as far as to apparently 'handicap' themselves to encourage younger partners (Tanner and Byrne, 2010). Nishida describes how young chimpanzees at Mahale not only use objects as 'tools for the solicitation of play ("play start"), but they also mock-compete for the possession of the item' (Nishida, 2004). However, this is the only mention of the behaviour, and does not necessarily imply any triadic or collaborative play – Sonso chimpanzees were observed to wrestle over Desplatsia fruit but with none of the hallmarks of collaboration described in the captive gorilla or bonobo groups (Tanner and Byrne, 2010, Pika and Zuberbühler, 2008).

Tomsello describes gestural communication as being used for 'evolutionarily less urgent' functions (Tomasello and Call, 2007); however, it is difficult to imagine which evolutionarily urgent functions would be available to captive chimpanzees. In contrast, there are several contexts experienced by wild chimpanzees that are associated with a high risk of injury or death. Hunting, intercommunity encounters, boundary patrolling, and consortships are all risky activities and in all of these cases there is a very strong selective pressure on limiting the spread of information. In a dense rainforest environment gestures, particularly silent ones, represent an extremely discreet means of communication.

Consortships are rare at Sonso; however, I was extremely lucky in being present for four events and observed extensive use of gestural communication by adult males initiating consortship. These observations are described in detail in Chapter 8. In contrast, patrolling behaviour, while also rare, was remarkable for its near total absence of any communication, gestural or otherwise. The group's behaviour was consistent with a strong desire to limit any noise; however this did not result in the promotion of gestural communication.

Patrolling behaviour

Patrolling behaviour was itself very rarely observed at Sonso; this may be due to the difficulty of observing what is an inherently silent and discreet behaviour, alternatively, the behaviour itself may be actually impeded by a human observer's presence. Despite our best efforts at stealth, researchers and to a lesser extent field-assistants are still in chimpanzee terms a noisy and at times unwelcome addition to the group or party. With hunting behaviour, the greatest risk is that the hunt fails and the community have to revert to a less desirable food source; however, in encounters with other chimpanzee communities, violence to the point of lethal aggression is a very real risk (Goodall, 1986, Boesch, 2009). On one hand we would appear to confer an advantage to the Sonso community, as only they are habituated to our presence, our being there at the moment when two communities meet is usually sufficient to ensure that the other community retreats. However, we are not always there, and there is evidence to suggest that chimpanzee inter-group encounters do not happen in isolation but build sequentially with raids back and forth (Boesch, 2009). On balance, our presence may increase the risk sufficiently that it's not worth pursuing boundary patrols when we're around. In consortship behaviour a considerable amount of energy goes into the early stage of encouraging the female away from the group and, as the risk of lethal aggression is less than in inter-group encounters, it may be worth continuing to pursue the behaviour with observing researchers in tow.

Another significant contribution to the absence of boundary-patrolling behaviour observations at Sonso may have been the small number of community males, combined with an apparently weak alpha male. Shortly before observation started the alpha male Duane, who had been in place for over 10-years, was usurped by Nick, a strong but very inexperienced young male in the community. Duane was considered by long-term researchers to be a reliable leader in whom the group displayed a lot of confidence; he was a large and powerful individual who had cultivated strong social bonds amongst both males and females. Nick, while physically capable of dominating other males individually, had few strong social allies and in fact allowed the usurped Duane to remain in the beta male position. Nick appeared inexperienced and socially unpredictable, even to the knowledgeable field assistants. He was observed on several occasions to lead the group in circles without apparent purpose until another individual would move forward and 'lead' the group towards a feeding tree. At times he was ignored and even threatened by the adult females, and he had aggressively attacked and seriously injured several young sub-adult males while apparently ignoring socially threatening behaviour from more dominant males. In addition to an inexperienced alpha, the Sonso community has a very small number of large adult males: at the start of observation there were nine, five of which died in the course of the study; of the remaining four, two are under 20-years old. If any of the remaining males were killed or seriously injured while on a boundary patrol this would further reduce the community's ability to defend its territory. Towards the end of the observation time, the community to the north-east boundary had started to make regular incursions into Sonso territory on an almost monthly basis, occasionally reaching even core areas. Although observations were very brief, this community appears to contain a large number of mature adult males (in one encounter 10 were counted); and on several occasions Nick ran away, leaving females and young juveniles at the front of the aggression. The current absence of boundary patrolling may represent unwillingness on the part of the group to take part in an extremely risky behaviour with such an apparently inexperienced leader.

However, even in the limited boundary-patrol behaviour observed there was no evidence for the use of any communication gestural or vocal. This reflects the findings in the Ngogo community, where despite regular observation of boundary patrols, little gestural communication has been observed in this context (Pika 2009, pers. comm.). This absence of communication while patrolling was also observed on hunting-patrols, where no communication was observed during the silent initial patrol; and no gestural communication during the subsequent chase and attack behaviours, although at this point vocalizations were prevalent. Given the speed and fluidity of the chase environment, and the fact that they usually occur in the dense upper canopy where visibility is limited at best, it is unlikely that gestural communication would prove an effective strategy at this stage.

One possible explanation for the absence of gestural communication in patrolling is that even silent gestures may be conspicuous to potential prey or a neighbouring group. While the movement of an individual gesture is unlikely to stand out amongst the movements of the chimpanzee party as it patrols, one factor I had not taken into account is the extreme difficulty of making any physical movement in the dense secondary forest environment without causing some degree of noise. Although an arm-swing or hand-shake has no intentionally audible component, they can easily connect with a low branch or stir through a pile of dried leaves. Potential noise from locomotion is an unavoidable risk in patrolling; however, the risk of accidental noise while gesturing may outweigh any benefits offered by the gestural communication.

Despite the apparent absence of communication while patrolling, the group appeared to move in a coordinated purposeful manner. Individuals within the patrol would pause, move position up and down the line; and the group as a whole would stop or turn in a new direction. Their behaviour at the time was reminiscent of watching a close-knit family, where their detailed knowledge of one another's behaviour results in a smoothly choreographed interaction without any obvious communication. This bears similarities to the co-regulated 'dance' of communication described by King (King, 2004); and supports the finding of Menzel (1973), who in a study leadership and communication in young captive chimpanzees found little evidence of clear signalling behaviour during co-ordinated travel, and instead argued that 'visual orientation and the locomotor postures and movements of the 'animal as a whole' contain sufficient information' (Menzel, 1973).

A more clear use of gestural communication was found in the extensive use of gesture during the meat eating following a successful hunt. The persistence in begging for the tiniest scraps of bone and fur appears to be surprising given the almost negligible nutrition benefit these must represent. The only other context where such long G-sentences were produced was *consortship* (and one case in *play*).

The sharing of large portions of meat by the alpha male with the beta male, Zefa, could be explained as an attempt to strengthen the social bond between them. However, there is an alternative possibility that would also explain the case in which he very unusually shared a large piece of meat with Tinka, who as a low-ranking and badly disabled individual was incapable of providing any significant support in future social interactions. In the case where only one individual within the group has meat, they are subjected to a constant barrage of begging gestures from other individuals, sometimes from up to eight individuals at a time. The individual holding the meat must remain on guard for individuals trying to steal the meat, frequently having to swat away over exuberant infants and more aggressively chase older individuals trying to pilfer discreetly. When two or more individuals have meat, the majority of begging tends to be directed towards the lowest-ranked individual. On the occasion where Nick shared with Tinka, a large party of very persistent adult female and juvenile beggars had surrounded him; he had moved several times in an apparent attempt to evade this clearly unwanted attention, but was unsuccessful. At this point he tore off a large piece of meat and gave it to Tinka, who was then immediately surrounded by the group leaving Nick to feed on his portion in peace. A similar effect was observed on the occasions where he shared with Zefa, while the individual sharing must ‘lose’ a portion of the meat, they gain the ability to feed completely (and in peace) on the remaining portion – a tactical trade-off.

7.4.1 Summary

Gestural communication was employed for a wide range of contexts in natural chimpanzee behaviour. As in captivity, *play* represented the dominant context for gesture use, and stood out as including the highly flexible use of gesture and as having the largest repertoire of gestures used on a regular basis. As in captive chimpanzee groups, there was no evidence for the use of gesture in triadic or collaborative play interactions.

There did appear to be a strong pressure towards silent behaviour when *patrolling*, however this did not promote the use of gestural communication. In contrast *consortship*, which was also hypothesised to promote silent behaviour, contained such large quantities of gestural communication that the following chapter has been devoted to a description of gesture use in this context. The variation in the use of gestural communication between the two contexts may be a result of a variation in the costs and benefits associated with the use of gesture. Even a silent gesture may produce an accidental noise; in consortship, discovery of the consorting pair by the other community males may lead to physical attack, but this is unlikely to lead to lethal aggression. In contrast when patrolling, the risk of discovery by a neighbouring community carries the very real risk of serious injury and possibly death. Furthermore it is possible that while there appeared to be no need for the use of gestural communication in order to successfully co-ordinate a patrol; a successful consortship may require the male to clearly communicate his intentions to the female. Gestural communication may then represent the optimum means by which this can be discreetly achieved.

Chapter 8. Consortships: the use of gesture towards an evolutionarily urgent function

'Primates also routinely communicate using manual and body gestures, mainly in close-range social contexts such as play, grooming, nursing and during sexual and agonistic encounters. These are in general less evolutionary urgent functions….' (Tomasello and Call, 2007, p.5).

8.1 Introduction

The quote above comes from Tomasello & Call's (2007) book detailing the extensive studies of great ape gesture in captivity. *Play* has repeatedly been described as the most prolific context for the use of gestural communication by captive great apes (chimpanzees: Tomasello et al., 1994, Liebal et al., 2004a; gorillas: Genty et al., 2009, Pika, 2007; bonobos: Pika et al., 2005b); and, as discussed in the previous chapter, is likewise the dominant context for the use of gestural communication in wild chimpanzees. However, it is not clear what, if any, contexts experienced by captive apes would require the communication of evolutionarily urgent functions. In contrast, a wild chimpanzee patrolling territorial boundaries, hunting, or initiating consortship behaviour, runs very real risks, up to and including their own death. In these situations they might be expected to employ communicative strategies that conserve these risks, by, for example, limiting messages to specific individuals. Unlike vocalizations, silent and contact gestures allow the signaller to communicate their intention without the risk of that message being overheard by other parties. In both boundary-patrolling and hunting the advantage is in restricting information transfer *outside* of the group, so that the risk of alerting a neighbouring community or potential prey is avoided. When initiating a consortship, an individual male aims to restrict sexual access to an individual female by escorting her away from the community, and must therefore avoiding notifying other males within the group of his intentions. Here the advantage is in restricting the information transfer *within* the group; although there may also be subsequent risks from outside the group once the pair leaves their own core-territory.

As shown in the previous chapter, there was no evidence within the Sonso community for the preferential use of gestural communication while engaged in boundary-patrol or hunting behaviour; however, gestural communication while on consortship represented the dominant context for gesture use by adult males. The inherently secret nature of consortship behaviour means that to date there has been very little empirical analysis of the way in which a consortship is initiated and the behaviour of the pair once they have moved away from the group. Here I take advantage of a recent cluster of observations in the Sonso community to discuss consortships and the role of gestural communication within them in more detail.

8.1.1 Chimpanzee sexual strategies

Chimpanzees live in stable, promiscuous, multi-male, multi-female communities; females emigrate from their natal group at around the time of sexual maturity, thus managing the costs of incest (although see also: Tutin, 1979, for observations on primary kin avoidance). As she approaches sexual maturity the female chimpanzee begins a regular cycle of oestrus that includes a dramatic swelling of the pink skin around her perineum. Tumescence is categorised in stages (at Sonso we define 5, from: 0=none to 4=maximum). Fertility, and the chance of conception, peaks during the peri-ovulatory period (POP), which occurs within one day of the end of maximal tumescence (Graham, 1979).

Early work in this field emphasised male sexual strategy (Tutin and McGrew, 1973, Tutin, 1979, Allen, 1981, Hasegawa and Hiraiwa-Hasegawa, 1983); thus sexual behaviour was defined in terms of male-male competition as either opportunistic (non-competitive mating, with free access to all males), or restrictive (access to the female is monopolised by a single male). These patterns were first distinguished at Gombe (Tutin, 1979), and have been consistently observed across sites (Mahale: Hasegawa and Hiraiwa-Hasegawa, 1983; Taï: Boesch and Boesch-Achermann, 2000; Sonso: Reynolds, 2005 #467).

Within the category of restrictive mating, we can discriminate two patterns of behaviour: *possessiveness*: where sexual access to a female is monopolized by a single male while remaining within the group; and *consortship*: where a single male monopolizes sexual access by escorting a female away from the group (Tutin, 1979). At Gombe, Tutin found that consortships were associated with a high probability of reproductive success (Tutin, 1979), although a genetic analysis of the Taï community suggests that this may vary between males (Boesch and Boesch-Achermann, 2000).

More recently, work on sexual strategy has emphasised the role of female choice in determining paternity (Stumpf and Boesch, 2006, Pieta, 2008, Thompson et al., 2008, Boesch, 2009, Stumpf and Boesch, 2010). This is particularly true in the case of consortship behaviour: here, where the consorting male must avoid detection by other group males, even a brief scream from the female may be enough to bring other males to investigate, particularly if she is known to be in oestrus. Aggressive coercion by the male is often observed in the initial stages of consortship behaviour (Goodall, 1986); and this necessity, to overcome apparent reluctance on the part of the female, has been used to suggest that promiscuity represents a more favourable strategy for female chimpanzees (Muller et al., 2007). However, a recent study showed that aggressive male coercion did not act to decrease female resistance (Stumpf and Boesch, 2010); and Nishida (1997) describes females at Mahale responding with 'blunt refusal of male courtship.' Co-operation on the part of the female may then be critical to the success of consortship behaviour. Tutin observed that males who frequently engaged in grooming and sharing food with oestrus females while they were with the group were more likely to then be successful in leading females away from the group on consortship (Tutin, 1979); and Goodall describes the use of grooming in consortship to reduce the anxiety of a reluctant female, making her easier to lead away (Goodall, 1986).

While the overall proportion of restrictive mating appears to be similar across sites (Gombe: 27%, (Tutin, 1979); Mahale 6-27%, Sonso: 15.8%, Oliver (unpublished) cited in (Reynolds, 2005)), the frequency with which consortships are employed, and the social-rank of the males involved, appears to vary. At Gombe consortships were observed regularly: Goodall (1986, pg458) reports up to 36 per year (mean 14.3 per year over 18 years); Tutin reported 15 cases in a 16 month study, involving approximately 50% of adult males, particularly individuals of lower social rank (Tutin, 1979), and McGinnis observed 40 cases in 30 months, but with no clear effect of social rank (McGinnis, 1979). At Mahale the behaviour is considered extremely rare Nishida (1997) makes no mention of the behaviour in a specific study of adult male sexual behaviour, although he does mention 5 observations of the behaviour in a more general report on Mahale social structure (Nishida, 1979). More recently, 1 case was reported in a 2-year study, although the authors acknowledge that the inherent secrecy of the behaviour may lead to its frequency being under-reported (Hasegawa and Hiraiwa-Hasegawa, 1983). The frequency of consortship behaviour at Sonso appears to be similar to Mahale, 3 cases in 15 years, all high-ranking males (Reynolds, 2005). Interestingly, at Taï, where levels of consortship behaviour appear to be intermediate (30 consortships in 8 years, mean 3.8 per year, varied between 0-10 per year), all consorting males were individuals who, while not currently alpha-male, had achieved, or would achieve, alpha male status during their lifetime (Boesch and Boesch-Achermann, 2000).

This variation between sites and individuals may be understood if we consider behaviour not just in terms of its immediate outcome, but also cumulatively over the course of an individual's life. Male lifetime reproductive success is optimized by selecting strategies that, for him as an individual, maximise his chance of fertilization while minimising the cost in terms of energy expenditure and risk. Restrictive mating patterns are advantageous in reducing competition from other males but are associated with increased energy input and risk (Tutin, 1979). Males who display overt possessive sexual behaviour towards oestrus females, risk an aggressive response from other higher-ranked males within their community (McGinnis, 1979). This response may vary depending on the time to the female's POP: in the early stages of oestrus when fertilizations is unlikely, high-ranking males are relatively tolerant of copulations by lower-ranking individuals, but become increasingly possessive as POP approaches (Deschner et al., 2004).

In the case of a possessive sexual strategy, where the pair remains within the group, the risk is limited to aggression from within community males; so that effectively only the alpha, as the largest, most dominant male in the group can usually restrict access to an oestrus female in this manner. For lower-ranking individuals to maintain possession of a female they must isolate her from their competitors by engaging in consortship behaviour.

Consorting males must invest time and energy in removing the female from the group. Lower-ranking individuals may have to initiate a consortship several days before POP, when the highly desirable female is likely to be surrounded by other more dominant would-be suitors. This may require days, or even weeks, of investment; and, once initiated, it is critical that the female be kept away from the group until POP has passed or the investment is wasted. In addition to the time and energy invested, consortship behaviour is also associated with increased risk; in this case for both the male and female. The consorting male risks aggressive attack from males within the community should they discover his attempt to remove the female, or when he tries to rejoin the group after the absence while on consortship (Riss, unpublished cited in: Tutin, 1979). This doesn't necessarily imply any intentional punishment for having monopolized the female. A consorting male may be absent from the group for days or even weeks, during this period previously lower-ranking individuals have the opportunity to move up into the absent male's social position, potentially forming new alliances and presenting a challenge on the his return. Both the male and female risk attack should they encounter another community, especially while isolated from the potential support of their own. Tutin cites intercommunity encounters as the highest source of risk for individuals already on consortship (Tutin, 1979). In attempting to avoid detection by their own group, consorting pairs are more likely to occupy peripheral areas of the community territory, increasing their chances of encountering individuals from neighbouring groups. For the male this may present a direct risk to his life as intercommunity encounters can result in lethal aggression (Goodall, 1986); females, particularly those in oestrus, are less likely to be killed, but may be aggressively herded into the neighbours community (Boesch, 2009). Here they risk attack by the community females (Townsend et al., 2007), and there is great risk to any dependent offspring travelling with them who may be killed (Suzuki, 1971, Reynolds, 2005, Townsend et al., 2007).

Any increase in investment (in terms of risk and energy expenditure) must be balanced by an increased payoff in order to make a restrictive sexual strategy worthwhile. Where the return on a restrictive sexual strategy varies between males there will be a differential uptake of the associated strategies. For example: the current alpha male of a community may be capable of maintaining exclusive sexual access to a female while remaining within the group, and is unlikely to be seriously challenged by other community males. Thus for him the within-community possessive strategy is a relatively medium-energy, low-risk strategy with a benefit of increased reproductive success. He would gain no additional pay-off by employing the increased-energy, high-risk consortship strategy (Tutin, 1979). A very low-ranking male may simply not be able to afford the investment of energy necessary to remove a female from the group, particularly if he must do so in advance of POP and keep her away for several days. Even if he could achieve this, the already high risk represented by an intercommunity encounter is much higher for a smaller, weaker male. Bearing in mind that the strategy may very well hinge on the co-operation of the female, low-ranking males may be better to remain within the community and employ an opportunistic strategy. Thus consortships represent an optimal strategy only for males who, while not currently alpha, are large dominant individuals; hence the finding at Taï that only future- or ex-alpha males engage in consortship behaviour (Boesch and Boesch-Achermann, 2000).

Aside from rank, payoff in sexual strategies may also vary with demographic factors such as instability in the male social hierarchy, which affects the likelihood of aggression or support from other community males; or even the male to female ratio in the community. At Mahale a decrease in available oestrus females coincided with an increase in restrictive mating patterns, this was interpreted as a response to the increased payoff of successfully monopolizing any one female (Hasegawa and Hiraiwa-Hasegawa, 1983).

8.1.2 The potential role of gestural communication when on consortship

Thus, the total return on investment in a consortship strategy depends on a number of factors including: time, energy, female co-operation, male-male competition and risk associated with intercommunity encounters. However, once the decision has been made to engage in consortship behaviour, in all cases there is therefore significant pressure on a consorting male to communicate his initial intention to the female in a discreet manner, and for both the male and female to avoid detection once on consortship. In this case gestural communication may represent an effective strategy. Here I am able to report on a recent peak in consortship behaviour within the Sonso community, and the high levels of gestural communication employed during these events.

8.2 Specific method

8.2.1 Procedure

Observations of consortship behaviour were recorded on an ad hoc basis during data collection for the ongoing project into chimpanzee gestural communication. All examples of consortship behaviour (as defined below) were recorded on miniDV tape using a Sony Handycam (DCR–HC-55).

8.2.2 Long-term data collection

In addition to direct observations I interrogated the 6 highly experienced, chimpanzee field-assistants (2 of whom have worked with the Sonso community for almost 20-years), in order to establish a more long-term record of consortship frequency. I also consulted the long-term events book, kept on site for the purpose of collating unusual or rare observations.

8.2.3 Defining sexual behaviour

I follow Tutin (1979), in assigning sexual behaviour as either opportunistic or restrictive. *Opportunistic* mating is defined as non-competitive sexual behaviour, where any male within the group may mate with a receptive female. *Restrictive* mating is defined as a situation where a male behaves in a manner that prevents other males from mating with a receptive female. Restrictive mating includes both: *possessiveness,* 'where a male established a special short-term relationship with a receptive female, and may prevent lower-ranking males from copulating with her'; and *consortship*, 'where a single adult male escorts a female away from the group and maintains exclusive copulatory access to her' (Tutin, 1979).

8.2.4 Specific terminology

Sexual swelling (hereafter swelling): The distinctive external swelling of the skin around the female genitalia associated with the period of peak fertility (Graham, 1979).

Oestrus female: A sub-adult or adult female chimpanzee that has commenced the regular cycle of sexual swelling to maximum tumescence.

8.2.5 Long and short-distance audible gestures.

In rainforests, the complicated acoustic environment leads to increased degradation and attenuation of acoustic signals (Wiley, 1991). Mitani et al. (Mitani et al., 1999) found that the long distance pant-hoot calls of different chimpanzee populations varied in a manner that maximized signal transmission with variation in the habitat acoustics. In dense, secondary rainforest such as that found at Budongo, the degradation of acoustic signals would be particularly high. Studies of chimpanzee vocal behaviour typically distinguish between shot and long-distance chimpanzee vocal behaviour (e.g. pant-grunt vs pant-hoot) (Van Lawick-Goodall, 1972, Crockford and Boesch, 2005), and I suggest that it is possible to distinguish audible gestures in the same way.

Although clearly audible, ‘object move’ and ‘object shake’ gestures appear to be quite limited in terms of their audible range. For example: when the highly experienced head field-assistant (20-years at Sonso) was trying to locate a consorting male who my field assistant and I observed to repeatedly produce ‘object shake’ gestures, he failed to do so until under 100m away, despite being aware of the pair’s approximate location (through contact with us). In addition to the short-distance over which they are heard, the audible component of these gestures comes from the rattling of leaves and foliage, something that can be caused by other large forest mammals such as bush-pigs, bush-buck (or field-researchers!); and as such they are not immediately acoustically identifiable as chimpanzee gestural communication.

In contrast certain gestures are audible over much greater distances, and are only associated with chimpanzee communication. These are the ‘drum object’ or ‘stomp on object’ gestures. When the object in question is one of the large tree buttresses regularly found throughout the forest and regularly employed by the chimpanzees for drumming and stomping actions, the gestures produce a distinctive deep boom that is audible to humans over 500m away. In many cases, individual idiosyncrasies allow us to identify not only the location but also the identity of the drumming chimpanzee: a highly effective long-distance signal. Several observations of solitary male chimpanzees repeatedly drumming and then waiting until there is a response from a party of chimpanzees before moving directly to them, suggests that the chimpanzees themselves are aware of the long-distance nature of these communications. Furthermore observations of the immediate change in behaviour when the drum of an individual from a neighbouring group is heard, strongly suggest that the chimpanzees are also capable of distinguishing individuals in this manner: an observation supported by similar reports from chimpanzees in the Tai forest (Boesch and Boesch-Achermann, 2000).

8.2.6 Levels of physical aggression

Physical attacks can be categorised according to the intensity of the physical violence inflicted. Goodall (1986) defines three categories, varying from mild to violent attack, with the duration of the attack critical to differentiating between level 2 and 3. As the duration of aggression events is not included in the long-term site records I define only 2 levels:

> Level 1: attack with low intensity or brief physical contact including hits, kicks or unspecified contact aggression. Corresponds to Goodall’s Level 1.
>
> Level 2: attack with high intensity or sustained physical contact including beating, biting, and anything resulting in physical injury. Corresponds to Goodall’s level 2 and 3.

8.2.7 Specific analyses

Data were converted to means for each individual, to remove any effect of pseudo-replication from the use of focal behaviour sampling. Only individual means calculated from 5 or more separate cases were included in any analyses. Analyses were carried out in SPSS v11, with α=0.05 required for significance. Means are given ± Standard Deviation, throughout.

8.3 Results Part 1: Consortship behaviour in Sonso chimpanzees

Opportunistic mating was regularly observed from adult, sub-adult, and juvenile Sonso males; however, restrictive mating behaviours were observed less frequently and only from adult males. Consortship behaviour was rarely observed, with only 10 events reported in the past 10-years (see Table 20).

The majority of these (7/10), by the ex-alpha male Duane (now deceased). 3 other cases were recorded from the 3 adult males: Black (ex-beta, now deceased), Maani (ex-beta, now deceased) and Nick (current-alpha male).Although neither reached alpha-male rank, both Black and Maani challenged (unsuccessfully) for the position on at least one occasion.

Table 20: Consortships reported during 1998-2008. The social rank of the male at the time of the consort, along with the highest rank that they achieved during their lifetime. The name of the female taken on consortship and the year in which the event occurred. Notification * represents an event reported by field-assistants for period 1998-2004 but with no consensus on date

	Rank at time	**Highest lifetime rank**	**Female**	**Year**
Nick	1	1	Nambi	2008
Duane	2	1	Zimba	2008
Duane	2	1	Zimba	2008
Duane	2	1	Lola	2008
Duane	1	1	Gonza	2004
Duane	1	1	Nambi	2002
Duane	1	1	Nambi	2002
Black	3	2	Kigere	2002/03
Duane	1	1	Mukwano	*
Maani	(2-4)*	2	Strange female	*

8.3.1 The distribution of consortship behaviour

Consortship frequency was not evenly distributed: 3 of the 4 consortships recorded in 2008 occurred within a 1-month period from mid January to mid February 2008. These 3 consortships were all initiated by the beta male Duane (1 failed with Lola and 2 successful with Zimba). The 4th (successful) event was initiated in October 2008 by the alpha male Nick (with Nambi). The last consortship event prior to these observations was reported in 2004, and prior to this there was another cluster of events around 2002.

8.3.2 The availability of oestrus females

In the 2-years prior to the study (Oct 05-Sept 07) the community contained 18 oestrus females (Flora, Gladys, Harriet, Janie, Kalema, Kewaya, Kigere, Kutu, Kwera, Lola, Melissa, Mukwano, Nambi, Ruhara, Sabrina, Sarine, Wilma, Zimba). No consortship behaviour was recorded during these 2-years. 11 of these females became pregnant or gave birth during this period, and were then in postpartum anoestrus for the duration of the study period.

During the 2-year study period (Oct 07-Aug 09) the community contained only 8 oestrus females (Juliet, Kigere, Kutu, Lola, Melissa, Nambi, Wilma, Zimba). However, Kutu became pregnant in November 2007 (gave birth in July 2008), Kigere became pregnant in February 2008 (gave birth October 2008), and so both were essentially anoestrus for the majority of the observation period. Of the remaining 6, Wilma (26-27years old, parous: single infant who died in 2001) cycled only irregularly and her prolonged period of barrenness suggests she may no longer be fertile. This left only 5 available oestrus adult females (Juliet, Lola, Melissa, Nambi and Zimba); 3 of these females were observed on consortships with Sonso males during this time.

8.3.3 The success of consortship strategy

5 females were impregnated during the study period: Kutu in November 2007 (gave birth in July 2008), Kigere in February 2008 (gave birth October 2008), Melissa in June 2008 (gave birth in January 2009); Zimba in August 2008 (gave birth in

March 2009) and Juliet in February 2009 (gave birth September 2009). None of these females were observed on consortship at, or near, the time of assumed fertilization.

8.3.4 The aggressive coercion of females on consortship

During the year 2008, a total of 331 aggression events were recorded in the Sonso community. 178 of these included physical contact: 116 level-1 minor attacks, and 63 more serious level-2 attacks. 25 of these level-2 attacks occurred during consortships (39.7% of level-2 attacks on 1.1% of observation days).

9 of the 25 adult Sonso females experienced a more serious level-2 attack during 2008. The majority (5/9) only experienced one or two of these level-2 attacks, however 4 females experienced higher levels (Janie: 3 cases; Melissa: 4 cases; Zimba: 14 cases (9 during consortships); Lola: 16 cases (16 during consortship)).

Lola experienced a total of 18 separate attacks while on consortship: 2 level-1, and 16 level-2 attacks that resulted in serious injuries. These attacks were particularly aggressive and prolonged: they included throwing her from trees from heights of over 15m and violent pounding and stamping on her body. The resulting injuries are thought to have contributed to her death 10 days later. See Appendix 3 for a complete description of the event.

Zimba experienced 9 level-2 attacks over the 2 consortships; these resulted in minor injuries and are summarized along with Lola's in Table 21. As the 2 attacks in the second consortship took place in heavy undergrowth it was not possible to film them; however, they have been categorised as level 2 because they resulted in physical injury (bite wounds). On 2 occasions, following a level-2 attack, Zimba succeeded in driving the attacking male Duane away. Nambi experienced only a single level-1 attack while on consortship, however as the consorting pair were lost after only 20min it is possible that further attacks went unrecorded.

Table 21: Details of level-2 type attacks experienced by females on consortship. The frequency, mean duration and resulting injuries of level-2 type aggressive attacks experience by the two females in the three consortship events.

Frequency level-2 attack			**Mean duration (range)**			**Resulting injuries**		
Lola	**Zimba 1st**	**Zimba 2nd**	**Lola**	**Zimba 1st**	**Zimba 2nd**	**Lola**	**Zimba 1st**	**Zimba 2nd**
16	7	2	13.9sec (4 - 90sec)	10.0sec (3 – 15sec)	No video data	Deep cuts to palm and swelling (>2”), blood in stool, pain standing or moving	Temporary discomfort moving and bite marks to head	Bite marks to back and abrasion to wrist

8.3.5 What female behaviour preceded physical attack?

The behaviour of the female immediately preceding a level-2 physical attack by the male is described in Table 22. This data does not include the 2 attacks during the second consortship with Zimba as the behaviour at the time was obscured by undergrowth.

Table 22: Female behaviour that preceded level-2 attack. Category and frequency of female behaviour that preceded a level-2 aggressive attack by the male while on consortship

Female behaviour	Lola	Zimba	**Total**
Failure to respond to male’s communication	15	2	17
Vocal communication with other individuals	0	3	3
Attempt to move away from male	1	2	3
Unclear	2	0	2

The majority of the attacks (17/25) followed a failure by the female to respond to the male’s communication. The function of the gestural communications produced in consortship is discussed in detail below but they were almost universally requests by the male that the female ‘follow’ him.

8.3.6 Non-aggressive coercion

Duane was the only male observed to consistently engage in consortship behaviour in the Sonso community (7 of the 10 recorded cases). He was described by the long-term field assistants at the site as being remarkable for the strength of his social bonds with adult females. He groomed the females on all three consortships but to a varying degree.

In his consortship with Lola he aggressively coerced her from the start, and grooming behaviour was negligible, with only two brief bouts, both under 10-seconds. During the first consortship with Zimba he was discovered grooming her in her sleeping nest before she had had time to climb down in the morning. He groomed her briefly once when she did climb down, and then following a period of more aggressive coercion he started grooming her for longer periods (>5min). On the second consortship, the beginning was again marked by a brief period of aggressive coercion followed by long bouts of grooming once they were away from the group. These grooming bouts lasted >10min, and he seemed to be paying particular attention to the back wounds that he had inflicted in the preceding attack.

8.3.7 Summary of consortship behaviour in Sonso chimpanzees.

Consortship behaviour is relatively rare at Sonso; it is usually initiated by large dominant males, and may be associated with periods when access to oestrus females becomes restricted. Consortships do not appear to represent a particularly successful sexual strategy for Sonso males. Males employed both aggressive and non-aggressive coercion; these tended to occur at different stages in the consortship process. Aggressive coercion resulted in serious injury to at least one of the females, and was usually preceded by the repeated refusal of the female to follow the male.

8.4 Results part 2: Gestural communication in the consortship context

As discussed in earlier chapters, the 266 days of observation between October 2007 and August 2009 produced a total 120 hours of footage, which on analysis contained 4346 intentional gestures. This footage included over 2 hours of behaviour recorded from the 4 consortships (total 2h24m37s: includes 17m30s kindly donated by other researchers); which provided 412 intentional gestures, contained within 286 G-clauses.

8.4.1 The levels of gesture use during consortships

Consortships were recorded on only 4 of the 266 days of observation (1.50%) but accounted for 412 of the 4397 gestures recorded (9.39%). Critically, gestures from consortships accounted for 62.18% of all adult male gesture use recorded during the study (393 of 632 gestures); with males producing almost all of the gestures used in this context (n=412, males: 393, females: 19).

8.4.2 The consortship repertoire of gestures

The complete Sonso gestural repertoire consists of 66 types of gesture, used flexibly across up to 10 different contexts (range 1-10, median 2, see Chapter 7 for details). 21 of these gesture types were recorded during *consortship*, 17 from males and only 4 gestures from females (predominantly the *Present-sexual* gesture, 16 of the 19 cases of female gesture). The young female Lola produced 15 of the 19 cases of female gesture, 13 of which were *Present-sexual* gestures.

The most frequently used gestures were the object related gestures: *Object shake* (222 cases), and *Object move* (41 cases); which together accounted for over 60% of all gestural communication in this context. I observed no consortship specific gestures; however the rare *Rump-rub* gestures were highly associated with the consortship context (26 of 29 observations) and are discussed in detail.

Rump-rub gestures

I observed 2 forms of Rump-rub gesture: *Rump-rub genital* and *Rump-rub body*. In these gestures the male signaller backs-up to the recipient and pushes his rump against either the genitals (*Rump-rub genital,* e.g. the swelling of an oestrus female) or torso of the recipient (*Rump-rub body*); this was accompanied by a small but rapid, vertical up-and-down, rubbing motion. *Rump-rubs* were often accompanied by a soft-pant vocalisation.

These rare gestures were recorded 29 times in gestural communications over the course of the study; 26 of these by a male during consort behaviour (*Rump-rub body*: 19/21 during consortship; *Rump-rub genital*: 7/8 during consortship). In other contexts (2 agonistic, 1 unknown) the gesture was used by a less dominant male to a more dominant male when apparently seeking affiliation or reassurance; however in the consortship context a dominant male signaller directed the gesture to a lower-ranking female recipient.

8.4.4 Gesture as discreet communication?

Perhaps surprisingly, audible gestures were extremely prevalent in consortship communications (334/412, 81.1%); even silent and contact gestures were accompanied by audible behaviours in a third of cases (26/78). Within male gestural communication 85.0% of gestures were audible gesture types (334/393, Duane: 321/379; Nick: 13/14); and 91.6% were either audible or accompanied by other audible behaviour (360/393, Duane: 347/379, Nick: 13/14). This actually represented an increase in the proportional use of audible gestures over use in other contexts, by both males (*Duane* consortship audible=321/379, non-consortship audible =7/17, Chi-square 2-tailed χ^2=21.67, df=1, p<0.0001. *Nick* consortship audible=13/14, non-consortship audible n=59/106; Chi-square 2-tailed χ^2=4.60, df=1, p=0.0319).

The prevalence of audible gestures was due to the prolific use of the object-shake and object-move gestures described above; critically these are all short-distance audible gestures. In other contexts short-distance audible gestures (object shake and object move) were used in the same G-sentence as long-distance audible gestures (drum object or multiple stomp on object) in a mean 8.5% of cases, see Table 23.

Table 23: Association of short and long-distance audible gestures. The frequency with which long-distance audible gestures (such as buttress drums) co-occur within the same gestural communication as short-distance audible gestures (such as object-shakes) in consortship behaviour and other contexts.

Short-distance audible gesture	n	Frequency co-occurrence with long-distance audible gesture	
		Other contexts	Consortship context
Object shake	327	11/201 (5.5%)	0/126
Object move	145	8/84 (9.5%)	0/29

However, despite the prevalence of the short-distance object-shake and move gestures in consortship communications, there were no cases of long-distance audible gestures during consortships (n=496, Chi-square 2-tailed: $\chi^2=14.06$, df=1, p=0.0002).

8.4.5 Vocalization during consortship

Male vocalization

Neither male produced any loud vocalization while on consortship. Duane was observed to produce soft-pant vocalizations in connection with the Rump-rub gesture described above. Nick was not observed to vocalize while on consortship.

Female vocalization

Lola and Zimba both produced loud vocalizations, such as screams, in the early stages of consortship; all of which were followed by an aggressive attack from Duane. Nambi was not observed to vocalize loudly when in consortship with Nick. On the first consortship between Duane and Zimba, a bout of screaming by Zimba resulted in the consorting pair being discovered by a group of males. On this occasion all of the newly arrived males were subordinate to the consorting male Duane and after a brief period of rest he escorted Zimba away again. The screaming from Lola is likely to have contributed to the eventual location of the pair by a party containing the alpha male, which resulted in the immediate termination of the consortship as Duane was chased away (but not attacked).

Zimba was frequently observed to produce a soft-bark immediately following a bout of gestural communication from Duane; she would then follow on shortly after. Interestingly this appeared to provide some satisfaction to Duane who would only resume gesturing if she continued to then make no further move towards him.

Vocalisation by others outside the consorting pair

On the first consortship between Duane and Zimba a neighbouring community was heard calling ahead; both individuals had been relatively relaxed at this stage, with Zimba following freely. Clearly nervous, Duane, who had been leading Zimba directly west towards the boundary of the Sonso territory, immediately turned due south away from the source of the calls, but still avoiding core Sonso territory.

8.4.6 The function of gestural communication in consortship

Function was measured at the level of the G-sentences and defined by the behavioural response that led to the end of the communication attempt (see Chapter 10 for a detailed discussion of function). Consortship communication included 127 separate bouts of communication (102 single G-clauses, and 25 G-sentences); 61 of which were successful and could therefore be used to defined function. Unsurprisingly, given the nature of consortship behaviour, the overwhelming majority of the gestural communications produced by both males had the apparent function that the female 'follow' him (Duane: 48/52 G-sentences, 92.3%; Nick: 5/6 G-sentences, 83.3%). Perhaps more surprisingly, only a very low number of G-sentences (total 2: Lola = 1 case; Duane = 1 case) were used for the function of acquiring 'sexual attention' (this function includes both inspection and copulation), see Table 24.

Table 24: Frequency of function of G-sentences within consortship behaviour. The frequency and percentage frequency of the functions of gestural communications in consortship behaviour.

Function	**Frequency: number of G-sentences (%)**
Affiliation	1 (1.7)
Direct attention	1 (1.7)
Follow	53 (88.3)
Move closer	1 (1.7)
Position	1 (1.7)
Sexual attention	2 (3.3)
Stop behaviour	1 (1.7)
Total	**60**

The function 'follow' was very rarely recorded outside of the consortship context, and never from adult males. During the study it was recorded in only 8 other G-sentences, all in the travelling context; and almost all (6/8), mother to offspring communications (1 case between brothers Zalu and Zed, 1 case between sub-adults Bahati and Hawa).

8.4.7 Response waiting in gestural communication on consortship

Response waiting is an indication of intentional communication and as such was already selected for within any analysis of intentional gesture; however, it is one of several criteria for intentionality and its distribution may vary within the data set (see Chapter 3 for details on general distribution).

Both adult males employed response waiting significantly more often following consortship communications as opposed to communication in other contexts (*Duane* response-waiting: consortship = 345/379, mean frequency =88.7%; other contexts: 5/17, mean frequency=29.4%, Chi-square 2-tailed χ^2=7.66, df=1, $p=0.0057$; *Nick* response-waiting: consortship =14/14, mean frequency =100.0%; other contexts =40/89, mean frequency=44.9%, Chi-square 2-tailed χ^2=14.70, df=1, $p=0.0001$).

8.4.8 Success of male communications in consortships

Figure 20 illustrates the variation in frequency of success of gestural communications *from* males within and outside of the consortship context, alongside the variation in frequency with which females provided a successful response *to* gestural communications within and outside of the consortship context. Alongside a total decrease in any level of success, there appears to be a large decrease in complete success, somewhat compensated for by an increase in partial success.

Full success

Duane experienced significantly lower success in consortship communication (successful G-clauses: consortship n= 229, mean frequency = 25.3%; other contexts n=16, mean frequency =75.0%. 2-tailed Fisher's exact test $p<0.0001$). There was no significant variation in the success of the alpha male Nick (successful G-clauses: consortship n=14, mean frequency = 42.9%; other contexts n=68, mean frequency = 58.8%. 2-tailed Fisher's exact test $p=0.377$.)

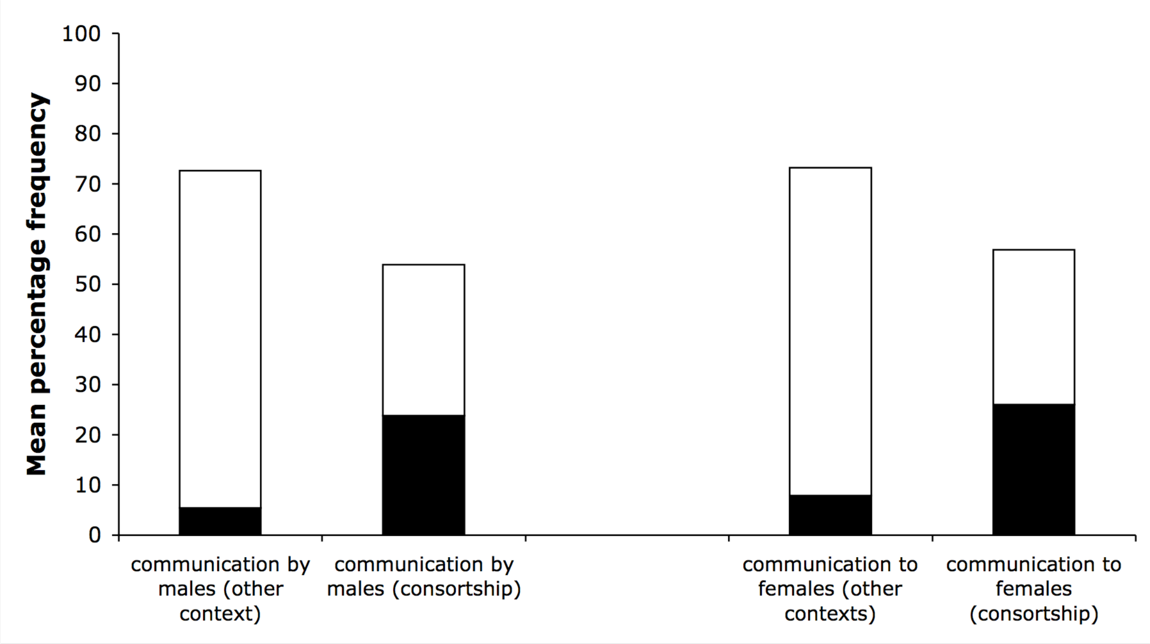


Figure 20: Variation in the frequency of success in communications *given* by males and *received* by females. The percentage of gestural communications produced by adult males that receive a successful or partially successful response is compared with the number of communications to which an adult female responds successfully or partially successfully in consortship behaviour and other contexts. Black bars represent partial successful communications; white bars represent completely successful communications.

Partial success

Again the alpha male Nick experienced no variation in partial success between consortship and other communications, however Duane experienced a significant increase in partially successful communication. (*Duane* partially successful G-clauses: consortship n= 229, mean frequency = 33.6%; other contexts n=16, mean frequency =0.0%. 2-tailed Fisher's exact test p=0.004. Nick partially successful G-clauses: consortship n=14, mean frequency = 14.3%; other contexts n=68, mean frequency = 13.2%. 2-tailed Fisher's exact test p=1.000.)

8.4.9 Female responsiveness to male gestural communication on consortship

The variation in rate of success and partial success experienced by the two consorting males may be due to a difference between the males (such as rank) or a difference in the response of the females with whom they attempted consortship.

Table 25 describes the variation in female responsiveness to gestural communication while on consortship when compared to that in other contexts.

The only significant change in behaviour was recorded from the female Zimba, with whom Duane consorted twice. She produced completely successful responses significantly less often, although she appeared to compensate for this by increasing the level of partially successful response rather than outright refusals.

Table 25: Variation in individual female response. The percentage of communications to which each individual female responds in a successful or partially successful fashion when on consortship and in other contexts. Notification * represents a significant variation between behaviour in consortships and other contexts.

Female	**Consortship**		**Other contexts**		**Fisher's exact test**
	n	**mean frequency %**	**n**	**mean frequency %**	**p**
Successful response					
Zimba	159	33.3	39	51.3	0.039*
Lola	70	7.1	11	27.3	0.072
Nambi	13	38.5	66	68.2	0.060
Partially successful response					
Zimba	159	38.4	39	5.1	<0.0001*
Lola	70	22.9	11	9.1	0.440
Nambi	13	15.4	66	6.1	0.255

Lola produced very low levels of successful responses on consortship behaviour (less than a third of either of the other 2 females) but this was not significantly lower than her level of response outside of consortships and she did not produce a significant increase in partially successful response behaviour as observed in Zimba. Nambi also made no significant change in her behaviour, although her level of successful response was much higher than that of Lola, and equivalent to that of Zimba.

8.4.10 Persistence in gestural communication on consortship

Sonso chimpanzees persist following the failure and in particular the partial failure of a gestural communication (see Chapter 3). When compared with communication in other contexts, persistence following total failure was significantly higher in consortship communication by Duane, and approached a significant increase in Nick. Persistence following partial success in consortship behaviour was high from both males, but the available data were limited and there was no significant variation between this and other contexts. See Table 26.

Table 26: Variation in individual male persistence. The variation in the percentage frequency with which each individual male persisted in further communication following the partial or total failure of the earlier communication when on consortship or in other contexts is compared using Fisher's exact tests. Notification * represents no cases observed in the category.

	Duane			Nick		
Persistence following:	Consortship (%)	Other contexts %	Fisher's exact p	Consortship %	Other contexts %	Fisher's exact p
Total failure	120/162 (74.1)	3/5 (60.0)	<0.0001	6/6 (100.0)	10/20 (50.0)	0.0532
Partial failure	98/114 (86.0)	*	-	2/2 (100.0)	5/11 (45.5)	1.00

8.4.11 The use of multiple gesture G-clauses and G-sentences by males on consortship

As persistence is implicated in G-sentences but not G-clauses, then increased levels of persistence should lead to longer G-sentences but not to longer G-clauses. As expected, I found no variation in the observed distribution of single and multiple gesture G-clauses produced while on consortship as opposed to any other context. (*Duane* consortship: range =1-6 gestures per G-clause, median =2; other contexts range =1-2 gestures per G-clause, median =1: Chi-square 2-tailed with Yates correction between single and multiple gesture G-clauses in consortship and other contexts: χ^2 =3.18, df=1, p=0.075. *Nick* consortship: range =1 gesture per G-clause, median =1; other contexts range =1-5 gestures per G-clause, median =1: Chi-square 2-tailed with Yates correction between single and multiple gesture G-clauses in consortship and other contexts: χ^2 =0.68, df=1, p=0.411).

However, strikingly, consorting males would then string up to 9 of the G-clauses together to form particularly long G-sentences; this led to significantly more

G-sentences (multiple G-clauses) as opposed to single G-clause communications. See Figure 21.

Figure 21: Distribution of G-sentence length in consorting males. The percentage of all G-sentences within consortships or other contexts accounted for by G-sentences of differing length (including G-clauses used individually). Black bars represent consortship communications; white bars represent communications in other contexts.

Duane: consortship range =1-9 G-clauses per communication, median =3; other contexts range =1-4 G-clauses per communication, median =1: Chi-square 2-tailed with Yates correction between single and multiple G-clause communications in consortship and other contexts: χ^2=14.50, df=1, p=0.0001. Nick: consortship range =1-4 G-clauses per communication, median =4; other contexts range =1-3 G-clauses per communication, median =1: Chi-square 2-tailed with Yates correction between single and multiple G-clause communications in consortship and other contexts: χ^2 =7.72, df=1, p=0.006

8.5 Discussion

Consortship behaviour at Sonso

Consortship behaviour is rare in the Sonso community; even with the additional observations described in this study the overall rate equates to less than 1 per year, slightly higher than Mahale, but much lower than Taï or Gombe.

Additionally, as at other sites, the variation in frequency between both years and individuals is high.

As discussed, the costs and benefits of a consortship strategy may vary between individual males. At Gombe, consortships represented the most successful sexual strategy for any individual except the alpha male, who was able to maintain an exclusive sexual relationship with an oestrus female while remaining with the community (Tutin, 1979). In contrast, at Taï only ex- or future-alpha males engage in consortship behaviour, possibly because consortships appeared to represent a less successful strategy than at Gombe (where apparent fertilization rates were extremely high) but were still associated with the high level of risk (Boesch and Boesch-Achermann, 2000)).

The pattern at Sonso is less clear-cut: approximately half of consortship events were initiated by ex or future, alpha or beta, males (close to the pattern at Taï); however, the remaining cases were initiated by the current alpha-male. Clearly at Sonso consortships are favoured by large dominant individuals, able to offset the cost and risk associated with consortship behaviour; however the tendency for even the alpha male to engage in consortship behaviour may suggest that the alpha male is less able to maintain an exclusive possessive relationship while within the community. As discussed, there are several factors that may affect the engagement in consortship behaviour by individual males. One particular issue at Budongo may be the forest environment. Budongo, as a secondary rainforest, contains much more dense undergrowth than a primary forest, such as Taï; this undergrowth leads to low levels of visibility throughout much of the Sonso range and may increase the opportunities for other males to steal opportunistic copulations from ‘under-the-nose’ of a possessive male, especially if the female co-operates. On the other hand, this pattern could also be the result of an individual preference in the behaviour of a single male: Duane. Individually responsible for the majority of consortship events, he was notable for his strong social bonds with adult females in the group and also for his tendency, even as alpha, to disappear for days and sometimes weeks. Following several of these disappearances he returned to the community with unknown young females (at least two of whom immigrated permanently to Sonso) and so he may have been extending his consorting behaviour even into other communities. Interestingly, while only very limited paternity data is available, there is no evidence that he successfully fathered any offspring while on consortship.

At Mahale the use of restrictive mating patterns increased when there were small numbers of available females (Hasegawa and Hiraiwa-Hasegawa, 1983). The recent small peak in consortship behaviour in the Sonso community coincided with a severe drop in the availability of oestrus females. During the 2-year study period, only five oestrus females were available to Sonso males, a legacy of the extremely successful period of child-bearing over the prior 2-years that left the majority of the adult female population in postpartum anoestrus. Three of these five available females were taken on consortship during this time.

Thus, the variation in the frequency of consortship behaviour between years and between individuals at Sonso is consistent with the suggestion that male participation in consortship behaviour is adjusted strategically as a result of variation in payoff due to social and demographic factors at any one time.

Was aggressive coercion an effective strategy for consorting males?

While consortship may represent an effective strategy for male reproductive success, it may not be in the female's interest to restrict her choice in this way (Muller et al., 2007). Males sometimes employ aggressive behaviour to coerce particularly reluctant females into following them away from the group ((Goodall, 1986) (Stumpf and Boesch, 2006)). However, at Mahale, Nishida (Nishida, 1997) describes female response to coercion as 'stubbornly' resistant; and reports that it was rarely effective, as the females would simply scream until a more dominant male intervened. A recent study at Taï confirmed no positive effect on female proceptivity following aggressive male coercion (Stumpf and Boesch, 2010).

Although all the observed consortships at Sonso included some aggression on the part of the male, the success of aggression as a strategy is unclear. Both consortship events with Zimba included aggressive coercion in the early stages, and both attempts led to her being successfully isolated from the group; however it is unclear that the one followed directly from the other. On two occasions Zimba's response to an aggressive attack was to drive Duane away, and both consortships were also characterized by extensive periods of Duane grooming Zimba. Furthermore on one occasion, following an aggressive attack, loud vocalizations from Zimba successfully brought other community individuals to the consorting pair. In this case the newly arrived individuals were all of low rank and the consortship resumed shortly afterwards; however, had more dominant individuals been near-by the outcome might have been quite different, as was the case with Lola.

The extremely high levels of aggressive attack to Lola did not cause her to follow Duane more freely; both individuals were left clearly exhausted and still well within Sonso territory when they were discovered by the alpha-male and the consortship terminated. The level of aggression in this case seems highly unusual, particularly for a within community event, although the case bears interesting parallels to another consortship event reported several years earlier, also involving Duane. In this case, the young nulliparous female Gonza (only 12-years old) experienced violent attacks following her repeated refusal to follow Duane away from the group. These attacks included a severe bite to the head, and although the consortship attempt failed when she eventually succeeded in escaping and running away, she was never seen again. The experienced field-assistant who observed the event (Monday Gideon), believed that, although it is possible she emigrated to an adjacent community, the severity of her injuries and her complete disappearance (emigrant habituated females at Sonso are usually observed to return on a number of occasions, particularly while they remain nulliparous), mean it is more likely that she died.

The repeated use of aggressive coercion may have been due to Duane's apparently high motivation to succeed in consortship behaviour at that time. Almost immediately following his unsuccessful consortship with Lola, he successfully removed Zimba on consortship twice. Very few oestrus females were available, so there was strong male-male competition for access to this limited resource; and, as he had recently been supplanted at the top of the male hierarchy, for the first time in 13 years he would not have been able to monopolize a female while remaining within the group. As an individual he was still a large, powerful male, with strong social alliances amongst the adult females. All of these factors combined to maximize the potential reward and minimise the risk of engaging in consortship behaviour. In this case the strategy was not effective, as Duane failed to impregnate any of the females he had engaged on consortship and shortly after these observations he died suddenly. He was believed to have been initiating another consortship with a female on that morning, when he quite literally dropped dead: the cause is still unknown. Zimba did become pregnant shortly afterwards suggesting that this had been an optimum period for him to invest in her.

While on consortship, levels of female responsiveness to male communication were generally low; however, Zimba appeared to compensate for infrequently responding with the desired 'follow' behaviour, by producing behaviours that were at least congruent with following behaviour more often. In practice this meant that although she did not follow him, she would turn to attend to his communication, and approach a little way towards him. Duane appeared visibly less tense as a result, his movements and gestures were more relaxed and eventually the pair moved freely together. While on consortship Zimba was accompanied by her young sons Zak and Zig; they would occasionally wander behind, and she would pause to wait for them. These partial responses may have represented an attempt on the part of Zimba to acknowledge Duane's communication, while at the same time giving her sons time to catch up before she followed on. In doing this she appeared to avoid the complete refusals that were characteristic of Lola's response to consortship communications.

There was no similar compensation from Lola, whose repeated refusals only seemed to increase the frequency, vigour and aggression of Duane's attempts. The high motivation to succeed in combination with the repeated frustration of his goal may have been the catalyst behind his unusually aggressive behaviour. Given that repeated complete refusal of the male's request most commonly preceded serious aggressive attack, this variation in female responsiveness may, at least in part, explain the variation in aggressive coercion experienced by the two females.

As well as experiencing lower levels of aggression, Zimba received much higher levels of grooming. Goodall suggested that the use of grooming by a consorting male might function to relax the female and give 'proof of his fundamentally friendly intent', making her easier to lead away ((Goodall, 1986), pp402). It is tempting to see the variation in the two forms of coercion as being related: a sort of – honey being more effective than vinegar – approach; however, there is no reason to assume that this is the case. Apart from the early grooming in the nest, grooming behaviour occurred only once Zimba started to follow more freely. As Lola was never observed to follow Duane freely this may explain the absence of any significant grooming behaviour on her consortship.

Grooming requires that both individuals are stationary for several minutes or more. While this may be appropriate once they have moved away from the main group, it could be extremely costly for the male to sit down while still 'under-the-nose' of the other community males, particularly if the female is still not entirely co-operative. The pattern of use at Sonso appears to suggest that aggressive coercion is used to initially 'dominate' the female; and that later, once the pair is away from the group and travelling freely together, the relationship is reinforced (or possibly repaired) through grooming. However, at this stage it may no longer be appropriate to consider the grooming as 'coercive'. It is extremely interesting then to note the use of the rump-rub gestures, which were directed to both females, and occurred predominantly before the female started to follow freely.

Outside of the consortship context, lower ranking males directed rump-rub gestures towards a more dominant individual when seeking reassurance or affiliation, and in a manner that suggested submissive behaviour. However, in the consortship context it was a very dominant male who employed this gesture towards the much lower-ranking females. This rare behaviour was documented at Gombe by Goodall (1968) as 'rump-turning':

> *'the dominant individual turns its rump towards the subordinate, and may even back towards the latter..... seven times when rump turning was shown in response to presenting this lead to the animals' pressing their bottoms together..'*

and in a captive group by Tutin & McGrew (1973) as 'bump rump':

> *'rubbing of the perineal areas of the two individuals. The active participant (male or female) backs towards the passive, usually prone recipient (always a somewhat swollen female), crouches quadrupedally, then repeatedly moves its perineum vertically against the other's, making contact on both upwards and downwards motions.*

Given the use of aggressive coercion towards a still-reluctant female, it seems puzzling that the dominant male would at this stage choose to employ a gesture whose physical form (a low crouch with the genitals exposed) is classically submissive, and that is associated with a submissive role in other contexts. However, the pant vocalisation that accompanied the gesture at times may give some clue as to his intention. This vocalisation is normally given to a trusted ally or family member in contexts such as food excitement or the arrival of a friendly other (M. Laporte 2009, pers. comm.; C. Crawford 2009, pers. comm.). The apparent submission implied by the use of the rump-rub gestures by the male may represent an attempt to reassure the female, while continuing to gesture and communicate his desire that she follow him. Thus the rump-rub gesture may function as a ‘quick-and-dirty’ communication of the consorting male’s essentially friendly intent: encouraging the female as she is being coerced into leaving the main group; but without the need for long relaxing bouts of grooming while the pair are still in the vicinity of other community males.

The use of gesture while on consortship

Rump-rub gestures, while extremely interesting, represented a tiny portion of the huge amount of gesture recorded within the consortship context. A successful consortship relies on the male being able to both successfully communicate to the female his desire to leave with her, while at the same time avoiding advertising this intention to any other males in the group. Chimpanzees not only use gesture to communicate their intention, but they intentionally alter the modality of their gestures with respect to other individuals’ state of attention (see Chapter 3). I hypothesised that, because of the pressure to limit the communication to a specific recipient, gestural communication -particularly silent and contact based gestures - would be selected for in the consortship context.

There is no doubt that gestural communication was particularly prevalent within the consortship context, accounting for a massive 62% of all cases of adult male gesture. The large percentage of adult male gesture in this context, only observed in wild chimpanzees, may explain the low frequency of adult male gesturing reported in captivity. However, extremely surprisingly, the overwhelming majority of this communication involved audible forms of gesture.

Did gestures represent a discreet means of communication for consorting males?

Given the loss of investment and risk should other individuals become aware of the consorting male's intentions, the use of audible gestures seemed initially counter-intuitive. In attempting to understand this, I developed the post-hoc hypothesis that, as with vocalizations, there may be different levels of 'audibility' within gestural communication.

All of the audible gestures used on consortship were short-distance gestures whose audible component (rustling leaves etc.) was not immediately associable with chimpanzee behaviour. None of the distinctive long-distance chimpanzee gestures such as object-drums were employed at any time, despite being associated with short-distance audible gestures in other contexts: therefore it is still appropriate to describe the gestural communication employed as discreet. This mirrors the pattern of vocalisations produced during consortship behaviour: males were only observed to produce soft-pant vocalisations and I found that, as McGinnis (1973) reported, loud vocalisations on the part of the female resulted in the threat or use of physical violence by the male: supporting the idea that consorting male chimpanzees are highly motivated to employ discrete methods of communication.

The function of gestural communication in consortships

The predominant function of almost all male gestural communication in this context was 'follow me'. As discussed, in order to maintain exclusive access to female at POP, it is necessary to remove her before she reaches this stage. It is then logical that the immediate function of the male's communication is to take the female away with him rather than engage in sexual behaviour. Almost all gestures with the function of obtaining sexual attention were produced by the females, and accounted for most female gestural communication in this context. The majority of these gestures were present-sexual gestures produced by the young female Lola. As described above she also experienced the highest levels of aggression, usually in response to repeated failure to comply with the male's apparent goal that she follows him. Her behaviour at the time strongly suggested that she was unclear as to the appropriate response to the male's behaviour. Prior to Duane's attempts to sequester her, she had spent that morning being courted by a number of younger males who had copulated with her, and her apparent confusion may have been exacerbated by the lack of immediate sexual motivation on the part of the consorting male. Duane displayed no signs of penile erection while initiating consortships. On the one hand this seems appropriate, given his immediate aim was to remove the female from the group rather than copulate with her. However this was highly unusual, in that normally the simple presence of a female in oestrus is sufficient for all the males in the party to maintain erections. It is conceivable that as a young inexperienced female, Lola may not have understood Duane's goal in leading her away, and her reluctance to comply may have been increased by the fact that she was being taken away from other males who were clearly sexually interested in her at the time.

The form of gestural communication in consortships

In comparison to contexts such as play or grooming, sexual behaviour - in particular risky sexual behaviour such as consortship - represents an evolutionarily more urgent function. The increased value of consortship communication is reflected in increased response-waiting, and (to an extent) increased persistence following failed communications. The increased level of persistence also explains the use of particularly long G-sentences. The length of G-clauses only increased very slightly, suggesting that the consortship context had little effect on the underlying reason for combining gestures in this manner.

8.5.1 Summary

The pattern of consortship use at Sonso supports the case that male chimpanzees are able to continuously evaluate the cost-benefit ratio of a sexual strategy, and to adjust their use appropriately. At Sonso a recent peak in consortship behaviour coincided with a period of high male-male competition, and consorting males tended to be large dominant individuals, able to withstand the high energetic demands and possible risks. Unusually, consortship behaviour appears to outweigh possessive behaviour even in the case of the alpha male. Gestural communication was extremely prevalent, and consortships represent the dominant context for the use of gesture by adult male chimpanzees: highlighting the necessity of examining communication in a natural context. There is no preference for the use of silent or contact gestures, however the audible component of the gestures used was limited and could not be clearly associated with chimpanzee behaviour; thus the gestural communication employed could still be considered discreet.

Consorting males appear to be highly motivated, and are more likely to wait for a response, and persist following the failure of their communications. Repeated refusal, or loud vocalisation, by the female can lead to aggressive attack and serious injury. Grooming was only employed once the female was already co-operative; however, the use of submissive-like Rump-rub gestures in the early stages of consortship may function to reassure the female during the highly stressful experience of being isolated from the community.

Chapter 9: Do wild chimpanzees use referential gestures?

One of the most familiar uses of language is to describe the outside world, through speech we are able to refer to specific objects and events in the world around us and draw another's attention to them: not just a seat, but that chair in the corner of the room; not just food, but that particularly large slice of cake. Similarly, one of the most familiar uses of human gesture is to direct attention to objects and events by pointing, whether this is in the form of imperative (I want that cake), or declarative (that chair is comfortable) communications.

In their description of pointing behaviour in humans Enfield et al. (Enfield et al., 2007) define pointing as: 'a communicative bodily movement which projects a vector whose direction is determined, in the context, by the conceived spatial location, relative to the person performing the gesture, of a place or thing relevant to the current utterance'. While something of a mouthful, it is interesting that in this detailed analysis of human pointing behaviour, the authors make no requirement that a finger, or even hand is extended in order to classify the action as pointing; instead, they detail this later as a specific subcategory of pointing gestures.

There is no doubt that in western cultures we are most familiar with the index-finger point; but this bias in our expectation can lead to other equally valid forms of pointing being overlooked. Pointing with all of the fingers extended (whole-hand points) is common in some cultures: the Tzotzil in Mexico (Haviland, 2000); and the Arrente in Australia (Wilkins, 1999); and pointing with the lips is frequently, and sometimes preferentially, used in others (again the Arrente in Australia; the Barai in Papua New Guinea (Wilkins, 2003); the San Blas Cuna in Panama (Sherzer, 1973); and in Laos (Enfield, 2001)). Indeed the Ugandan and Kenyan field-assistants, with whom I work at Budongo, when asked to point out directions in the forest, regularly use their lips. This habit is often initially to the bemusement of visiting western researchers who fail to understand that this is in any way meant to direct their attention. In an interesting reversal of the western bias towards finger pointing, the lip-pointing Barai people of Papua New Guinea are described by a visiting linguist as having not only no form of pointing with their hands, but also no understanding that his doing so was meant to function referentially (Olsen, pers. com. cited in: Wilkins, 2003). Despite this variability, there are no reports to suggest that any human culture lacks the ability to communicate referentially to outside objects, and yet the absence of naturally occurring index-finger pointing in great apes has been employed to argue just this (Povinelli and Davis, 1994).

Pointing indicates the cognitive capacity to not only recognise and accommodate another individual's perspective, but to direct it to external objects. Thus, the question of whether, and to what extent, pointing exists within other species is of great interest. Building on earlier descriptive observations (de Waal, 1982, Savage-Rumbaugh et al., 1986), there is now an extensive body of research into whether apes do (Apes: Gómez, 2007, Gómez, 2009; Chimpanzees: Leavens et al., 1996, Leavens and Hopkins, 1998, Leavens and Hopkins, 1999, Leavens et al., 2004, Leavens et al., 2005a; Orang-utans: Call and Tomasello, 1994; Orang-utans and Bonobos: Zimmerman et al., 2009); or do not point (Povinelli et al., 1997, Povinelli and Vonk, 2003, Tomasello, 2005).

Captive chimpanzees do occasionally spontaneously exhibit pointing with an extended index finger (Leavens et al., 1996); however, they are more frequently seen to use what Leavens and Hopkins describe as 'whole-hand points' where all of the fingers are extended (Leavens and Hopkins, 1999). Despite the presence of the same form of pointing behaviour in the human cultures described above, some studies categorise these actions by great apes as simply being 'reaches' for unreachable food (Povinelli and Davis, 1994). However, as Leavens and Hopkins discuss (2004), we have to question the implication that great apes reared in captivity would so seriously fail to understand the limitations of their physical environment. Why would an adult chimp born and raised in a captive environment still try to reach for items that are clearly out of reach? Even more critically, the non-communicative reaching explanation fails to explain the increase in this pointing behaviour exhibited in the presence of a human observer. In their 1996 study Leavens et al. report on 3 untrained laboratory chimps that spontaneously developed both index finger and other referential pointing. Here 254 of the total 256 observed points were produced in the presence of a human, and were accompanied by both attention getting behaviours (vocalisations) and gaze alternation (Leavens et al., 1996). This 'audience-effect' on pointing behaviour has been demonstrated in both chimps (Leavens et al., 2004) and orang-utans (Call and Tomasello, 1994), and is specifically used elsewhere as a means to identify cases of intentional communication in general gestural use (Tomasello et al., 1994, Liebal et al., 2004a, Genty et al., 2009).

In addition to discriminating different physical forms of pointing, the physical act of pointing can be categorised along a spatial axis from *contact* (where the gesture touches the object) to *distal* (where the object indicated is out of reach). We can also distinguish an intermediary stage: *proximal*, where the object is within reach but not touched (Miklósi and Soproni, 2006). Although contact gestures may function referentially to direct another individual's attention to an object or location (Pika and Mitani, 2006), the definition of *pointing* usually requires that the gesture projects a vector towards the object (see (Enfield et al., 2007, Povinelli et al., 1997), rather than contacting it directly. Thus, the majority of pointing studies focus on the use of proximal or distal gestures (for review see: (Miklósi and Soproni, 2006)).

Despite the accumulation of evidence for pointing in captive apes, there remains very little evidence for its use in the wild, where to date there exists only a single anecdotal description of two cases of distal pointing from a wild bonobo (Vea and Sabater Pi, 1998). Given the virtual absence of distal (or proximal) pointing cases in the wild, great interest was generated by Pika and Mitani's (2006) report of the widespread use of a contact referential gesture in the wild Ngogo chimpanzee community: the 'directed scratch'. Here a loud deliberate scratch on the signaller's own body, appears to be used to direct grooming to the scratched location.

To address the question of whether wild chimpanzees use referential gestures, this chapter is divided into two sections. The first addresses the case for pointing (proximal or distal); I describe 4 potential cases of whole-hand pointing in the Sonso chimpanzees and address the question of whether or not the conditions necessary to promote the use of pointing exist for wild chimpanzees. The second section addresses the question of contact referential gestures by examining the case for the intentional use of a 'directed-scratch' gesture in the Sonso community.

Chapter 9, Section 1: Where's the point? Is referential communication in wild chimpanzees non-existent or simply not recognised?

'one reasons that chimpanzees very seldom point manually is that *they do not have to*' (Menzel, 1973, p.218).

9.1.1 Introduction

The increasing body of evidence for pointing in captive apes described in the main chapter introduction makes the disparity with the near complete absence of evidence from wild chimpanzees all the more striking. As the captive evidence demonstrated that there was no biological impediment to the development of pointing in wild apes, this led Leavens, Hopkins and Bard to suggest that its apparent absence in wild populations can be explained through environmental factors (Leavens et al., 2005a). They argue that the development of pointing can be attributed to the combination of two environmental factors that are regularly experienced by both captive chimpanzees and young humans, but not wild chimpanzees. Namely that:

1. There are physical barriers to the ability to obtain desirable objects.
2. There is a reliable history of provisioning by adult/human caretakers

The regular experience of these two factors in tandem then creates the environment for the development of communications that rely on a *triangle of reference* formed between the signaller, recipient, and external object. In the absence of either one of these factors the triangle fails. As wild chimpanzees do not experience either the physical restrictions, or regular provisioning then the authors argue that pointing is simply not an effective strategy. In other words it's not that wild chimpanzees can't point – but that they have no reason to. As they put it 'what's the point'? (Leavens et al., 2005a).

While it is no doubt true that the environmental factors they describe do not exist in wild populations; I would argue that there are equivalent environmental circumstances that, while perhaps rare, do exist; and that where they occur these may also act to promote the use of pointing gestures in wild chimpanzee populations.

It is true that wild chimpanzees experience very few physical barriers to desirable objects such as food. There are no cages or bars in the forest, and close relatives are frequently seen to carry younger individuals up the more difficult trees. Young chimpanzees also experience very little physical restraint on the part of their caregivers and are relatively free to move about at will from a only few months old. However, there may be other factors that restrict access to desirable objects. For example: there are some highly desirable foods that can be easily monopolised by either a single individual or a small group of chimps. These include items such as meat, or the much sought-after pith of the decaying Raphia palm (*Raphia farinifera*) only accessible through a small hole gnawed through the trunk. While there are no physical barriers in accessing these foods there may be significant *social barriers* to doing so.

The presence of a dominant unrelated adult chimpanzee that is monopolising a particular resource could be considered to pose an even greater barrier to a young chimp's access than the bars on a cage. Other members of their community generally tolerate the social faux pas of very young babies; and adults may overcome social barriers by offering sexual access (females) (Gomes and Boesch, 2009), or social support (males) (Mitani and Watts, 2001). However, to older infant and juvenile chimpanzees, who have less social currency to offer, the barrier is a highly effective one. Their best chance of overcoming this and gaining access to the food is with the aid of a third party. To achieve this they would then need to communicate their desire not just for help, but also for help in relation to a specific object.

Several studies in captivity have demonstrated the apparent reluctance of chimpanzees to share food even when at relatively little cost to themselves (Vonk et al., 2008, Hare et al., 2007). Young chimpanzees at Sonso are frequently seen to pilfer food both from family members and some unrelated group members; however, although less frequent, genuine giving or provisioning was also observed. As would be expected these cases were normally limited to mother-offspring interactions, or very close social allies (for example following a hunt, the alpha male Nick was observed to give large portions of meat to the beta male Zefa on several occasions).

While perhaps not a regular occurrence, these factors may then combine to create a situation whereby an older infant, or young juvenile, wishing to gain access to a food that is being monopolised by a more dominant individual, may benefit from being able to communicate this desire to a close family member such as their mother or older sibling. In this situation pointing becomes a potentially effective strategy for wild chimpanzees.

From the broad study of gestural communication, I examined all clips containing object-related begging behaviour for examples of potentially referential gestures, with specific attention to begging-reach type gestures that may function as whole-hand points. In order to classify the reaches as clear cases of referential communication, only cases where the reach was produced towards an external object (rather than a third individual) were considered for analysis.

9.1.2 Results

79 video clips contained object-related begging gestures; the majority (62/79) of these surrounded periods of meat consumption following a hunt. Unfortunately, when feeding, the individual monopolizing the meat usually holds on to it at all times. It then becomes difficult to objectively distinguish between gestures the signaller directs towards the meat while communicating to a third party, and gestures directed towards the individual holding the meat. Instead, only in examples where Raphia pith was the desirable object, was the object sufficiently distant from any potential recipient to create a clear triangle of reference necessary to isolate potential cases of referential gesture.

12 bouts of Raphia feeding were recorded; however, 5 of these were from either single individuals or small ‘mother + offspring’ parties. In the remaining 7

bouts there was the combination of a dominant unrelated individual who might act as a social barrier, and a potentially helpful ally such as a mother or older sibling.

In one of these bouts, 3 cases of potentially referential whole-hand points were identified and are described in full below. A 4th example that occurred outside of the expected feeding context is also described.

1. *19th June 2008*

While other dominant chimps (the alpha male and his mother) feed on a Raphia palm, a young female Monika (5 years old) approaches the palm and starts to whimper; she is followed by her mother (Melissa), who stops approximately 5m behind her. Monika's attention is focused on the palm, with occasional glances back at her mother who is paying attention to her. She whimpers and reaches her left hand out (all fingers extended) towards the access hole in the Raphia palm while glancing back at her mother. Her mother approaches to approximately 2.5m, but then stops. Monika continues to wait but on getting no further response she approaches her mother to within 1m. She reaches to her mother, while whimpering and glancing back at the palm. As her mother approaches she moves back closer to the palm. She then gestures requesting to nurse (causing her mother to move even closer) but stops nursing after only 3 sec before continuing to gesture to the palm – see no. 2

2. *19th June 2008*

Monika stops nursing after 3 seconds and again moves back toward the palm, whimpering and reaches across her body with her right hand towards the hole in the Raphia-palm where the dominant individuals are feeding. There is no immediate response from her mother and she gestures to her mother requesting to nurse. Her mother approaches and she nurses, but she again stops after a few seconds and moves towards the Raphia, this process is repeated several times each time the result is that her mother moves closer to the Raphia palm. They are now sitting less then 0.5m from the feeding individuals who would have been extremely unlikely to tolerate Monika approaching directly (even the mother of the alpha male was slapped by him when she briefly impeded his access to the hold). At this point Monika drops any pretence of nursing and peers intently at the feeding individuals while chewing on scraps of Raphia palm. Unfortunately at one point the alpha male moves suddenly, although there appears to be no obvious immediately aggressive intent, Monika screams in apparent fear and at this point he chases both her and her mother away. Interestingly, the alpha male doesn't return to feed after this disturbance and shortly afterwards following a third bout of gesturing (see 3. below) Monika succeeds in feeding at the palm.

3. *19th June 2008*

After the disturbance Monika and her mother re-approach the Raphia palm, her mother appears reluctant to approach and sits down; Monika reaches to her whimpering. At the same time she reaches out towards the Raphia palm and glances towards it while looking at her mother. Her mother then approaches and picks her up, carrying her to within 2m of the Raphia palm. Monkia climbs off her mother and approaches the tree, shortly afterwards she starts to feed.

4. *16th December 2008.*

One further example occurred outside of the expected feeding context. Here, Night, the particularly well-habituated juvenile daughter of the dominant female, approached me to under 0.5m while I was seated filming her. She was quite relaxed and peered intently at the camera in my hand; she suddenly started and backed-away to her mother having apparently caught a glimpse of either herself or some movement in the camera lens. As she moves back to her mother she turns and reaches out towards me (or the camera), glancing back at me while looking at her mother and then sits next to her mother who has looked up at the disturbance. Although she does direct gestures towards me occasionally, the response-waiting behaviour following this gesture suggests that it was directed towards her mother rather than towards me. While there was clearly no physical or social barrier inhibiting her from approaching me initially, the small fright she had seemed to cause a temporary reluctance on her part to come close again. The camera certainly represents an object of great desire to her, as an individual she is particularly interested in the objects that I carry around, and is remarkable as the only Sonso chimpanzee that has shown any interest in these. The camera and other items such as water bottles are of such interest to her that I must pay careful attention to avoid her stealing them even while they're attached to the pack I'm wearing. She could have been requesting her mother's support in this desire, though in this case the outcome was negative.

Were there effective social barriers to desirable objects?

Interestingly the frequent use of begging-reaches directed towards individuals with meat, supports the argument that there are social, if not physical, barriers to desirable objects for wild chimpanzees; and that gestures provide an effective strategy to overcome these.

Were there potentially helpful allies present?

Both individuals who produced the whole-hand points were 5-year old juveniles communicating to their mothers. Furthermore, these were the only two juveniles in the Sonso community not to have a younger baby, or infant, sibling at the time. This means that helpful action on the part of the mother in overcoming the social barrier; would only put herself, and not any fragile younger babies, at risk.

Were there examples of alternative forms of pointing such as 'lip-pointing' in chimpanzee behaviour?

It is interesting, given the prevalence of lip-pointing in human culture, to briefly consider the case for other potentially referential actions outside of manual based pointing; however, I observed nothing to suggest the use of the lips in a referential manner. I chose not to analyse facial expressions in this study because previous work has suggested that they represent a relatively fixed automatic response, rather than flexible intentional communication (Tanner and Byrne, 1993). However, despite not attending to fine facial movements, I don't believe that I missed regular use of a lip-pointing gesture. Unlike the hand and arm, to point at something not located immediately in front of you requires that you rotate, at the least, your head, if not also your neck and shoulders (just try to pointing at something in your peripheral vision without doing so!). Moreover, in the Ugandan and Kenyan field-assistants, lip-pointing is characteristically accompanied by a small but clear jerk of the head in the direction indicated. Together, particularly for a researcher focused on the intentional use of body movements, I would anticipate that this pattern of action would be relatively easy to observe if chimpanzees regularly employed lip-pointing. Instead I observed nothing consistent with any of these actions; and, as there is no discussion of it in the extensive captive literature, I don't believe lip-pointing is a part of the chimpanzee communicative repertoire.

9.1.3 Discussion

Taken individually these 4 cases fulfil the criteria for whole-hand points. They are all extensions of the arm and fingers directed towards a desirable but unavailable object, within bouts of intentional communication directed to an individual who may act as a potentially helpful ally. There are no physical or behavioural reasons not to categorise them as pointing; rather it is only their scarcity that brings into question whether or not these factors all combined in accidental rather than intentional pointing.

While the overall frequency is certainly very low, it is comparable to the recorded frequency of other rare gesture types reported in this study. For example: 21 of the 115 detailed gesture types recorded were only observed on 1 or 2 occasions, and a further 14 were seen on 5 or fewer occasions (Arm swing under (3); Beckon (5); Bow (4); Feet shake (4); Foot present (4); Hands shake (3); Hit with object (5); Knock object (5); Look (5); Slap object with object 2-handed (3); Stomp other ritualized (3); Tap object (single) (3); Tapping object (3); Water-splash (5)).

Furthermore, over the 2-years of field time I observed only 7 occasions where all of the necessary factors combined to create a situation whereby pointing represented an effective strategy. On one of these, 3 cases of whole-hand pointing were recorded; thus, while it is accurate to describe the context in which pointing represents an effective strategy as rare in wild chimpanzees, the frequency with which the behaviour was observed within this context was relatively high.

The circumstances for the use of referential pointing in wild chimpanzees do not occur on a regular basis. Not only must a single individual monopolize a highly desirable food source; but also to create a clear triangle of reference the food source itself must be spatially distinct from the individual who is monopolizing it. This was made particularly apparent in the case of reaches produced during begging to obtain meat; where, because the individual usually holds onto the meat, it was very difficult to objectively distinguish between a referential begging-reach pointing *towards the meat* and directed to a potentially helpful third-party; and a straightforward begging-reach *towards the individual holding the meat*. As I adopted the conservative approach of requiring that there be no potential recipient in the direction of the reach, this led to the elimination of the majority of reaches as possible cases for whole-hand pointing.

Only in the case of Raphia pith was the desirable object clearly separate from the individual monopolizing access to it. However, observations of Raphia feeding behaviour became increasingly difficult to record over the course of the study, as this now rare species is threatened by its overuse in the local tobacco industry (Reynolds et al., 2009). During the final 4-month period of fieldwork, a specific effort was made to film social interaction around Raphia palms; however in over 16-weeks, no cases of Raphia feeding were observed. Instead the chimpanzees were feeding on an alternative species (*Cleistopholis patens*). As this tree decays the entire trunk falls and the decayed wood can be accessed at any point, eliminating the opportunity for individuals to monopolize the food source.

The restrictions defined by the social requirements (presence of both a dominant individual and a potentially helpful ally) further diminish the frequency with which pointing would be promoted in wild chimpanzee communication. Given the limited circumstances where all of the necessary factors for the development of pointing come together then a low observation frequency is to be expected.

Finally, while there has been extensive study of wild apes for over 40 years, to date there has been no systematic analysis of their gestural communication. There were no obvious differences between the referential whole-hand reach gestures and begging-reach gestures in the physical action of reaching; it was only the manner of their use (directionality and accompanying behaviours) that categorised the behaviour as part of a triadic rather than dyadic communication. The accurate analysis of gestural communication requires months of training, and field observations in particular are often hindered by difficult environmental conditions. Given that even in captivity referential whole-hand points were repeatedly categorised as simple reaches, such errors would be even more likely to occur in field-studies, further reducing the frequency with which pointing cases may be reported.

Thus, the low frequency of observation need not be interpreted as an absence of pointing behaviour in wild chimpanzees, but rather as a consequence of the low frequency with which pointing represents an effective strategy for wild chimpanzees. This supports the conclusions of Leavens et al. that the apparent absence of pointing behaviour in wild chimpanzees is less to do with the question of whether or not wild chimpanzees *can* employ referential communication; and more the question of whether or not there is an ecologically valid reason *why* they should employ referential communication in the wild.

Chapter 9, Section 2: The ‘Directed’ Scratch?

18th July 2009
Night is sitting behind Rachel, grooming her back. After a while she stops, and in a loud deliberate way she scratches her left arm while looking at Rachel. Rachel, who has been facing the other way, turns round and looks at Night. Once Rachel turns round, Night lies down and presents her back to be groomed, Rachel immediately starts to groom the area presented.

9.2.1 Introduction

Given the apparent absence of referential gesture in wild apes, great interest was generated by Pika and Mitani’s report of the widespread use of scratching in such as way that it appeared to function as a referential gesture (Pika and Mitani, 2006). They describe the use of a clear deliberate ‘scratch-gesture’ by the adult males of the Ngogo community in Uganda, which resulted in grooming being relocated to the scratched area in the majority (64%) of cases. The majority of these gestures were produced when both individuals in the grooming pair were high-ranking males. Pika and Mitani use this effect of rank to argue against the hypothesis that the scratch-gesture is simply an effective action, with no intentional communicative function.

To date their study remains the only evidence for the regular use of a referential gesture in a wild population; thus, there would be considerable value in replicating the findings, particularly within a new population of chimpanzees. In my initial field period I regularly observed the use of gestural communication during bouts of grooming (as in the interaction described between Night and Rachel above) and felt that my work on the gestural communication of the Sonso chimpanzees might provide just the opportunity to expand the work on directed-scratches, although the results were not quite as anticipated.

9.2.2 Specific method

Gesture types

Pika and Mitani describe their directed-scratches as ‘relatively loud and exaggerated scratching movement on a part of his body, which could be seen by his grooming partner’ (Pika and Mitani, 2006). I followed their general example and categorised all easily audible, exaggerated scratching movements within the grooming context as potential directed-scratches but employed the more neutral term: Big Loud scratch (BL-scratch). In addition I chose to initially include all easily audible, exaggerated scratches, and then considered the sub-group of those given in full view of the recipient separately. In order to assess whether there is any intentional use of visual information in the BL-scratch gestures, I compare its use with that of a visual-only (silent) gesture: the Present-groom, defined as ‘a body movement to deliberately expose an area to the recipient within a grooming context’.

Procedure

During a 14-week period (May-Aug 2009) all cases of BL-scratch gestures were recorded. All observed social interactions that had the potential for social grooming, and where both individuals could be clearly seen at the outset were recorded on miniDV tape using a Sony Handycam (DCR-HC-55). I defined the potential for social grooming as any situation with more than one chimpanzee present, where one individual was at least 3 years old and where at least one individual was not involved in social activity with a third party.

Judgements of location matching in gesture and action

A location-match refers to the case where the place on the body of subsequent grooming is the same as the place of the earlier gesture. All body parts were considered to have a maximum of 6 basic planes (top, bottom, front, back, left side and right side); obviously in most cases there would be fewer (e.g. forearm: top, bottom, left side and right side). The visual information contained in BL-scratches can be more easily localized than that of the Present-groom gesture; for example, it is possible to scratch a tiny 1cm^2 area on the front of the forearm, but only the whole front of the forearm can be presented. In order to judge the location-matching of both gestures at a similar level I used a generous definition whereby a match was recorded where subsequent grooming was initially directed to the same plane of the same body part that had been either scratched (BL-scratch) or presented (Present-groom).

Statistical analyses

Data were converted to means for each individual, to remove any effect of pseudo-replication from the use of focal behaviour sampling. Only the data from gestures that successfully elicited a bout of grooming were included in analyses. Analyses were carried out in SPSS v11, with $\alpha=0.05$ required for significance. Means are given ± Standard Deviation, throughout.

9.2.3 Results

I collected 6hrs, 3min and 37seconds of grooming behaviour video suitable for analysis. The video was broken down into 448 clips, 136 of which contained gestural information appropriate for coding. A total 147 BL-scratch and 50 Present-groom gestures were coded, 98 of these gestures successfully elicited grooming: 50 BL-scratch and 48 Present-groom.

9.2.3.1 Use of BL-scratch and Present-groom gestures

The BL-scratch gesture was recorded from both male and female individuals, and in all age classes from juvenile to adult chimpanzees (not in infants). Present-groom gestures were also recorded from both sexes and in all age classes including infant chimpanzees (youngest example: 2-year old male Klaus).

Does the location of the response match the location of the gesture?

In successful grooming requests the location of Present-groom gestures matched the location of subsequent grooming with almost 100% accuracy (mean=96.7% ±11.6); unlike BL-scratches, which were significantly less successful (Mann-Whitney U=33.50, n=42, $p<0.0001$) with only a mean location-match of subsequent grooming in 22.6% ±35.1 of cases, see Figure 22.

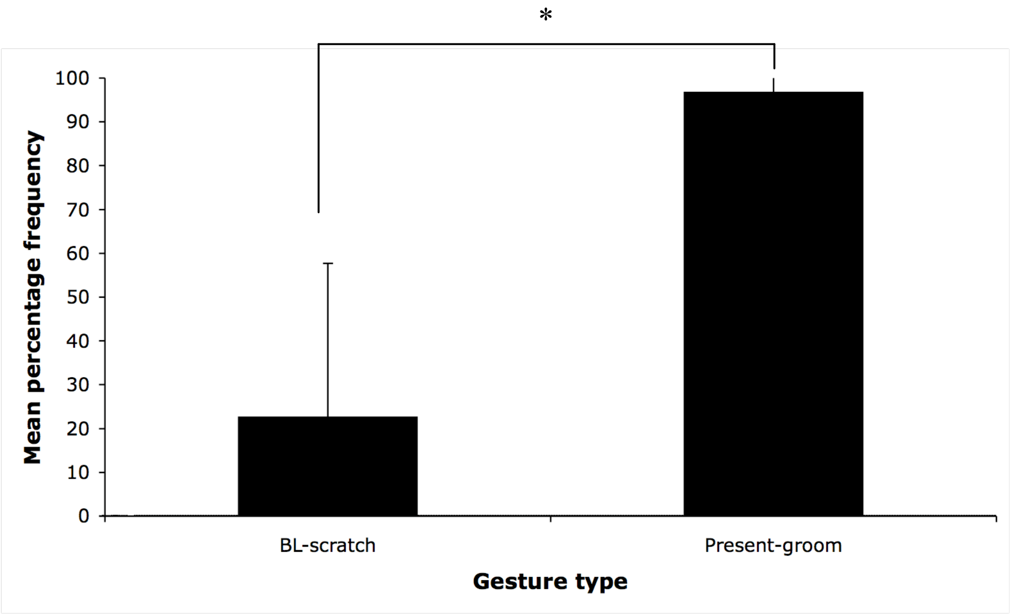


Figure 22: Frequency of successful location-matching with type of gesture. This frequency with which the recipient grooms the signaller in the same location as the signaller 'indicated' in the gestural communication. Notification * represents p<0.0001

Are the gestures directed to recipients who are able to receive visual location information?

There was no significant difference in the frequency with which BL-scratch gestures were used towards attentive recipients, able to see the location of the gesture (recipient attending, mean = 38.6% ±43.9); or inattentive recipients, unable to see the gesture (recipient out of sight, mean = 23.3% ±36.0) (T-test: t=-1.17, df=42, p=0.25). In contract the Present-groom gesture, was used significantly more frequently to attentive recipients able to see the gesture (recipient attending, mean: 70.0 ±38.1; recipient out of sight, mean = 23.3 ±12.2; data transformed to correct for positive skew with √(x): T-test t=-7.77, df=38, p<0.0001), see Figure 23.

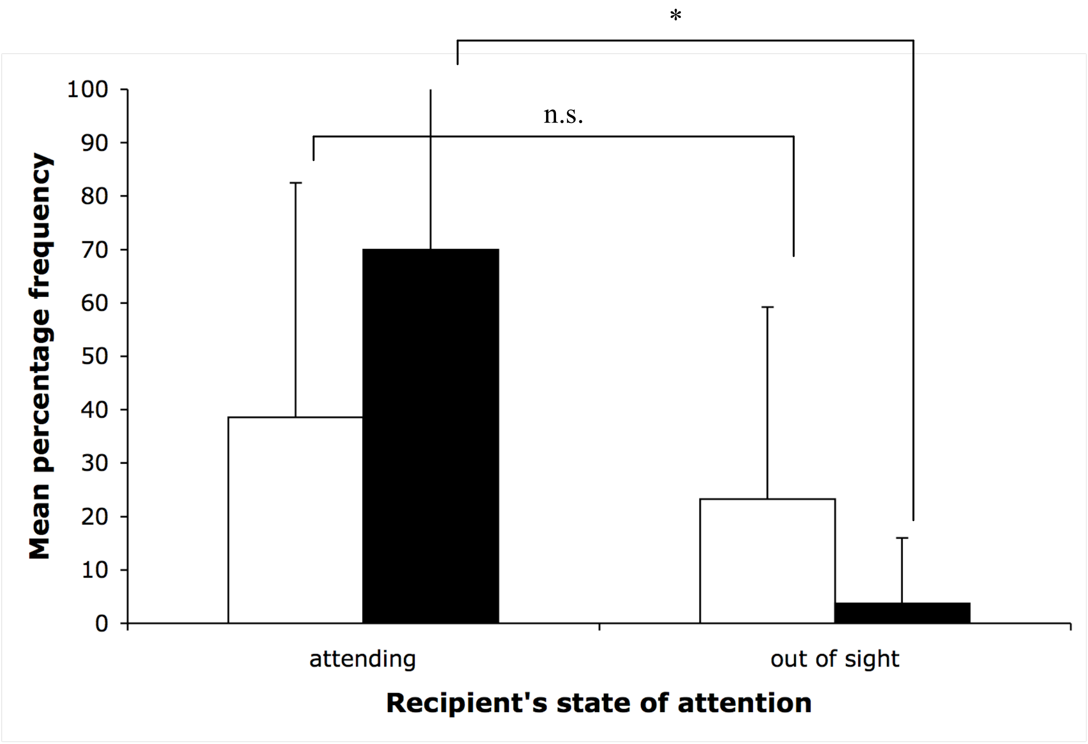


Figure 23: Variation in frequency of gesture use with variation in recipient's state of attention. The percentage frequency with which the two types of gesture were produced when recipient's were either attending or unable to see the signaller. White bars represent BL-scratch gestures, black bars represent Present-groom gestures. Notification * represents p<0.0001, and n.s. represents no significant difference.

Did the recipient's state of attention affect the frequency with which they groomed in the location of the gesture?

There was no difference in the success rate of location matching for BL-scratches when the recipient was in (18.8% ±32.2) or out (17.3% ±37.1) of sight (data transformed to correct for positive skew with √(x): t-test t=0.34 df=19 p=0.57). The Present-grooming gesture was 100% successful in location matching when used to an attending individual; there were not sufficient examples of its use to out of sight recipients to calculate its success in this situation, see Figure 24.

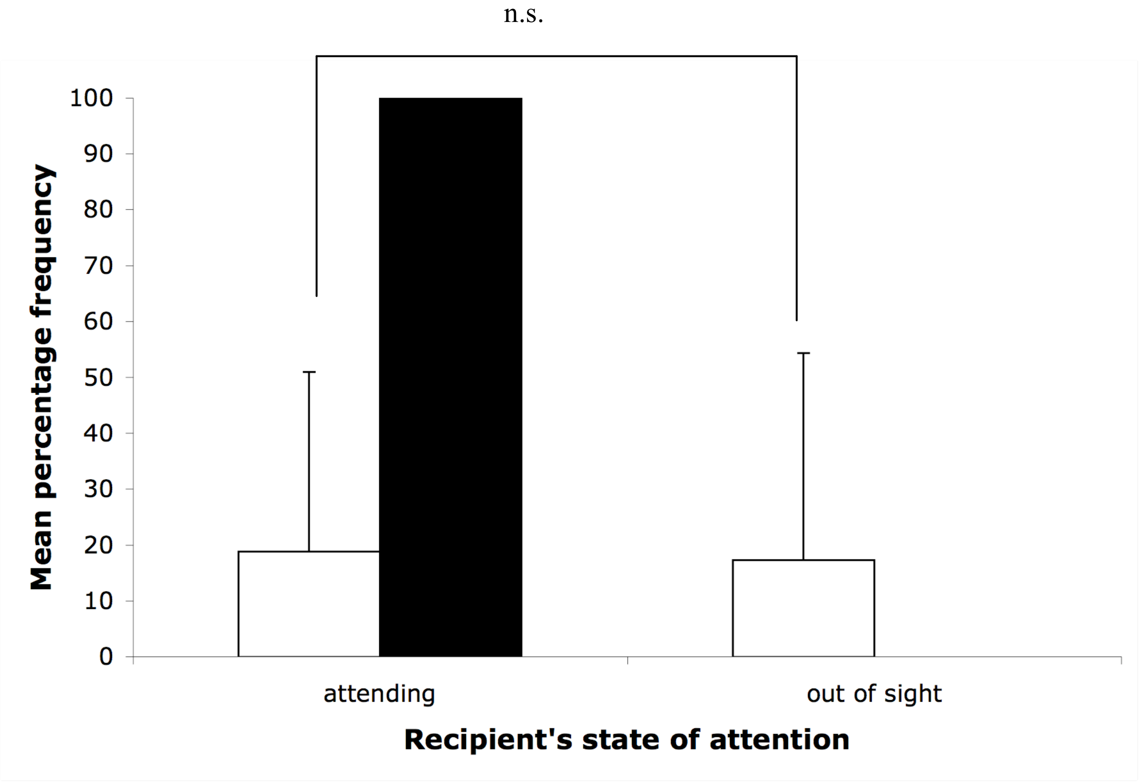


Figure 24: Frequency of successful location matching with variation in recipient's state of attention. The percentage frequency of each gesture with which the recipient grooms the signaller in the same location as the signaller 'indicated' when the recipient was either attending or unable to see the signaller. White bars represent BL-scratch gestures, black bars represent Present-groom gestures. Notification n.s. represents no significant difference.

These findings demonstrate that grooming responses were not significantly matched to the location of BL-scratch gestures; that the recipient's ability to receive any visual location information was not taken into account in the use of BL-scratch gestures; and that even when recipient's were in a position to passively receive visual information they were no more likely to groom the scratched-location than recipient's who were unable to see where the scratch had occurred. This contrasts strikingly with Present-groom gestures: these were used in a targeted fashion towards attentive recipients and subsequent grooming responses did match the indicated location.

9.2.3.2 The use of gesture combinations

Did the location of gestures remain consistent with repetition?

Gestural communication can consist of strings of multiple gestures; these can involve simple repetition of a single gesture or complex combinations of several. These gestures are assumed to be part of the same communication and have the same function. 21.13% of BL-scratches occurred in multiple BL-scratch communications; however, 100% of these communications contained variations in the location of the BL-scratches. For example: a BL-scratch on the arm, might be followed by response-waiting and then a second BL-scratch this time on the head. There were no examples of repeat Present-groom gestures within a single bout of communication.

Was there any evidence for combinations of different categories of gesture?

The paragraph at the start of this chapter describes the use of a BL-scratch to an inattentive recipient, followed by response waiting by the signaller and, when the recipient starts to pay attention, the production of a silent Present-groom gesture. Although observations such as this one initially suggest the possibility of a basic syntax in an attention getter + informative gesture combination, this is not the only interpretation. It is equally possible that both gestures function as intentional requests, each with a ‘groom me’ function, and the variation in the modality of gesture simply reflects the appropriate modification of the signaller’s use of gesture to the recipient’s state of attention.

As discussed in Chapter 3, I consistently found no evidence for any category of ‘attention-getter’ gestures. This is again supported here; where, of the 23 cases of combined BL-scratch + Present-groom gestures, the majority were (16/23) contained within single G-clauses with no response waiting between the gestures. This, along with the independent use of BL-scratch gestures, supports the definition of the BL-scratch as a functional audible gesture, which is employed as a basic ‘groom me’ communication; rather than any form of attention-getter with no inherent meaning.

Instead of the use of ‘attention-getters’ to inattentive recipients, individuals would either produce communicative audible, or contact gestures; or would relocate to a position where the recipient was in full view of any silent gestures. On two occasions, young chimpanzees positioned their mothers with repeated directed-pushes so that their mothers turned around to face them, before the young chimpanzee then produced silent Present-groom gestures. In both of these situations, the mothers were engaged in grooming the signaller’s siblings and simply moving into a position where the signaller could produce a silent gesture may not have been an effective solution.

9.2.3.3 Use of BL-Scratches in contexts outside of grooming

BL-scratch gestures were also observed outside of the grooming context. The distribution of the gesture across contexts in the complete gesture data set is described in Table 27.

Table 27: The distribution of BL-Scratch gestures in different situational contexts

Context	Frequency
Affiliating	2 (0.85%)
Feeding	1 (0.43%)
Grooming	207 (88.09%)
Play	2 (0.85%)
Resting	1 (0.43%)
Travelling	22 (9.36%)

Although the dominant context of use was grooming, almost 10% of cases were reported in the travelling context. These gestures were usually produced by resting individuals shortly before moving off; for example in one typical case Kwera was sitting with her sub-adult son Kwezi and daughters Karo (juvenile) and Karibu (infant). Kwera produced a BL-scratch, waited for a response but got none, she moved off a little way and repeated the gesture. At this point Kwezi produced a BL-scratch, Kwera replied with another BL-scratch, Kwezi got up and moved towards her, she repeated the gesture and they moved off together, followed shortly after by the two sisters.

The majority (18/22) of BL-scratch gestures used in travelling were produced between mothers and their dependent offspring in this way. Although this bias may simply be a result of the fact that in Budongo many of the travelling parties consist of individual family units. The function of the gesture in this context remained unclear; however, again it did not appear to function referentially but as a communicative audible gesture.

9.2.4 Discussion

I found no evidence to suggest that Big Loud-scratch gestures served to draw attention to a desired location for grooming. That purpose was achieved much more successfully by the silent Present-groom gesture. In fact I found no evidence that either the signaller, or recipient, treated the BL-scratch gestures as having any visual information.

There was no modification of the use of BL-scratches with regards to the recipient's ability to see the gesture, and so any visual location information it might contain. This contrasted strikingly with the use of silent Present-groom gestures, which were produced almost exclusively to attentive recipients, and functioned very effectively to direct grooming to the indicated location. This failure to adjust to the attention state of the audience might suggest that the BL-scratch was not in fact a gesture, and was simply an effective self-grooming scratch.

Even without any intent to communicate referentially, scratching may still function to passively direct the recipient's attention to the location of scratch. When observing chimpanzee grooming, it is obvious to see the immediate interest in the discovery of a parasite. The attention of both groomer and groomie becomes highly focused, and the groomer may produce lip-smacking and teeth-clacking behaviours. Sometimes the parasite is carefully transferred to a leaf for closer inspection, and even bystanders may approach for a closer look. Loud obvious scratching by one individual may suggest the presence of parasites and this alone may serve to draw the attention of a potential groomer to the location of the scratch. Pika and Mitani (2006) argue that the variation in use of the gesture with rank argues against this interpretation as an 'unintentionally' communicative signal. While the use of the gesture by all age-sex classes at Sonso did not lend itself to an analysis by rank, there were 2 other findings that supported the case for a 'gestural' interpretation of the scratch behaviour.

Firstly the slow deliberate action that defines a BL-scratch was quite different from the short, rapid motion of effective self-grooming scratches. In addition to this, all actions coded as gestures within this study were accompanied by some measure of intentionality, such as response-waiting or persistence. So rather than suggesting that the BL-scratches were effective actions not being used in an intentionally communicative manner, I suggest that the failure to modify the gesture to the recipient's attentional state was simply due to their use as a purely audible signal with no visual content.

This is supported by the fact that, unlike the Ngogo community, Sonso recipients also failed to treat the signal as containing any visual information, even when they were in a position to do so. If they were simply motivated by an attraction to a potentially interesting parasite, I would still expect any subsequent grooming to be matched to the location of the scratch. However, the frequency of location matching for attentive recipients capable of receiving any location information (intended or otherwise) was still below 40%, and no different to that of inattentive recipients who had no means of knowing where the gesture had occurred. It is more likely that any successful location matching at Sonso reflected a chance base rate, given that there are only so many possible convenient locations for grooming to occur.

Finally if the BL-scratch did serve to indicate a specific location for grooming then repetition of the gesture within a single bout of communication should be restricted to the same location on the signaller: but this was not the case. Instead BL-scratches were performed in multiple locations within the same request for grooming, again suggesting that the gesture was used as an audible 'groom me' request with no specific location information.

Once again I find no evidence for the use of gestures as simple 'attention-getters', instead I find, as Liebal found (Liebal et al., 2004a), that signallers would either use gestures appropriate for inattentive recipients, such as audible or contact gestures; or they would move into a position where the recipient could clearly see any silent gestures. Of far greater interest are the two cases where the individuals persisted in gesturing repeatedly to achieve the result that the recipient turned to face them, before then producing silent 'present-groom' gestures. In both cases the recipient was occupied in grooming another individual, and the position of the group (strung out along a branch/fallen tree trunk) prevented the normal tactic of the signaller simply moving around into a position where the silent groom me gesture could be perceived. Instead they employed the 'direct-push' gesture, usually used to position a recipient to *receive grooming* (for example: a direct-push to the arm so that the signaller can groom the underarm area); but in this case they employed it to position the recipient to then *receive their second communication* 'direct your attention here'. As I found no evidence for a class of 'meaningless' attention-getting gestures, this seems to reflect the use of a primary gesture towards one goal, *in order* to produce a secondary gesture towards an ultimate goal. Both gestures are meaningful functional communications; however in order to communicate the ultimate goal: 'direct your attention here'; they must first communicate a prior step on the way to achieving this: 'move into position'.

The absence of directed-scratch behaviour at Sonso leads to one of two possible conclusions, that there are either: no referential scratch gestures within the Sonso community, or, there are no referential scratch gestures in wild chimpanzees but a group specific variation in the way in which recipients respond to BL-scratches.

The case for the intentional use for referential scratch gestures at Ngogo contains one serious flaw: the authors include in the definition of the directed-scratch gesture that it 'could be seen by his grooming partner' pp191 (Pika and Mitani, 2006). In doing so they presuppose the visual nature of the gesture by selecting for cases given in full view of the recipient, and then use the response of the individual to the visual information to argue that the gesture functions referentially.

In other words they assume the gesture has visual content that is used in an intentional manner by the signaller, and then argue that the response of the *recipient* shows that the *signaller* is using the gesture in an intentional referential manner. The only way to confirm that a gesture is being intentionally used as a visual signal by the signaller is to check that, as with other primarily visual gestures such as silent types, it is preferentially used towards attentive recipients by examining all uses of the gesture (see Chapter 1). However, Pika and Mitani's definition leads them to discard any cases of a loud exaggerated scratch gesture given when the recipient is not attending. This means that they only consider cases produced in full view of the recipient and are therefore unable to verify that the gesture is *intentionally produced* towards attentive recipients. At Sonso, less than 40% of all BL-scratch gestures were directed towards an attentive recipient. Had I followed Pika and Mitani's definition over 60% of all cases would have been discarded, despite clear evidence that they were being used in intentional gestural communication. It was only in considering these cases that I was able to demonstrate that Sonso chimpanzees make no attempt to focus their use of BL-scratch gestures towards attentive recipients, suggesting that they do not intend to communication any visual information, such as location.

The failure by Pika and Mitani to consider the case for BL-scratch gestures produced to inattentive recipients is a serious one; and, without revisiting this, their conclusions can only be considered tentative. However, even when we consider the sub-group of BL-scratches produced to attentive recipients, the frequency of location matching at Sonso is much lower than at Ngogo, suggesting that there may be a consistent group difference in the behaviour of the recipients. The data described are consistent at least with the suggestion that within the Ngogo community *recipients* benefit from the visual component of this audible gesture to direct their grooming. However, the intentional use of the visual channel by the *signaler*, i.e. the targeted use of the gesture towards attentive recipients able to see where the scratch is produced, must be shown before any conclusions about its use as a referential signal can be confirmed at Ngogo or elsewhere.

At Sonso the non-targeted use of BL-scratches across attentive and inattentive recipients, the inconsistency of location in repeated communications, and the failure of the recipients to adjust their responses in line with the gesture's location, clearly demonstrates that BL-scratch gestures are not used referentially in the Sonso community. Instead individuals are able to direct the attention of a grooming partner with the very effective Present-groom gesture. It may be possible to argue that the Present-groom gesture functions as a very weak referential communication; however there is a distinct difference between drawing your partners attention to the ball in the corner by pointing to it, and by drawing their attention to it by bringing it to them and holding it in front of their face. When grooming an individual, it is simply much easier to groom the area presented to you than it is to either move yourself, or reposition the individual. Thus, as was the case in whole-hand pointing, it would be more appropriate to describe the Sonso community as simply having no need for a referential scratch gesture in the grooming context.

Chapter 10. Function: what does it all mean?

10.1 Introduction

Perhaps the most obvious question when examining any communication is: what does it mean? It is then surprising that the meaning of gestural communications is barely touched upon in the literature to date. The much-touted flexibility of gestures, described by Tomasello and colleagues as the use of 'the same signal for different ends, and … different signals for the same end' (Tomasello et al., 1994, p151), is reported in terms of the number of *contexts* in which the gesture is observed; and Liebal et al. clearly state that 'the function of a gesture is defined by the context in which is used' (Liebal et al., 2004a, p394).

Undoubtedly, it is possible to draw parallels between context and meaning: in general, communications produced within the context of play will have a meaning associated with play behaviour. My own analyses of flexibility have followed the existing methodology of using context to describe flexibility, partly to allow for comparison with the existing literature, but partly because there are very practical reasons for using context rather than meaning in the analysis of gesture. The context in which behaviour is produced is an external set of observable environmental and behavioural circumstances that can be objectively defined; in contrast, describing what an individual 'means' by a gesture requires an explanation of the individual's invisible internal thought processes. These sort of assertions about what we 'know' someone to be thinking are usually rather precariously founded on assumptions that we extrapolated from our own understanding of the world.

Even within our own species, an everyday assumption about what was 'meant' by another individual of our own age and culture can be easily misplaced; nevertheless, in this situation the objective scientist (or the friend with their foot in their mouth) can simply enquire as to what the individual actually meant. In contrast, if we consider the case of pre-linguistic human infants, let alone individuals from other species, the task of objectively defining meaning becomes considerably more difficult. Mothers regularly ascribe meanings to their infant's early attempts at vocalization (Papaeliou et al., 2002), yet the majority of us have no memory of our pre-linguistic phase, and by definition pre-linguistic infants are unable to tell us whether or not our assumptions about the meaning of their communications are accurate. In a similar fashion the physical similarity we have to many other primate species can easily lead the interpretation of meaning into the murky swamp of anthropomorphism. As Morris notes:

> '*If a zoologist sees that an animal such as a fish has, say, a 'fierce expression' he will be in little danger of drawing the conclusion that this generally indicates an aggressive motivation… but when an observer notes a 'fierce expression' on the face of a monkey or ape, he is less likely to discard it.*' (Morris, 1967, p.2).

Thus, in using context as an approximate, but objective, substitute for meaning, we are able to avoid the hazard of attempting to interpret the inner thoughts of another species; and yet to have to make do with an approximation seems rather unsatisfactory given the importance of meaning in communication. To return to the case of communication in play behaviour, it is possible that individual gestural communications produced during play have very different meanings, for example: 'start playing with me', and 'stop playing with me' would both be lumped by a context driven method but represent polar opposites in terms of the actual meaning to the recipient of the communication. On the other hand, stop playing with me, and stop begging from me would be separated by a context based method but have much more in common in terms of the desired change in the recipient's behaviour. Perhaps most worryingly for the argument in favour of the flexible use of gesture, if a single gesture had the single meaning 'stop behaviour' it could be used in multiple contexts and would appear, when using a context based methodology, to be flexible when in fact it was fixed.

One solution to this problem is to approach the definition of meaning from another perspective, not by asking what does the communication mean, but what is it for? In other words what is the function of the communication?

In a broad sense communications function to alter the behaviour of the recipient towards a specific goal: once that goal is achieved, intentional communication would be expected to stop. By this logic we can define the function of an intentional communication in terms of the change in the behaviour of the recipient that leads to the cessation of communication. As the change in behaviour will, in many cases, be an observable external event, we avoid the pitfalls of attempting to 'mind-read' the intention of the signaller. This method is somewhat conservative; it prevents the assignation of function to any unsuccessful communications, and also cannot account for communications that are produced with the function of preventing any change in the recipient's behaviour. Nevertheless, taking this approach, 2 recent studies of great ape gesture found ample cases for analysis; and were able to show that individual gestures were: used flexibly towards a number of functions, had a specific distribution of functions for which they were used, and usually had one or two dominant functions for which they were usually used (gorillas: Genty et al., 2009; orang-utans: Cartmill and Byrne, 2010).

In this chapter I define the range of functions for which gestural communication was employed; and, where sufficient data are available, I examine whether or not individual gesture types are associated with specific functions and to what extent a gesture's meaning can be defined as specific or ambiguous.

10.2 Specific method

10.2.1 Detailed definition of function

As discussed in the main method I define the likely function of a communication in terms of the behaviour that appears to satisfy the gestural communication, i.e. the one that immediately precedes the cessation of attempts to communicate by the signaller.

Where a G-clause fails and the signaller persists in further communication, I define any additional G-clauses as produced towards the same function as the first; hence function was assigned at the level of the G-sentence. As function is defined in terms of a successful response (that results in the cessation of communication), all unsuccessful cases are assigned the function 'unknown'.

In order to be defined as a function, the behaviour in question must fit a plausible biological need on the part of the signaller. Certain behavioural responses were therefore ruled out as failures; for example: it is extremely difficult to think of a plausible biological need on the part of the signaller to be aggressively chased by the recipient. Following this logic a simple change in attention was not considered to be a successful behavioural response; particularly given the growing body of evidence which argues against the existence of gestures which serve simply to get the recipient's attention (Liebal et al., 2004a, Call and Tomasello, 2007, Genty et al., 2009).

Behaviours considered failures:

- Recipient changes attention state but makes no further response.
- Recipient leaves without this resulting in any plausible biological advantage to the signaller.
- Recipient physically prevents the signaller from continuing to gesture.
- Recipient aggressively chases the signaller away.
- No change in the behaviour of the recipient.

During the study I observed on a number of occasions that individuals approaching high-ranking males would produce the submissive pant-grunt vocalisation and gesture at the same time. It is usual in chimpanzee society to produce submissive pant-grunt vocalisations when approaching, or approached by, a higher-ranking individual. This behaviour is so consistent researchers use it as the basis for defining an individual's social rank within the community: all individuals to whom you pant-grunt are considered higher ranking, and all those who pant-grunt to you are considered lower ranking. Typically the response of the individual to whom you pant-grunt is to make no change in their existing behaviour (in contrast, failing to pant-grunt can lead to threat and/or attack from the higher ranking individual). Similarly a gesture given while pant-grunting received no response from the recipient; however, the signaller rarely persisted in further communication. I felt that these gestures might function as a request for the higher-ranking individual to 'remain in the same state'. However, it was impossible to confirm if this was in fact the true function of the behaviour, as it was impossible to objectively distinguish these cases from those where the lack of response was due to the failure of another communicative function.

For this reason ‘remain in the same state’, while a possible function of chimpanzee communication, has not been included in this analysis.

10.2.2 The distribution of functions in gesture use

In their study of gorilla gesture, Genty et al. showed that gestures were not produced for a single function, but were instead produced flexibly towards a range of functions with varying degrees of frequency (Genty and Byrne, 2009). For example: the gesture ‘arm swing’ is predominantly produced as an invitation to start play, and this would be described as its *primary function*. However, it may also, occasionally, be produced in order to displace an individual or to request an object etc. these, in rank order of frequency, are referred to as the *secondary function* and *tertiary function* and so on. The *distribution of functions* describes the frequency with which each of the possible functions is observed in any one type of gesture.

Following the protocol defined in Genty et al. (Genty et al., 2009), the total distribution of functions in the data set (produced by pooling the data across gesture types), served as a null distribution against which the distribution of functions for any individual gesture type could be compared; this is referred to as the *general distribution of functions.*

10.2.3 Specificity of meaning

In their paper on semantic meaning in orang-utan gesture Cartmill and Byrne (2010) adopt a different approach to specifying the meaning of a particular gesture. They defined a gesture as having a ‘tight’ meaning in cases where a gesture was found to have a single function in over 70% of cases and where this function was observed three-times as often as the next most common. A ‘loose’ meaning was assigned where a single function accounted for 50-70% of cases and was observed twice as often as the next most common. All other cases were assigned as having ‘ambiguous’ meaning.

A gesture may have a *primary* function that is observed significantly more often than any other function but this primary function may account for less than 50%

of use. Thus, a gesture may have a dominant *primary* function and still be classified as having a 'loose' or 'ambiguous' meaning.

In order to discuss the functions for which chimpanzees use gestures I first considered whether or not individual gestures had a dominant primary function and then also whether or not this could be classified as a tight, loose or ambiguous meaning.

I restricted my detailed analysis of function to gestures with 5 or more cases from 5 or more individuals; however, only 14 gestures met the criteria for inclusion. In order to provide an overview of meaning within the wider repertoire, I also combined all individual data and analysed the use of any gesture that was produced at least 4 times towards any one function. This broad analysis follows the protocol used by Cartmill and Byrne in their analysis of the semantics of orang-utan gesture (2010) and, thus, provides an equivalent level for comparison. 50 of the total repertoire of 66 gestures met the conditions for analysis in this case.

10.2.4 Choice of statistical analyses

My initial analysis of the distribution of function in individual gestures followed Genty et al. (Genty et al., 2009), by running a series of Chi-square tests comparing the observed distribution of functions for which a gesture-type was used, with the 'null' general distribution of functions within the data set. However, as this method fails to take into account the effect of pseudo-replication within the data set I followed this with a second more detailed parametric analysis. Here individuals only contributed the mean of their data, eliminating the possibility that one particularly prolific individual would skew the group findings towards their own behavioural norm.

Procedure for detailed parametric analysis of function

I calculated the mean distribution of functions for each individual's use of a gesture by dividing the number of cases of use for that function (n) by the total number of cases of that gesture (N) for each individual. Critically the total number of cases of that gesture (N) included all use of the gesture, not just where it was possible to define a function (i.e. it included cases where the function has been assigned as unknown). By including cases with an unknown function in the total N, I eliminated the possibility of a forced dependency between gesture and function that would have rendered the data unsuitable for parametric analysis.

Next, in all cases where the resulting mean value (n/N) was equal to 0 or 1, I re-scaled the values using the following substitutions: where $x=1$, the value was replaced with $x=1-(1/4N)$; where $x=0$, the value was replaced with $x=1/4N$. I then applied the transformation: Arcsine($\sqrt{x}$) uniformly across the data set. These steps correct for non-homogenous distribution of variation and render the data suitable for parametric analysis with uni-variate ANOVA (following method recommended in: Snedecor and Cochran, 1989).

I addressed three questions in this more detailed parametric analysis:

1. *Was there any effect of gesture type on the distribution of function?*

Using a 2-way Uni-variate ANOVA comparing the distribution of function between all gesture types. As different individuals contributed data to different gesture types, individual identity was coded and treated as a random factor in the analysis.

2. *In which (if any) gestures, did the distribution of function vary from the null distribution of function?*

Using a series of planned separate Uni-variate ANOVAs for each gesture comparing the distribution of function for that gesture with the general (null) distribution of function across gestures (again including individual identity as a random variable). This step is the equivalent of the chi-square analyses described in section 8.2.3 above; in this case a significant interaction between gesture (specific gesture vs. null (all gestures)) and distribution of function, would signify that the distribution of function for the specific gesture type varied from the general distribution of function in the data set. I again checked for a significant main effect of the random variable: individual identity, as this might suggest that any other significant findings were the result of variation between individual chimpanzees.

3. *Were individual gestures significantly associated with a single primary function?*

Finally, to establish whether or not individual gestures were predominantly used for a single primary function, I ran a series of planned paired t-tests, comparing the frequency of the most frequent (primary) and second most frequent (secondary); functions within each gesture.

10.3 Results

10.3.1 What were the functions of chimpanzee gestural communication?

1651 cases of communication (1194 single G-clauses used individually, and 467 G-sentences) were followed by a successful response that led to the cessation of communication. From these I identified the following 17 functions:

1. Climb on: recipient climbs on signaller's body (n=52, 3.2%)
2. Climb on you: recipient permits signaller to climb on them (n=9, 0.6%)
3. Direct attention: the recipient adjusts their behaviour to focus attention on the location indicated in the signaller's gestural communication (n=202, 12.5%)
4. Follow: recipient follows signaller (n=59, 3.7%)
5. Give affiliation: recipient gives signaller affiliation, usually in the form of physical contact such as hugging, touching etc. (n=60, 3.7%)
6. Give object: recipient gives signaller object (e.g. food, leaf sponge, etc.) (n=45, 2.8%)
7. Give sexual attention: recipient gives signaller sexual attention (e.g. inspection, copulation etc.) (n=87, 5.4%)
8. Groom me: recipient grooms signaller (n=45, 2.8%)
9. Groom you: recipient accepts grooming from the signaller (n=3, 0.2%)
10. Move away: recipient moves away from signaller (n=61, 3.8%)
11. Move closer: recipient moves towards signaller (n=48, 3.0%)
12. Play change chase-contact: the recipient changes the type of play from chasing play to contact (e.g. wrestling) play (n=18, 1.1%)

13. Play change contact-chase: the recipient changes the type of play from contact (e.g. wrestling) to chasing play (n=3, 0.2%)
14. Play continue: the recipient resumes playing after a pause in the activity (n=126, 7.8%)
15. Play start: the recipient starts to play (n=641, 39.8%)
16. Position: the recipient moves and holds a body part in the indicated position (n=79, 4.9%)
17. Stop behaviour: the recipient either stops a behaviour previously directed towards the signaller or changes their behaviour to direct it towards another individual (n=73, 4.5%).

All 17 functions were imperative requests for a change in the recipient's behaviour. 15 were positive requests to encourage further interaction such as Groom me, Climb on me, or Play change chase-contact. 2 of the functions, Stop behaviour and Move away, were negative requests to prevent or discourage further social interaction.

The most prevalent function was *Play start* (n=641, 39.8%), followed by *Direct attention* (n=202, 12.5%) and *Play continue* (n=126, 7.8%). *Play change* communications were dominated by requests to move from chasing to contact play, rather than vice versa (ratio of respective frequencies 6:1).

10.3.2 Were gestures used flexibly for multiple functions?

Sonso chimpanzees used individual gestures flexibly for a mean 4.0 ±2.7 functions (range 1-11, mode =2); and used a mean 15.6 ±14 gestures per function (range 3-57, mode =3). However, there was a significant correlation between the number of cases of a gesture and the number of functions with which it was recorded (gestures with 5 or more cases, Pearson's correlation: r=0.72, n=58, p<0.001).

10.3.3 Were there significant differences in the flexible use of gesture as described by function as opposed to context?

17 functions were identified, in contrast to the 10 contexts. Gestures were recorded as used with slightly more functions (mean functions per gesture =4.0 ±2.7)

than contexts (mean contexts per gesture =3.5 ±2.3), Paired 2-way t-test: t=2.796, df=60, p=0.007.

10.3.4 Did individual gestures have a specific distribution of functions?

14 gestures met the conditions for individual analysis; these gestures were associated with a mean 2.30 functions (±1.06). Arm swing (2.56 functions ±1.59); Big loud scratch (2.11 ±0.60); Dangle (2.18 ±0.98); Directed push (3.00 ±1.66); Grab (1.92 ±0.79); Object move (2.60 ±0.55); Object shake (2.64 ±1.01); Present grooming (1.18 ±0.40); Present sexual (1.80 ±0.84); Reach (2.70 ±0.82); Slap object (2.80 ±1.14); Slap other (2.00 ±0.89); Stomp (2.63 ±0.92) and Stomp 2-feet (2.00 ±0.63).

The general distribution of functions was calculated by summing the distribution of function across the 14 gesture types. As with the total data set, within the general distribution of this subgroup the most common function was again *Play start* (580/1316 cases, 44.1%), but *Follow* (161/1316, 12.2%) was the second most frequently observed function, and then *Move closer* (101/1316, 7.7%) (see table 28 for the details of each individual function). The distribution of function in each of the 14 gestures varied from the general distribution in a highly significant fashion (see Chi squares in Table 28). However, as there was the potential for pseudo-replication in the raw data, I checked these findings with more rigorous parametric analyses of average values (see Table 29 for mean distribution of functions).

Here, I found that the distribution of functions varied significantly between gestures (f=22.76, df=238,2177 p<0.0001); and that, again, in each individual gesture the distribution of function varied significantly from the general distribution (see Table 30, anova results). As highlighted in Table 30, I find a main effect of individual identity in only one gesture: Big loud scratches, in this case the variation in the distribution of functions may be as a result of individual differences in use between chimpanzees.

Table 28: Function of individual gestures (raw frequency data)
The notations * and ** refer to a Chi-square result of $p=0.01$ and $p<0.0001$ respectively, representing a significant deviation from the overall 'null' distribution of functions; numbers in **bold** represent the primary function for each gesture type.

	Function																
Gesture	Climb on me	Climb on you	Direct attention	Follow	Give affiliation	Give object	Give sexual attention	Groom me	Groom you	Move away	Move closer	Play change chase-contact	Play change contact-chase	Play continue	Play start	Position	Stop behaviour
Arm swing **	0	0	0	15	0	1	0	0	0	0	14	3	0	10	**57**	0	1
Big loud scratch **	0	0	**9**	4	0	0	0	**38**	**6**	0	0	0	0	0	0	0	0
Dangle **	0	0	0	0	0	0	0	0	0	0	8	1	0	21	**171**	0	0
Directed push **	17	0	5	1	0	0	0	0	0	10	25	0	0	0	1	**48**	0
Grab **	1	2	1	0	0	0	0	0	1	2	0	4	0	17	**93**	0	0
Object move **	0	0	0	28	1	0	1	0	0	2	7	0	0	3	**16**	0	0
Object shake **	0	0	0	**102**	0	0	27	0	0	19	35	0	0	2	47	0	5
Present (grooming) **	0	0	**79**	0	0	0	0	2	0	0	0	0	0	0	**0**	0	0
Present (sexual) **	0	0	1	0	2	0	**44**	0	0	1	0	0	0	0	1	0	0
Reach **	0	1	1	0	3	**27**	4	0	0	0	2	0	0	2	22	0	2
Slap object *	0	0	0	7	0	0	2	0	0	5	5	1	0	8	**54**	0	4
Slap other **	0	0	0	0	0	0	1	0	0	0	0	0	0	6	**44**	0	1
Stomp **	0	0	0	4	1	0	1	0	0	0	4	1	0	7	**45**	0	2
Stomp 2-feet **	0	0	0	0	0	0	0	0	0	0	1	0	0	3	**29**	0	4
General distribution	*18*	*3*	*96*	*161*	*7*	*28*	*80*	*40*	*7*	*39*	*101*	*10*	*0*	*79*	***580***	*48*	*19*

Table 29: Function of individual gestures (individual mean data)
The individual distribution of all gestures deviated significantly from the general distribution of functions (individual ANOVAs all p<0.0001, see table 30 for details); numbers in **bold** represent the primary function for each gesture type.

	Function: mean frequency ±s.d.																
Gesture	Climb on me	Climb on you	Direct attention	Follow	Give affiliation	Give object	Give sexual attention	Groom me	Groom you	Move away	Move closer	Play change chase-contact	Play change contact-chase	Play continue	Play start	Position	Stop behaviour
Arm swing	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	8.8 ±26.3	0.0 ±0.0	0.5 ±1.5	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	9.8 ±10.9	2.0 ±4.5	0.0 ±0.0	8.4 ±9.6	**70.1** **±33.1**	0.0 ±0.0	0.5 ±1.5
Big loud scratch	0.0 ±0.0	0.0 ±0.0	12.1 ±14.7	10.0 ±28.3	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	**67.1** **±24.3**	10.8 ±12.7	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0
Dangle	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	4.5 ±6.8	0.3 ±1.1	0.0 ±0.0	8.8 ±8.7	**86.4** **±11.5**	0.0 ±0.0	0.0 ±0.0
Directed push	17.2 ±22.9	0.0 ±0.0	9.2 ±26.6	0.3 ±1.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	5.5 ±6.7	13.1 ±25.1	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	1.4 ±4.2	**53.3** **±32.8**	0.0 ±0.0
Grab	1.1 ±3.8	1.8 ±6.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	1.0 ±3.4	1.5 ±3.5	0.0 ±0.0	2.2 ±5.0	0.0 ±0.0	9.1 ±13.7	**83.2** **±16.8**	0.0 ±0.0	0.0 ±0.0
Object move	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	29.9 ±41.0	2.5 ±5.6	0.0 ±0.0	4.0 ±8.9	0.0 ±0.0	0.0 ±0.0	3.6 ±8.1	6.4 ±10.1	0.0 ±0.0	0.0 ±0.0	9.0 ±8.8	**44.5** **±41.8**	0.0 ±0.0	0.0 ±0.0
Object shake	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	8.4 ±22.5	0.0 ±0.0	0.0 ±0.0	22.7 ±29.0	0.0 ±0.0	0.0 ±0.0	17.9 ±20.3	7.8 ±7.4	0.0 ±0.0	0.0 ±0.0	2.1 ±4.6	**37.9** **±34.6**	0.0 ±0.0	3.3 ±11.0
Present (grooming)	0.0 ±0.0	0.0 ±0.0	**97.2** **±6.3**	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	2.8 ±6.3	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0
Present (sexual)	0.0 ±0.0	0.0 ±0.0	2.0 ±4.5	0.0 ±0.0	10.0 ±22.4	0.0 ±0.0	**84.8** **±21.1**	0.0 ±0.0	0.0 ±0.0	1.2 ±2.6	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	2.0 ±4.5	0.0 ±0.0	0.0 ±0.0
Reach	0.0 ±0.0	1.4 ±3.9	1.3 ±3.5	0.0 ±0.0	7.5 ±17.5	**42.9** **±31.6**	10.4 ±14.6	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	2.5 ±7.1	0.0 ±0.0	0.0 ±0.0	3.2 ±5.9	27.8 ±28.3	0.0 ±0.0	3.1 ±8.8
Slap object	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	6.0 ±18.0	0.0 ±0.0	0.0 ±0.0	1.7 ±5.1	0.0 ±0.0	0.0 ±0.0	8.4 ±11.6	4.2 ±8.5	1.6 ±4.8	0.0 ±0.0	9.4 ±11.2	**62.9** **±30.6**	0.0 ±0.0	5.9 ±7.4
Slap other	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	1.1 ±2.7	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	10.8 ±10.7	**85.8** **±13.3**	0.0 ±0.0	2.4 ±5.8
Stomp	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	10.0 ±28.3	0.7 ±2.0	0.0 ±0.0	2.5 ±7.1	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	6.0 ±9.6	2.5 ±7.1	0.0 ±0.0	12.7 ±14.5	**62.4** **±32.9**	0.0 ±0.0	3.2 ±5.9
Stomp 2-feet	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	3.7 ±10.5	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	4.0 ±7.8	**77.5** **±27.1**	0.0 ±0.0	4.3 ±10.4
General distribution	1.4 ±6.8	0.2 ±1.5	6.1 ±23.4	3.3 ±16.7	1.3 ±6.8	6.3 ±19.5	8.6 ±24.4	4.5 ±19.1	0.1 ±0.9	2.6 ±8.0	1.9 ±9.8	0.4 ±2.2	0.0	5.6 ±13.3	**47.0** **±40.0**	2.8 ±13.9	3.1 ±13.4

Table 30. The deviation of each gesture from the general distribution of function. The results of 13 Uni-variate 2x17 ANOVAs comparing the distribution of function for each specific gesture with the null distribution (including individual identity as a random variable). Notification * refers to a significant main effect of individual identity.

Gesture	**Chi square (df = 15)**	**Uni-variate 2x17 ANOVA with individual identity as a random factor**	
		Interaction between specific gesture distribution of function and general distribution of function (df=1,16)	Main effect for individual identity (df=43)
Arm swing	χ^2 =44.88, p<0.0001	f =4.42, p<0.0001	f =1.06, p =0.398
Big loud scratch*	χ^2 =917.27, p<0.0001	f =15.56, p<0.0001	f =1.70, p =0.036
Dangle	χ^2 =170.38, p<0.0001	f =13.72, p<0.0001	f =1.01, p =0.464
Directed-push	χ^2 =791.06, p<0.0001	f =6.84, p<0.0001	f =1.45, p =0.225
Grab	χ^2 =116.11, p<0.0001	f =11.44, p<0.0001	f =0.93, p =0.605
Object move	χ^2 =82.25, p<0.0001	f =1.73, p<0.0001	f =1.18, p =0.252
Object shake	χ^2 =320.90, p<0.0001	f =2.81, p<0.0001	f =1.32, p =0.108
Present groom	χ^2 =977.50, p<0.0001	f =69.16, p<0.0001	f =1.06, p =0.396
Present sexual	χ^2 =617.23, p<0.0001	f =5.24, p<0.0001	f =0.62, p =0.851
Reach	χ^2 =531.75, p<0.0001	f =10.41, p<0.0001	f =0.93, p =0.602
Slap object	χ^2 =36.80, p=0.0014	f =4.03, p<0.0001	f =1.00, p =0.484
Slap other	χ^2 =45.65, p<0.0001	f =3.30, p<0.0001	f =0.98, p =0.511
Stomp	χ^2 =32.90, p=0.0048	f =3.04, p<0.0001	f =0.80, p =0.806
Stomp 2-feet	χ^2 =48.99, p<0.0001	f =4.52, p<0.0001	f =0.58, p =0.953

10.3.5 Did individual gestures have a dominant primary function?

I compared the frequency of the first and second most frequently observed functions in each gesture type, to establish whether the most frequently observed primary function was observed significantly more often than any other function, the results are summarized in Table 31.

Table 31. The primary function of individual gestures. The mean frequency of the primary and secondary function of each gesture was compared in a series of planned paired t-tests. Notification * represents a non-significant result at α=0.05.

	Mean % frequency (sd)		
Gesture	**Primary function**	**Secondary function**	**Paired t-test**
Arm swing	Play start (70.1% ±33.1)	Move closer (9.8% ±10.9)	t=8.25, df=10, p<0.0001
Big Loud Scratch	Groom me (67.1% ±24.3)	Direct attention (12.1% ±14.7)	t=10.35, df=10, p<0.0001
Dangle	Play start (86.4% ±11.5)	Play continue (8.8% ±8.7)	t=13.67, df=12, p<0.0001
Directed push	Position (53.3% ±32.8)	Climb on me (17.2% ±22.9)	t=3.07, df=8, p=0.015
Grab	Play start (83.2% ±16.8)	Play continue (9.1% ±13.7)	t=8.35, df=17, p<0.0001
Object move	Play start (44.5% ±41.8)	Play continue (9.0% ±8.8)	t=5.40, df=9, p<0.0001
Object shake	Play start (37.9% ±34.6)	Sexual attention (22.7% ±29.0)	t=2.58, df=17, p=0.20
Present (grooming)	Direct attention (97.2% ±6.3)	Groom me (2.8% ±6.3)	t=22.85, df=11, p<0.0001
Present (sexual)	Sexual attention (84.8% ±21.1)	Affiliate (10.0% ±22.4)	t=3.62, df=5, p=0.015
Reach*	Give object (42.9% ±31.6)	Play start (27.8% ±28.3)	t=1.87, df=22, p=0.074
Slap object	Play start (62.9% ±30.6)	Play continue (9.4% ±11.2)	t=7.81, df=13, p<0.0001
Slap other	Play start (85.8% ±13.3)	Play continue (10.8% ±10.7)	t=9.29, df=6, p<0.0001
Stomp	Play start (62.4% ±32.9)	Play continue (12.7% ±14.5)	t=5.47, df=14, p<0.0001
Stomp 2-feet	Play start (77.5% ±27.1)	Stop behaviour (4.3% ±10.4)	t=7.00, df=9, p<0.0001

13/14 gestures had a primary function that was observed significantly more often than the secondary function. The exception was the gesture Reach, where the difference between the frequency of the primary and secondary functions only approached significance; however, in this case both the primary function: Give object, and secondary function: Play start, were observed significantly more often than the tertiary function: Sexual attention (mean frequency 1.4% ±4.8; variation in frequency from primary function: paired t-test, $t=6.41$, $df=22$ $p<0.0001$; variation in frequency from secondary function: paired t-test, $t=3.83$, $df=22$ $p=0.001$).

10.3.6 Did individual gestures have specific meanings?

Although almost all gestures (13/14) were associated with a dominant primary function that was observed significantly more often than the next most frequent function, only 7 of the 14 gestures had 'tight' meanings (Arm swing, Dangle, Grab, Present-groom, Present-sexual, Slap other, and Stomp 2-feet). A further 4 had 'loose' meanings (Big Loud-scratch, Directed push, Slap object, and Stomp) and 3 had 'ambiguous' meanings (Object move, Object shake, and Reach). The majority (5/7) of tight meanings were *play-start*, with one *give sexual attention* (Present-sexual) and one *direct attention* (Present-grooming). See Table 29 for details.

In the broad analysis of the use of gestures by the group as a whole, 30 of the 50 gestures had tight meanings, 15 loose and 5 ambiguous. As with the detailed analysis the majority (22/30) of tight meanings were *play-start.* Some functions were only observed as secondary and tertiary functions. The tight or loose association of gestures with a function is detailed in Table 32.

10.3.7 Were there categories of meaning?

Within the set of 17 functions, I defined 8 categories of semantic meaning. The 15 positive functions could be grouped into 7 categories which encouraged further social interaction: *Affiliate* (Give affiliation, Move closer), *Co-locomote* (Climb on, Climb on you), *Follow* (Follow), *Groom* (Direct attention, Groom me, Groom you, Position), *Object desire* (Give object), *Play* (Play change chase-contact, Play change contact-chase, Play continue, Play start), *Sexual contact* (Give sexual attention). The two negative functions were grouped into a single category: *Negate* (Move away, Stop behaviour) of active refusal or prevention of social interaction (as opposed to a passive refusal such as turning away or ignoring). See Table 32.

Table 32. Specificity of gestural meaning. Gestures with a primary function that was classified as being in tight or loose association with a particular function.

Semantic category	***Function***	**Tight gestures**	**Loose gestures**
Affiliate	*Give affiliation*	Embrace	Shake hands
	Move closer		
Co-locomote	*Climb on*	Present climb-on	
	Climb on you		
Follow	*Follow*	Slap object with object	Object shake, Throw object
Groom	*Direct attention*	Present-groom	
	Groom me	Big Loud-scratch	
	Groom you		
	Position	Directed push	
Negate	*Move away*	Hand fling	
	Stop behaviour		Pirouette
Object desire	*Give object*	Mouth stroke	Reach
Play	*Play change chase-contact*		
	Play change contact-chase		
	Play continue		
	Play start	Arm shake, Bite, Dangle, Drum object, Drum other, Gallop, Grab, Hand shake, Head nod, Head stand, Kick, Knock object, Leg shake, Leg swing, Object in mouth, Object move, Poke, Pounce, Punch object/ground, Roll over, Slap other, Stomp, Stomp 2-feet	Arm swing, Grab-pull, Hand on, Side roulade, Slap object, Somersault, Tap other
Sexual contact	*Give sexual attention*	Leaf clipping	Present-sexual

Within the broad analysis of the whole repertoire, 45 gestures were categorized as having tight or loose meanings. The majority of these were in the category *play.* See Figure 25.

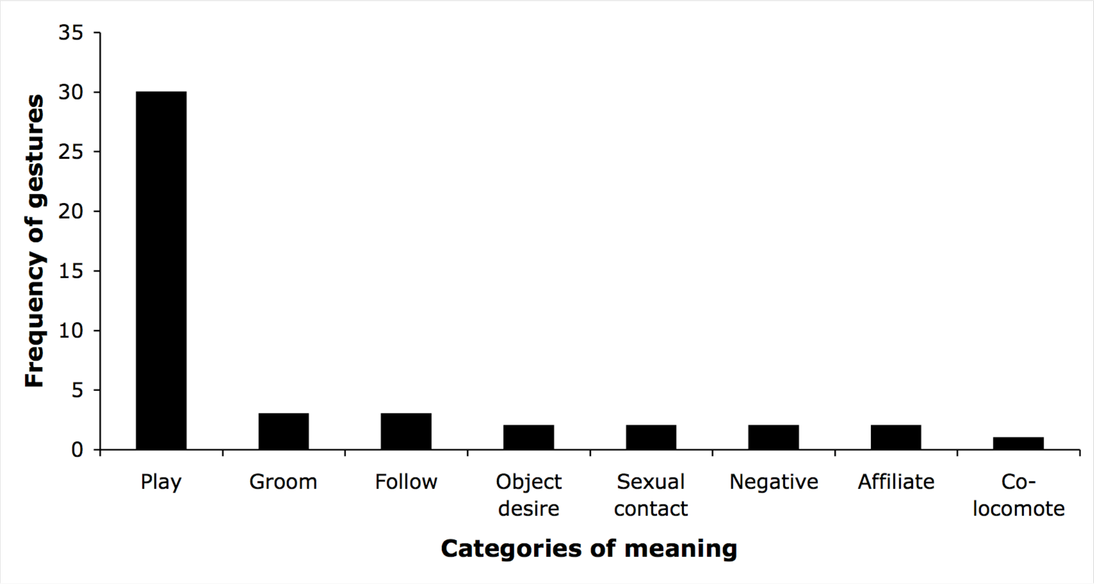


Figure 25. Distribution of gestures across categories of meaning. The number of gestures defined as having a tight or loose meaning within each category. Ambiguous gestures were excluded.

10.3.8 Ambiguous meanings

There was no strong evidence for a general effect of individual use on the meaning of gestures. Of the 14 gestures analysed in detail, the dominant function remained the same when analysed by total number of cases (total frequency of use, see Table 28), or by individual mean frequency of use (corrected for pseudo-replication, see Table 29). However, in one gesture – object shake- which was defined as having an ambiguous meaning, the dominant function changed from an ambiguous association with a primary function *follow* when measured by the straight frequency of cases (see Table 28), to a ambiguous association with a primary function *play-start* when measured by the mean individual usage (see Table 29).

10.3.9 Was there a species overlap in the function of individual gestures?

Genty et al. (2009) describe 10 functions in gorilla gestural communication; 8 of these functions had direct correlates in the gestural communication of Sonso chimpanzees, 1: Attention getter, was not considered to be a function in this analysis, leaving only the Calm down request function as distinct to the gorilla group, although as noted this behaviour may have been occasionally included within the Stop behaviour function at Sonso (see Table 33). For example: when a juvenile became overly boisterous in play with a young infant it was not uncommon for the mother of the infant to intervene to stop the behaviour; this may have been similar to the Calm down requests coded by Genty et al.

Cartmill and Byrne (2010) describe 8 functions in orang-utan gestural communication; 6 have direct correlates with the Sonso chimpanzees. As with the gorilla function ‘Attention getter’, the orang-utan function ‘Look towards signaller’, was not considered to be a function in this analysis but may have some overlap with the Direct attention function. This left only the Look at/Take object function as possibly orang-utan specific. Offering objects such as food was observed in the Sonso chimpanzees, however these were considered to be the effective action of giving, rather than a true gestural communication. 3 functions: Groom me, Groom you and Position appeared to be specific to chimpanzee behaviour.

Of the 10 gestures for which the individual distribution of function was described in gorilla communication, 2: Grab and Slap other, were included in the detailed chimpanzee analysis above (section 8.3.5). In gorilla communication Grab was described as having a primary function as a Contact play invitation, which corresponded to the chimpanzee primary function as a Play start invitation. Similarly the secondary function of Slap other was again as a Contact play invitation, corresponding to the chimpanzee primary function as a Play start invitation. Of the 29 orang-utan gestures identified as having ‘tight’ meanings, 4: Dangle, Shake-object, Hit ground/object (Sonso – Slap object) and Simultaneous hit (Sonso - Slap other), were included in the chimpanzee analysis. All 4 gestures were defined as having the primary chimpanzee function of Play start, and the Orang-utan function of

Affiliate/Play. However, Play invitations represented the most frequently observed functions in all three species; and, as there were only 6 cases for comparison, this overlap may simply have been a coincidence.

Table 33. Overlap in functions described for great ape gestural communication.

Chimpanzee functions	**Gorilla functions**	**Orang-utan functions**
Climb on	*Travel invitation*	*Co-locomote*
Climb on you	-	*Co-locomote*
Direct attention	*Attention getter* (not considered a plausible function but may be some overlap)	*Look towards signaller* (not considered a plausible function but may be some overlap)
Follow	*Travel invitation*	*Co-locomote*
Give affiliation	*Cuddle invitation*	*Affiliate/Play*
Give object	-	*Share food/object*
Give sexual attention	-	*Sexual contact*
Groom me	-	-
Groom you	-	-
Move closer	*Approach invitation*	-
Move away	*Displace*	*Move away*
Play change chase-contact	*Contact play invitation*	*Affiliate/Play*
Play change contact-chase	*Chase invitation*	*Affiliate/Play*
Play continue	-	*Affiliate/Play*
Play start	-	*Affiliate/Play*
Position	-	-
Stop behaviour	*Stop, Stop approach,* may be some overlap with *Calm down request*	*Stop action*

In contrast the Pirouette gesture was the only gesture described as having the primary function Stop in gorilla communication, with a secondary function as a Chasing play invitation. Although there were insufficient cases of pirouette gestures in the Sonso community to have included it in the detailed analysis, the pattern of use did appear to mirror that described for gorillas. At Sonso, 10 cases of pirouette gestures were recorded from 7 individuals: 6 with the function ‘stop behaviour’, 2 with the function ‘play continue’, and 2 with the function ‘play start’.

10.4 Discussion

The Sonso chimpanzees use gestural communication for a range of at least 17 separate functions all of which can be defined as imperative requests, these included 4 contrasting pairs such as groom me & groom you. 15 were positive requests that enabled further social interaction, the remaining 2 were negative requests that actively discouraged further social interaction: stop behaviour and move away. This imbalance between positive and negative requests was also found in orang-utan gesture (6 positive, 2 negative) (Cartmill and Byrne, 2010), and may be due to the very general nature of the stop behaviour request, which can be applied to a broad range of behaviour categories; however, despite the broad nature of the negative requests, they still accounted for less than 10% of all gestural communications.

The commonest function was a request for play to start, which corresponds with the finding that play was the behavioural context in which gestural communication was most frequently used. As in gorilla and orang-utan gestural communication (Genty et al., 2009, Cartmill and Byrne, 2010), Sonso chimpanzees used individual gestures flexibly towards a range of functions, and communicated individual functions using a range of gestures. Moreover, individual gestures had a specific distribution of functions, each of which varied from the general distribution of functions as a whole. Finally, while the full range of functions for which a gesture was used did increase with the number of cases of the gesture, chimpanzee gestures were almost all associated with a single dominant function observed more frequently than any other function. Only Reach gestures were used in slightly less specific fashion with two dominant functions observed more frequently than any other function.

The range of functions described was almost twice as large as the range of behavioural contexts; despite this, individual gestures were used towards only slightly more functions than contexts. Thus, I don't believe that the flexibility of gestural communication has been misrepresented by the use of contexts to describe it. However, as discussed in the introduction it is not appropriate to use context alone to define the meaning of gestures; and instead I suggest that, in terms of a single factor for analysis, function provides an equally objective and much closer representation of meaning.

While most gestures had a dominant primary function, fewer gestures were associated with tight meanings (approximately half of those in the detailed analysis and two thirds of those in the broad analysis). Thus chimpanzee gestural communication employed the use of gestures which vary from the tightly specific to the ambiguous in meaning.

Cartmill and Byrne (2010) suggest that orang-utan functions can be divided into 5 classes of desire, 4 positive: Social affiliation, Co-locomotion, Object transfer, Sexual interaction, and a negative or refusal class. Similarly, within the 17 functional requests used by Sonso chimpanzees, I could define 8 broader categories of semantic meaning (7 positive and 1 negative), although these overlapped with those described in orang-utan gesture there were some differences. Unlike Cartmill and Byrne, I distinguished *affiliate* and *play* as separate categories as, in the Sonso chimpanzees, they represented requests for different forms of social interaction. Similarly, I distinguished *follow*, from other requests for *co-locomote*, as *follow* was almost exclusively used by males escorting a female on *consortship*, while *co-locomote* normally involved requests between mothers and dependent offspring – two very different functions. As in Cartmill and Byrne, I defined a single category of active discouragement: *negate*. This category contained the stop behaviour and move away functions that were used to discourage social interactions in 6 of the 7 areas of positive semantic meaning (*affiliation, co-locomotion, groom, play, object desire, sexual contact*) but were not observed in behaviour related to *follow*.

I included Cartmill and Byrne's suggested category of *sexual contact*, as this was regularly observed in chimpanzee communication. As well as species differences in sexual behaviour, the low levels of *sexual contact* requests reported in the orang-utans may be the result of the low levels of opportunity for sexual contact provided by the captive environment. As reported in the orang-utan gesturing I found a striking dominance of the meaning category *play*. Not only were the majority of gestures with tight functions (22/30) assigned to this category, but more than half of (9/17) gestures with a primary function in an alternative category of meaning contained a secondary function within the category of *play*.

This dominance may reflect the very broad nature of play behaviour. The frequent use of gestures that had specific tight meanings *outside* of *play*, to also communicate a social desire *within play*, suggests that *play* may serve as an exploratory arena within which young chimpanzees experiment with the use of gestures. In the way that when a child learns a new meaning such as 'I love', he explores it's function by producing it widely in a highly variable fashion: I love my cat/house/mother/bike/ice-cream, but with maturity the usage is narrowed to focus on a more specific meaning: I love my wife. One consequence of the proliferation of gesturing during *play,* is that, when considering the meaning of gesture across individuals and contexts, the 'real' tight meaning may be disguised by the use in play so that it appears to be one of two or more loose or ambiguous meanings. For example, when analysed by straight frequency (as opposed to individual mean values) the 'object-shake' gesture was 'loosely' associated with both the meaning category *follow* and *play*. A large proportion of object-shake gestures produced with the function *follow* came from a male chimpanzee escorting a female away from the group into a consortship (Duane, see Chapter 8), the remainder were mostly produced by young chimpanzees in play. Thus, this important and very 'real' tight function of the object-shake gesture for adult chimpanzees was diluted to a 'loose' function because of the regular use of the same gesture within *play*.

Of course in reality, the interpretation of a communication's meaning requires the incorporation of information about both function and context. As established by Smith in his early discussion of the topic (1965), 'the "meaning" of a signal to a recipient should be considered with reference to context, since, for the recipient, context is unavoidable' (Smith, 1965, p.406). Furthermore, as well as the normal function and current situational context of the communication, chimpanzees may take into account a complex range of social information about the signaller as part of the full context of the communication. In a systematic series of experimental playback studies on vocal behaviour, Cheney and colleagues have demonstrated that old world monkeys incorporate information about the past behaviour of the signaller (Cheney and Seyfarth, 1988), and about the signaller's relationship to both the recipient

(Cheney et al., 1995) and to other members of the group (Cheney and Seyfarth, 1999, Wittig et al., 2006). Early findings from a series of ongoing studies at Sonso employing the same methodology, suggest similar capacity in chimpanzee vocal behaviour (C. Crockford 2009, pers. com.); and I would anticipate that in interpreting the meaning of gestural communications chimpanzees would employ the full range of these skills.

Finally there is the tantalizing hint that, as with as the large overlap in the gestural repertoire described in chapter 1, there may be some species overlap in function. Not only were the majority of functions described in the gesturing of several captive gorilla and orang-utan groups also seen in Sonso chimpanzees; but also, in the few specific cases available for comparison, all three species appeared to use the same gestures for similar functions. The only chimpanzee specific functions were all employed within the context of grooming, which, while a key part of the chimpanzee social environment, is a relatively rare and more utilitarian activity in orang-utan and gorilla behaviour (MacKinnon, 1974, Schaller, 1963), and is thus less likely to involve gestural communication.

The use of pirouette gestures represents a particularly interesting case: as in gorilla communications, its dominant function at Sonso appears to be as a ‘stop behaviour’ request, a relatively unusual primary function. On a small number of occasions I observed 2 different sub-adult chimpanzees directing this gesture to researchers following closely along a transect line in the forest. While juvenile and infant chimpanzees did occasionally gesture towards the researchers and field assistants, similar behaviour from sub-adult and adult chimpanzees was much more rarely observed; they were much more likely to simply ignore us. The use of the pirouette gesture in this way appeared to reflect a desire by the two younger sub-adults for the researchers to stop following so closely. This supports the finding that while chimpanzees can use gestures flexibly; they tend to use them for a single dominant function, in this case even when gesturing to individuals of another species.

Chapter 11. General Discussion

The aim of my study was to provide the first systematic investigation of gestural communication in a wild chimpanzee population. Previous studies of gesturing in great apes have focused on the systematic study of captive groups (Tomasello et al., 1985, Tomasello et al., 1994, Tanner and Byrne, 1999, Pika et al., 2005b, Genty et al., 2009, Cartmill and Byrne, 2010), or the focused analysis of single gestures in wild populations (Nishida, 1980, McGrew et al., 2001, Pika and Mitani, 2006). Captive studies are vulnerable to the effects of the captive environment and human influence; and studies of single gestures, while providing interesting cases of group-wise variation, are unable to address broader questions about the nature of intentional communication. Thus, in order to address questions about gestural communication from an evolutionary perspective, I undertook an in-depth study of gestural communication in the wild Sonso chimpanzee community living in the Budongo forest, Uganda.

11.1 Summary of findings

11.1.1 Repertoire: size and variation

Captive chimpanzees: A long-term study of chimpanzee gesture in the captive Yerkes group described a repertoire of 33 different gesture types (Tomasello et al., 1985, Tomasello et al., 1989, Tomasello et al., 1994), and new types of gesture continued to be added with each new study (e.g. (Call and Tomasello, 2007, Pollick et al., 2007)). Repertoires varied widely between individuals and across time periods, and included large numbers of idiosyncratic and one-way forms (Tomasello et al., 1994).

Sonso chimpanzees: The Sonso group repertoire contained 66 gesture types, with no idiosyncratic gestures and only a low level of one-way gestures (18% in the individuals with the largest repertoires). The group repertoire only approached asymptote following 266 days of observation. No individual repertoire reached the group total of 66 within the course of the study. The largest was 41; however, the size of any individual (or age group) repertoire was closely predicted by the quantity of gesturing recorded for that individual, suggesting that most individual repertoires had yet to reach asymptote. Thus, it may be inappropriate to describe gestures as idiosyncratic or one-way following shorter observation periods. When individual repertoires were plotted on the same graph as the community repertoire over time, the majority fell close to the cumulative curve, supporting the suggestion that they had yet to reach asymptote. This finding suggests that the variation between individual repertoires can be explained as a sampling artefact, rather than, as Tomasello and colleagues (1994) suggest, a difference in the individuals.

11.1.2 The intentional use of gestures

Captive chimpanzees: Several studies have reported that chimpanzees use gestures flexibly across different contexts, so that a single gesture may be used in many contexts, or several gestures within a single context (Tomasello et al., 1989, Call and Tomasello, 2007). Choice of gesture is adjusted in order to accommodate a specific target audience, so that silent gestures are used when the recipient is already attending to the signaller (Tomasello et al., 1994). Chimpanzees wait for their recipients to respond, and if they do not, or the response is not the desired one, they persist with further gestures (Leavens et al., 2005b).

Sonso chimpanzees: All of the indications of intentional communication demonstrated in the gesturing of captive chimpanzees were also present in wild chimpanzee gestural communication. Individual gestures were used flexibly across different contexts, and multiple gesture types within single contexts; and signallers accommodated their target audience by adjusting the use of particular modes of gesture so that the recipient could perceive them. Although the general use of silent gestures towards attentive recipients has been shown in captive chimpanzees (Tomasello et al., 1994), I was able to demonstrate that individual chimpanzees actively adjust their use of different modes of gesture to accommodate the recipient's state of attention. This means that silent gestures were produced more towards attentive recipients, and contact gestures more towards inattentive recipients. When gesturing, Sonso chimpanzees waited for a response, and, where this failed to meet their goal, persisted in gesturing again. Individuals were more likely to persist following a partially successful response from the recipient (71% of cases), than when the communication failed completely (48% of cases). This pattern of persistence replicates a recent finding in captive orang-utans (Cartmill and Byrne, 2007), suggesting that, as in the orang-utans, signallers receive some form of positive reinforcement from the partial success, which encourages them to persist in the attempt to communicate.

11.1.3 Ontogeny of gestural communication

Captive chimpanzees: In their study of the captive Yerkes group, Tomasello and colleagues reported that gesture-like actions were produced from approximately 1-year old, but these only started to be accompanied by indications of intentional use at 2-years, and were considered to be produced in a fully intentional manner at 3-years old (Tomasello et al., 1985). Gesturing appears to peak in the juvenile age group (5-9 years) and then declines, with little use of gesture reported in adulthood (Call and Tomasello, 2007).

Sonso chimpanzees: I recorded the use of a limited number of gestures in an intentional manner from individuals as young as 4-months old. Initially their use of gesture was minimal, but by the end of their first year, when they were able to move independently of their mother, gesturing increased rapidly. This age of onset was consistent with descriptions from another wild population (Plooij, 1978). As in captivity, the use of gesture peaked in the juvenile period; nevertheless, in the Sonso community all age groups, including mature adults, regularly employed gestural communication across a range of contexts.

11.1.4 Contexts of gesture use

Captive chimpanzees: In captivity the majority of gesture use occurs in the context of *play*, and for other ‘less evolutionarily urgent functions’ ((Tomasello and Call, 2007) p.5), such as in grooming or agonistic encounters.

Sonso chimpanzees: While *play* remained the dominant context for gesture use in wild chimpanzees, a far wider range of contexts was available in a natural environment, and gestural communication was employed in almost all of these. I defined 10 situational contexts, and found gestural communication in 9; the exception was in *patrolling* where no clear cases of communication, gestural or vocal, were observed. Gesturing was employed in frequently experienced contexts such as grooming, along with more rarely experienced activities such as begging for meat. Adult male chimpanzees used gestural communication extensively in the evolutionarily urgent context of coercing and escorting a sexually receptive female into *consortship*.

11.1.5 Referential gestures

Captive chimpanzees: spontaneously use single digit and whole-hand pointing to direct human and conspecific attention in requests for desired objects that are out of reach (Leavens and Hopkins, 1999, Leavens et al., 2004).

Wild Ngogo chimpanzees: Pika & Mitani (2006) report that chimpanzees in the wild Ngogo population regularly use a referential ‘directed-scratch’ gesture in order to direct grooming to a specific location on the signaller’s body.

Sonso chimpanzees: I observed a limited number of potential cases of whole-hand pointing in the Sonso chimpanzees. Although these were at a level comparable to other rare gesture types, they were insufficient to confirm the existence of referential pointing in a wild population.

Sonso chimpanzees did employ a scratch-based gesture, but used this as a purely audible signal. Signallers produced the ‘Big-loud scratch’ gesture to attentive and inattentive recipients equally, and recipients did not actively adjust their subsequent grooming to match the location of the signaller’s gesture. Sonso chimpanzees were able to successfully guide grooming into a desired location by positioning the relevant area of the body so that it became the most convenient area for grooming as part of a ‘Present-groom’ gesture.

11.1.6 Functions in gestural communication

Captive chimpanzees: In captivity the behavioural context in which a gesture was produced has been regularly substituted for the gesture’s function (Tomasello et al., 1994) (Liebal et al., 2004a). This method allowed the objective assessment of external, observable events, but, as a gesture could theoretically have a single function (e.g. stop current behaviour) and still be used across multiple contexts, this protocol was vulnerable to exaggerating the flexibility of gestures.

Sonso chimpanzees: Two recent studies of gorilla (Genty et al., 2009) and orang-utan (Cartmill and Byrne, 2010) gesture, employed the recipient response that appeared to satisfy the signaller as an externally observable means to interpret the function of the signaller's communication. By following a similar protocol I was able to demonstrate that Sonso chimpanzees employed individual gestures flexibly for a range of at least 17 separate functions, all of which took the form of an imperative request. As in gorilla gesturing individual gestures were usually associated with a single dominant primary function, and, as found in orang-utan gesture, gestures varied from the ambiguous to the specific in meaning. Gesture functions could be classified into 8 categories of meaning, 7 which encouraged further social interaction: *play, groom, follow, object desire, sexual contact, affiliate and co-locomote*, and one *negate*, which discouraged further social interaction.

11.2 The big questions

From these findings I can now attempt to answer four key questions: how do chimpanzees acquire their gestures; when do chimpanzees use their gestures; do chimpanzees use any gestures referentially; and what are gestures used for, in general?

11.2.1 How do chimpanzees acquire their gestures?

The theory of Ontogenetic Ritualization (OR) has dominated the literature on the acquisition of gesture by great apes for 25 years (Tomasello et al., 1985, Tomasello et al., 1989) (Tomasello et al., 1994, Call and Tomasello, 2007, Pollick and de Waal, 2007). OR argues that the majority of intentional gestures are acquired through the ritualization of effective actions into 'intention-movement' gestures. There is no understanding of the signaller's intention, simply an anticipation of their future actions, so gestures must be ritualized anew with each recipient. Thus, OR predicts that gestural repertoires will be characterized by high levels of idiosyncratic and one-way gesture forms, and that the physical form of gestures acquired through ontogenetic ritualization should match the physical form of the early movements of the physical actions from which they are ritualized.

As all studies of gesture include the intentional use of a number of gestures whose physical form is incompatible with an origin in an effective action (e.g. a pirouette or drum); OR also necessarily includes additional categories of gesture. One such example is the suggested category of 'attention-getters'. Attention getters are described as having no intrinsic meaning and function only to draw the recipient's attention to an accompanying 'meaningful' signal, which may take the form of a further gesture or an unlearned facial expression or posture. Although still described as acquired through a process of ontogenetic ritualization, these gestures are distinct from the category of 'intention-movements' in that it is the recipient's reaction, rather than the physical form of the gestures that is ritualized. Further categories of gesture are necessary to account for the intentional use of silent gestures that have no possible origin in effective action. However, despite describing attention-getting gestures as less intentional, Tomasello and colleagues do not distinguish them from intention-movements in their analyses of intentional gestural communication and several studies have found no justification for a category of pure attention-getters (Liebal et al., 2004a) (Genty et al., 2009).

Thus, while OR was able to explain the individual variability reported from captive studies (Tomasello et al., 1994), it contained a number of serious theoretical and empirical weaknesses, and was recently challenged by new evidence from a systematic study across several gorilla groups that supported an alternative, species-typical explanation (Genty et al., 2009).

The evidence from wild chimpanzee gesturing supports this new alternative theory of a species-typical repertoire. I found no evidence to support the differentiation of potentially ritualized intention-movements from other intentional gestures in either flexibility across contexts, or in the accommodation of the signaller's state of attention, as would be predicted by OR. Critically there was also no evidence for idiosyncratic gestures, or for large numbers of one-way gestures, and the physical form of specific gestures did not match the actions from which they were presumed to have been ritualized. Furthermore, there was significant evidence to suggest that much of the variation between individuals and demographic groups in the quantity of gesturing and the size of the available repertoire actually stems from sampling artefacts, rather than any variation between individuals.

In short, there was no evidence that supported OR as the main means by which chimpanzees acquire their gestural communication. Instead, the pattern of data strongly supported the theory that chimpanzee gesture is founded upon the intentional use of a large, flexible, species-typical repertoire. OR requires multiple categories of gestures, with varying levels of intentional use, and the acquisition of even a portion of the repertoire would require large numbers of repeated dyadic interactions. In contrast, the alternative theory of a species-typical repertoire represents both a better fit for the data and a simple more parsimonious explanation.

Of course the elimination of OR as a likely means of acquisition does not necessitate a species-typical means of acquisition; social learning mechanisms such as imitation remain possible explanations. However, as I found no evidence that required, or suggested, a more complex social learning explanation, the more parsimonious species-typical theory is sufficient to explain the acquisition of the gestural repertoire.

One theme throughout the literature on OR is the avoidance of terms such as ‘biologically-inherited’ or ‘species-typical’ when discussing intentional communication; this may have been a conscious effort to avoid parallels with the fixed repertoire of vocalizations. However, as discussed above, in order to account for common gestural forms regularly reported across chimpanzee populations, OR required the addition of sub-categories such as ‘attention-getters’ or ‘phylogenetically ritualized’ gestures.

In fact, the misperception that species-typical gestures were produced in a less intentional manner, and that gestures with a possibly ritualized origin were characterized by idiosyncratic forms and more intentional use, may have stemmed from a relatively simple experimenter bias in the ease with which we are able to distinguish physical movements as intentional cases of gesture in another species.

Tomasello and Call themselves describe ‘intention-movement’ gestures as ‘very subtle ritualizations (incipient movements) of important social behaviours’ (Tomasello et al., 1985, p.179), and highlight that they can be difficult to distinguish from normal non-communicative physical behaviour. In contrast, other gestures, by definition, do not resemble important social behaviour, and therefore stand out clearly from the normal physical repertoire. As well as being physically distinctive, these gestures also tend to be noisy. Of the group of gestures whose physical form excluded them as candidates for a potentially ritualized origin, 51.8% were audible and 10.3% silent (as opposed to 19.4% audible and 44.4% silent, in the potentially-ritualized gesture forms). Thus, gestures that do not fit the pattern of ontogenetic ritualization tend to be noisy and obvious.

Noisy obvious gestures are much more likely to be reported across individuals and groups, and may be noted in studies which do not specifically focus on gestural communication. In contrast, gestures that are subtle, and quiet are less likely to be observed and reported. This, then, would tend to create the perception that the noisy obvious gestures are species-typical, while the subtle quiet ones are limited to a few individuals, or idiosyncratic.

In addition, audible gestures are the only category of gesture not adjusted to accommodate the audience’s state of attention. The production of audible gestures whether or not the recipient is attending can lead them to appear superficially less directed, and more akin to the fixed expressions of mood such as facial-expressions and postures. Indications of their intentional use such as response waiting can be limited to subtle glances, and the production of further gestures may not be perceived as persistence but as a new communication. In contrast, silent gestures, once identified, are much more easily classified as cases of intentional gesture. Signallers must verify their target’s ability to see the movement immediately prior to producing it, and, where necessary, may locomote around into a position where the recipient is capable of receiving the gesture: both easily distinguished signs of the intent to communicate.

To summarise: noisy, obvious gestures tend to be easily identifiable and, thus, may appear more species typical. They also tend to be accompanied by small subtle indications of intentional use and, thus, may appear to be used in a more reflex way. In contrast, small, subtle gestures are less likely to be reported across individuals, and tend to be accompanied by clear, obvious indications of intentional use.

It is only with the systematic long-term study of gestural communication that the widespread use across individuals of subtle, silent, gesture forms becomes clear; and, it is only with the detailed analysis of a large database of gesture cases, that the intentional use of noisy, obvious, gesture forms become apparent. At this point the fully intentional use and species-typical nature of the whole repertoire becomes clear.

Further evidence for the species-typical nature of the chimpanzee gestural repertoire is provided by a comparison across wild populations. Although no other systematic study of gesture exists for a wild population, it was possible to construct group repertoires from the detailed descriptions of gesture included in the long-term studies of the Gombe and Mahale groups. The gestural repertoire of three wild populations is broadly similar (Sonso: 66, Mahale: 69 (Nishida et al., 1999), Gombe: 61 (Goodall, 1968, Plooij, 1984)). While the repertoire described for the captive Yerkes group is much smaller (33, (Tomasello et al., 1985, Tomasello et al., 1989, Tomasello et al., 1994)), the addition of new types of gesture with each new study (Call and Tomasello, 2007, Pollick et al., 2007), suggests that it has yet to approach asymptote. Across all four groups of chimpanzees there was almost no evidence for group specific gestures (3 possible cases), with a near 100% of those reported at Gombe, Mahale and Yerkes, also present in the Sonso repertoire. Remarkably, when the complete Sonso repertoire was compared to that described in studies of gorilla and orang-utan gesture, there was an impressive overlap of over 60% in both cases, suggesting that a significant portion of the gestural repertoire is in fact ‘family-typical’, as we might expect for a biologically given trait.

The evidence for imitation

The evidence for imitation in great apes comes from two bodies of captive studies. The first demonstrated the capacity shown by both chimpanzees (Whiten et al., 1996) and gorillas (Stoinski et al., 2001) to match a demonstrated action in opening a puzzle-box. However, what is learned here is not a new action, but the circumstances to deploy an existing familiar one. A second body of work focused on the imitation of gestures. Encouraged by the abilities of sign-language trained apes to acquire large repertoires of novel gestures in ASL, these studies trained subjects to match a demonstrated action and then presented novel actions for them to imitate. While there was some degree of matching, these 'imitations' were normally imperfect and in a longitudinal study of gorilla gesture, Byrne and Tanner (2006) were able to demonstrate that they could in fact be accounted for by the facilitation of rare actions within the large species-typical repertoire.

Thus all of the evidence for chimpanzee imitation can be explained as either the reproduction of existing behaviour in a new environment (contextual imitation), or as the facilitation of an existing behaviour from within the large species-typical repertoire. In this context, it is extraordinary that I have evidence that can only be explained as program imitation.

In their imitation of Tinka's disability-specific grooming technique, the Liana-scratch, Sonso chimpanzees demonstrated the capacity to acquire a novel behavioural pattern through imitation. At Sonso, young chimpanzees were observed to employ the Liana-scratch, a grooming technique specifically developed by the severely disabled male Tinka, despite the fact that for these healthy individuals it represented a functionless behaviour. While each of the action elements was part of the normal chimpanzee repertoire, the specific combination of these into the liana-scratch technique had never been reported in other Sonso individuals, or at other sites, and so was not simply a rare part of the normal chimpanzee repertoire. Only individuals who had the opportunity to regularly observe Tinka acquired the technique; other similar-aged individuals whose regular range was outside of Tinka's failed to do so. Thus, the acquisition of the liana-scratch by other young Sonso chimpanzees can best be explained as production imitation: the acquisition of a novel sequence of actions through imitation.

While the findings from wild chimpanzees suggest that the gestural repertoire of chimpanzees is biologically given, it remains possible that alternatives such as the conventionalization of action into gesture or the imitation of another individual do occasionally occur. For example, acquisition through imitation may best explain the small number of idiosyncratic gestures with no possible origin in effective action that has been documented in captive apes (e.g. the Disco arm shake in a young female gorilla (Genty et al., 2009), or the Spit-water gesture at Yerkes (Tomasello et al., 1994)). Captive apes are usually kept in small stable groups and have regular opportunities to observe both individuals within the group and the behaviour of other species. They are under less pressure to fulfil basic biological requirements in foraging and feeding, and may be presented with new contexts outside of those in which the species-typical repertoire developed. Thus, the captive environment may promote the occasional addition of new gestures to the species-typical repertoire through means such as imitation.

11.2.2 When do chimpanzees use their gestures?

In sequences

One of the most characteristic features of human language is its open nature, made possible by the unlimited potential for recombination from a finite set of elements. Therefore the frequent use of gesture sequences by great apes is of great interest; however, to date, only two previous studies have undertaken a systematic analysis of gesture sequences and these found conflicting results.

Liebal et al. found that sequences produced in chimpanzee gesturing were predominantly repetitions of the same gesture type, and suggested that they were produced in response to the failure of single gestures (Liebal et al., 2004a). In contrast, Genty & Byrne found that sequences in gorilla gestural communication contained few repeated forms and found no evidence of an increase in the effectiveness of gesture sequences over single gestures. These authors suggested that sequences functioned as a form of ongoing gestural modification of behaviour within a dynamic environment (Genty and Byrne, 2010). But, there was a key difference between the studies in the manner in which they defined a sequence: Liebal et al. included in a single sequence gestures separated by bouts of response-waiting, while Genty & Byrne treated these as separate communications. In fact, both approaches are correct. It is appropriate to treat gestures produced after response waiting as related to any earlier gestures, after all they are a part of the same communicative goal; and, it is also appropriate to treat gestures produced in a rapid sequence as distinct from subsequent gestures produced after response waiting, as one stems from the signaller's decision to combine gesture types prior to any recipient response, and one from a response to the recipient's behaviour (or lack of it). Thus, the detailed analysis of gestural sequences in great ape communication requires that the two different forms of gesture are distinguished and considered separately.

Sonso chimpanzees did persist in producing additional gestures following the failure of earlier communications; however, this form of gestural sequence was distinct from the combination of gestures into rapid sequences. Immature Sonso chimpanzees regularly produced rapid sequences composed of a broad range of different types of gesture. These rapid sequences were often unsuccessful, and the immature chimpanzees frequently persisted in producing further communications following the recipient's apparently undesirable response (or lack of one). However, within the Sonso group repertoire certain gestures were inherently more successful, irrespective of whether the individual using them was immature or mature. These high-success gestures were not only more effective when used individually, but their inclusion in a rapid sequence of gestures increased the likelihood that the sequence would be successful. Mature individuals employed these high success gesture types in the majority of their gesturing, and high-success gestures tended to be used individually, reducing the number of rapid sequences produced. As the initial gestural communications were more successful, there was less need for persistence and the use of additional gestures after response waiting also decreased.

Given the large ratio of gesture types (66) to the number of functions (17) identified in gestural communication, I suggest that the use of rapid sequences of gestures is the result of a conservative strategy, wherein young chimpanzees 'hedge their bets' on obtaining the desired response by producing a range of gestures together. The low frequency of repeated gesture types within these rapid sequences strengthens the argument that they represent a shotgun approach to the selection of gestures. In mature individuals gesture use becomes more targeted, as experience of increased success in communications that include high-success gestures, selectively reinforces the use of the more effective gesture types.

The difference between the motivation to produce rapid sequences of gestures and the motivation to persist in producing additional gestures after waiting for a response is nicely illustrated in the use of gestural communication in *consortship*. When gesturing to a female in *consortship*, mature males continue to persist in gesturing for longer than in other behavioural contexts, with further gesturing following up to eight bouts of response waiting in a single communication. Consortships represent a large investment in terms of time, energy and associated risk, particularly on the part of male chimpanzees; thus, it makes sense to invest in further communication when gesturing fails. In contrast, there is no increase in the length of rapid gesture sequences, because as mature males with an established repertoire of effective gesture types, there would be no benefit to producing additional gestures in rapid sequence.

The perceptual tuning of a large species typical repertoire, to distinguish between and reinforce the production of the most useful elements, underlies several processes in human cognition, including linguistic capacities such as our ability to hear the range of phonemes in a language (Oyama, 1976, Kuhl et al., 2003). In a similar fashion, the very large species-typical repertoire of chimpanzee gestures may be, with experience, restricted to a reduced repertoire of regularly used, highly successful, gesture types. As there is no reason to assume that the highly successful gesture types are the same across chimpanzee groups, I would predict that this process might lead to group-typical repertoires of regular use in *mature* individuals.

This hypothesis explains not only the form and function of gestural sequences, but also the tendency for the recorded repertoire of mature individuals to be smaller than that of immature individuals (see: Tomasello et al., 1985). As the use of the repertoire becomes focused on the most effective gesture types, the less effective gesture types are used less and a portion of the biologically given repertoire thus becomes dormant - in much the same way that our ability to hear a particular phoneme is lost if it is not reinforced by exposure and experience (Burnham, 1986). The imperfect imitation of ‘new’ gestures by captive apes can be explained as the facilitation of forms from the dormant portion of the species-typical repertoire (Byrne and Tanner, 2006).

Does gesture use differ across contexts?

Play

As has been found in captive apes (Tomasello et al., 1994, Liebal et al., 2004a, Pika et al., 2005b, Genty et al., 2009), *play* represented the dominant context for gesture use in the Sonso chimpanzees. This was the case for both gesturing in general and in each age group from babies to young adults, highlighting the importance of play in chimpanzee behaviour even in a natural population. *Play* also contained the regular use of a wide range of gesture types from the repertoire, and the particularly flexible use of individual gestures towards a wide range of functions. This varied flexible pattern of use contrasted strongly with other prominent contexts such as feeding or grooming, where a much more limited range of gesture types accounted for the majority of gesture use. Unlike Tanner (2010), working with gorillas, I found no evidence for the use of gesture in triadic or collaborative interactions involving object play. Instead objects were used as a means to initiate play, as in the ‘object in mouth’ gesture, but were then discarded once play started.

Patrolling

Although there were few opportunities to observe patrolling, either in the form of boundary or hunting patrols, gestural communication does not appear to play a part in the regulation of group behaviour in this context. Despite the absence of gestural or vocal communication, the patrolling individuals appeared to co-ordinate their behaviour in a purposeful manner, pausing, moving off, and changing direction together. This behaviour was reminiscent of King’s description of great ape communication as a ‘dynamic dance’ in which behaviour is co-regulated between partners in a fluid fashion (King, 2004). She compares this co-regulation to the way that musicians that have played together for many years are able to co-ordinate an improvised segment of music without any obvious external signs of communicating to each other. In a similar fashion several captive studies have noted the capacity for chimpanzees to regulate their behaviour ‘by means of inferences and anticipations’

(Tomasello et al., 1985, p.179); see also (Menzel, 1973), and this appears to be sufficient for a chimpanzees to co-ordinate their behaviour when on patrol.

Consortships

In stark contrast to the absence of gestural communication in patrolling, gestural communication was used prolifically in consortship behaviour and represented the dominant context for gesture use by adult male chimpanzees. Male chimpanzees produced almost all (95.4%) of the gestural communication within this context; they used a range of 17 gesture types, predominantly to request that the female follow them away from the group. Perhaps surprisingly, considering the pressure to avoid detection by other chimpanzees (either by other Sonso males, or by other communities), the majority of gesture types used in consortship were audible forms of gesture. However, audible gesturing while in consortship was restricted to short-distance audible gestures such as object-shakes. These gestures were not only limited in terms of the range that the communication would travel, but their audible component was not immediately associable with chimpanzee behaviour. For example, any large animal passing through the forest could have made the rustling of foliage noise made by an object-shake gesture. There was no use of the long-distance drumming gestures that are immediately identifiable as chimpanzee communication. Thus, the gesturing still appeared to provide a discreet means to communicate in the dense secondary forest environment.

Consortships represent an understudied area of chimpanzee behaviour. Irregular, infrequent, and inherently secret, they are particularly difficult to observe, however, they provide an insight into an unusual form of social relationship in chimpanzee behaviour: an isolated male-female pair. At Sonso, as at other sites, the use of consortship behaviour as a sexual strategy by community males appears to be based on an assessment of several factors, including the availability of oestrus females (as at Mahale, see: Hasegawa and Hiraiwa-Hasegawa, 1983), as well as the male's social rank and relationship with community females, both of which may influence his ability to successfully engage, and then keep, a female in consortship (as at Tai, see: Boesch and Boesch-Achermann, 2000). Despite the evidence for male choice in the timing and frequency of consortship behaviour, the influence of female choice should not be under-estimated, with a well-timed scream able to bring other community males quickly into the vicinity (see also: Nishida, 1997).

The motivation to succeed in a consortship, as evidenced by unusually high levels of response waiting and persistence when gesturing, can also be judged by the level of aggressive coercion employed by consorting males. While brief fights are not unusual in chimpanzee behaviour, prolonged bouts of severe aggression are rare, particularly between males and females. The repeated and violent attacks the young female Lola experienced while in consortship almost certainly resulted in her death, and a similar pattern of events led to the disappearance and likely death of the young female Gonza several years earlier. Only one other case of confirmed intra-community killing has been recorded at Sonso, that of Zesta, a young male killed in a highly aggressive attack by the alpha and two other community males. The young male had, unusually, been the most frequent grooming and copulation partner of the only female to be in oestrus. This ‘breaking of rank’ appeared to motivate the serious attack instigated by the alpha and beta males who would normally have expected to maintain almost exclusive access to this valuable female (Fawcett and Muhumuza, 2000). Thus, all three possible cases of intra-community killing in the Sonso chimpanzees can be connected to sexual competition. Intra-community killings are extremely rare, and at other sites have usually been connected with contests for alpha male status (Nishida, 1995, de Waal, 1982). Along with the killing of Zesta, the evidence from the observation of consortships at Sonso suggests that periods of intense sexual competition may also represent a sufficiently high-stakes context in chimpanzee behaviour for the normal social regulation of aggressive behaviour to break down.

Perhaps the most surprising, and somewhat tragic, aspect of the extreme aggression displayed in consortships was its failure to achieve the apparent goal of the male. Both Lola and Gonza’s consortships were cut short by the arrival of other community males, almost certainly drawn to the pair by the female’s screams. Even in the successful consortships of Duane and Zimba, both included an aggressive attack by the male in the early stages, one of which led to the arrival of other community males. Extensive grooming of the female did occur on both successful consortships, but only after the female started to follow freely and the pair had moved away from the core Sonso territory. Thus, it appeared to function less as a form of coercion and more as a means to re-establish the social bond between the pair following the earlier aggression. This makes the repeated use of the rare ‘rump-rub’ gesture at the earlier, more aggressive, stage in the consortship particularly interesting. Usually used outside of consortship by a lower-ranking individual towards a more dominant one, in requests for affiliation or reassurance; the use of the rump-rub by the male to the female, during the period of aggressive coercion, may function as a ‘short-hand’ communication of his essentially friendly intent. A rump-rub can be employed in the initial stages of consortship, when the pair remain in the core of the communities territory and a more time consuming alternative, such as grooming, risks their discovery by other community males.

The extensive gesturing by adult males in consortship differs dramatically from the low frequency of adult male gesturing reported in captivity, and represents the first description of gesture use in an “evolutionary urgent” context. Gestural communication offers male chimpanzees the opportunity to communicate their intentions to the female they wish to engage in consortship, while minimising the risk of also advertising these intentions to other community males. This finding highlights the importance of studying behaviour in a natural population where the full range of environmental and social contexts is available.

What determines the choice of communication or co-regulation?

Both *patrolling* and *consortship* are contexts in which there appears to be a strong selective pressure towards discreet communication. In *patrolling* this appeared to result in a subtle co-regulation of the group’s behaviour without any clear cases of gestural or vocal communication. In stark contrast, consortships represented one of the most intensive contexts for the use of gestural communication.

While other factors, such as the lethal risk involved in patrolling, undoubtedly also affect the form of communication. I would highlight the role of the extent to which the goals of the individuals involved are compatible. For example, once on patrol the decision to engage has been made and, thus, within those individuals participating in the patrol there is a general consensus of goal. From this point forwards, the group may be considered to have a single goal with minor decisions over in what manner to achieve this (the exact path to take or the position of different individuals within the group) resolved through subtle co-regulation in a mutual two-way manner. In contrast, in a consortship, the desired outcome for the male (to isolate the female from the group) appears to be broadly incompatible with that of the female (who is more likely to benefit from remaining within the group). Thus, one individual must 'lose' and a means to communicate your intentions in a clear one-way fashion may be more appropriate.

A more day-to-day example of this difference can be found in the context of grooming. Where grooming takes place between a mother and her offspring, or between immature siblings, it may serve both a practical function of parasite removal and also a social-bonding function, but both individuals can achieve their own goals in a mutual fashion. Gestural communication in this context tends to be rather brief, with grooming and the shifting of positions taking place in a fluid manner. In contrast, where two similarly ranked males both wish the other individual to groom them, there may be much at stake, in terms of social hierarchy, over who is willing to cede their own goal of being groomed in order to groom the other. Even when the final outcome is that both individuals engage in mutual grooming, one individual must 'give in' and groom the other first. In this case there are frequently long bouts of gesturing back and forth between the individuals, with exaggerated response waiting that includes very pointed looks towards the other individual. In this case where the goal of each individual (to be groomed first) is incompatible with the goal of the other, clear deliberate communication of this goal can be achieved through gestural communication.

11.2.3 Do chimpanzees use their gestures referentially?

There is a substantial body of evidence that captive apes are able to point in a clear referential fashion, in dramatic contrast with the absence such of evidence from wild populations. If chimpanzees can point, why wouldn't they be doing it all the time? Fruit in trees, paths through the forest, individuals joining the group: there appear to be myriad practical applications for pointing in wild chimpanzee behaviour.

Given the evidence for the capacity in captive apes there appears to be no biological impediment to the development of pointing; thus, Leavens and colleagues (2005) suggested that the absence of pointing in wild apes could be explained through environmental factors. In order to develop pointing, they suggest, an individual must regularly experience an environment where there are physical barriers to desirable objects, *and* where there are individuals present who, in the past, have regularly provided them with desirable objects. The presence of these two factors in tandem establishes a 'triangle of reference' between the signaller, recipient, and the desired object, creating an environment in which pointing represents an effective strategy. These authors argue that as wild chimpanzees experience neither physical restrictions to desirable objects, nor regular provisioning, then pointing is simply not an effective strategy and thus does not develop within wild populations (Leavens et al., 2005a).

While provisioning is not a frequent event in wild chimpanzee behaviour, I did regularly observe Sonso chimpanzees actively sharing desirable food items such as meat with close relatives (normally mother to offspring) or social allies (for example, the alpha and beta males). Moreover, while Sonso chimpanzees do not experience physical barriers to desirable objects, they do experience *social* barriers. The frequent use of begging for rather than simply taking desirable food demonstrated this clearly. And indeed, within a context that provided both a social barrier and a potentially helpful ally, I *was* able to observe a small number of whole-hand reaching gestures that could be described as referential pointing. The social nature of the barrier may provide an explanation for the absence of regular pointing behaviour, as, when a social barrier is in place, it may simply be more effective to communicate with the individual creating the barrier: for example through begging gestures, rather than attempting to elicit the assistance of a third party.

Furthermore, the development of any referential behaviour may require a context in which it represents an effective strategy for which there is *no existing alternative* in the behavioural repertoire. Thus, it may not be sufficient that an environment contains both a barrier and a potentially helpful ally, because the option of overcoming the social barrier in another fashion (for example by begging) must also be unavailable. For example, would a captive ape with experience of desirable, out-of-reach objects, and regular provisioning, develop communicative pointing if an alternative mechanical solution (e.g. a rake) were also available?

This point is clearly illustrated in the case of the supposedly referential 'directed-scratch' gestures (Pika and Mitani, 2006). Although the Sonso chimpanzees do have an intentional scratch gesture in their repertoire, signallers did not use it in a referential fashion to direct the attention of the recipient; nor did recipients take advantage of any un-intentional information in the signal to direct their grooming to the location of the scratch. Accompanied by both response waiting and, where necessary, persistence, the Big Loud-scratch was a clearly intentional gesture, however, it functioned as a purely audible communication, closely associated with the request 'groom me', but also used in requests to 'groom you' and 'follow me'. Instead if a signaller wished to receive grooming in a specific location it was able to achieve this by the alternative means of a Present-groom gesture. Here the signaller orientated its body so that the area it wished to receive attention was conveniently located for grooming.

Although there was no evidence for a 'directed-scratch' gesture within the Sonso chimpanzees, this might have been attributable to a group difference between the Sonso and Ngogo community. There certainly appeared to be a group difference in terms of the recipient response to the scratch gestures, as Ngogo recipients, unlike Sonso recipients, did match their subsequent grooming to the location of the scratch. However, the case for an *intentional referential* signal within the Ngogo community is not clear. Pika and Mitani define directed-scratch gestures as those produced in full view of the recipient (2006). By limiting their analysis to gestures produced in full view, they are unable to show whether or not signallers adjusted their use of the gesture to accommodate the recipient's state of attention. This means that although their observations are consistent with the interpretation of the 'directed-scratch' as a referential gesture in the Ngogo community, they are not sufficient to confirm that the signallers intend to produce a visual referential signal.

11.2.4 What are gestures used for?

When I explain that I study the gesturing of wild chimpanzees, the first thing most people ask is not, how do they learn gestures? Or, how do they use them? But, *what do they mean?*

It is perhaps the most obvious question in the study of any system of communication, particularly if we aim to address the evolutionary perspective. Behaviour does not occur in an isolated vacuum, but in an environment to which it has adapted over time. Selection acts upon the likelihood that a particular behavioural trait will promote that individual's chances of passing the trait on to the next generation. In other words, selection acts upon what that trait brings to that individual: upon its function. Thus, when studying gestural communication from an evolutionary perspective, it is not enough to describe simply the form and use of gestures; we must also address their function.

Despite this there has been very little empirical study of function in gestural communication, with the first studies to address this in gorilla and orang-utan gesture only published in the past year (Genty et al., 2009, Cartmill and Byrne, 2010). Earlier work on the flexible nature of gesture concentrated on the use of behavioural contexts as a proxy for function (Tomasello et al., 1994, Liebal et al., 2004a). The use of context allowed for the objective analysis of observable factors such as grooming or feeding, and avoided the precarious pitfalls involved in interpreting the 'meaning' of another species' behaviour. Nevertheless, this approach risked exaggerating the flexibility with which gestures are used, as a gesture may have a single function, such as 'stop', and still be used across a number of contexts: a potentially serious problem given that this flexibility is considered a key distinction from the fixed nature of the vocal repertoire.

In order to address this, Genty et al. (2009) approached the problem from a different perspective: if gestural communication is goal-directed, then the goal (or function) of that communication can be defined in terms of the behavioural outcome which appears to satisfy the signaller. This approach allowed for a more accurate analysis of a gesture's function while steering clear of attempting to 'mind read' internal thought processes. Following this approach I identified 17 separate functions in chimpanzee gestural communication, all imperative requests. This was a much larger repertoire of functions than that found in gorilla (10) (Genty et al., 2009), or orang-utan (8) (Cartmill and Byrne, 2010) gesturing; but it replicated the finding that great ape gestural communication appears limited to imperative requests which act to regulate social interactions, rather than communicating information in a specific word-like fashion (Cartmill and Byrne, 2010).

Fifteen of the chimpanzee functions were positive requests that promoted social interactions such as grooming, or sharing food, while two were negative requests that functioned to discourage or prevent social interaction. This apparent bias towards positive requests may, in part, be due to the very general nature of the negative 'stop behaviour', which could be applied across a wider range of behaviour than specific positive requests such as groom me, or move closer. However, together the negative requests accounted for less than 10% of all gestural communication, which is approximately equivalent to the proportion of functions they represented (2/17 or 11.8%). Thus, it appears that the general 'stop behaviour' category represented an appropriate level of categorization, and that further splitting was unnecessary at this stage.

Sonso chimpanzees used individually gestures flexibly towards a range of functions, however, where detailed analysis was possible, there was a striking association with a single primary function (observed significantly more often that the secondary function) in 13 of the 14 gestures. At the same time only 7 of these 13 gestures were classified as having a 'tight' association of meaning with this primary function (over 70% of cases and 3x more frequent than the secondary function). Thus, chimpanzee gesturing appears to involved the use of both highly specific and ambiguous gestures.

As with orang-utan and gorilla gestural communication, the majority of chimpanzee gestures functioned to start, continue, or change play (Genty et al., 2009, Cartmill and Byrne, 2010). This corresponds with the finding that *play* accounted for the majority of gesture cases, and was the dominant context for gesture use in all age groups of chimpanzees under 25-years old. Not only did the majority of gestures have a primary function *play,* but more than half gestures with an alternative primary function, also had a secondary function in *play*. Interestingly there was the suggestion that, in some cases, gestures were defined as having only a 'loose' or 'ambiguous' meaning because of the prevalence of their use towards a secondary or tertiary *play* function.

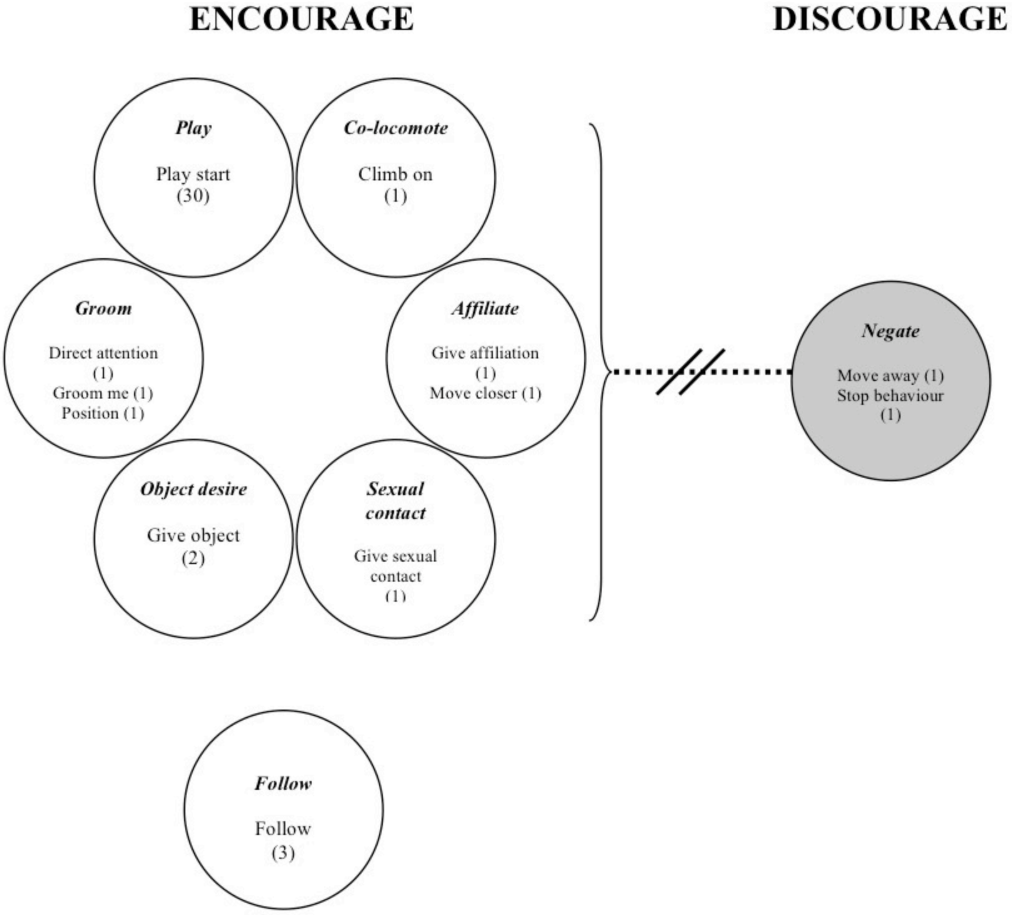


Figure 26. Semantic contrasts evident in chimpanzee gestures. The unshaded circles represent the 7 categories of positive meanings (named in bold ***italics***) that encouraged further social interaction, the shaded circle represents the category of negative meaning (*negate*) which actively discouraged social interaction. The functions within each category are listed within the circles; the numbers in brackets represent the number of gestures associated with each function (through either a tight or loose association).

As in orang-utan gesture (Cartmill and Byrne 2010), I was able to distinguish broad categories of semantic meaning with the functions of chimpanzee gestural communication. These included 7 positive categories that encouraged further social interaction and 1 negative category that actively discouraged further interaction. These active discouragements were relatively infrequent, as in many cases social interaction was refused through passive discouragement such as the recipient turning away, or studiously ignoring the signaller.

Negate was comprised of the two functions: ‘stop behaviour’ and ‘move away’; however, it may be the case that rather than communicating distinct meanings, these two functions represent more (move away) or less (stop behaviour) emphatic versions of the same communicative meaning. *Negate* communications were observed in contexts that related to 6 of the 7 categories of positive social request (see Figure 26). The single positive area of meaning in which no active negative communications were observed was *follow.* Follow was very closely associated with consortship communication, in these cases, where even passive refusal resulted in violent attack, it would be extremely unlikely that female chimpanzees would risk actively communicating their refusal of the male’s desire for them to follow him away from the group.

11.3 Where do we go from here?

The systematic study of gesture across populations.

I find that the gestural communication of wild chimpanzees supports the new theory that the gesturing of great apes is founded upon the intentional use of a large species-typical repertoire. As this represents a new and radical shift away from the long-standing theory that intentional gestures are acquired through ontogenetic ritualization, it would be valuable to test the species-typical theory further.
One prediction of a species-typical theory is that there would be no significant variation between chimpanzee groups in the available gestural repertoire, thus, one means to test it would be to extend the systematic study of gesture into other chimpanzee populations, to allow for more detailed comparison.

The systematic study of gesturing across populations would also provide the opportunity to test for group-differences: for example, in the gesture types regularly used by mature individuals. I find evidence that although the available repertoire is species-typical, the use of this repertoire undergoes a process of tuning, so that with maturity gesturing becomes focused on a sub-set of high-success gesture types. This tuning opens up the interesting possibility of group differences in the adult repertoires of different populations. While there is no evidence for group specific repertoires in captive apes (Genty et al., 2009), captive studies have tended to focus on the gesturing of immature individuals (Tomasello et al., 1994, Pika et al., 2005b, Genty et al., 2009), and no study has compared mature repertoires in isolation.

Group differences may be created through the cultural transmission of preferences for certain gesture types, for example through the imitation of mature individuals. However, this is not necessarily the case, as a similar result of consistent group differences could be effected through selection to the local environment. For example, in the same manner that the song frequency of certain birds varies within the species depending on the local acoustic environment of the singer (Slabbekoorn and Peet, 2003, Kirschel et al., 2009); certain gestures may be more effective within certain environments, such as audible gestures within dense secondary forest environments, or silent gestures in more open primary forest environments. Group specific differences in repertoire may permit the identification of a mature individual's natal group from their adult repertoire, and the extent to which repertoires differ between neighbouring groups might have significant implications for the gestural communication of females, who emigrate away from their natal groups at maturity.

Inter-generational changes in gesturing

In addition to possible between-group variation in the mature repertoire, there may be a drift across generations of the same population. For example, while I would not expect the addition of many new gesture types to the Sonso repertoire, it is possible that the repertoire of regular use could shift over time, so that the relative frequency of different gesture types may change in future generations. Establishing whether or not this was the case would require a long-term study of gesturing over several generations within the Sonso community.

The development of gestural communication

One further means to test theories regarding the acquisition of gesture would be to conduct a longitudinal study within a single cohort of chimpanzees in a natural population. Tomasello and colleagues undertook a long-term study of gesturing in captive chimpanzees (Tomasello et al., 1994); however, this was a series of snapshots of gesturing recorded several years apart, from a very limited number of individuals in a restricted captive environment. In order to directly examine the development of gesture it would be extremely valuable to have true long-term records of the gestural communication of a larger number of chimpanzees living in their natural habitat.

The intentional use of other species-typical behaviours

If great ape gesturing is based on the *intentional* use of a large species-typical repertoire, as the evidence from both gorilla (Genty et al., 2009), and now chimpanzee, gesturing suggests. It may be the case that the intentional aspects of species-typical communicative behaviour in other species have been over-looked. Ristau's (1991) studies of the 'broken-wing' display of the piping plover suggest that this may be the case. Widespread among the subfamily to which plovers belong, therefore undoubtedly biologically given, the piping plovers adjust the location of their display in order to accommodate the visual field of the potential predator (Ristau, 1991). It may then be interesting to employ the methodology used in the identification of intentional cases of gesture use in the study of biologically-given displays in other species.

11.4 What are the implications for the theory that human language originated in gesture?

Chimpanzees represent our closest biological relative, and, while modern chimpanzees have undergone their own evolution in the 6-8 million years following the divergence of our species lines, we are able to predict the cognitive capacities of our last common ancestor by looking at areas of overlap in the behaviour of both modern species. In the case of gestural communication, areas of horizontal overlap between the gestural communication of chimpanzees and the language capacity of humans, provide a means of tracing the origin of our communicative capacity back through the vertical evolutionary time line, and address questions such as whether or not gestural communication may have provided a platform for the development of human language.

The nature of gesturing in wild chimpanzees strengthens the argument for a gestural origin of human language. Although captive studies of great apes have provided compelling evidence that the elaborate and flexible nature of gesture provided an appropriate platform for the development of language, there was the inevitable concern that the artificial, restricted nature of the captive environment, and the potential for human influence may have distorted the findings.

In fact, when compared with the gesturing of captive chimpanzees, wild chimpanzee gestural communication appears to be *more elaborate*: it includes a larger repertoire of gestures combined in different forms of sequence; and *more flexible*: it is regularly used in an intentional manner by a wider range of individuals (4-months to over 44-years old) in a wider range of situational contexts, including in evolutionarily urgent behaviour. It is used in a targeted fashion in order to communicate specific, imperative requests, in a predictable manner that act to regulate social interaction. Furthermore, wild chimpanzee gestural communication appears to undergo a process of perceptual tuning, similar to that observed in several aspects of human cognition, including language. Thus, the evidence from the gesturing of wild chimpanzees strengthens the argument that gestural communication provided a platform for the development of human language.

It seems likely that the capacity for referential pointing existed prior to the divergence of the human line. Although on the evidence from wild chimpanzees it would appear that pointing is a uniquely human trait, it is impossible to ignore the compelling evidence for the capacity in captive apes. Thus, I would suggest that the capacity for referential pointing did exist in the shared ancestral line, but would only have been expressed in contexts where the environmental pressures promoted its usefulness as a communicative strategy.

One puzzling finding may point to a possible area of difference that arose after the divergence of the chimpanzee and human lineages. If great apes are capable of using a large repertoire of gestures in an intentional fashion, and are capable of acquiring new patterns of behaviour through imitation or social learning, as has been shown in manual food processing skills (Byrne and Byrne, 1993) and in the acquisition of Tinka's unique liana-scratch by the young Sonso chimpanzees (see Chapter 6); then why do they not regularly extend this repertoire?

In wild populations of great apes, the species-typical repertoire of gestures may have evolved to accommodate communication under all normal circumstances, rendering further augmentation largely unnecessarily. Captive great apes are capable of acquiring large repertoires of communicative signs in ASL, and, not only readily acquire new signs when instructed by humans, but also spontaneously invent novel signs, for example by combining existing signs, when faced with novel situations (Gardner and Gardner, 1969). Nevertheless, despite demonstrating the capacity to extend their communicative repertoire in this manner, it appears that the semblance of innovation in naturalistic gesturing is largely illusory (Byrne and Tanner, 2006). Thus, it may be that the apes simply do not appreciate the potential of referential communication, and that this capacity may be specific to the human lineage.

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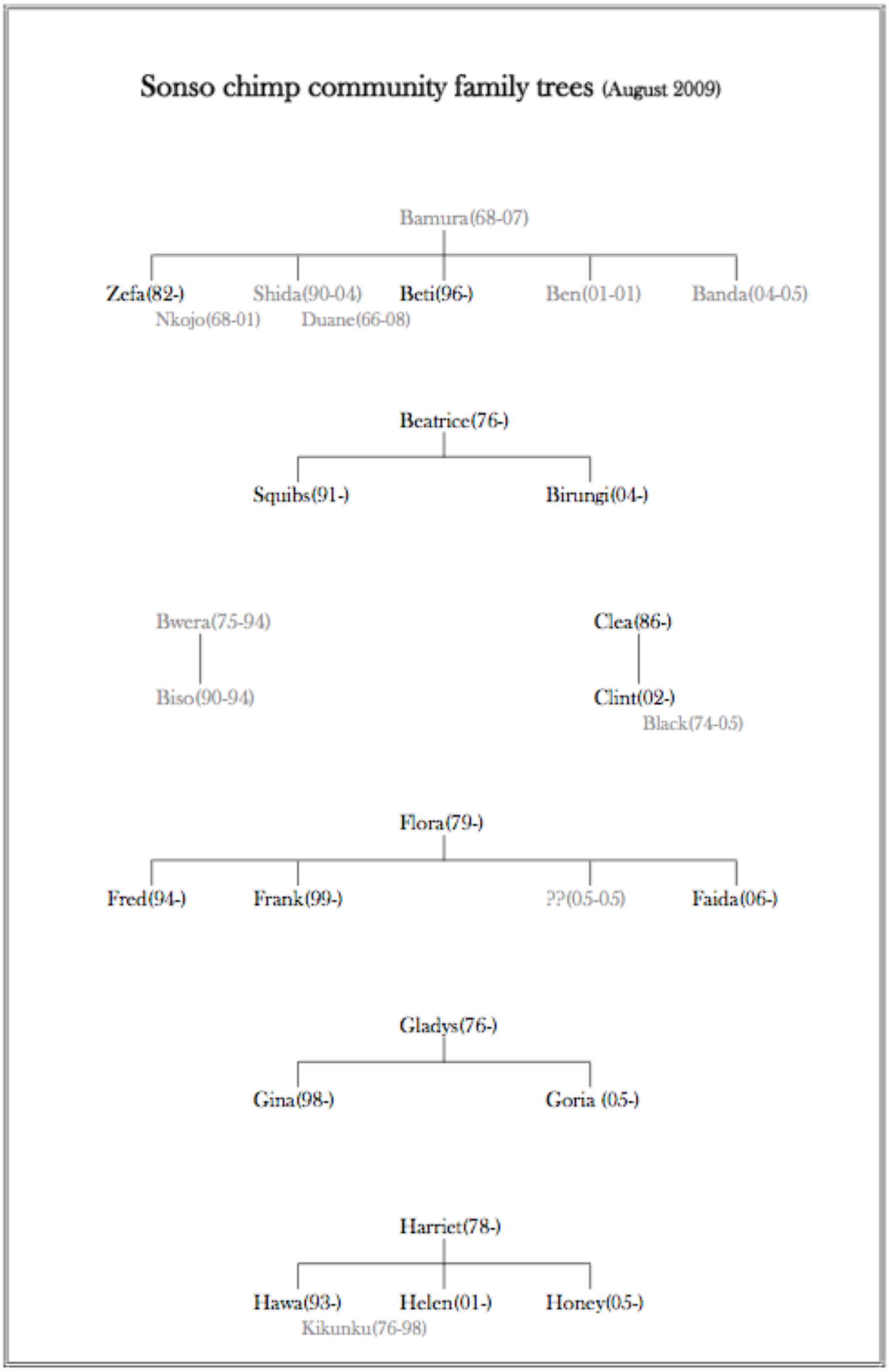
Appendix 1: Sonso community individuals: names, ages and female ranging status.

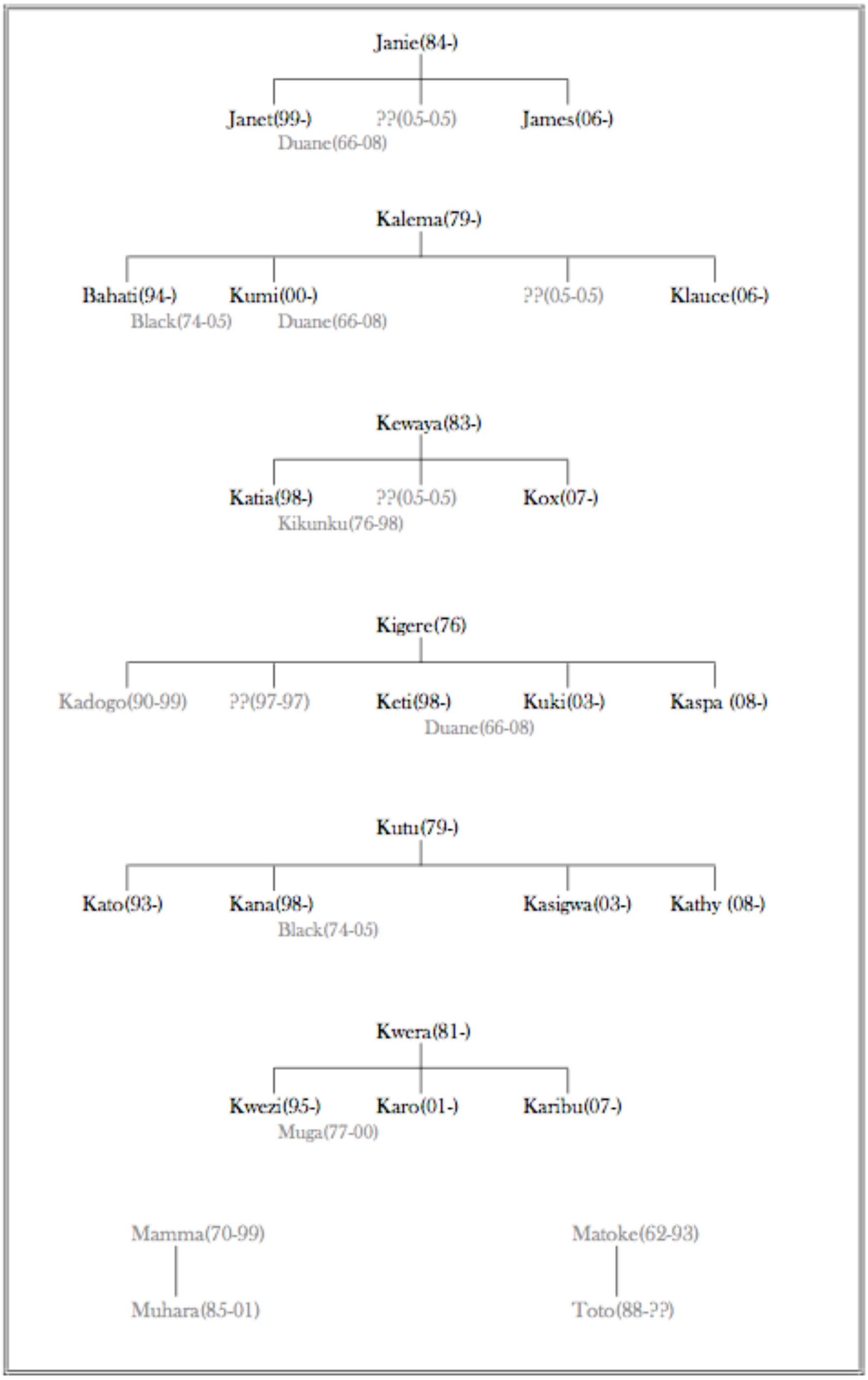
Numbers in brackets are ages in years, valid for 2009. Individuals in *italics* are dead as of end of the study in 2010.

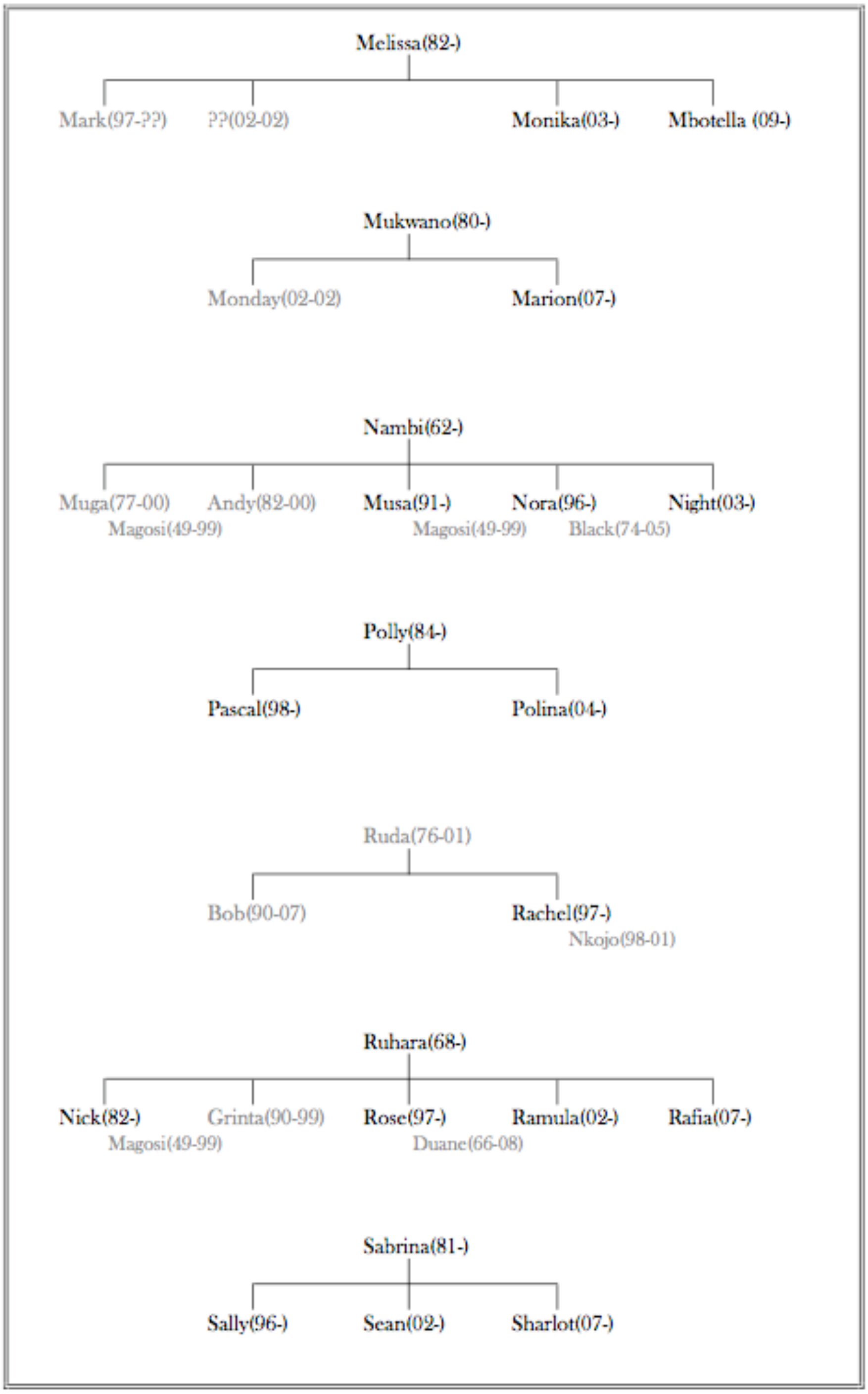
		Known offspring			
Adult females		**Adult**	**Sub-adult**	**Juvenile**	**Infant**
Core	Juliet (19 ±1)				
	Kalema (30 ±1)	Bahati (15)		Kumi (9)	Klaus (3)
	Kewaya (26 ±1)		Katia (11)		Kox (2)
	Kutu (30 ±1)		Kato (15) Kana (11)	Kasigwa (6)	Kathy (1)
	Kwera (28 ±1)		Kwezi (14)	Karo (8)	Karibu (2)
	Lola (20 ±1)				
	Nambi (47 ±3)	Musa (18) *Andy Muga*	Nora (12)	Night (5)	
	Zana (26 ±1)		Zalu (14)	Zed (8)	
	Zimba (41 ±3)	Kewaya (26)	Zig (12) *Gonza*	Zak (7)	*Zip*
Peripheral	Beti (15)				
	Flora (30 ±1)		Fred (15) Frank (10)		Faida (3)
	Harriet (31 ±1)	Hawa (16)		Helen (8)	Honey (4)
	Janie (25 ±1)		Janet (10)		James (3)
	Melissa (27 ±1)			Monika (6)	Mbotella (<1)
	Mukwano (29 ±2)				*Monday* Marion (2)
	Ruhara (41 ±3)	Nick (27 ±1)	Rose (12)	Ramula (7) *Grinta*	Rafia (2)
	Sarine (38 ±5)	Simon (16)			Sokomoko (3)
	Tanja (t.b.c.)				
	Verena (12±1)				
	Wilma (28 ±1)				*Willis*
Rare	Anna (19 ±1)				
	Beatrice (33 ±5)	Squibs (18 ±1)		Birungi (5)	
	Clea (23 ±2)			*Clint*	
	Emma (18 ±2)				
	Gladys (33 ±5)		Gina (11)		Goria (4)
	Kigere (33 ±5)		Keti (11)	*Kadogo* Kuki (6)	
	Polly (24 ±2)		Pascal (11)	Polina (5)	
	Ruda (25 ±1)		*Bob* Rachel (12)		
	Sabrina (28 ±1)			*Sally*	*Sean* Sharlot (2)

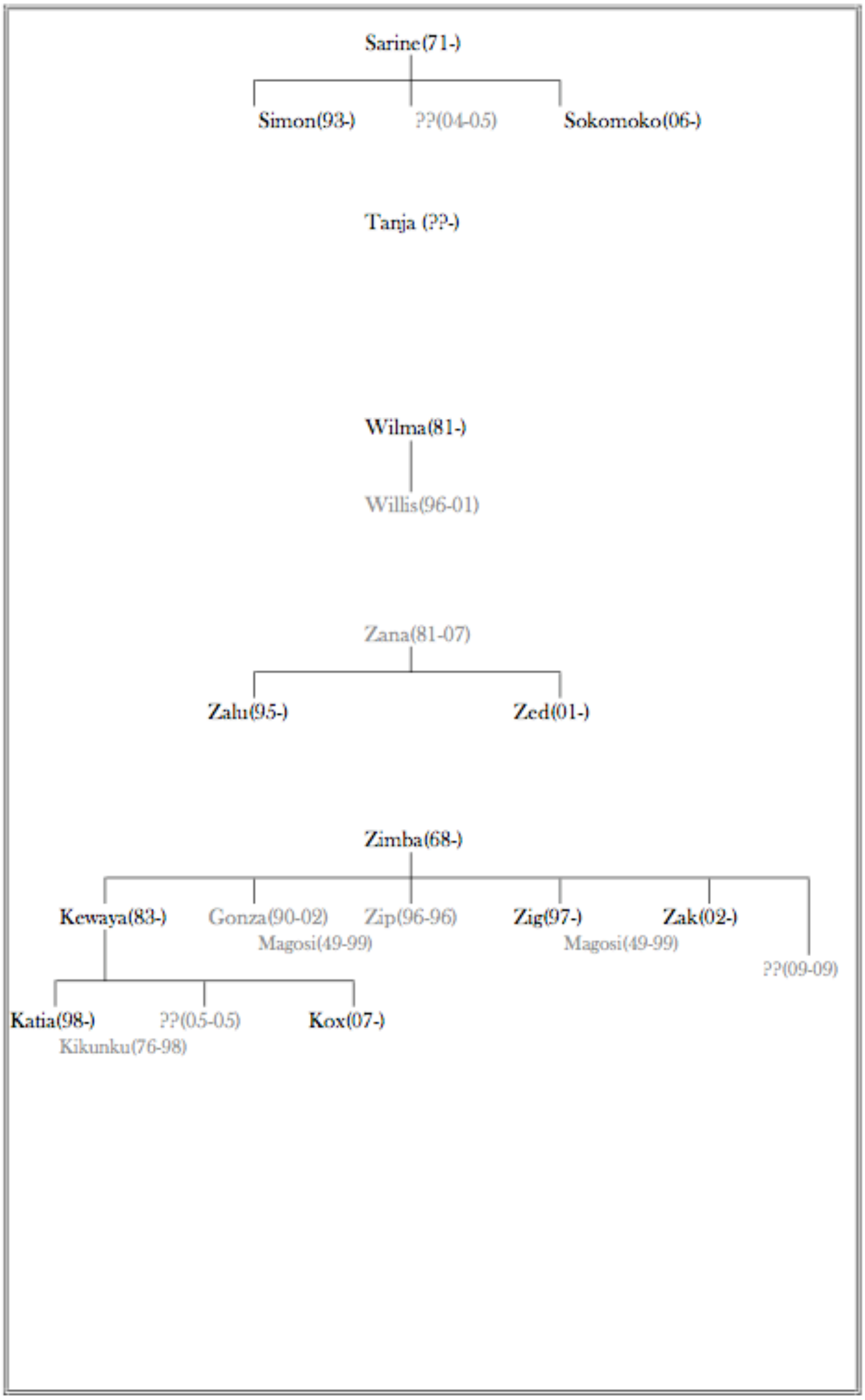
Other Adult males: *Bwoba (21 ±1), Duane (42 ±2), Gashom (21 ±1), Maani (50 ±5), Tinka (48 ±3),* Zefa (27 ±1)

Appendix 1 continued. Sonso family trees

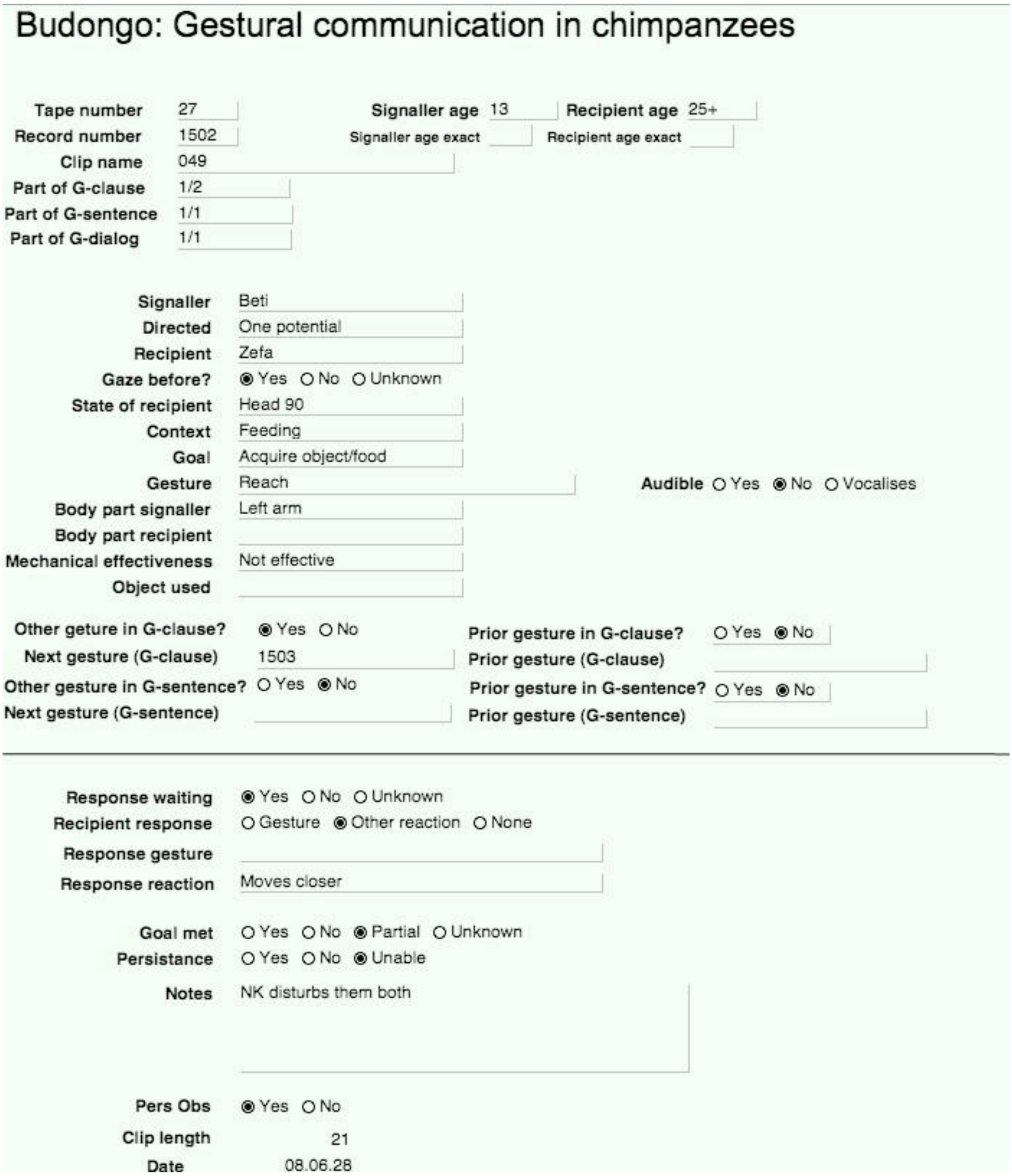



Janie(84-)
Janet(99-)
??(05-05)
James(06-)
Duane(66-08)
Kalema(79-)
Bahati(94-)
Kumi(00-)
??(05-05)
Klauce(06-)
Black(74-05)
Duane(66-08)
Kewaya(83-)
Katia(98-)
??(05-05)
Kox(07-)
Kikunku(76-98)
Kigere(76)
Kadogo(90-99)
??(97-97)
Keti(98-)
Kuki(03-)
Kaspa (08-)
Duane(66-08)
Kutu(79-)
Kato(93-)
Kana(98-)
Kasigwa(03-)
Kathy (08-)
Black(74-05)
Kwera(81-)
Kwezi(95-)
Karo(01-)
Karibu(07-)
Muga(77-00)
Mamma(70-99)
Muhara(85-01)
Matoke(62-93)
Toto(88-??)


Melissa(82-)
Mark(97-??)
??(02-02)
Monika(03-)
Mbotella (09-)
Mukwano(80-)
Monday(02-02)
Marion(07-)
Nambi(62-)
Muga(77-00)
Andy(82-00)
Magosi(49-99)
Musa(91-)
Nora(96-)
Magosi(49-99)
Night(03-)
Black(74-05)
Polly(84-)
Pascal(98-)
Polina(04-)
Ruda(76-01)
Bob(90-07)
Rachel(97-)
Nkojo(98-01)
Ruhara(68-)
Nick(82-)
Grinta(90-99)
Magosi(49-99)
Rose(97-)
Duane(66-08)
Ramula(02-)
Rafia(07-)
Sabrina(81-)
Sally(96-)
Sean(02-)
Sharlot(07-)


Sarine(71-)
Simon(93-)
??(04-05)
Sokomoko(06-)
Tanja (??-)
Wilma(81-)
Willis(96-01)
Zana(81-07)
Zalu(95-)
Zed(01-)
Zimba(68-)
Kewaya(83-)
Gonza(90-02)
Zip(96-96)
Zig(97-)
Zak(02-)
Magosi(49-99)
Magosi(49-99)
??(09-09)
Katia(98-)
??(05-05)
Kox(07-)
Kikunku(76-98)

Appendix 2: Example Filemaker Pro gesture coding sheet



Budongo: Gestural communication in chimpanzees

Tape number 27
Signaller age 13
Recipient age 25+
Record number 1502
Signaller age exact
Recipient age exact
Clip name 049
Part of G-clause 1/2
Part of G-sentence 1/1
Part of G-dialog 1/1

Signaller Beti
Directed One potential
Recipient Zefa
Gaze before? ● Yes ○ No ○ Unknown
State of recipient Head 90
Context Feeding
Goal Acquire object/food
Gesture Reach
Audible ○ Yes ● No ○ Vocalises
Body part signaller Left arm
Body part recipient
Mechanical effectiveness Not effective
Object used

Other geture in G-clause? ● Yes ○ No
Next gesture (G-clause) 1503
Other gesture in G-sentence? ○ Yes ● No
Next gesture (G-sentence)
Prior gesture in G-clause? ○ Yes ● No
Prior gesture (G-clause)
Prior gesture in G-sentence? ○ Yes ● No
Prior gesture (G-sentence)

Response waiting ● Yes ○ No ○ Unknown
Recipient response ○ Gesture ● Other reaction ○ None
Response gesture
Response reaction Moves closer

Goal met ○ Yes ○ No ● Partial ○ Unknown
Persistance ○ Yes ○ No ● Unable
Notes NK disturbs them both

Pers Obs ● Yes ○ No
Clip length 21
Date 08.06.28

Appendix 3: Field reports of consortship behaviour and background

The three main consortship events occurred on:
1. 05.01.2008 Duane and Lola. 98 clips, 45min and 50sec of video (unsuccessful)
2. 20.01.2008 Duane and Zimba. 100 clips, 53min and 15sec of video (successful)
3. 03.02.2008 Duane and Zimba, 64clips, 28min, 2sec video (successful).

A fourth consort event was recorded from the alpha male Nick to the dominant female Nambi who was in oestrus 4 (and increasing) on the 04.10.2008, however the pair were lost after less than 20min. Nick returned to the group on the 7th October and Nambi reappeared with oestrus 1 and decreasing a day later on the 8th October.

Individual history at the time of the consortship events

Duane: male, born 1966±2years, age 41years. A highly dominant individual (alpha for 13 years, an unusually long period of time) he had been recently been supplanted at the top of the male hierarchy by the younger male Nick. After the contest Nick relied heavily on Duane's support allowing him to maintain the beta male position. Duane still commanded a significant amount of influence in the community, and he maintained the support of the dominant females.

Zimba: female, born 1968±2years, age 39years. A dominant resident female and the only confirmed grandmother in the community. She has been a successful and productive mother with at least 5 children: *Kewaya* f, 1983 (mother of: Katia f, 1998; baby, 2005 (deceased); Kox f, 2007); *Gonza* f, 1990; *Zip* sex unknown, 1996(deceased); *Zig* m, 1997; *Zak* m, 2002. At the time of the consortship Zimba was in the process of weaning her youngest son Zak, she had resumed her oestrus cycle and when in swelling was highly sought after by all the community males.

Lola: female, born 1988±1year, age 19years. First seen in 2003 and named in 2005 she was a recently immigrated nervous young female who had not yet formed strong ties with anyone in the community. She had no known offspring and was assumed to be nulliparous at the time of the consortship.

Duane and Lola, 05th January 2008

Lola is in maximal swelling and has spent the morning grooming with the sub-adult male Hawa, he is not exhibiting any herding or possessive behaviour but Lola follows him all morning and there is at least one confirmed copulation between them. At 10.27am the young adult male Musa joins them and shortly after at 10.59am, Duane also arrives. Lola is resting in a tree with the female Zimba and her offspring; the males remain on the ground. At 13.56pm Hawa and Musa leave and Duane climbs and starts to display at Lola, this is the start of his consortship behaviour towards her. She screams in fear and tries to escape through the canopy, he chases and attacks her; a level 3 fight ensues during which Lola falls from a height of >15m, Duane drops and continues to attack her on the ground. She is badly injured, including deep cuts to her palm and swelling – she defecates and there is blood in the stool. This pattern of display-refusal-attack continues for almost 2hours until 15.33pm.

Over this time Lola is slowly herded away from the group but experiences 18 separate attacks, two of which are level 3 aggression events where she is thrown or falls from the canopy at over 15m. The 14 level two events are all short (<20s) but highly aggressive attacks during which Duane wrestles, bites, throws her bodily around and jumps up and down on her. Duane mounts Lola 10 times but he shows minimal penile erection and it is not clear that intromission is ever achieved; all follow level 2 or higher aggression events. Duane never made any clear attempt to invite her to copulate (penis display, leaf clipping etc.), at no point was he seen at maximum erection. There was no normal post-copulatory behaviour (penis smelling or wiping). During the consortship Duane displays almost no affiliative behaviour only very briefly grooming Lola (2 occasions, both <10sec). On 7 occasions, following an attack Lola presents her swelling to Duane and he turns and rubs against it with his anus while audibly panting (anal-rub gesture to swelling). She appears to be unsure of the correct response to this behaviour – on one occasion she presents twice, both times Duane responds with an anal-rub. None of the anal-rub gestures result in her moving towards him or following, all of them are followed by further displays from Duane, and on 4 occasions her refusal to follow results in an attack. By 15.00pm both of them are breathing hard and clearly exhausted spending longer and longer resting on the ground, Lola's swelling has noticeably decreased; they have moved less than 500m. At 15.33pm Musa returns with the alpha male Nick. Duane immediately moves away from Lola and Nick briefly chases him, but does not attack.

Lola moves away and Musa follows, Nick moves off in the direction that Duane left in.

Follow up

11th Jan - Lola was seen again for the first time, she is limping on the hand that was cut.

15th Jan – Lola is found dead in the morning. The position of the body and the vegetation around it seems to indicate that she has fallen from the tree above and was probably unconscious or dead at the time of falling. An autopsy reveals a broken collarbone on the left side with severe haemorrhaging around it, and a second haemorrhage on the brain. Post-mortem lividity indicated she died in the position the body was found on the ground face-down.

Duane and Zimba, 20th January 2008

Early in the morning we find Duane in Zimba's nest grooming her, he has climbed in early before she has had a chance to move off. Her two dependant sons Zig and Zak are with them. At 8.23am Duane climbs down and starts to display, Zimba follows slowly and presents to him. He rubs his anus against her swelling and moves off; he displays again and she comes to him, this time he carefully inspects her, smelling and tasting. She is in swelling stage 1(increasing) with only early indications of oestrus. He grooms her briefly and a pattern of display – slow approach follows. When she approaches he frequently rubs his anus against either her swelling if she presents or her chest if she simply follows. Her eldest son Zig calls and she moves to him and away from Duane, although she has barely moved a meter Duane immediately attacks; as she screams others from the community respond near by and she moves towards their calls, Duane attacks again but this time Zimba drives him off. He anal rubs against her side, and while they rest the others call again – Zimba screams and he attacks her a third time but is again chased off. Although Zimba is still slow to follow, unlike Lola she usually responds at least partially to Duane's requests, often barking softly to acknowledge his communication and then moving a few meters towards him. At 9.03am the other party joins up with them – the two males Tinka and Gashom come, led by Zig; however Duane is the most dominant male and Zimba continues to follow him. The group travels together for a short while but by

9.12am Duane has isolated Zimba again and they move off together. Zak continues to move with his mother but Zig remains behind with the other males.

Over the next hour as well as leading her away Duane grooms Zimba twice for 5min, she now follows him easily and both individuals are quite relaxed. He only attacks her once more, at 10.32am after she responds to the group they left behind who are calling again – this is violent but very brief (<5sec) and afterwards she remains silent despite them continuing to call. At 10.44am another community is heard calling ahead, Duane immediately changes direction to move around them and Zimba now follows him quickly, apparently nervous of encountering the others. By 11.41am they have been travelling together for over 3hours, Zimba has experienced 7 level 2 attacks, 6 in the first 20min; but all of them brief and she doesn't appear injured. Unlike Lola, Zimba fought back and on 3 occasions successfully drove him off, at no point does Duane try to copulate with her and he is not showing any erection. They have now been travelling comfortably together for hours, they have moved over 1500m and both are relaxed, Duane grooms her and at times even briefly leaves her alone to climb and find young leaves to feed on. They move off the grid system together and are lost in a thick tangle of swamp.

Follow up

Duane returns to the community on the 27th Jan, and Zimba a day later with a swelling at level one and descending. It appears as though he has successfully isolated her for the entire duration of her oestrus cycle, however within only 4 days she is back at swelling level 3.

Duane and Zimba, 3rd February 2008

Zimba has been in stage 3 swelling for 2 days; on the 2nd Feb Duane carefully inspects her but doesn't take any further action. On the 3rd Feb at 10.00am in the morning he and Zimba are travelling together as part of a larger group, they (along with her two offspring Zak, and Zig and the young male Pascal) drop to the back of the group and she climbs a tree allowing the others to move ahead. Duane starts to display and she climbs down, over the next 20min he attacks her twice, wrestling and biting. She sustains two bites to the back and an abrasion to the left wrist but doesn't appear to be seriously injured. Duane continues to display and succeeds in leading her away from the direction the main group have moved in; Zak travels with them, while Zig and Pascal re-join the main group. The previous pattern of display – slow follow is repeated, with Duane also frequently using the rump-rub gesture against her chest. Interestingly Zimba doesn't present her swelling to Duane, who is only showing a very small degree of erection throughout the day. He only mounts her once (10.36am), and appears to copulate for 14 seconds but intromission is not confirmed and there is no post-copulatory behaviour. Once they are isolated they move quickly and quietly away together with no further aggression and little hesitation on the part of Zimba. By 10.44am they have moved into the outskirts of the Sonso territory and Duane feels comfortable enough to climb up a fig and feed for several minutes.

They have now travelled together for 40min, and have moved over 1000m; Zimba sustained only 2, level 2 attacks both in the first 20min, which left her with minor injuries. Duane now grooms her for long periods (one >10min) paying particular attention to the bite wounds to her back, which he inflicted earlier. At 11.46am they encounter bush-pigs in a thick area on the border of the swamp, the young infant Zak meets them first and panics, and they all run in fear. Zimba could easily have taken this opportunity to escape but instead follows Duane and they all move off together into the swamp.

Follow up

Duane returns to the community the next day, Nick follows him and twice chases and mounts him before he is allowed to rejoin the community. Zimba rejoins the group on the 7th of February; her swelling is reducing at the time but returns to maximal (swelling 4) oestrus only a few days later on the 9th Feb.

Long-term follow up

26th Feb 2008 Duane is seen in the morning displaying at Kigere (who is probably pregnant but is in oestrus at the time), he is believed to be initiating consortship behaviour when he disappears through some undergrowth and is found dead on the other side. There were no prior indications of ill health, and to date the cause of death is unconfirmed.

On the 8th March 2009 Zimba gives birth to a baby boy: average 7.5month gestation suggests conception in July 2008. This rules out insemination during either of the consortships but suggests that she was in, or approaching a period of highly fertility.