MEANING AND CONTEXT IN THE GESTURAL COMMUNICATION OF WILD BILIA (BONOBO: *PAN PANISCUS)*

Kirsty E. Graham

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

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Kirsty E. Graham

University of
St Andrews

This thesis is submitted in partial fulfilment for the degree of PhD
at the
University of St Andrews

September 2nd, 2016

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Abstract

Studying the communication of our closest living relatives, the great apes, can inform our understanding of language evolution. Great ape gestural communication has been well-documented in captivity, but less so in the wild, with the exception of the chimpanzee. My research on the gestural communication of wild bonobos (at Wamba, Democratic Republic of the Congo) aims to fill one of the gaps in our knowledge. In my thesis, I first describe the gestural repertoire of wild bonobos –the physical form of the gestures that they use. The Wamba communities of wild bonobos use 68 gesture types. I then look at the meaning of gestures by analysing the Apparently Satisfactory Outcome (ASO) that they achieve. Of the gesture types that are suitable for analysis, about half have only one ASO, while the other half achieve multiple ASOs. Where these meanings are ambiguous, with one gesture type achieving multiple ASOs, I look at potential modifiers: syntax-like sequence ordering, and behavioural and interpersonal context. There is no effect of sequence order on the meaning of gestures; rather, the behavioural and interpersonal context explains the apparent ambiguity. Gesture types mean different things in different contexts. Finally, I take my findings and compare them to data from wild chimpanzees at Budongo, Uganda. The gestural repertoire (the physical form of the gestures) overlaps by 88-96%, and many ASOs are achieved by the same gesture types. However, the distribution of gesture types for each ASO is different between species, possibly as a result of different contexts arising from differences in social behaviour.

Table of Contents

Acknowledgements....4
Abstract....5
Index of Tables....9
Index of Figures....10
Chapter 1 – Introduction....11
  1.1 What do I study?....11
  1.2 What is a bonobo?....11
  1.3 What is gestural communication?....14
    1.3.1 Human gestures....14
    1.3.2 Great ape gestures....17
  1.4 Why is this topic interesting?....24
  1.5 Outline of my Thesis....26
Chapter 2 – General Methods....28
  2.1 Introduction....28
  2.2 Field-site and subjects....28
  2.3 Data Collection....37
    2.3.1 GPS Data....38
    2.3.2 Video recording....40
    2.3.3 Focal individual sampling....41
  2.4 Video Coding....44
  2.5 Conclusion....49
Chapter 3 – Expressed and understood repertoires....51
  3.1 Background....51
    3.1.1 Human vocabularies & animal repertoires....51
    3.1.2 Teaching animals "Language"....54
    3.1.3 Natural great ape gestural repertoires....56
    3.1.4 Bonobo gestural repertoire....59
  3.2 Specific Methods....63
  3.3 Results....65
    3.3.1 Community repertoire....65
    3.3.2 Individual repertoires....72
    3.3.3 Who expresses and understands which gestures?....73
  3.4 Discussion....78

3.4.1 Bonobo gestural communication 78

3.4.2 The bigger picture 83

3.5 Conclusion 85

Chapter 4 – Gesture dictionary: Meaning of bonobo gestures 87

4.1 Background 87

4.1.1 Meaning in human language 87

4.1.2 Function in animal communication 89

4.1.3 Function or meaning? 90

4.1.4 Meaning in great ape gestural communication 91

4.2 Specific Methods 94

4.3 Results 94

4.3.1 Which gesture types are satisfied by which ASOs? 94

4.3.2 Which ASOs are achieved by which gesture types? 98

4.3.3 Do different gesture types achieve different ASOs? 101

4.3.4 Are different ASOs achieved by different gesture types? 106

4.3.5 Is requesting GG-rubbing different from requesting copulation? 108

4.4 Discussion 109

4.4.1 Bonobo gestural communication 109

4.4.2 The bigger picture 111

4.5 Conclusion 114

Chapter 5 – Syntax and context: Modifiers of bonobo gestures 115

5.1 Background 115

5.1.1 Human syntax & context 115

5.1.2 Animal signal combinations 117

5.1.3 Bonobo syntax 120

5.1.4 Great ape gesture sequences 121

5.2 Specific Methods 123

5.3 Results - Syntax 124

5.3.1 Do gesture types achieve the same ASOs when they are used singly as when they are used in sequences? 124

5.3.2 Should “Groom me” and “Groom you” be combined into one ASO? 128

5.3.3 Are certain gesture types more likely to appear at a specific position in a sequence? 131

5.3.4 Does the position of a gesture in a sequence affect the meaning? 134

5.4 Results – Context 137

5.4.1 Can behavioural context explain the ambiguity of gesture meanings? 137

    - 5.4.2 Does interpersonal context further disambiguate gesture meaning? 143
  - 5.5 Discussion..147
    - 5.5.1 Bonobo gestural communication 147
    - 5.5.2 The bigger picture 151
  - 5.6 Conclusion...153
- Chapter 6 – Comparing bonobo and chimpanzee gestures 154
  - 6.1 Background 154
    - 6.1.1 Bonobo and chimpanzee geography, evolution, and physiology........................154
    - 6.1.2 Bonobo and chimpanzee behaviour 157
    - 6.1.3 Bonobo and chimpanzee communication 163
  - 6.2 Specific Methods...165
  - 6.3 Results 167
    - 6.3.1 Do bonobos and chimpanzees use the same gestures?......................................167
    - 6.3.2 Do bonobos and chimpanzees use the same gestures for the same ASOs?........168
    - 6.3.3 Do bonobo and chimpanzee gestures share meanings in the same proportions? 172
  - 6.4 Discussion...176
  - 6.5 Conclusion...181
- Chapter 7 – General Discussion 182
  - 7.1 Gestural repertoires..182
  - 7.2 Gesture meanings 184
  - 7.3 Context affects meaning 187
  - 7.4 The BIG Conclusion 192
- References 193
- Appendices...210
  - Appendix 1. Focal behaviour and individual sampling categories for “behaviour” 210
  - Appendix 2. Focal behaviour and individual sampling categories for “posture” 211
  - Appendix 3. Focal behaviour and individual sampling categories for “general context” .212

Index of Tables

Chapter 2 – General methods

Table 2.1. Information for members of E1 Group (2014-2015) 32

Table 2.2. Information for members of P Group (2014-2015) 34

Chapter 3 – Expressed and understood repertoires

Table 3.1. Description of the bonobo gestural repertoire 66

Chapter 4 – Gesture dictionary: Meaning of bonobo gestures

Table 4.1. Proportion of ASOs achieved by each gesture 95

Table 4.2. Proportion of gesture types that achieve each ASO 99

Table 4.3. ANOVA of ASO distribution for each gesture type 102

Table 4.4. ANOVA of gesture type distribution of each ASO 107

Chapter 5 – Syntax and context: Modifiers of bonobo gestures

Table 5.1. ASOs achieved by each gesture type singly and in sequences 126

Table 5.2. Distribution of ASOs for each gesture type singly and in sequences 127

Table 5.3. ASOs achieved when "Groom me" and "Groom you" are combined 131

Table 5.4. Position of each gesture type in sequences 132

Table 5.5. ASOs achieved by each gesture type in each position 135

Table 5.6. Distribution of ASOs for each gesture type in each position 136

Table 5.7. ASOs achieved ≥5 times for a given gesture type 137

Table 5.8. ASOs for each gesture type in each behavioural context 142

Table 5.9. ASOs for each gesture type in each interpersonal context 145

Table 5.10. Gesture meanings that are disambiguated by context 149

Chapter 6 – Comparing bonobo and chimpanzee gestures

Table 6.1. Bonobo and chimpanzee gesture types used to achieve each ASO 172

Table 6.2. ANOVA of distribution of gesture types across ASOs for both species 175

Index of Figures

Chapter 2 – General methods

Figure 2.1. Map of bonobo group ranges at Wamba (Tashiro et al., 2007) 31

Figure 2.2. Daily attendance during study periods 37

Figure 2.3. Map of study site location and range of E1 and P Group (2014-2015) 39

Figure 2.4. Blank FileMaker Pro coding sheet used for video coding 45

Chapter 3 – Expressed and understood repertoires

Figure 3.1. Illustration of *Begging* gesture (Plooij, 1978) 57

Figure 3.2. Photograph of *Reach out side* gesture (Pollick & de Waal, 2007) 60

Figure 3.3. Asymptote of community gestural repertoire 72

Figure 3.4. Expressed and understood repertoires of all individuals 74

Figure 3.5. Index of expressed and understood repertoire by number of instances 75

Figure 3.6. Expressed and understood repertoires by age and sex 77

Figure 3.7. Photograph of adult male carrying juvenile male 80

Chapter 4 – Gesture dictionary: Meaning of bonobo gestures

Figure 4.1. Proportional histogram for ASOs achieved by each gesture type 97

Figure 4.2. Scatterplot of number of ASOs by number of instances 98

Figure 4.3. Scatterplot of number of gesture types by number of instances 101

Figure 4.4. Interaction plot of ASO and gesture type for copulation and GG-rubbing .. 109

Chapter 5 – Syntax and context: Modifiers of bonobo gestures

Figure 5.1. Proportion each gesture type (single or sequence) achieved each ASO 125

Figure 5.2. Proportion of ASOs when combined “Groom me” and “Groom you” 130

Figure 5.3. Proportion of ASOs for each gesture type in each position 135

Figure 5.4. Proportion of ASOs achieved ≥5 times for a given gesture type 140

Figure 5.5. ASOs achieved by each gesture type in each behavioural context 142

Figure 5.6. Proportion of ASOs by gesture type for remaining ambiguous gestures 144

Figure 5.7. ASOs achieved by each gesture type in each interpersonal context 146

Chapter 6 – Comparing bonobo and chimpanzee gestures

Figure 6.1. Venn diagram of bonobo-chimpanzee repertoire overlap 168

Figure 6.2. Matrix of bonobo-chimpanzee gesture meanings 170

Figure 6.3. Comparison of matrices with different constraints 171

Figure 6.4. Proportion of gesture types achieving each ASO for each species 174

Chapter 1 – Introduction

1.1 What do I study?

When I describe my research topic to family and friends, I first have to explain what a "bonobo" is, before I can get into describing how they use gestures. Most people are quite interested, but I always imagine that their first thought is "*Why on earth would anyone want to study how monkeys move their arms?"* It has taken me three years to adequately answer this question. First of all, bonobos are not monkeys – they are apes, just like you and me. Long-armed and tailless. The second part of the question is more complicated, and I will spend the next tens of thousands of words demonstrating what we can learn by studying bonobo gestural communication.

1.2 What is a bonobo?

The bonobo (*Pan paniscus*) is a species of great ape, a family that also includes the chimpanzee, orangutan, gorilla, and human. Bonobos were only declared a separate species in 1933, before which they were thought to be chimpanzees, and even their first name "pigmy chimpanzee" reflected the similarity between the two species (Coolidge, 1933). The name "bonobo" was more recently adopted, and is likely derived from Bolobo, a town outside of the bonobo distribution from where the first bonobo specimens were shipped (Kortlandt, 1995). Throughout this thesis, I will refer to *Pan paniscus* as "bonobo", but I wish to recognise that most people living in the bonobo range know them as “bilia” (Kano & Nishida, 1999), as I have referred to them in the title of this dissertation. Although it is difficult to re-name a species, it is important for biologists to acknowledge the local name for endemic species.

When I encounter non-primatologists who *have* heard of bonobos, they give a knowing look, “oh, they’re the ones that…” Yes, bonobos are popularly known as a highly promiscuous species of ape, even though chimpanzees also exhibit promiscuous mating strategies (Tutin, 1979). The bonobo reputation probably stems from their homosexual behaviour; they frequently engage in female-female genito-genital rubbing (GG-rubbing), a behaviour that is much rarer in other species of great ape (but see Grueter & Stoinski, 2016). However, as I explain in my comparison of bonobos and chimpanzees in Chapter 6, bonobo and chimpanzee heterosexual behaviour is not so different (i.e. they both copulate dorso-ventrally and ventro-ventrally), although bonobo females are sexually receptive for a longer period (Furuichi & Hashimoto, 2002).

Bonobos are noted for their matriarchal, egalitarian society, in which females maintain the peace by forming strong bonds through female-female sexual relationships (Furuichi, 2011). While there are very real differences between bonobo and chimpanzee behaviour, we need to be careful not to exaggerate (Stanford, 1998). Much bonobo research comes from captivity, where the range of behaviour is limited and groups are small and artificial – often fewer than 10 individuals, whereas in the wild group sizes range from 20-40 individuals (Chapman, White, & Wrangham, 1993; Furuichi et al., 1998; Pika, 2007; Pollick, Jeneson, & de Waal, 2008). Hierarchies that do emerge in captivity are thus only shallow representations of what happens in the wild. Captive bonobos don’t have to forage for food, and have much more time to play.

If we only ever compare captive bonobos to wild chimpanzees, we will necessarily find differences, and so making wild-wild comparisons is imperative.

On the other hand, studying bonobos in the wild is notoriously difficult, as they live only in the Democratic Republic of the Congo, south of the Congo River. Research in this region has been patchy, because of two recent civil wars, ongoing instability, and poor infrastructure. I was fortunate enough to have a supportive university risk assessment team, and to conduct my research at Wamba, the longest-standing bonobo study site. As I will describe in my methods in Chapter 2, bonobos at Wamba are well-habituated, so while observation is not as clear as in captivity, it is still a relatively easy field site to work at.

When deciding on a research topic, I did not adamantly want to work with bonobos, but ended up studying them through a series of fortunate events. I'm happy that I did, as it was an exciting opportunity to learn more about our lesser-known cousins. Although there have been a number of studies on captive bonobo gestural communication (de Waal, 1988; Genty & Zuberbühler, 2014; Orr, 2014; Pika, 2007; Pollick et al., 2008), much less has been done in the wild (but see Douglas & Moscovice, 2015; Fröhlich et al., 2016; Vea & Sabater Pi, 1998). I was therefore left with a plethora of research questions: What gesture types do bonobos use and what do the gestures mean? Do they have ways of modifying the meaning of their gestures? How does bonobo gestural communication differ from that of the chimpanzee? Do the two species' differing social structures affect gesture use and gesture meaning?

1.3 What is gestural communication?

1.3.1 Human gestures

Gestures are mechanically ineffective limb and body movements that are used to communicate (Gomez 1994). Human gesturing is a universal behaviour. People point, wave, stick out their lips, shake their heads, and present certain fingers. Humans use gestures alongside speech; the co-occurrence of speech and gesture is so strong that we even use gestures while talking on the phone, when our audience is unable to see us. In a series of studies, participants were asked to describe “Greebles”, digital 3D objects, but were not explicitly told to use gestures (Hoetjes, Krahmer, & Swerts, 2015). The participants used spoken words to describe the objects, but they also accompanied their speech with gestures. Most people gestured regardless of whether or not their audience could see them, much like talking on the phone. The difference was that when the audience could see the person, the gestures were larger than when the audience could not see them. Gesture may be used as a tool to help us to think through tasks, like when you are looking for scissors and walk around the room making a ‘scissor gesture’ with your fingers. There is an undeniable link between gesture, language, and cognition.

Gestures help us to think, and are linked to numeracy abilities in young children (Gunderson, Spaepen, Gibson, Goldin-Meadow, & Levine, 2015). Gesture also develops alongside language acquisition. Young children reach to request for things, and children as young as 11-12 months point as a way of referring to objects (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Tomasello, Carpenter, & Liszkowski, 2007). Pointing is a *deictic gesture* – it refers to the object towards which it is directed. Deictic gestures are not limited to pointing with the index finger, which is the familiar way of pointing for most Europeans, but also include pointing with other fingers, full-hand pointing, and lip pointing (Wilkins, 2003). Pointing combined with one or two noises can be used to attribute those noises to the referent, so that from pointing people can begin to talk about the world around them (Butterworth, 1998). *Iconic gestures* are another important variant – they are gestures that convey their meanings because they resemble the referent, and both signaller and recipient see the resemblance, e.g. making scissor movements with your index and middle finger. Iconic gestures can also link vocal communication to an object; by using iconic gestures that physically resemble the referent, the signaller is able to attribute noises to that object. Deictic and iconic gestures are potential entry points for reference in communication.

But many gestures do not physically resemble or point towards the thing that they refer to – rather, we have attributed meaning to arbitrary body movements, much as we have attributed meaning to arbitrary sounds (Sebeok, 1996). These are *conventionalised gestures*, gestures that we learn and that are shared by a linguistic community (Kendon, 1997). Conventionalised gestures are regularly used for greeting (hand waving, bowing); approving (thumbs up, head nodding, clapping); disapproving (thumbs down, head shake); and swearing (middle finger, middle and index finger, chin flicking). None of these gestures are deictic or iconic, nor in any way are they inherently connected to the referent – they are culturally-specific gestures that must be learnt to be understood. Conventionalised gestures demonstrate that gestures can convey a lot of information, but far more impressive is the fact that people who are unable to speak can *replace* speech with gesture, in the form of sign language.

Gesturing is clearly different from using sign language – sign languages are formally recognised languages with robust grammar structures and expansive vocabularies/sign systems. Nevertheless, the physical way in which we produce gestures and signs, namely with limb and body movements, is the same. That language so easily co-opts gesturing when speech is unavailable, illustrates the link between language and gesture. Sign languages are used in deaf communities around the world, and there is growing recognition of deaf culture (Ladd, 2003). Historically, deaf children were forced to try to learn to speak, but now several countries teach sign languages, such as British or American Sign Language, in school. When deaf children are not given formal sign language schooling, 'home signing' usually emerges, wherein the child and parent(s) develop their own system of signs to communicate (Frishberg, 1987). In Nicaragua, deaf children, many of whom had their own home signs, were systematically institutionalised and a new Nicaraguan Sign Language (NSL) emerged (Pyers, Shusterman, Senghas, Spelke, & Emmorey, 2010). The emergence and evolution of NSL followed the pattern of spoken pidgins and creoles[1]: first, at the pidgin stage, the students taught one another their own home signs without a formal grammar, and then a grammar structure emerged, becoming a creole after several generations (Pyers et al., 2010). AlSayyid Bedouin Sign Language, which has emerged over the last three generations in a Bedouin-Palestinian community with high instances of congenital

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[1] Pidgin languages occur when many people from different linguistic communities are brought together (often in a colonial context), and they begin to form a new, shared vocabulary from a combination of their known languages. A pidgin does not have a formalised grammar structure. After a number of generations, a formal grammar structure crystallises, at which point the language is known as a creole.

deafness, has followed a similar process of creolisation (Sandler, Meir, Padden, & Aronoff, 2005; Senghas, 2005).

Sign language is the epitome of gestural communication, demonstrating that a complete language is possible using gestures alone. But even those of us who do not know a sign language use gestures in our everyday lives. It seems that gesture is profoundly linked to language. Cognition and language are undoubtedly related, and the overlap seems to extend to gestures as well. As a linguistic species, we are able to use sign language and conventionalised, deictic, and iconic gestures. But humans are not the only species that produce gestures; all great ape species use gestural communication. Do other species of great ape also use conventionalised, deictic and iconic gestures? Or is there another variety of gestures available to them, and by extension us?

1.3.2 Great ape gestures

The study of natural gesture in apes came out of a long history of trying to get them to use language: first by teaching spoken language, then sign language. Several attempts were made at teaching chimpanzees to speak: Lightner Witmer tried to teach language to an ex-circus chimp (Witmer, 1909); Nadezhda Ladygina-Kohts raised a chimpanzee to the age of four, looking at its communication and comparing her findings to her own son (Ladygina-Kots, 2002); similarly, the Kellogg family studied the development of chimpanzee Gua, raised alongside a human child (Kellogg & Kellogg, 1933); and Catherine and Keith Hayes hand-reared a chimpanzee, Viki, explicitly in an attempt to teach her to speak (Bryan, 1963; Hayes & Hayes, 1951).

Although Viki grew up in the same environment as the Hayes' own daughter, she never learned more than a few unconvincing words – chimpanzee vocal production was apparently not malleable enough for human speech (Bryan, 1963; Hayes & Hayes, 1951).

Researchers then moved on to teaching apes sign language, as hand and arm movements fall within the physical abilities of chimpanzees. After 21 months, chimpanzee Washoe acquired over 30 signs; after 30 months, gorilla Koko acquired around 100 signs; and in total, chimpanzee Nim acquired around 125 signs (Gardner & Gardner, 1969; Patterson, 1978; Terrace, Petitto, Sanders, & Bever, 1979). The apes learned these signals by hand-moulding and demonstration, along with association training, whereby the subject learns to associate a gesture or picture symbol with a desired object or activity in exchange for a reward. Unfortunately many of these studies were abandoned after concerns were raised about methodological weaknesses, with signals and signal series being unintentionally primed by experimenters (Terrace et al., 1979; Umiker-Sebeok & Sebeok, 1981). However, not all ape language research was equally flawed. The Savage-Rumbaugh group particularly, which trained apes on symbol keyboards, still contributes towards our understanding of great ape communication (Savage-Rumbaugh & Lewin, 1994; Savage-Rumbaugh et al., 1993; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert, 1986).

In the wild, Goodall and, in particular, Plooij were the first to look at the natural gestural communication of chimpanzees, noting the capacity that they had for using gestures in different contexts (Goodall, 1986; Plooij, 1978). Subsequently, the most rigorous studies have been done in captivity (Call & Tomasello, 2007; Cartmill & Byrne, 2010; de Waal, 1988; Genty, Breuer, Hobaiter, & Byrne, 2009; Liebal, Call, &

Tomasello, 2004; Pika, Liebal, & Tomasello, 2005; Pollick & de Waal, 2007), cataloguing the gesture types that great apes use (which I'll cover in Chapter 3), the meanings that they have (Chapter 4), and the sequences that they use and contexts in which they occur (Chapter 5). Although there are more and more studies on great ape gestural communication in the wild (Douglas & Moscovice, 2015; Fröhlich et al., 2016; Genty et al., 2009; Hobaiter & Byrne, 2011b; Roberts et al., 2012), they do not cover all species equally and the methods are largely not comparable. However, the studies that *have* been conducted in the wild have highlighted the need for more wild research, and momentum seems to be building to take gestural (and multimodal) communication research in that direction.

Great ape gestural communication is of particular interest because the apes produce gestures *intentionally*. That is to say, great ape gestures meet criteria for first order intentionality. Intentionality, as described by Dennett, is divided into levels that can be iterated ad infinitum (Dennett, 1983). The most parsimonious explanation for most animal communication (and perhaps some human communication) is that it's zero-order intentional; the signal is automatically produced in response to a stimulus (Dennett, 1983; Sebeok, 1996). In first-order intentional communication, such as great ape gesturing, the signaller aims to alter the behaviour of the recipient, e.g. "*I want you to…*". In second-order intentional communication, the signaller wants to change the mental state of the recipient, e.g. "*I want you to think that…*". Third-order intentional communication is the next step, "*I want you to think that I believe that…*". The levels progress from there. Grice believed that everyday language use can operate on at least fourth order intentionality, "*thinking about knowing about believing about* *wanting"*, although many exchanges probably take place at a lower order (Grice, 1969; Millikan, 1984).

Researchers have developed a set of criteria to assess first-order intentionality in individuals of non-human species whom we cannot ask "what are you thinking?" (Bates, 1976; Gomez, 1994; Liebal et al., 2004, Call & Tomasello, 2007; Cartmill & Byrne, 2007; Hobaiter & Byrne, 2011). First, the signal must be directed towards a target audience, showing that the signaller is communicating with a specific individual and not just making random body movements on their own. A mechanically ineffective movement is not communicative unless directed towards another individual. Second, the signaller monitors the attentional state of the recipient, i.e. makes eye contact or looks in their direction (Bates, 1976; Gomez, 1994), and adjusts gestures accordingly (Liebal et al., 2004). In human developmental studies, eye contact is a sign of ostension – the signaller wants the recipient to be aware of their communicative attempts (Bates, 1976). Like the first criteria, this demonstrates that the signaller is targeting a specific individual and is making the recipient aware of their communication, either by coming into their visual field or by using a contact or audible gesture that does not require visual attention. Third, the signaller waits for a response, and fourth, the signaller persists or elaborates if their goal is not met (Cartmill & Byrne, 2007). These last two criteria show that the signaller aims to alter the behaviour of the recipient in a specific way, and waits to receive that reaction, or if they do not receive a reaction they continue to communicate. Intentional communication is goal-directed communication, and so criteria demonstrating this goal-directedness are imperative. To be included in analysis in most studies, gestures must meet at least one intentionality criterion.

The final criteria, that signallers persist or elaborate when they are unsuccessful, has been elegantly shown in captive orangutans (Cartmill & Byrne, 2007). If the gesture that an orangutan subject used to request a food item was partially successful, then they persisted in using that same gesture type, whereas if the gesture was unsuccessful, they elaborated by using a different gesture type (Cartmill & Byrne, 2007). This clearly demonstrated that the orangutans were directing their gestures towards a goal and if they were unsuccessful in achieving that goal, they continued to gesture. More strikingly, it showed that orangutans distinguished among different reactions of the target audience and adjusted their gesturing accordingly. If the audience apparently misunderstood their basic aims, they used a completely different gesture type (elaboration); if the audience apparently half-understood, they continued to use the same gesture type (repetition).

After completing the first full-draft of my thesis, a paper was published with new intentionality criteria, many of which are similar to those mentioned previously, but are framed in a way that can be applicable to all modalities of communication (Townsend et al., 2016). Developing criteria that are relevant to all communication systems is imperative for comparative research. Although I only look at gestural communication in my thesis, the interplay of gestures, vocalisations, and facial expressions will doubtless be a fruitful area of research in future. The new criteria proposed by Townsend et al. emphasise the social-use of signals, the aim towards a goal, and the reaction of the recipient – all similar to the way in which I assess intentionality of gestures in my thesis.

Several great ape gestures have been noted to resemble the action that they aim to elicit, and are then called “iconic”. The gesture *Beckon* resembles a movement in which the recipient comes towards the signaller, and may go so far as to direct a final destination for the recipient (Genty & Zuberbühler, 2014). A similar gesture, representing the path of travel towards a successful mating, has been described for the gorilla (Tanner & Byrne, 1996). Female bonobos use a *Hip shimmy* gesture, wriggling side to side in a way that resembles GG-rubbing (Douglas & Moscovice, 2015). But are these iconic gestures in the same way that humans use iconic gestures, where both parties recognise that the gesture resembles the referent and encode/decipher the meaning because of that? In a way, many (but not all) gesture types resemble the signaller's part of the action. For example, when an infant uses *Reach* to request being picked up, or an individual uses *Present (grooming)* to request being groomed, they are gesturing in a way that fulfils their part in the final action. I extend my arm so that you can respond and take it to pick me up. I show you my shoulder so that you can groom it. Perhaps gestures are ubiquitous through a community and a species because they are a natural action for what is wanted, and therefore everyone can use and understand them in a communicative system. One possible way in which the form of gestures could have come to resemble the final action is through what Lorenz called "Phylogenetic Ritualization", in which initially non-communicative, goal-directed actions gradually evolve to become part of the species' communicative repertoire (Lorenz, 1966). Alternatively, gestures could be acquired by "Ontogenetic Ritualization", in which initially non-communicative, goal-directed actions become ritualised between two individuals becoming part of the individuals' communicative repertoires (Tomasello et al., 1997; Tomasello, Gust, & Frost, 1989).

There is sparse evidence of deictic gesturing in great apes. In captivity, chimpanzees (particularly language-trained apes) are known to point (Leavens, Hopkins, & Bard, 1996; Leavens & Hopkins, 1999). The two beckoning gestures from the previous paragraph could also be considered deictic – pointing towards the desired location – and appear iconic because that is how an arm must move to point that way. However, pointing is hardly ever seen in wild chimpanzees (Hobaiter, Leavens, & Byrne, 2014). Chimpanzees may use a “directed scratch” to refer to a specific location for the recipient to groom the signaller, effectively pointing towards that location (Pika & Mitani, 2006). Pointing has anecdotally been reported in bonobos (Vea & Sabater Pi, 1998), but not in a systematic study on gestures. Recently, a study argued that bonobo females point toward their genital swellings with their feet (Douglas & Moscovice, 2015). However, this case of deictic gesturing is contentious – from the supplemental video footage, it seems that as the bonobo performs a *Leg swing* or *Leg flap* gesture their foot points in all directions, occasionally coincidentally pointing towards the genital swelling. Given such little support for iconicity and deixis in great ape gestural communication, it seems like we are looking at different kind of gesture – not iconic, or deictic, or symbolic.

My research does not involve the neurobiology of great ape gesturing, but it would be amiss to completely ignore the discoveries in that area. While non-human great ape gestures do not resemble human language, neurological studies reveal structural similarities in brain regions associated with language. In humans, language is usually lateralised in the left hemisphere of the brain, and the communication region in chimpanzees also appears to be lateralised (Cantalupo & Hopkins, 2001; Hopkins, Marino, Rilling, & MacGregor, 1998; Taglialatela, Cantalupo, & Hopkins, 2006). Moreover, chimpanzees have areas homologous to human Broca’s and Wernicke’s areas, which are associated with language comprehension and production

(Cantalupo & Hopkins, 2001; Hopkins et al., 1998; Taglialatela et al., 2006). The link between gestural communication and language is a large part of why I'm studying gestures in the first place.

1.4 Why is this topic interesting?

One reason to study bonobo gestures is obvious: to compare them to human gestures and, more importantly, human language. I have always been interested in languages. I speak four languages, and am currently learning a fifth; comparative linguists sometimes learn 60 or 70. The ability of humans to acquire languages is astounding. But I find it even more puzzling to think about how this language ability evolved.

In my undergraduate program, I began by reading Chomsky and Pinker, who argue that we have an innate language instinct, a module in our brain that supports whatever individual language we learn (Chomsky, 1972; Pinker, 1994). It is a simple and elegant solution, but one that perhaps over-simplifies the different abilities that are also required for language, and begs the question "where did this module come from so suddenly? How did it evolve?" Tomasello purports that Theory of Mind is integral to language use (Tomasello, 2009); in order to communicate using language, we must recognise the mental states of others. Bloom followed a similar train of thought, accepting the idea that we have a biological capacity for language but suggesting also that we acquire a language through input that requires a metalizing ability (Bloom, 2002). I also took an Evolutionary Psychology class, and was struck by the range in academic rigour – from thought experiments imagining an Environment of Evolutionary Adaptiveness (Foley, 2005), to full cross-cultural studies. But throughout it all, what appealed to me most was that we can study our closest living relatives as a way of deducing what our last common ancestor may have been like.

Primate communication has long been studied with the view of revealing precursors to human language. The field of primate gestural communication, although relatively young, has already been fruitful. Given that human speech is vocal, it might seem more natural to study vocalisations, but given the interrelatedness of gesture and language in humans, it is important to study both forms of communication in primates. Gesture may be integral to the origins of language, either alone or alongside vocalisations and facial expressions (Corballis, 2009). There is however, still a long way to go –we still do not fully understand how great apes use gestures, and the bonobo represents a significant gap in our knowledge. Humans shared a common ancestor with bonobos and chimpanzees 4-8 MYA, and bonobos and chimpanzees subsequently diverged 0.8-1MYA (Bradley, 2008; Lander, Reich, Gnerre, Patterson, & Richter, 2006). Despite the fact that chimpanzees and bonobos are equally related to humans, bonobos have been studied less and their gestural communication in the wild has never been systematically catalogued, with emphasis put on discovering the meanings of gestures and the way that bonobos modify the meaning of gestures.

By studying the gestural communication of great apes, we can gain insight into the evolution of human gesture and, indeed, human language. But we need a more complete picture – one that includes the study of *wild* great apes, and *all species* of great ape. Only once we can directly compare the gestures and their meanings across all great ape species will we have a clearer image of the gestural communication of our last common ancestor. And only once we have that base, can we work forward in reconstructing the evolutionary trajectory of human language.

1.5 Outline of my Thesis

In this thesis, I build from which gestures bonobos use, to what they use them for, to how they use them in combinations and in different contexts, and finally compare my findings with data from wild chimpanzees. I review the literature for specific topics in the introduction of each relevant chapter.

Chapter 2, “General Methods”, describes the methods that are used throughout all of the following data chapters. I describe the field site, study subjects, and data collection. Methods specific to each chapter are given in those chapters.

Chapter 3, “Expressed and Understood Repertoires”, explores which gestures to include in an individual’s repertoire. To date, researchers have only reported the *expressed* repertoire, the set of gesture types that an individual uses. Here, I argue that also reporting the *understood repertoire*, the set of gesture types that an individual understands, gives a more complete picture of each individual’s overall repertoire. I also examine whether there are any “one-way gestures” or gestures specific to a subset of individuals – gesture types that are expressed by one individual or set of individuals but received and understood by another.

Chapter 4, “Gesture Dictionary: Meaning of Bonobo Gestures”, explores how we study meaning in animal communication. I attribute meaning to intentionally produced gestures by looking at the Apparently Satisfactory Outcomes (ASOs). I then look at the specificity of gesture meaning –the degree to which a gesture type has an ambiguous meaning.

In Chapter 5, "Syntax and Context: Modifiers of Bonobo Gestures", I try to explain this ambiguity of meaning by looking at ways in which bonobos may modify their gestures. I begin by looking at the occurrence of gestures in sequence, to see whether presence or position in a sequence affects the meaning of a gesture, as it does in the syntax of many human languages. I then look at behavioural and interpersonal context, to see whether gestures mean different things in different contexts.

Chapter 6, "Comparing Bonobo and Chimpanzee Gestures", brings my findings from Chapters 3 & 4 together and compares them with data from wild chimpanzees at Budongo, Uganda. Bonobos and chimpanzees, although closely related, have markedly different social behaviour. I compare the repertoire and meaning of gestures between the two species. Although I do not compare meaning in different contexts between the species, I propose an idea for how it might look.

Then I'll wrap it all up with a discussion and conclusion, by which point you should hopefully be convinced about "*why on earth anyone would want to study how ~~monkeys~~ great apes move their arms*".

Chapter 2 – General Methods

2.1 Introduction

In this chapter, I describe the general methods used to collect data for all following chapters, which all use parts of the same dataset but analyse it in different ways. For statistical analysis I use R 3.2.3 with the R Commander package, and frequently use the packages ggplot2, lmer, MASS, and plyr. Here, I describe my field-site (Wamba, Democratic Republic of the Congo) and my study subjects. I outline my data collection methods, and broadly describe how I code my video footage. Each of the following data chapters will include "specific methods" sections that detail which part of the dataset I use and how I analyse that data.

2.2 Field-site and subjects

I conducted fieldwork at Wamba, Luo Scientific Reserve, Province de l'Équateur, Democratic Republic of the Congo (00° 10' N, 22° 30' E). The forest at Wamba can be split into three main types, as classified in a study using Landsat data, and reflect forest density: (1) dry forest, including primary and old secondary forest (regrown, no dense understorey); (2) swamp forest, bordering the Luo and Kofola rivers; and (3) disturbed forest, including young secondary forest and cultivated land (Hashimoto, Tashiro, & Kimura, 1998). The bonobos use all three forest types. The terrain is flat, with the exception of steep embankments surrounding the swamp forest of the Luo and Kofola rivers (Kano, 1980). Annual rainfall at Wamba is 2000 mm (Hashimoto et al., 1998), and my study periods were selected to avoid the severe rainy season from September through November, although they coincided with the light rainy season from March to May.

Wamba is a field-site of Kyoto University's Primate Research Institute. Research began at Wamba in 1974 when Kano and Kuroda established the study site and began habituation (Kano, 1980; Kuroda, 1979). Research at Wamba has been continuous, except in 1991-1994 because of increased conflict and rioting in Zaire, and in 1996-2003 during the country's two civil wars (Idani et al., 2008). There are currently 8 operating bonobo research sites (with varying levels of focus on research or conservation): Wamba, LuiKotale, Kokolopori, TL2, Lukuru, and Lac Tumba (Furuichi & Thompson, 2008), Lomako, and the newly-established Malebo. Wamba is the longest standing field-site; although Lomako was also founded in the 1970s, it was abandoned during the two Congo civil wars, and regular research has yet to be resumed. Though several other research sites were established in the early 1990s, they too were interrupted by civil war, and research only began properly in the years following 2002. These few field-sites, combined with captive work, provide our current understanding of bonobo behaviour.

There is some controversy in the bonobo research community because Wamba began as a provisioned field-site, wherein researchers gave sugar cane and pineapples to the bonobos at select provisioning sites. Some researchers feel that provisioning has altered the "natural behaviour" of bonobos at Wamba (Stanford, 1998). However, provisioning occurred only 2-3 months a year, periodically from 1976 to 1996 (Hashimoto et al., 2008; Kano, 1980). Also, provisioning targeted the main study group at the time, “Kame Kake” (E Group), which then split and through civil war and natural immigration of adolescent females, is now comprised of a largely different set of individuals than those who experienced provisioning. Also, there is another study group at Wamba, P Group, that were not the target of provisioning (though they may have occasionally visited the provisioning site). Because my research involves both groups, and also because there are few remaining members of E1 who experienced provisioning, I am confident that my findings do not reflect altered behaviour, above and beyond the usual impact of habituation.

At Wamba, there are two current study groups: E1 Group (sometimes referred to as Kame Kake) and P Group. In 1974, researchers began studying E Group, which later split into two groups, E1 and E2, between 1982 and 1983 (Hashimoto et al., 1998). It is possible that they were originally two separate groups that only appeared to be united because of the provisioning site (Tetsuya Sakamaki & Nahoko Tokuyama, personal communication). E1 Group was followed as the main study group, although five other unit groups (E2, P, B, K, S) were known to share overlapping ranges (Hashimoto et al., 2008). When researchers returned to Wamba in 2002 after the civil wars, E1 Group remained; E2 and P Groups had displaced their ranges; and no evidence was found of B, K, and S Groups (Idani et al., 2008; Tashiro, Idani, Kimura, & Bongori, 2007) (Figure 2.1). Currently, research continues with E1 and P Group. If anything, the ranging behaviour of E1 Group seems to have been affected more by the extermination of neighbouring groups than by periodic provisioning (Tashiro et al., 2007).

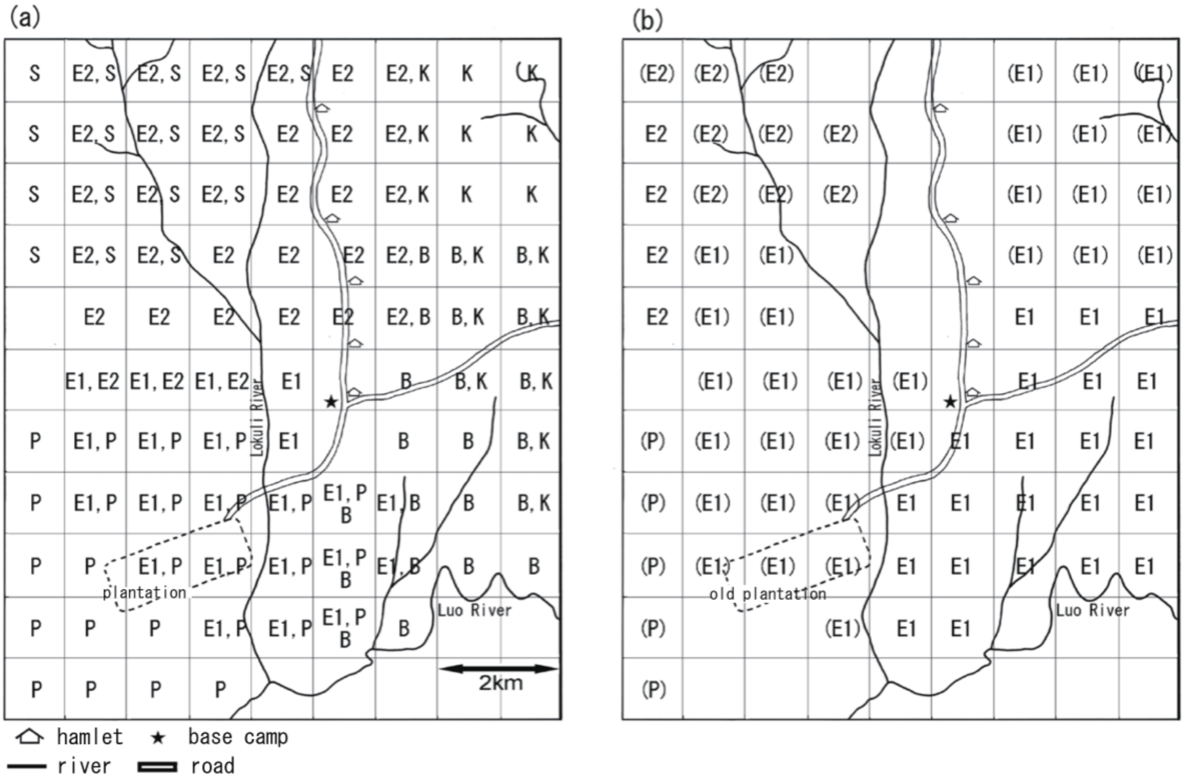


Figure 2.1. Map of bonobo group ranges at Wamba from (Tashiro et al., 2007)– "Fig. 2. Change in home range area from each bonobo group in Wamba Forest. One grid square represents 1 x 1 km. Each letter signifies the group (E1, E2, P, B, K, S). (a) Home range area of size groups in 1995. (b) Home range area of three groups in 2005. Home range data in parentheses are based on information from co-researchers and research assistants."

Throughout my study periods, E1 Group had 39 individuals and P Group had 30 individuals. Both groups are well habituated; as previously mentioned, habituation for E1 Group began in 1974 with provisioning, and habituation for P Group began in September 2010, without provisioning but simply by following the bonobos persistently. In 2014, the total sample size was 63 individuals, with 28 adults (16 females, 12 males), 12 adolescents (7 females, 5 males), 9 juveniles (6 females, 3 males), and 14 infants (8 females, 6 males). In 2015, the total sample size was 64 individuals, with 30 adults (18 females, 12 males), 8 adolescents (3 females, 5 males), 10 juveniles (7 females, 3 males), and 16 infants (10 females, 6 males). Throughout both study periods, I observed a total of 70 individuals (although one immigrant female Iyo was only seen for several weeks). For analysis, I divided age into classes following Hashimoto's bonobo age classifications: infant (<4 years), juvenile (4-7 years), adolescent (8-14 years), and adult (15+ years) (Hashimoto, 1997). In general, infants are dependent on their mothers; juveniles are weaned and less dependent on their mothers, but still travel with them; adolescents are sexually mature but socially immature; and adults are socially and sexually mature (Hashimoto, 1997).

The rank hierarchy for E1 group was taken on Tetsuya Sakamaki's advice, based on his longterm observations, and corroborated by other researchers at Wamba. Because rank and aggression were not my main focus, I did not collect the "all observance" data that would have been necessary to calculate rank. However, if, in my preliminary assessment, rank seems to influence gestural communication, then I will collaborate with other researchers at Wamba to properly delineate the hierarchy. The rank for P group reported here is from Nahoko Tokuyama's research, who overlapped with my study periods at Wamba and looked specifically at rank and aggression.

Table 2.1. Information for members of E1 group during 2014 and 2015 study periods.

Abbr.	Name	Sex	Age Class	D.o.B.	Imm. (F)	Mother	Rank
TN	Ten	M	Adult	1970		Sen	Medium
TW	Tawashi	M	Adult	1974		Kame	Low
LB	Loboko	M	Adult	1991-94*		?	Low
GC	Gauche	M	Adult	1984-89*		?	Low
NB	Nobita	M	Adult	1989*		Kiku	High
JD	Jeudi	M	Adult	1991*		?	Medium
DI	Dai	M	Adult	1985*		?	Medium
JR	Jiro	M	Adolescent	2002-03*		Jacky	-
No	Nao	F	Adult	1971*	11.1983		High
+Ne	Namee	F	Infant	10-13.04.15		Nao	-
Nt	Natsuko	F	Juvenile	05.2009		Nao	-
Ki	Kiku	F	Adult	1974*	12.1984		High

Ka	Kalin	F	Infant	30.01-03.02.14		Kiku	-
KY	Kiyota	M	Juvenile	07.2009		Kiku	-
KT	Kitaro	M	Adolescent	02.2004		Kiku	-
Hs	Hoshi	F	Adult	1981-85*	08.2003**		Medium
Ha	Hanna	F	Infant	07.02.2014		Hoshi	-
HC	Hachiro	M	Juvenile	08.2009		Hoshi	-
Sl	Sala	F	Adult	1991-92*	08.2003**		Medium
SE	Seko	M	Infant	12.2011		Sala	-
SB	Shiba	M	Adolescent	11.2004		Sala	-
Yk	Yuki	F	Adult	1981-85*	04.2004**		Medium
Ym	Yume	F	Juvenile	10.2009		Yuki	-
YD	Yoda	M	Infant	31.03-07.04.14		Yuki	-
Jk	Jacky	F	Adult	1986-90*	04.2004**		Medium
Jl	Jolie	F	Infant	01.2012		Jacky	-
JO	Jo	M	Juvenile (2014)/ Adolescent (2015)	10.2006		Jacky	-
Nv	Nova	F	Adult	1994-95***	08.2007		Low
Nl	Nimba	F	Infant	07.2013		Nova	-
Na	Nadir	F	Juvenile	09.2008		Nova	-
Ot	Otomi	F	Adult	1997***	06.2008		Low
+OS	Osamu	M	Infant	05.04.15		Otomi	-
Ok	Otoko	F	Infant (2014)/ Juvenile (2015)	01.2011		Otomi	-
Fk	Fuku	F	Adult	1998***	06.2008		Low
Fa	Fua	F	Infant (2014)/ Juvenile (2015)	01.2011		Fuku	-
Zn	Zina	F	Adolescent	2001***	10.2011		Imm
Pf	Puffy	F	Adolescent	2004***	10.2013	Pao (P)	Imm
- An	Anna	F	Adolescent		01.04.14		Imm
- Iy	Iyo	F	Adolescent				Brief Imm
+Ik	Ichiko	F	Adolescent	2008*		Ichi (P)	Imm

* Estimates of age from Hashimoto et al., 2008

** Immigration possibly took place earlier during conflict, but individuals were only identified after researchers returned to Wamba

*** Estimates of age from unpublished data

- Not present in 2015

+ Added in 2015.

Table 2.2. Information for members of P group during 2014 and 2015 study periods.

Abbr.	Name	Sex	Age Class	D.o.B.	Imm. (F)	Mother	Rank
GI	Gai	M	Adult	1972-77*			Medium
TK	Turkey	M	Adult	1982*			High
ML	Malusu	M	Adult	1987*			Medium
DN	Daniel	M	Adult	1995*			Low
SN	Snare	M	Adult	1990*			High
IR	Ikura	M	Adolescent	2002-3*		Ichi	-
Bk	Bokuta	F	Adult	1962*			High
Kb	Kabo	F	Adult	1972*			High
KL	Kale	M	Infant	03.2012		Kabo	-
- Kk	Kaboko	F	Adolescent	2005-06*		Kabo	-
Hd	Hide	F	Adult	1972*			High
HO	Hideo	M	Infant(2014)/ Juvenile (2015)	02.2011		Hide	-
- Hk	Hideko	F	Adolescent	2005-06*		Hide	-
Mt	Maluta	F	Adult	1985*			Medium
Mz	Mazy	F	Infant	11.2012		Maluta	-
- MC	Michio	M	Adolescent	2005-06*		Maluta	-
Ic	Ichi	F	Adult	1989*			Medium
Is	Isha	F	Infant	~25.03.2015		Ichi	-
IA	Isao	M	Infant	04.2012		Ichi	-
- Ik	Ichiko	F	Juvenile	2008*		Ichi	-
Po	Pao	F	Adult	1989*			Medium
Pk	Pukka	F	Infant	05.2013		Pao	-
Pp	Pipi	F	Juvenile	2009		Pao	-
Sk	Saku	F	Adult	1995*			Low
So	Sato	F	Infant	06.2013		Saku	-
Sc	Sachi	F	Juvenile	2009*		Saku	-
Mr	Marie	F	Adolescent (2014)/Adult (2015)	2000*	11.2011		Imm (2014) / Low (2015)
+Ma	Marina	F	Infant	14.07.2014		Marie	-
Nr	Nara	F	Adolescent (2014)/Adult (2015)	2001*	08.2012		Imm (2014) / Low (2015)
+Ns	Narisa	F	Infant	06.07.2014		Nara	-

* Estimates of age from unpublished data
- Not present in 2015
+ Added in 2015.

Because E1 Group is larger than P Group and has been studied for much longer, there is more complete information available for biological and social relationships among E1 members. However, habituation of P Group has been very successful, and genetic analysis is now being used to determine biological relationships. It was originally thought that P Group consisted of two sub-groups: P-East and P-West, who co-range more regularly than would be expected of separate groups (Tetsuya Sakamaki, personal communication). However, currently it is thought that they are indeed separate groups that encounter frequently, because during and following encounters the group membership remains stable (i.e. individuals do not switch group after encountering). For the remainder of this dissertation, I will refer to P-East as "P Group", which is the accepted name used by Wamba researchers. As I did not study "P-West", I don't mention them again in this dissertation.

I chose to work with both E1 Group and P Group in order to increase my sample size, as well as to determine whether any inter-group, potentially cultural, differences exist in terms of gestural communication. P Group is particularly interesting to follow in this regard; because of their frequent encounters with P-West, I am able to see them using gestural communication with members of a different group. E1 and P Group do encounter each other, but I did not observe such an event during my study period. Working with two bonobo groups also increased opportunities for observation in months when party size is more variable. In 2008-2009, E1's daily association size, the number of individuals seen together throughout the day, compared to total group size was roughly 80-100%, with lower percentages of roughly 40% in March and December (Sakamaki, 2013).

During my study periods, daily attendance data was collected by the field assistants, and I was allowed to use this data to determine the daily association size of groups during the study periods. For each day, I calculated daily association as:

$$Daily\ association = \frac{\#\ of\ individuals\ observed\ throughout\ day}{Total\ \#\ of\ individuals\ in\ group}$$

I found that during my 2014 study period, E1 group's daily association was, on average, 0.78 ± 0.21 (range 0.14-1.00); during my 2015 study period, E1 group's daily association was, on average, 0.76 ± 0.22 (range 0.18-1.00). During my 2014 study period, P group's daily association was, on average, 0.90 ± 0.15 (range 0.37-1.00); during my 2015 study period, P group's daily was, on average, 0.90 ± 0.18 (range 0.19-1.00). Monthly averages for both groups for both years are shown in Figure 2.2. These high daily association rates made it possible to collect adequate data for all individuals. There is some discussion among researchers at Wamba that E1 group may be splitting into parties for longer periods because of reaching such a high number of individuals, and may eventually split into separate groups (Tetsuya Sakamaki, personal communication).

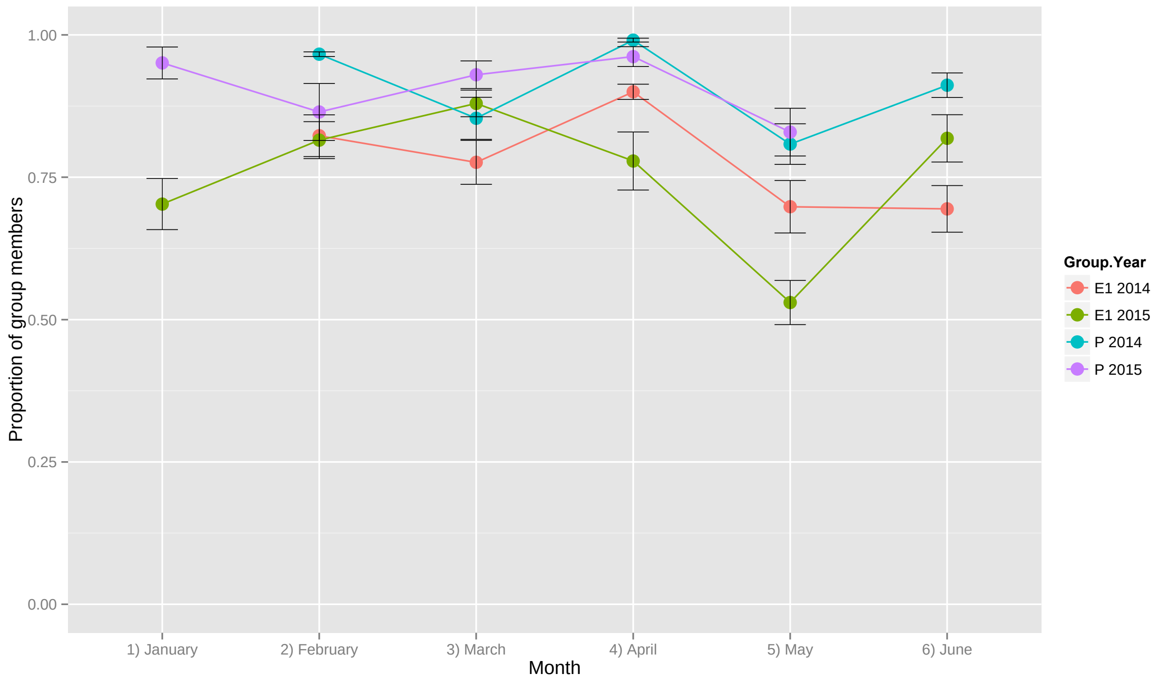


Figure 2.2. Average proportion of daily attendance over total group size for each month, with separate lines for both groups in both years. Error bars show the standard error for each month.

2.3 Data Collection

I collected data over two 6-month study periods, from February to June 2014, and January to June 2015. Each day, I woke up at 04:00 and left camp by 04:40 to arrive at the nest-site by 05:50. Sometimes the bonobos were further away and so I had to leave camp earlier, since we always aimed to be at the nest site at 06:00, before the bonobos started to travel. In the morning, I was accompanied by two field assistants and sometimes one other researcher. We followed the bonobos until meeting the afternoon team of two field assistants, who left camp at 10:00 to reach us by ~12:00. To find the morning team, the afternoon team walked the trails looking for signs where we had crossed, and once the two teams were close enough, we co-ordinated between teams with Motorola walkie-talkies. Once the two teams met, I would return to camp with the morning team. The afternoon team followed the bonobos until they made their night nests, usually at ~17:00, and the next day those same two field assistants would work in the morning.

I followed this daily schedule for four days on and one day off. Rain made data collection prohibitively difficult because a) the bonobos usually stay in nests, b) if they do travel, it is hard to follow them, c) rain affects visibility for filming, and d) the water could damage the camera. Therefore, if it rained heavily, I took the morning off and went in the afternoon. If one group was lost or consisted only of a small party of frequently observed individuals, I followed the other group. I observed bonobos on a total of 204 days amounting to ~1159 hours of observation time and 900 hours of focal individual data (or 1272 hours, including focal data for infants and juveniles collected simultaneously to their mothers). I divided time between the two communities, E1 and P Group, to allow an equal amount of observation for each individual, but roughly followed two days with E1 Group then two days with P Group then one day off, with additional days intermittently given to E1 because of the larger group size. Thus divided, I observed E1 Group on 118 days, amounting to 671.5 hours of observation time, including 517 (or 712 with infants/juveniles) hours of focal individual data. I observed P Group on 86 days, amounting to 488 hours of observation time, including 383 (or 560 with infants/juveniles) hours of focal individual data.

2.3.1 GPS Data

I collected GPS data to illustrate the range of E1 and P Groups during the study periods. Each day, at first visual contact with the bonobos, I began to record the daily range using the track function on a Garmin GPSmap 62, which continued recording until stopped at the last visual contact. I created a map of the ranges of both groups using ArcGIS (Figure 2.3). Although E1 and P Group did not encounter during either of my study periods, E1 Group sometimes ranged in the normal range of P Group, illustrating where intergroup encounters may occur.

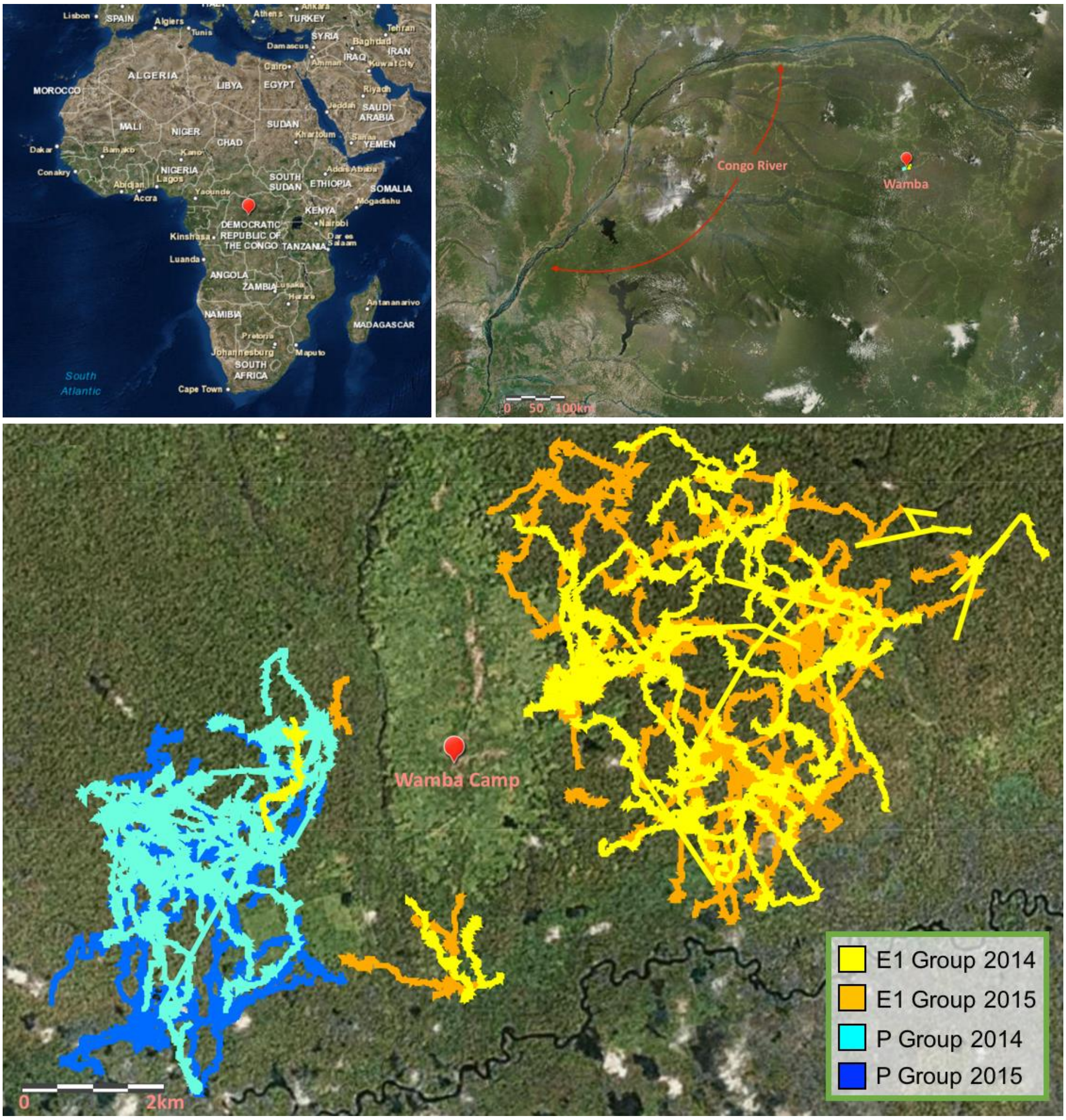


Figure 2.3. Maps created using ArcGIS. Top left map shows location of Wamba in the Democratic Republic of the Congo. Top right map shows the location of Wamba in relation to the Congo River. Bottom map shows the range of both E1 and P Group in 2014 and 2015, and the location of the research station.

2.3.2 Video recording

Filming was my most important data collection method, enabling me to record footage of gesturing in order to code and analyse it. I also collected focal individual data, and this ensured constant awareness of one individual. To capture gestures that precede social interactions, I began filming whenever two or more individuals approached within 5 metres of one another. I recorded all occurrences for the focal individual, but if the focal was resting or not engaging with others, I recorded ad libitum for all other individuals. I tried to film individuals engaging in social behaviour deemed most likely to elicit gestural communication: grooming, co-feeding, co-locomotion, play, sexual, and agonistic. I also prioritised individuals for whom I had less video footage. I recorded video using a Panasonic HDC-SD90 video camera, which has a pre-record feature that continually records the previous three seconds – an extra assurance that I would catch the start of gesturing. While filming, I recorded, by speaking into the microphone, the same information as for focal individual sampling (see following section), in addition to details about behaviour prior to filming. Using this method, I recorded 339.5 hours of video footage. Each day, after returning to camp, I uploaded the video footage to a MacBook laptop and sorted it into a library that I catalogued using FileMaker Pro.

2.3.3 Focal individual sampling

I collected focal individual data (by writing in a notebook) for all individuals in order to examine activity budgets and social interactions as possible factors affecting gestural communication. I have not used these data in my thesis, but plan to use them in the future for social network analysis and to chart individual behavioural differences, factors that could lead to differences in gesturing.

Most importantly, focal individual sampling facilitated video recording. For a single focal sample, I followed one individual for 2 hours, recording their instantaneous behaviour at 5 minute intervals, i.e. every five minutes I wrote down what the focal individual was doing at precisely that moment. When possible, I chose the focal individual based on frequency of past observations, so that I observed each individual for the same total number of hours; however, sometimes I had to choose individuals simply based on their availability, when alternatives were infeasible. If filming was on-going at the time of instantaneous recording, I recorded focal data by speaking into the camera microphone. I was able to collect focal individual data while filming individuals other than the focal individual, because local field assistants could continue to follow the focal individual while I was filming. If the focal individual left the party during filming of another individual, I abandoned following the focal individual. For each focal scan I reported the following information, which will be defined below: *date, time, ID of focal individual, behaviour (in a category), interaction partner (if any), position, height (ground, low, mid, canopy), forest density, general context of the group,* and *3 nearest neighbours*. I also recorded one-hour party size: at the beginning of the hour I began recording all individuals observed within the party, restarting every hour (Chapman, Wrangham, & Chapman, 1995; Doran, 1997; Furuichi, 2009; Hashimoto, Furuichi, & Tashiro, 2001). In consequence, if the focal individual was in a smaller party for less than one hour, but at some point joined with more group members, the smaller party size is not represented in the data. It is possible that one-hour party size underestimates the number of individuals present, because some individuals may be ranging peripherally and unobserved (Furuichi, 2009; Hashimoto et al., 2001). If I was following a parous female, then I simultaneously also recorded the aforementioned data categories for her infant or juvenile offspring, and additionally recorded the distance between mother and offspring.

For "behaviour", I recorded the behaviour in which the focal individual was engaged at the time of sampling, divided into: *agonistic, drag branch, feed, groom, being groomed, groom/being groomed, groom self, nest, other, out of sight, rest, sexual, social play, social play with object, solitary play, solitary play with object*, and *travel* (see Appendix 1). For social behaviour (*agonistic, groom, being groomed, groom/being groomed, sexual,* and *social play*) I recorded the interaction partner(s) as the individual(s) with whom the focal individual was engaged in a social activity. I did not include the interaction partner as one of the nearest neighbours. For mothers and infants when travelling, I did not specify the interaction partner, although if for example the infant's posture was *cling (back)* and the distance to mother was *contact*, it shows that the infant was riding on their mother's back. I used the category *other* for unusual, infrequent behaviour types and wrote a more complete description in the comments section. When an individual was *out of sight,* I recorded the general context and gave the height and vegetation for where the majority of the party was located. If an individual was out of sight for more than 20 minutes, I stopped following them and moved to the next focal individual.

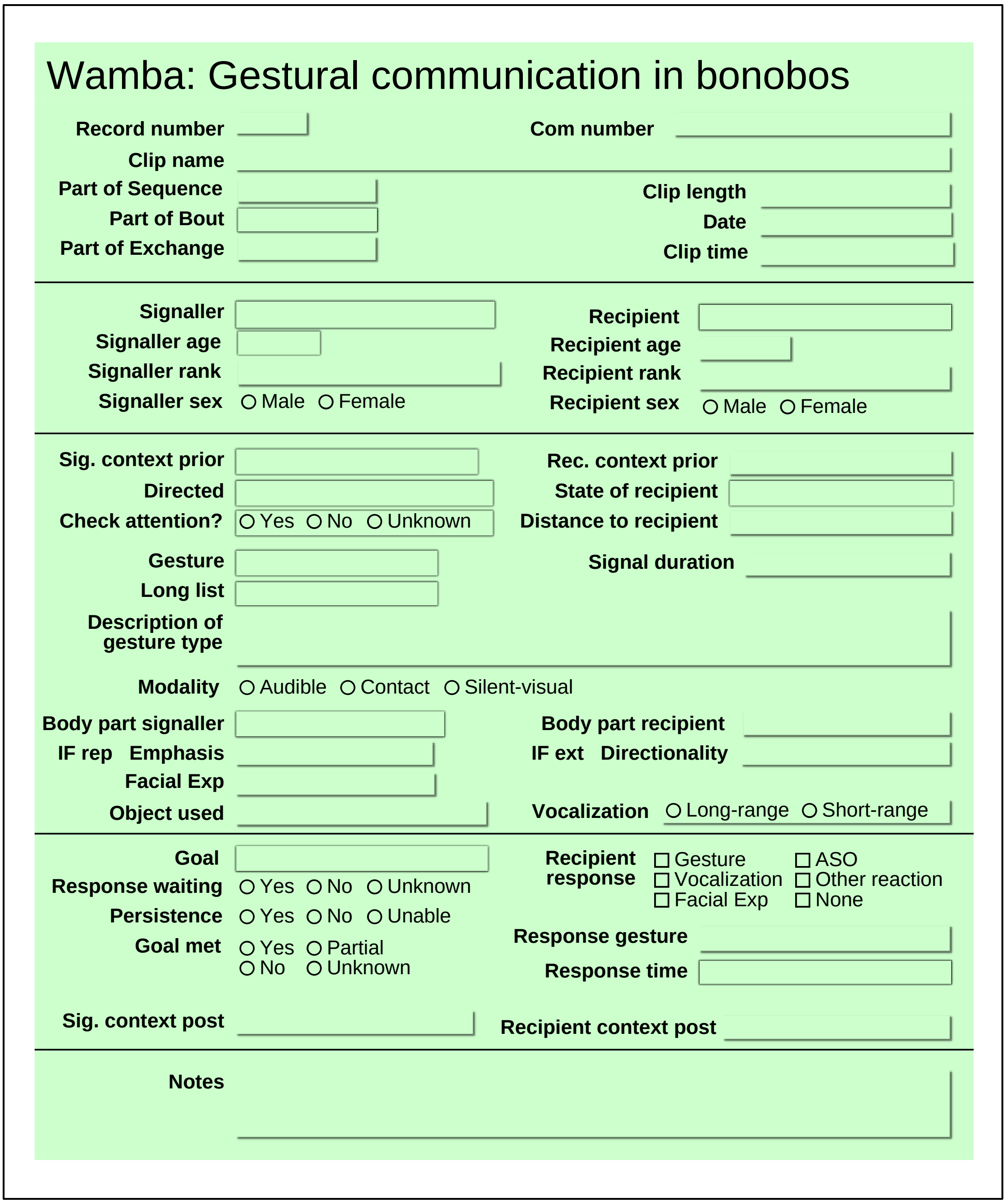
"Position" was categorised as *climb, cling, cling (belly), cling (back), hang, lie, roll, run bipedal, run quadrupedal, sit, stand bipedal, stand bipedal with support, stand quadrupedal, walk bipedal,* and *walk quadrupedal* (see Appendix 2). If the individual exhibited an unusual posture, I recorded the most similar posture but included more details in the comments section. "Height" was whether the individual was on the ground, in the low storey (<10m), in the mid-storey, (10m-canopy), or in the canopy. I considered fallen logs lying on the ground as *ground*, and fallen logs that remained elevated as *low*. Canopy height could vary between forest types. I estimated vegetation density at observer's eye level, to give a general impression of forest type and cover. "Density" was classified as *low* (visible beyond 10m), *medium* (5-10m), and *high* (<5m).

"General context" was the behaviour in which the majority of party members were engaged, and could therefore differ from the behaviour of the focal individual. Categories for general context were the same as those for "behaviour", although they were not directed, thus there was only one *groom* category (see Appendix 3). I recorded "general context" as only one activity, unless evenly split, in which case I recorded both activities. In such circumstances, I ordered the contexts alphabetically, for example *food/travel* or *groom/rest*.

The identity of and distance to the three nearest neighbours and the distance to offspring were reported in categories, due to the difficulties of accurate measurement at great distances: *contact, <1m, 1-2m, 2-5m, 5-10m, 10-15m, 15-20m, >20m*. Nearest neighbours were the closest visible individuals that could be successfully identified. In cases of dense vegetation, it was possible that no neighbours were visible, or that movement was visible but the neighbours were not identifiable. In most cases where individuals were in contact, they were interacting together and thus classified as interaction partner. I used the same distance categories to record distance between mothers and offspring.

2.4 Video Coding

I also used FileMaker Pro to code all of the video footage. To code it, I watched each video clip at normal speed and when I saw a gesture I paused and re-watched the gesture in slow motion reporting information in the sheet (Figure 2.4). I watched the gesture repeatedly, as many times as necessary to fill in the data sheet.



Wamba: Gestural communication in bonobos

Record number
Com number
Clip name
Part of Sequence
Clip length
Part of Bout
Date
Part of Exchange
Clip time

Signaller
Recipient
Signaller age
Recipient age
Signaller rank
Recipient rank
Signaller sex ○ Male ○ Female
Recipient sex ○ Male ○ Female

Sig. context prior
Rec. context prior
Directed
State of recipient
Check attention? ○ Yes ○ No ○ Unknown
Distance to recipient
Gesture
Signal duration
Long list
Description of gesture type
Modality ○ Audible ○ Contact ○ Silent-visual
Body part signaller
Body part recipient
IF rep Emphasis
IF ext Directionality
Facial Exp
Object used
Vocalization ○ Long-range ○ Short-range

Goal
Recipient response ☐ Gesture ☐ ASO ☐ Vocalization ☐ Other reaction ☐ Facial Exp ☐ None
Response waiting ○ Yes ○ No ○ Unknown
Persistence ○ Yes ○ No ○ Unable
Response gesture
Goal met ○ Yes ○ Partial ○ No ○ Unknown
Response time
Sig. context post
Recipient context post

Notes

Figure 2.4. Blank FileMaker Pro coding sheet used for coding information about each gesture instance.

For each gesture instance – that is the occurrence of a single gesture – I coded: *date, clip, clip time, part of exchange, part of bout, part of sequence, signaller, recipient, signaller age/sex/rank, recipient age/sex/rank, signaller behaviour prior, recipient behaviour prior, gesture type (short list and long list), description of gesture, modality, directed, check attention, recipient attentional state, body part of signaller, body part of* *recipient, vocalization, facial expression, object used, distance to recipient, response waiting, recipient response, persistence, intensity, response gesture, goal*, and *goal met* (Figure 3.4).

"Date" is the date on which the clip was recorded. "Clip" is the name of the video file. "Clip time" is the time within the clip at which the gesture occurred, by minutes and seconds 00:00:00 (hh:mm:ss). An "exchange" is when two individuals both participate in the communication event, and so the part of exchange divides the dialogue into how many times it went back and forth. A "bout" is defined as a series of gestures or sequences of gestures (given by the same signaller and targeted at the same recipient) that are separated by >1s. A "sequence" is defined as a series of gestures (given by the same signaller and targeted at the same recipient) that are separated by <1s. My criterion for the end of a communication event was behavioural – if the signaller stopped gesturing and started engaging in another behaviour (e.g. feeding, grooming, playing), then the communication event was over. If, after engaging in another behaviour, they resumed gesturing to the same individual, then it counted as a new communication event.

"Signaller" is the gesturing individual, and "recipient" is the individual to whom the gesture is directed. "Signaller age" and "recipient age" are the ages from Tables 2.1 and 2.2. An individual's rank is based on information given by Dr Tetsuya Sakamaki, and confirmed by other researchers at Wamba. "Rank" is divided into categories high, medium, and low, to assess whether there is any trend towards rank differences (assignment of rank was described in Section 2.2). In the future, I plan to collaborate with Dr Nahoko Tokuyama, who specifically looked at the dominance hierarchy in P

Group, to better analyse effects of rank. “Signaller (and recipient) behaviour prior” uses similar categories to ‘behaviour’ in the focal individual sampling (see Appendix 1).

“Gesture type” is what form of gesture was used, and will be described in more detail in Chapter 3, on the gestural repertoire. I selected the gesture type from both a short list, based on Hobaiter and Byrne’s chimpanzee gesture types (Hobaiter & Byrne, 2011b), and a long list from Catherine Hobaiter’s original coding. I added novel gesture types that I found during my study (*Arm up, Bipedal rocking, Bipedal stance, Bounce, Hip thrust, Leaf drop, Leg flap, Rocking*; description in Chapter 3). I also had a FileMaker Pro field in which I could write out a description of the gesture in more detail, and that I used for writing descriptions of novel gesture types in Chapter 3. I divided “modality” into three categories: *audible, silent-visual*, and *contact*. Audible gestures are gestures that create a sound perceptible to the recipient; silent-visual gestures rely on visual attention of the recipient as they are neither heard nor felt; and contact gestures are gestures in which the signaller makes contact with the recipient.

“Directed” specifies whether the gesture was targeted at *one certain individual, one potential individual, several potential individuals (but directed)*, or *several potential individuals*. Directedness of the gesture is determined by which individual(s) is in the visual field of the signaller or, in the case of contact gestures, with which individual the signaller makes contact. If directedness was not evident, then I did not code the movement, as it did not meet the definition of intentional communication, i.e. communication aimed at changing the behaviour of another individual. I report whether the signaller checked the attention of the recipient before signalling, as *Yes, No*, or *Unknown*. “Recipient attentional state” marks where the signaller is in the recipient’s visual field*: attending, head in direction, head at 90°, body contact but not* *attending, not attending, out of sight*. “Body part of signaller” is the body part used by the signaller for gesturing, and for contact gestures I recorded the “body part of recipient” as the body part with which the signaller makes contact.

When they occurred, I noted “vocalization” and “facial expression” to examine whether such additions act as syntactic modifiers. I did not determine specific vocalization type, but recorded presence or absence of vocalization, and if present, whether the vocalization was a short-range or long-range call type. I categorised facial expressions using de Waal’s ethogram (de Waal, 1988). If the signaller used an object as part of their gesturing, I recorded what object was used. “Distance to recipient” is the distance between the signaller and recipient in metres. “Response waiting” is a *yes* or *no* category, whether or not the signaller pauses for >1s after gesturing while maintaining visual contact. “Recipient response” is the behaviour by the recipient following the signaller’s gesturing. “Persistence” is whether the signaller continued to gesture after a period of response waiting when the recipient failed to respond in a satisfactory way. “Intensity” of the gesture is a rough measure of how forceful or exaggerated the gesture was. Intensity was only recorded by comparing the same gesture type in the same communication event (“less”, “more”, or “same” intensity), in order to avoid subjectivity of between-communication and between-subject comparison. If the recipient reacted with a gesture, then I recorded the gesture type of that “response gesture”.

I assigned the signaller’s “goal” in one of two ways. If the goal was met, with the signaller’s satisfaction shown by cessation of gesturing after the signaller’s reaction, then the recipient’s reaction stands for the goal as the Apparently Satisfactory Outcome (ASO). If the goal was not met then the ASO cannot be determined, and instead I only assigned the assumed goal, i.e. the ASO in similar cases, to make it possible (in the future) to examine gestures that failed to elicit the ASO, and to ask questions about why they were unsuccessful.

In order to ensure my coding was accurate, a second experienced coder, Dr Catherine Hobaiter, coded 100 gestures instances for the following information: gesture type, audience checking, persistence, and signaller apparently satisfied. I then assessed inter-observer reliability by Cohen's Kappa, which for these respective variables was 0.87 (almost perfect), 0.56 (moderate), 0.70 (substantial), and 0.63 (substantial) (Altman, 1991). Such agreement adequately shows that my coding method could be replicated by another experienced coder, and also knowing that our coding techniques were in agreement allowed me to compare my bonobo data with Dr Hobaiter's chimpanzee data.

2.5 Conclusion

By studying a wild population of bonobos, my data allow me to explore the natural gesture usage of bonobos. I worked at the longest standing bonobo field-site, Wamba, Luo Reserve, Democratic Republic of the Congo, which allowed me to make the most of my study periods, as the individuals were already identified and habituated. Before starting my first study period, I could already identify all members of E1 Group (as I had previously worked at Wamba as a research assistant), but had to learn to identify P Group, for which I am very grateful to the field assistants who helped me. I collected data using focal individual sampling and focal behaviour filming. In total, I collected 900 hours of focal individual data and 339.5 hours of video footage, comprising 4381 video clips. After coding the video clips, I found 4639 gesture instances. Given my sample size of 70 individuals, this dataset is more than adequate to move forward with meaningful statistical analyses. In the following chapters, I provide specific methods that delineate which data are used (i.e. which fields from the Filemaker Pro datasheet), as well as explaining my analyses.

Chapter 3 – Expressed and understood repertoires

3.1 Background

This chapter is the starting point for my analysis, and each of the following chapters builds on the previous. In this chapter, I present the community repertoire for bonobos at Wamba. I also examine the gestures that each individual uses and the gestures that they receive and understand, as a way of elucidating the role of the recipient in communication.

3.1.1 Human vocabularies & animal repertoires

An educated, adult, native-language speaker is estimated to have a receptive vocabulary of ~17,000 word families, with one word family including the base word and its derivative forms (Goulden, Nation, & Read, 1990). This estimate does not include “proper names, compound words, abbreviations, and foreign words” (Nation & Waring, 1997). Language’s heavy burden on learning and memory is impressive; we acquire an average of 2-3 words per day until adulthood (Goulden et al., 1990). But historically, production and comprehension have been seen as the most interesting aspects of language. They were also considered to be separate mechanisms occurring in separate brain regions, Broca’s and Wernicke’s areas respectively (Dronkers, Plaisant, Iba-Zizen, & Cabanis, 2007; Wernicke, 1969), although more recent neurological studies recognise that it’s a bit more complicated than that (Dronkers et al., 2007; Price, 2000). Still, the notion of separation of production and comprehension is reflected in how linguists talk about vocabularies. A *productive vocabulary* includes only the words that a person uses. A *receptive vocabulary* includes all of the words that a person understands regardless of whether they use them. In childhood development, the receptive vocabulary emerges earlier than the productive vocabulary, but there is a lot of variability in the rate of growth for both (Fenson et al., 1994).

Not all psychologists and/or linguists have the chance to follow study subjects throughout their lifetimes, although they may remark upon their own child's linguistic development (for example, see Gelman, 2005), and yet there are methods that allow them to measure a person's productive and receptive vocabularies. For productive vocabularies, subjects are asked to report words that they know and might use, whereas for receptive vocabularies they just have to know the word at all (Teichroew, 1982). To assess a person's receptive vocabulary, the researcher may ask the subject whether they know a particular word, or they may give instructions to a young child and see if the child responds correctly (Fenson et al., 1994). In the former example, the subject does not necessarily need to give a dictionary definition, but the researcher must ascertain that the subject is at least fairly certain of the meaning of the word (Goulden et al., 1990). This can be done by asking the subject to rate their confidence in their answers and also by inserting "non-words", fake words as controls, into the test to see how much the subject overrates their answers (Goulden et al., 1990). For productive vocabularies, it is possible to record spontaneous speech and to scale up the number of words used, but that is obviously not possible for receptive vocabularies (Teichroew, 1982). Because receptive vocabularies comprise *all* of the words that a person knows, they are more desirable objects of study.

While these methods are informative for human subjects, reliance on verbally *asking* the subjects about their understanding makes it impossible to use the exact same methods on non-human animals. Animal researchers have therefore largely fallen to looking at the equivalent of productive vocabularies, here called *expressed repertoires*, by reporting only the signals that individuals produce. This is unfortunate, because in human research we can clearly see the benefit of also studying receptive vocabularies. Human vocabularies are expansive, and in every language there are words that are used less frequently, as well as words that we rarely or never use but still understand. Even if you have never said 'soliloquy', you may still know what it means. By ignoring the signs that individuals understand, here called the *understood repertoire*, we may be grossly underestimating individual repertoire sizes.

Moreover, one of the ways in which great ape gesturing may be similar to human language is whether all individuals are able to use and understand all signals. Whereas some animal displays are restricted to members of one sex, all humans have the potential to use the same words. Across human individuals there is large overlap between productive and receptive vocabularies. That being said, a person may be more likely to have a word in their productive (and receptive) vocabulary depending on their profession, hobbies, social class, level of education, race/ethnicity, gender identity etc., and certain of these factors (i.e. socioeconomic and racial/ethnic, which are often correlated) may even affect absolute vocabulary size (Farkas & Beron, 2004; Hoff, 2006). But if it were merely a question of physical ability, most speakers would be able to acquire a similar vocabulary.

In most animal communicative systems, however, one would not expect expressed and understood repertoires to overlap, with the signals that an individual can use being strictly limited by their age, sex, or social position. For example, in the visual displays of lekking bird species (Endler & Thery, 1996), peacock spiders (Girard, Kasumovic, & Elias, 2011), smooth newts (Halliday, 1974), and ring-tailed lemurs (Sauther, Sussman, & Gould, 1999), the males signal and the females respond. Conversely, for the bioluminescent signals of fireflies (Lewis & Cratsley, 2008), or cowbird wing strokes (West & King, 1988b), the females signal and the males respond. For cowbirds, this visual signal given only by females is in response to a vocal signal given only by males (West & King, 1988a), illustrating that although both sexes are signallers and recipients, they are not signallers and recipients of the *same* signal. Mutually understood communication systems are rare in the animal kingdom, but great ape gestural communication is a good candidate, given that many social interactions (such as grooming and food-sharing) could conceivably be desired and provided by all individuals. Such signal production and comprehension was the focus of pioneering ape language studies.

3.1.2 Teaching animals "Language"

Aptly named "ape language" research purported to look at the capacity for production and comprehension of language in human-reared great apes. As I mentioned in Chapter 1, early attempts to teach apes to speak were unsuccessful. Hand-reared chimpanzees just could not learn human speech – their vocal production was apparently not malleable enough (Bryan, 1963; Hayes & Hayes, 1951). Other, more distantly related species, are much better vocal production learners, particularly when it comes to making human-like sounds. A grey parrot, Alex, raised by Irene

Pepperberg, learned over 100 labels for different objects, actions, and colours (Pepperberg, 1983). Viki's abilities pale in comparison.

Fortunately for the researchers, great apes did much better at acquiring sign language (typically American Sign Language (ASL), taught by moulding the apes' hands) and learning to use symbol keyboards. After 21 months, chimpanzee Washoe acquired over 30 signs; after 30 months, gorilla Koko acquired around 100 signs (the current estimate from the Gorilla Foundation/Project Koko put the final count at 1000+ signs, but this source is not peer-reviewed ("Progress & Plans," 2016)); and in total, chimpanzee Nim acquired around 125 signs (Gardner & Gardner, 1969; Patterson, 1978; Terrace et al., 1979). The Savage-Rumbaugh group taught their apes to use symbol keyboards, and were the first to document a conversation between two chimpanzees, Sherman and Austin, using taught signs (Savage-Rumbaugh, 1986). Another of their apes, a bonobo called Kanzi, began learning the symbol keyboard by watching his mother Matata, and at last count could use 348 signs (Raffaele, 2006; Savage-Rumbaugh et al., 1986). Kanzi's spontaneous acquisition meant that he naturally produced and comprehended the same signal, whereas other projects had to teach production and comprehension separately. The apes learned that each sign refers to (or is associated with) an object or activity, and many of them refer to types of food or play. The way that the apes learned to both use and respond to each sign means that the signs are included in their expressed *and* the understood repertoires. The overlap of the expressed and understood repertoires is complete, suggesting that great ape communication could potentially be a mutually understood communication system.

Ape language research relied on first teaching language to apes and then testing their abilities. In this way, it was not particularly informative about how the animals naturally communicate, although it was useful in exploring the abilities underpinning their communication in general. The research also pioneered methods for determining when a non-human animal comprehends a signal – namely by responding with an appropriate action. Following from ape language research, many more studies have gone on to examine the natural gestural repertoires of great apes in captivity and in the wild.

3.1.3 Natural great ape gestural repertoires

Goodall first noted the use of facial expressions, postures, and tactile gestures in communication by chimpanzees at Gombe (Goodall, 1971, 1986). Plooij followed with a more systematic study of gestural communication at Gombe, naming a handful of gesture types: *Hands around head, Lies down on back, Arm-high, Begging, Leaf grooming, Running away with an object,* and *Beckoning* (Plooij, 1978). It was clear that chimpanzee communication extended beyond vocalisations, and more researchers became interested in chimpanzee gestures. After the early wild studies, much of the research to categorise gestural repertoires was done in captivity. From captive studies, the repertoire size for orangutans is 29-62 gesture types (Call & Tomasello, 2007; Cartmill & Byrne, 2010); for chimpanzees is 25-30 gesture types (Call & Tomasello, 2007; Pollick & de Waal, 2007); and for gorillas is 30-102 gesture types (Call & Tomasello, 2007; Genty et al., 2009). There is some variation in repertoire size due to splitting and lumping levels used by the researchers – ranging from distinguishing gestures by individual digits to entire limbs. Also, these repertoire sizes may be lower than in the wild, because the apes experience only a limited number of contexts (e.g. there is no long-distance travelling or complicated foraging) and many live in smaller groups with different compositions than would occur in the wild.

Figure 3.1. Illustration of *Begging* gesture (that in my study is called *Mouth stroke*) from Plooij, 1978– “Fig.5. “Begging” in adult chimpanzees. From left to right, Hugo, Figan and Mike. Mike is begging from Hugo.”

Compared to the repertoire size for captive chimpanzees, the repertoire found in a long-term study on wild chimpanzees was much higher (Hobaiter & Byrne, 2011b). The repertoire size for the whole community at Budongo, Uganda, was estimated at 66 gesture types: roughly double the size reported in captivity, but again, perhaps for methodological reasons. Regardless, the community repertoire appeared to have reached asymptote and so researchers are unlikely to discover many more gesture types. But compared to the 66 gesture types at the community level, the average individual (expressed) repertoire size was only ~10 gesture types and none of the individuals were close to asymptote (Hobaiter & Byrne, 2011b). To record an individual's complete repertoire would require many more years of research and funding. However, all of the studies mentioned so far looked only at the gestures that an individual expressed, ignoring potentially valuable data on the gestures that an individual understood. For charting individual repertoires, reporting both the understood *and* expressed repertoires could maximize the available evidence. It is also a useful way of examining who uses which gestures: are there sets of gesture types expressed exclusively by one subset of individuals and understood by another?

Great ape gestural communication has the potential to be expressed and understood by individuals of all age-sex groups; signallers and recipients are in principle interchangeable for all signals. Because gestures are movements of limbs, head, or body, they could physically be produced by any individual. Many situations that elicit gestures, such as grooming or begging for food, are not experienced exclusively by one age-sex group, but there are some physical demands that could restrict interchangeability of signals. Mother-offspring relationships provide the most obvious example; adult females carry infants and juveniles, and therefore may be the only subset to deploy gestures that mean "climb on my back". Even in that example, as I reveal later in this chapter, adult females may not always be the *only* individuals to carry young, and though a behaviour may be rare, individuals may still be equipped with the gestures to deal with it. Finally, some gestures may be limited to certain individuals and specific audiences because of subtle differences in developmental experience.

Here, I examine individuals' expressed repertoires, as did previous studies, but also their understood repertoires. But first, I present what we already know about the gestural repertoire of my study species: the bonobo.

3.1.4 Bonobo gestural repertoire

The bonobo gestural repertoire has only been reported in captive studies. De Waal first described the gestural repertoire for a group of captive bonobos (de Waal, 1988). More recently, that catalogue was updated in a comparison with chimpanzee gestures (Pollick & de Waal, 2007). They identified 31 gesture types, 3 of which were unique to chimpanzees, and 2 unique to bonobos (Pollick & de Waal, 2007). Here is the complete catalogue:

> arm raise, arm wave, beckon, beg with hand, bent wrist, clap hands/feet, clasp self, dab, finger flex, finger/hand in mouth, flail, flap, foot/leg gesture, gentle touch, hand lead, hard touch, hunchover, pat, point, poke, rap knuckles, reach out down, reach out side, reach out up, shake wrist, slap ground, slap stomp, stomp, swing, throw aimed, throw hold (Pollick & de Waal, 2007).

Another captive bonobo study reported a repertoire of 20 gesture types, including 8 "tactile" gestures that I would call "contact" gestures (grab, grab-push-pull, kick, pull, punch, push, slap, touch) and 12 visual gestures that I refer to as "silent-visual" gestures (bow, gallop, ice skating, jump, look at, move, peer, present, reach arm, shake, somersault) (Pika et al., 2005).

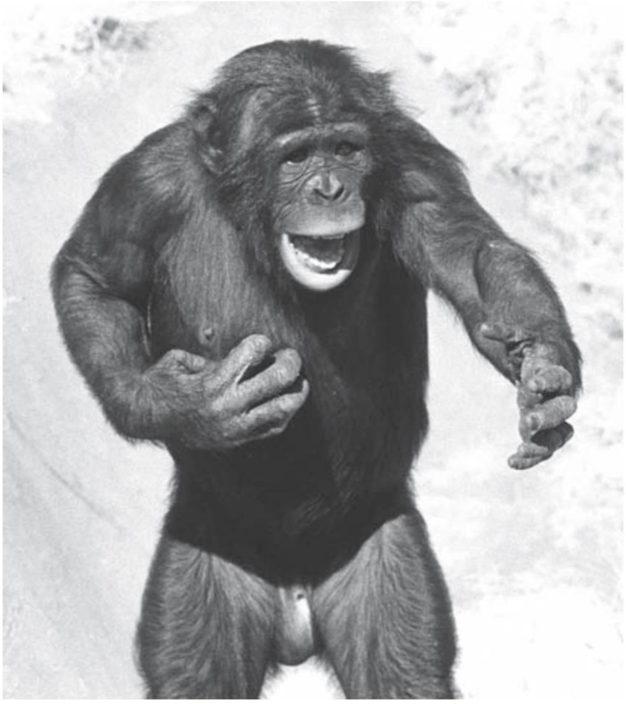


Figure 3.2. Photograph of *Reach out side* gesture from Pollick & de Waal, 2007– "Fig. 4.3 Multimodal communication: a bonobo gestures and vocalizes simultaneously (Photograph by Frans B.M. de Waal)."

Both of these studies had small sample sizes, of 13 and 7 bonobos respectively, and in the latter, all individuals were immature: 5 infants, 1 juvenile, and 1 adolescent (Pollick & de Waal, 2007; Pika et al., 2005). Moreover, the total observation time for each study was 300 hours of video with an additional 73 hours of focal observation, and 235 hours of observation with 33 hours of video, respectively (Pika et al., 2005; Pollick & de Waal, 2007). It is possible that the slightly larger repertoire in the first study is a result of larger sample size and more observation time. Comparing the description of each gesture type also shows differences in how both research groups split the gesture types, for example Pika et al.'s *reach arm* could plausibly be divided into de Waal and Pollick's *reach out down*, *reach out side*, and *reach out up* (Pika et al., 2005; Pollick & de Waal, 2007). Pika et al. reported a number of so-called "idiosyncratic" gesture types that were only produced by one individual during the study period. Such idiosyncratic gestures had also been reported in captive chimpanzees (Tomasello et al., 1997; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994; Tomasello et al., 1989), but the finding was not corroborated in wild studies (Hobaiter & Byrne, 2011b). What Tomasello et al. meant by idiosyncratic was that the gesture had been used by one individual in one study period, so that if another individual used the same gesture in a different study period, the gesture was still considered idiosyncratic. Perhaps if they had reported gestures across study periods, as did Hobaiter and Byrne (2011), they would have found fewer "idiosyncratic" gestures.

While captive studies do give a firm base for studying gestural communication, more observation hours with a larger sample size would lead to a more complete description of the bonobo gestural repertoire. The resulting increase in number of examples for each gesture type would facilitate more appropriate splitting of gesture types. Although more observation hours should be possible in captivity, the number of study subjects is strictly limited. To bridge the difficulties of fieldwork with the limitations of captive work, naturalistic sanctuaries may provide a partial solution. Lola ya Bonobo is a bonobo sanctuary in Kinshasa, Democratic Republic of the Congo, with naturalistic conditions and large study groups. Several studies on bonobo vocal and gestural communication indeed come from Lola ya Bonobo (Genty, Clay, Hobaiter, & Zuberbühler, 2014; Genty, Neumann, & Zuberbühler, 2015; Genty & Zuberbühler, 2014). However, these studies have not specifically listed the gestural repertoire. In one study on multi-modal communication, they reported only the 33 gesture types that accompanied contest hoots (Genty et al., 2014):

> Arm swing, Arm swing with object, Flap, Flap with object, Hit with object, Hit ground with object, Kick, Object shake, Push, Rap object, Rhythmic stomp, Slap other, Slap object, Stomp, Throw object, Bipedal swagger, Object dragging, Push object, Stiff trot, Arm raise, Arm raise with object, Grab, Grab-pull, Hand wave off, Hand-down reach, Hand-side reach, Hand-up reach, Stretch over, Touch, Wrist shake, Bipedal present, Concave back present, Rump present.

In another study on complex patterns of signals, they reported only the 10 gesture types used in sexual solicitation "*Bipedal present, Concave back present, Exaggerated concave back present, Rump present, Ventral present, Arm raise, Arm(s) up, Hand reach, Stretch over, Touch*" (Genty et al., 2015). Another study looked at spatial reference in one particular gesture type, *Beckon* (Genty & Zuberbühler, 2014). While all of these studies help us to better understand bonobo gestural communication, they must be accompanied by wild studies to get the full picture.

The first reports of wild bonobo gesturing were ad-hoc observations of gestures, such as pointing (Vea & Sabater Pi, 1998). Though the literature is growing, there are still sparse references, with one focusing only on two gesture types and arguing that bonobos have iconic and deictic gestures (Douglas & Moscovice, 2015), and another on co-operative turn taking in gestural communication (Fröhlich et al., 2016). We should expect more publications to come from this last research group in the near future, many of them focusing on gesture acquisition and development. It is somewhat surprising that researchers have jumped to describing detailed gestures or complex processes, without first assessing the complete gestural repertoire. I aim to fill in that gap by cataloguing the gestural repertoire for wild bonobos at Wamba, Democratic Republic of the Congo.

3.2 Specific Methods

In this chapter, I examine the community repertoire, and I also analyse the repertoires for all individuals, comparing their expressed and understood repertoires. By *understood* repertoire, I mean the set of gesture types that an individual receives and subsequently responds to in a way that satisfies the signaller. The term 'understand' is loaded with anthropocentric meaning, but what it broadly means is 'to know and correctly respond to a signal'. Here, an individual is said to understand a gesture if they respond with an Apparently Satisfactory Outcome (ASO) – a reaction (change in behaviour) that satisfies the signaller, shown by cessation of gesturing. Great apes intentionally deploy gestures (Leavens, Russell, & Hopkins, 2005; Tomasello et al., 1989), and the meaning of a gesture can be determined by the ASO (as I will examine in Chapter 4), and so by reacting with an ASO, the recipient can be said to have understood that gesture, and that gesture is part of their understood repertoire. Note that the ASO requires a *change* in behaviour, so that if a gesture was given and the recipient kept doing what they were doing, I would not count that as an ASO. This eliminates any error in judgment, at the minor cost of ignoring gestures that might mean "keep doing exactly what you're doing".

Examining not only the expressed repertoire, but also the understood repertoire will allow a more detailed understanding of the role of signaller and recipient in gestural communication, potentially revealing how this dyadic interaction may shape the evolution of communication and language. It is obvious that it takes more than one person to have a conversation, and so looking at an individual's role as both a signaller *and* a recipient is equally important. If gestures are indeed mutually understood, then it would be valuable for researchers to be able to include them in an individuals' overall repertoire.

Data collection and video coding was described in the general methods, Chapter 2. From that dataset, I extracted the following coded information: signaller, recipient, signaller age/sex, recipient age/sex, gesture type, part of sequence, part of bout, audience checking, response waiting, persistence, and signaller apparently satisfied (all terms were described in Chapter 2). I only analysed gestures that were used intentionally – I required that *all* gestures be directed towards a target individual (Gomez, 1994) *and* meet one of the other intentionality criteria (audience checking, response waiting, or persistence) – giving me 4256 gesture instances. It is standard for studies on great ape gestural communication to only require one or two of the intentionality criteria, but perhaps in future we will become stricter in our selection. For inclusion in the understood repertoire, the recipient had to respond to the gesture (or the sequence in which the gesture occurred) with an ASO.

3.3 Results

3.3.1 Community repertoire

I found a community repertoire, the sum of gestures types used by both E1 and P Group, of 68 gesture types:

> Arm raise, Arm shake, Arm swing, Arm up, Arm wave, Beckon, Big loud scratch, Bipedal rocking, Bipedal stance, Bite, Bounce, Bow, Dangle, Directed push, Embrace, Foot present, Gallop, Grab, Grab-pull, Hand fling, Hand on, Hand shake, Head butt, Head rock, Head stand, Hip thrust, Hit with object, Jump, Kick, Knock object, Leaf drop, Leg flap, Leg swing, (Look), Mouth stroke, Object move, Object shake, Pirouette, Poke, Pounce, Present (climb on), Present (grooming), Present (genitals backward), Present (genitals forward), Punch other, Push, Reach, Rocking, Roll over, Rump rub, Shake hands, Side roulade, Slap object/ground, Slap object with object, Slap other, Somersault, Stiff walk, Stomp, Stomp other, Stomp 2-feet, Stomp 2-feet other, Stroking, Tandem walk, Tap object, Tap other, Throw object, Touch other, Water splash (Table 3.1).

Look is reported here, as it was in chimpanzees, but I do not consider it gestural. Look, or “peering”, may be communicative but may also simply be inspection (Yamamoto, 2015). By the very nature of *Look,* described by Hobaiter and Byrne as “Signaller holds an eye-contact position with the recipient–minimum duration 2 s" (Hobaiter & Byrne, 2011b), it meets the criterion of "check attention" for intentionality. Therefore, given the difficulty in disentangling the gesture from the very criterion that makes it an intentional gesture, I do not count it in analysis and only mark it here for comparison with the chimpanzee.

Table 3.1. Description of the bonobo gestural repertoire compatible with the chimpanzee gestural repertoire described by Hobaiter and Byrne, 2011. Changes to the descriptions in Hobaiter and Byrne, 2011 have been marked in square brackets: [ ]. New gesture types and gesture types that were not described in Hobaiter and Byrne, 2011 are marked in **bold text**.

Bonobo gestures	Hobaiter & Byrne 2011	Description of gesture types
Arm raise	Arm raise	"Raise arm[(s)] and/or hand[(s)] vertically in the air"
Arm shake[1]	Arm shake	"Small repeated back and forth motion of the arm"
Arm swing	Arm swing	"Large back and forth movement of the arm[(s)] held below the shoulder"
Arm up[2]	-	**NEW: Extend straight arm(s) out to side and away from body**
Arm wave	Arm wave	"Large repeated back and forth movement of the arm[(s)] raised above the shoulder"
Beckon	Beckon	"Hand is moved in an upwards sweep from the elbow or wrist towards [the] signaller"
Big loud scratch	Big loud scratch	"Loud exaggerated scratching movement on the signaller's own body"
Bipedal rocking[3]	-	**NEW: Stand or walk bipedal, rock forward and back or side to side, repeated (includes rare 'Quadrupedal rocking')**
Bipedal stance[3]	-	**NEW: Stand bipedal, arms out to side, back arched**
Bite	Bite	"Recipient's body is held between the teeth of the signaller"
Bounce[2]	-	**NEW: Standing quadrupedal, bend elbows and knees to move up and down repeatedly**
Bow[1]	Bow	"Signaller bends forward from the waist while standing [bipedal]"

-	Clap	"Both palms mov[e] towards each other and are brought together with an audible contact"
Dangle	Dangle	"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"
Directed push	Directed push	"A light short non-effective push that indicates a direction of desired movement, immediately followed by the recipient moving as indicated"
-	Drum object (palms)	"Short[,] hard[,] audible contact of alternate palms against an object"
-	Drum other	"As '[D]rum object (palms)' but contact is with recipient's body"
Embrace	Embrace	"Signaller wraps [one or] both arms around the recipient and maintains physical contact"
-	Feet shake	"Repeated back and forth movement of feet from the ankles"
Foot present	Foot present	"Sole of the foot is presented to the recipient"
Gallop	Gallop	"An exaggerated running movement where the contact of the hands and feet is deliberately audible"
Grab	Grab	"The hand[(s)] is firmly closed over part of the recipient's body"
Grab-pull	Grab-pull	"As 'Grab' but closed hand contact is maintained and a force exerted to move the recipient from their current position"
Hand fling	Hand fling	"Rapid movement of the hand or arm in the direction of the recipient" **Includes "Swat" - NEW: Swipe hand in sharp downward motion without making contact with the recipient**
Hand on	Hand on	"Palm[(s)] of the hand[(s)] is placed on the recipient, contact lasts for more th[an] 2 s"
Hand shake[1]	Hand shake	"Repeated back and forth movement of hand from the wrist"
Head butt	Head butt	"Head is briefly and firmly pushed into the body of the recipient"
Head rock	Head nod	"Repeated back and forth [or side to side] movement of the head" (as for Hobaiter & Byrne 2011, includes 'Head nod' and 'Head shake')[4]
Head stand	Head stand	"Signaller bends forward and places head

		on the ground”
-	Hide face	“Face is hidden by the hands and/or arms”
Hip thrust[3]	-	**NEW: Sitting, crouching, or standing, thrust hips forward (single or repeated)**
Hit with object[1]	Hit with object	“An object is brought into short[,] hard contact with the body of the recipient”
Jump	Jump	“While bipedal[,] both feet leave the ground simultaneously, accompanied by horizontal displacement through the air”
Kick	Kick	“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’])”
Knock object[1]	Knock object	“Back of the hand or knuckles are brought into short[,] hard[,] audible contact with an object”
-	Leaf clipping	“Strips are torn from a leaf (or leaves) held in the hand using the teeth; produces a conspicuous sound”
Leaf drop	-	**NEW: Pick leaf(s) and drop it, usually signaller is above recipient**
Leg flap	-	**NEW: Sitting with knees bent, open and close one or both legs to side (single or repeated)**
Leg swing	Leg swing	“Large back and forth movement of the leg from the hip”
(Look[5])	Look	“Signaller holds an eye-contact position with the recipient–minimum duration 2 s”
Mouth stroke	Mouth stroke	“Signaller[‘]s palm and fingers [are] repeatedly run over the mouth area of the recipient”
-	Object in mouth approach	“Signaller approaches recipient while carrying an object in the mouth (e.g. a small branch)”
Object move	Object move	“Object is displace[d] in one direction, contact is maintained through movement” (as for Hobaiter & Byrne 2011, ‘Object move’ includes ‘Branch drag’)[4]
Object shake	Object shake	“Repeated back and forth movement of an object” (as for Hobaiter & Byrne 2011, ‘Object shake’ includes ‘Object shake tandem’)[4] **Object shake tandem: As ‘Object shake’ but object is in contact with the recipient**
Pirouette[1]	Pirouette	“Signaller turns around their bod[y’]s vertical axis while also displacing along the ground”

Poke	Poke	“Firm, brief push of one o[r] more fingers into the recipient’s body”
Pounce	Pounce	“Signaller displaces through the air to land quadrupedally on the body of the recipient”
Present (climb on)[6]	Present climb on me	“Arm or leg is extended to young recipient in order to facilitate them climbing onto the signaller[‘]s body (normally mother to infant)”
Present (grooming)[6]	Present grooming	“Body is moved to deliberately expose an area to the recipient[‘]s attention which is immediately followed by grooming of the area”
Present (genitals backward)	Present sexual	“Signaller approaches recipient backwards, exposing the swelling or anus to the recipient[‘]s face” (as for Hobaiter & Byrne 2011, includes ‘Present genitals forwards’ and ‘Present genitals backwards’)[4] **Present genitals forwards: the signaller sits and spreads their limbs displaying their genital swelling or erect penis**
Present (genitals forward)		
-	Punch object/ground	“Movement of whole arm, with short[,] hard[,] audible contact of the closed fist to an object or the ground”
Punch other	Punch other	“As ‘[P]unch object/ground’ but contact is with recipient’s body”
Push	Push	“Palm in contact with recipient’s body and force is exerted in an attempt to displace recipient”
Reach	Reach	“Arm extended to the recipient with hand in an open, palm upwards[, downwards, or sideways] position” (as for Hobaiter & Byrne 2011, includes ‘Reach – palm down’, ‘Reach – palm side’, ‘Reach – palm up’, and ‘Reach – wrist first’)[4]
Rocking[3]	-	**NEW: Sitting, rock forward and back or side to side, repeated**
Roll over	Roll over	“The signaller rolls onto their back exposing their stomach, normally accompanied by repeated movements of the arms and/or legs”
Rump rub[1]	Rump rub	“Push/rub rump against the body/swelling of recipient”
Shake hands	Shake hands	“Signaller grasps recipient’s hand in their own hand and then makes small repeated back and forth movements from the wrist”

Side roulade	Side roulade	“Body is rotated around the head-feet axis while lying on the ground with horizontal displacement along the ground”
Slap object/ground[1]	Slap object	“Movement of the arm from the shoulder with hard[,] short contact of the palm of the hand to an object [or the ground]”
Slap object with object[1]	Slap object with object	“As ‘[S]lap object’ but the hand holds an object which is brought into contact with another object [or the ground] (e.g. a branch is slapped against a tree)
Slap other	Slap other	“As ‘[S]lap object’ but the palm is brought into contact with the recipient’s body”
Somersault	Somersault	“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 a sitting position”
Stiff walk[1]	Walk (stiff)	“Walk quadrupedally with a slow[,] exaggerated movement”
Stomp	Stomp	“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 other	Stomp other	“As ‘[S]tomp’ but contact is made with recipient
Stomp 2-feet	Stomp 2-feet	“As ‘[Stomp]’ but both feet used, normally alternately”
Stomp 2-feet other	Stomp 2-feet other	“As ‘[S]tomp 2-feet’ but contact is made with the recipient”
Stroking	-	**NEW: Run palm of hand gently over recipient’s body repeatedly** (in Hobaiter & Byrne 2011, ‘Stroking’ was included in ‘Touch other’)
Tandem walk	Tandem walk	“[Signaller] positions arm over the body of the recipient and both walk forward while maintaining position”
Tap object[1]	Tap object	“Movement of the arm from the wrist of elbow, with firm[,] short contact of the fingers to the object (single/multiple)”
Tap other	Tap other	“As [T]ap object’ but contact is with the recipient’s body”
Throw object[1]	Throw object	“Object is moved and released so that there is displacement through the air after moment of release”
Touch other	Touch other	“Light contact with the palm and/or fingers on the body of the recipient, contact under 2 s” (as for Hobaiter & Byrne 2011, ‘Touch other’ includes ‘Knock

		other')[4] **Knock other: As "Knock object" but make contact with the recipient**
Water splash[1]	Water splash	"Hand is moved vigorously through the water so that there is audible displacement of the water"

[1] Observed at Wamba fewer than 2 times.
[2] Seen at Bossou, not at Budongo (Catherine Hobaiter, personal communication)
[3] Seen, but not reported, at Budongo (Catherine Hobaiter, personal communication).
[4] These gesture types were lumped for comparison with Hobaiter & Byrne, 2011. Future studies should use ASOs to consider whether they should be split, if they have different meanings.
[5] 'Look' behaviour was observed in bonobos at Wamba, but not considered gestural.
[6] 'Present climb on me' and 'Present grooming' are currently lumped for comparison. In future, we propose using 'Present body part', to disassociate the gesture form from the meaning.

To determine whether the community repertoire has reached asymptote or whether it is likely to continue to increase with further observation time, I plotted the cumulative repertoire size over the chronological gesture instances (Figure 3.3). This graph shows that the community repertoire has indeed reached asymptote at 65-67 gesture types after ~2000 gesture instances.

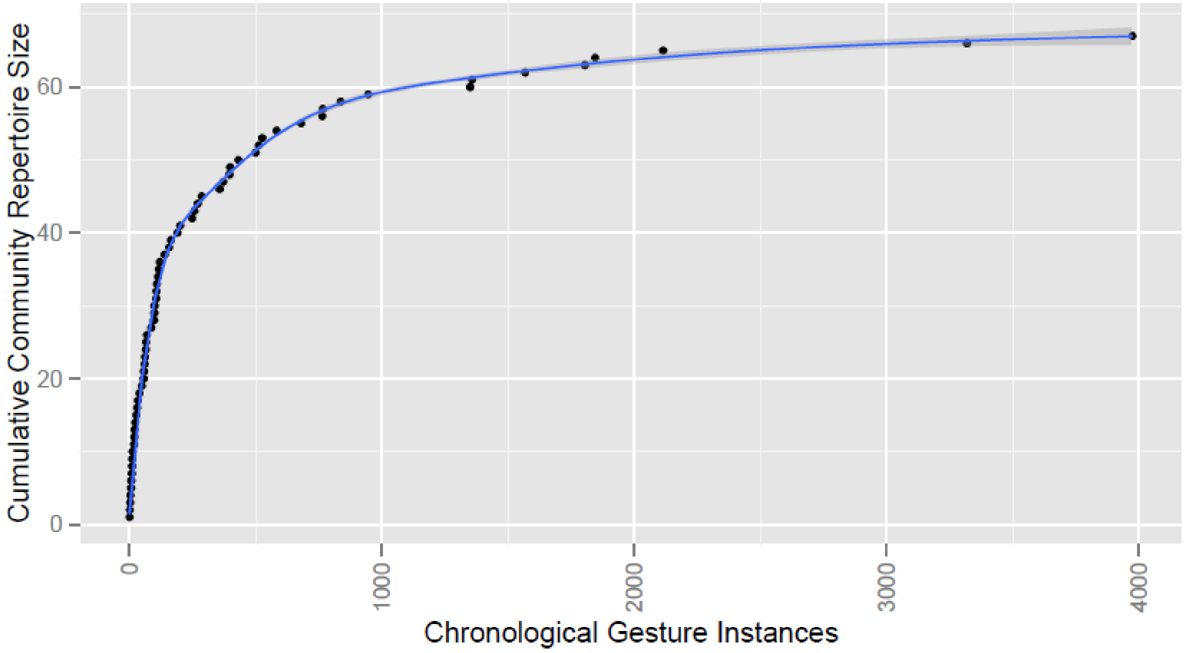


Figure 3.3. Scatterplot showing the cumulative number of gesture types in the community repertoire by the number of observed gesture instances in chronological order. The blue line is a locally weighted polynomial curve, with the surrounding dark grey representing the 95% confidence area (a very thin area).

3.3.2 Individual repertoires

For individuals, the mean expressed repertoire size was 14.40 ± SD 7.69 gesture types, N = 65 (range 1-35). After including the understood repertoire, with a mean of 10.48 ± SD 5.86, N = 65, range 0-30, the mean overall repertoire increased to 18.82 ± SD 9.07 gesture types, N = 65 (range 1-42). I conducted a one-way paired t-test with the null hypothesis that the overall repertoire is not higher than the expressed repertoire, and found it to be significantly larger ($t64 = -11.29$, $p < 0.01$).

3.3.3 Who expresses and understands which gestures?

I then examined whether any gesture types were used by a certain subset of individuals but received and understood by another subset. To do this, I only analysed gesture instances (alone or in sequences) that successfully achieved an ASO in both the understood *and* expressed repertoire, which left 2694 gesture instances and 60 gesture types. This allowed me to match expressed and understood gesture instances, to know who expressed the gesture and who received it. I calculated an index for each gesture type:

$$= \frac{\#\ individuals\ both\ Expressed\ and\ Understood}{\#\ individuals\ either\ Expressed\ or\ Understood}$$

With sufficient data, gesture types with values that are closer to 1 are both expressed and understood by most individuals, whereas gesture types with values that are closer to 0 are expressed and understood by different individuals. Index values ranged from 0.00 to 0.89 (Figure 3.4).

Figure 3.4 (next page). This spreadsheet with individuals along the top (split into female and male, and ordered by age from oldest to youngest) and gesture types down the side shows the number of gesture instances per gesture type that each individual either expresses or understands, or both expresses and understands. Gesture types that an individual only expresses are in yellow, only understands are in blue, or both expresses and understands are in green. The overall repertoire size for each individual is at the bottom. Four columns on the far right side show (a) number of individuals that both express and understood the gesture type, (b) the number of individuals that either express or understand the gesture type, (c) the index of a/b, and (d) the total gesture instances for each gesture type.

Gesture Type	Individual																																																																				
	Adult Female																		Adolescent F.						Juvenile Female								Infant Female							Adult Male												Adolescent M.						Juvenile M.			Infant M.								
	Old --> Young																																						Old --> Young																													
	Bk	No	Kb	Hd	Ki	Yk	Hs	Mt	Jk	Po	Ic	Sl	Nv	Sk	Ot	Fk	Mr	Nr	Zn	An	Pf	Kk	Hk	Ik	Pp	Sc	Na	Ym	Nt	Ok	Fa	Jl	Mz	Pk	So	Ka	Ha	Ma	Ns	TN	TW	GI	DI	LB	JD	ML	TK	GC	NB	SN	DN	JR	KT	IR	SB	MC	JO	KY	HC	HO	SE	KL	IA	NI	YD	a)	b)	c)	d)
Bow	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	1	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	1	0	0	2	0.00	2
Hand shake	0	0	0	0	0	0	0	0	0	1	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	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	2	0.00	2
Head butt	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	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0.00	2
Head stand	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	1	1	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	2	0.00	2
Rump rub	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	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.00	2
Shake hands	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	0.00	2
Slap ground/object	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0.00	2
Slap object with object	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	0.00	2
Somersault	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	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0.00	2
Stiff walk	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	2	0.00	2
Stomp 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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0.00	2
Tap object	0	0	0	0	0	0	0	0	0	0	0	1	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	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0.00	2
Throw object	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	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	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.00	2
Side roulade	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	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	4	0.00	4
Tap other	0	0	0	0	0	0	0	0	0	0	0	2	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	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0.00	4
Gallop	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	1	2	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	2	0	1	0	0	0	0	1	4	0.25	6
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	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	3	0	0	0	0	1	4	0.25	6
Poke	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	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	2	0	1	0	0	0	5	0.00	8
Pounce	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	1	0	0	0	2	2	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	0	0	0	0	2	4	0.50	8
Arm wave	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	9	0.00	10
Head rock	0	0	0	0	0	0	0	0	2	0	0	2	1	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7	0.14	10
Hip thrust	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	10	0.00	10
Roll over	0	1	0	1	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	7	0.00	10
Bite	0	2	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	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	6	0.00	12
Foot present	0	0	0	0	1	0	0	0	0	0	1	1	1	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	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	1	0	0	0	10	0.00	14
Object move	0	0	2	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	3	0	0	0	1	10	0.10	14
Jump	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	3	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	3	1	1	0	0	0	12	0.00	16
Stomp	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	3	2	2	0	0	1	9	0.11	16
Tandem walk	0	1	0	1	1	2	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0.08	16
Leg flap	0	1	0	1	1	0	1	0	1	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	1	0	2	0	0	0	1	0	0	0	0	0	0	0	1	14	0.07	18
Stomp 2-feet other	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	0	2	1	0	0	0	2	13	0.15	18
Leg swing	0	0	0	1	0	0	0	0	3	1	0	0	0	1	1	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	17	0.06	20
Punch other	0	1	0	1	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	1	1	0	0	17	0.00	20
Push	0	0	1	0	0	0	1	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	2	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	2	1	1	0	0	0	20	0.00	22
Stroking	0	0	1	0	3	0	1	0	4	0	0	3	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	2	16	0.13	24
Beckon	0	2	0	0	2	0	1	0	0	1	0	2	1	1	3	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	1	19	0.05	26
Kick	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	0	4	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	3	2	2	2	2	0	0	0	5	15	0.33	26
Bipedal rocking	0	0	0	0	0	0	1	0	6	0	1	4	0	1	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	2	0	2	2	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	19	0.11	30
Hand fling	0	1	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	1	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	2	0	2	1	2	0	2	1	1	2	1	0	1	0	1	0	0	1	25	0.04	32
Embrace	0	4	0	0	1	1	3	0	0	0	1	4	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	3	0	3	0	1	0	0	2	17	0.12	34
Slap other	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	0	4	1	1	2	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	2	3	4	1	2	1	0	2	0	4	20	0.20	36
Arm-up	0	6	2	1	1	0	4	0	6	0	0	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	6	0	1	7	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	2	2	0	0	1	1	20	0.05	50
Present (genitals backward)	0	1	0	2	2	0	2	0	3	0	0	2	2	0	0	3	3	0	1	0	1	0	0	0	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	3	0	2	0	0	2	2	3	0	1	1	7	5	1	0	0	1	1	0	1	0	0	0	0	6	27	0.22	58
Object shake	0	1	3	3	1	0	0	0	0	0	5	3	0	0	2	2	1	0	2	3	5	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	1	0	0	0	4	1	2	0	3	5	2	0	4	0	0	0	0	8	23	0.35	60
Bipedal stance	0	2	0	1	3	0	2	0	6	0	0	7	5	0	1	4	2	0	6	0	2	0	0	3	0	0	0	0	1	1	1	3	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	4	0	0	2	1	0	3	0	0	6	0	0	0	0	0	0	0	11	25	0.44	70
Rocking	0	4	2	2	4	1	3	1	1	2	0	11	0	2	4	2	8	0	2	0	0	0	0	0	1	0	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	4	3	0	0	0	0	1	0	2	1	0	0	1	3	0	0	0	0	0	0	11	27	0.41	72
Dangle	0	0	2	3	0	0	2	0	1	0	2	3	0	0	4	2	2	3	0	1	0	2	0	1	3	5	3	1	2	2	2	5	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	2	1	3	0	1	10	4	1	0	0	13	33	0.39	78
Hand on	0	5	0	0	7	1	2	2	1	2	2	7	1	1	1	1	3	1	0	0	1	0	0	1	0	0	1	0	6	0	0	2	0	0	1	4	0	0	0	0	1	0	0	0	0	0	0	0	3	0	0	0	1	1	2	1	0	4	4	0	5	3	1	0	1	7	34	0.21	80
Mouth stroke	0	0	7	6	0	0	3	2	0	6	2	5	0	0	0	0	3	9	0	0	3	0	0	0	1	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	2	0	3	5	1	0	0	0	0	0	0	0	2	3	5	2	2	1	0	5	28	0.18	80
Present (climb on)	0	4	4	3	0	0	2	0	7	1	1	10	0	1	3	5	1	0	0	0	1	0	0	0	0	0	0	0	4	3	5	8	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	5	10	4	1	0	0	0	26	0.00	90
Reach	0	5	9	2	2	0	2	1	1	3	1	7	2	4	0	4	0	0	0	0	0	0	0	0	2	0	0	0	5	0	5	1	1	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	4	2	8	7	0	4	0	12	29	0.41	92
Arm swing	0	2	3	4	2	0	2	2	6	0	0	9	3	0	3	3	4	0	0	2	3	0	0	0	0	0	3	2	4	0	1	2	2	0	0	0	0	0	0	0	0	0	3	1	1	1	1	0	1	1	1	3	2	0	3	0	1	3	4	5	4	4	0	1	0	19	38	0.50	102
Grab	0	2	0	3	2	0	3	2	2	0	2	3	4	0	4	4	1	0	0	0	1	0	2	0	1	1	3	2	3	2	1	2	0	1	0	1	0	1	0	1	2	0	0	0	0	2	2	2	7	0	3	0	5	1	3	1	1	1	7	2	5	1	4	0	1	11	44	0.25	104
Directed push	0	2	1	1	0	0	25	3	7	1	4	6	2	0	3	1	1	0	1	0	1	0	0	4	0	0	1	1	2	4	1	7	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	24	0	5	1	3	2	0	1	117	0.01	118
Big Loud Scratch	0	6	7	8	6	3	5	3	11	5	4	2	4	2	2	1	8	3	0	1	1	0	5	2	4	2	0	1	3	1	0	0	0	0	0	1	0	0	0	1	1	0	2	6	2	6	1	0	3	0	0	1	2	0	2	0	11	0	1	0	0	0	0	0	0	20	40	0.50	140
Touch other	0	4	1	7	1	2	15	4	8	0	2	11	3	0	5	3	6	1	1	0	2	0	0	5	0	0	3	1	2	2	2	10	3	0	1	0	0	1	0	2	1	0	0	2	0	1	0	0	4	0	0	2	4	2	3	0	0	9	20	3	5	3	3	2	0	22	44	0.50	172
Arm raise	1	8	4	6	6	0	21	2	14	3	5	10	4	1	5	1	5	2	3	0	4	1	3	4	2	0	2	1	3	1	1	10	0	1	0	0	0	0	0	0	0	1	2	0	3	1	1	1	1	2	2	2	3	0	4	0	3	11	19	1	6	5	2	0	0	23	49	0.47	204
Grab-pull	1	9	3	2	11	8	16	4	5	2	3	7	16	3	5	5	4	2	4	0	1	0	2	7	0	3	5	4	6	3	1	1	0	0	0	0	0	0	0	2	3	0	1	4	4	2	3	7	13	2	1	5	9	1	1	2	3	6	6	2	3	0	1	0	0	30	51	0.59	224
Present (genitals forward)	17	27	11	21	38	8	47	15	85	33	14	114	32	8	43	54	37	7	44	9	26	6	5	24	18	7	22	2	5	4	1	1	0	0	0	0	0	0	0	4	0	1	3	3	5	9	17	0	11	12	5	8	31	9	10	3	7	17	5	5	11	3	1	1	0	42	55	0.76	966
Present (grooming)	1	37	145	95	68	69	90	90	110	52	76	25	83	24	84	64	55	61	34	7	45	7	15	26	15	11	9	35	6	1	2	0	1	0	0	0	0	0	0	19	20	17	23	70	56	55	60	13	57	50	25	34	70	23	9	16	46	10	11	2	1	2	0	0	0	49	55	0.89	2132
OVERALL REPERTOIRE	**4**	**25**	**19**	**28**	**21**	**7**	**27**	**18**	**25**	**15**	**19**	**34**	**17**	**15**	**21**	**27**	**24**	**11**	**14**	**9**	**23**	**5**	**6**	**16**	**17**	**6**	**21**	**16**	**25**	**18**	**23**	**24**	**10**	**8**	**8**	**6**	**0**	**3**	**0**	**8**	**10**	**11**	**12**	**12**	**10**	**15**	**19**	**8**	**18**	**11**	**15**	**17**	**18**	**13**	**21**	**8**	**17**	**24**	**37**	**19**	**37**	**25**	**18**	**9**	**3**				**5388**

To determine whether sufficient data were indeed available, or alternatively whether the index was still partly a function the number of gesture instances, I plotted the index, as a dependent variable, against the total number of gesture instances as the independent variable, for each gesture type (Figure 3.5). Indeed, the index *does* increase with the number of gesture instances, with an asymptote of ~0.9 at ~2000 gesture instances. This suggests that for most gesture types the index seriously underestimates signaller/recipient interchangeability. Given enough gesture instances for all gesture types, most of them would have indices of 0.9-1.0.

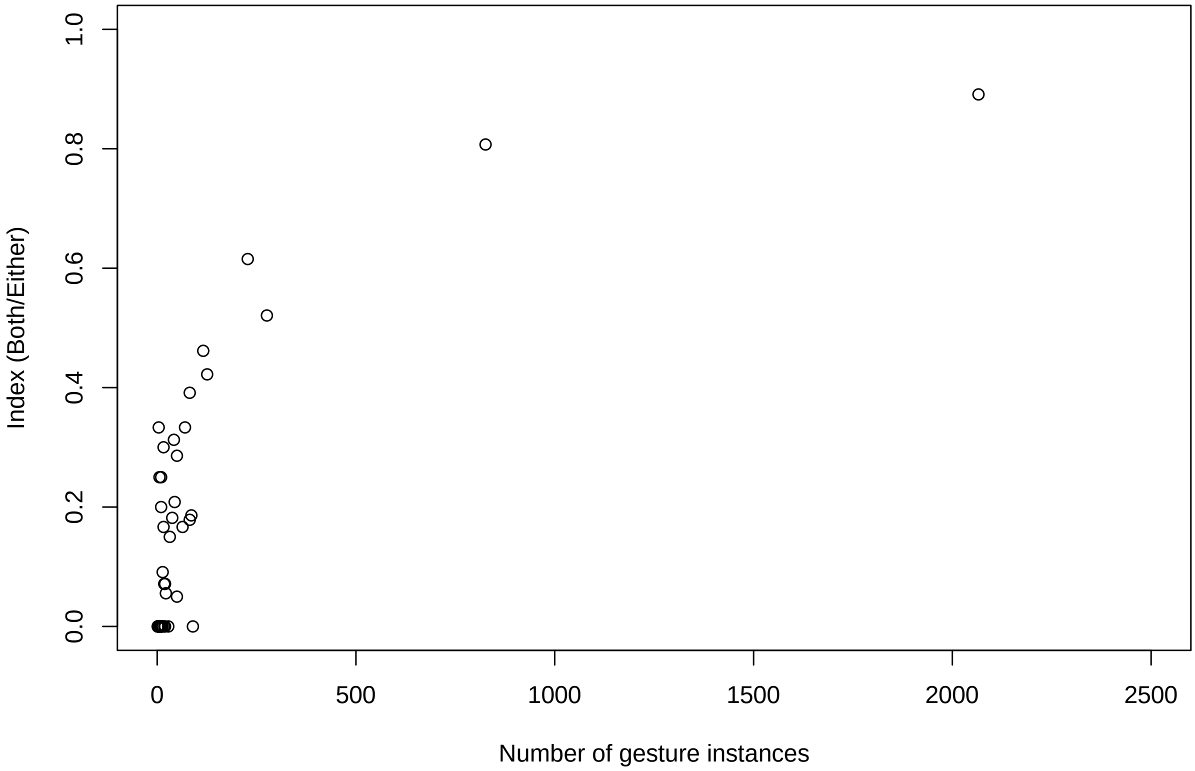


Figure 3.5. This graph plots the index (# of individuals that both express and understand/# individuals that either express or understand) over the number of gesture instances for each gesture type. The line curves, reaching asymptote at over 0.8 for over 2000 gesture instances.

To see whether any gesture types were expressed or understood exclusively by one sex, I grouped individuals by sex and plotted the number of individuals that express, understand, or both express and understand each gesture type (Figure 3.6). All gesture types that were observed >3 times (47 gesture types) were both expressed and understood by members of both sexes, with the exception of *Leg flap*, which was expressed but not received and understood by males.

Finally, to see if age-group had an effect on expressed or understood repertoires, I grouped individuals by age ("adult + adolescent" and "juvenile + infant") and plotted the number of individuals that express, understand, or both express and understand each gesture type (Figure 3.6). Most gesture types that were observed >3 times were both expressed and understood by members of both age-groups. However, three gesture types, *Bite*, *Arm up*, and *Present (climb on)*, were expressed but not received and understood by adults and adolescents. Three gesture types, *Bite*, *Beckon*, and *Present (climb on)*, were received and understood but not expressed by juveniles and infants; and one gesture type, *Roll over*, was expressed but not received and understood by juveniles and infants.

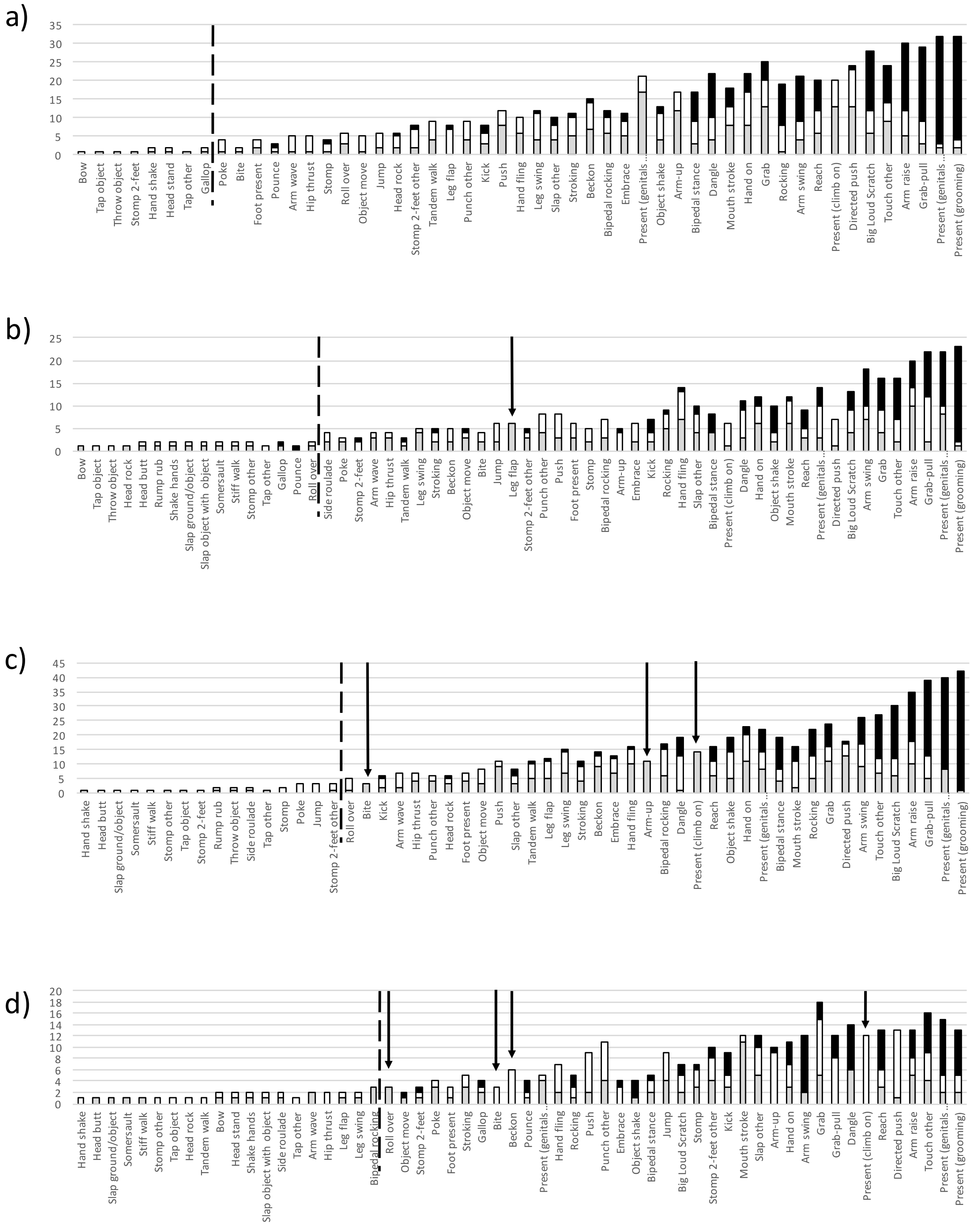


Figure 3.6. For these histograms the entire dataset is divided into (a) female and (b) male, and into (c) adults and adolescents and (d) juveniles and infants. Each histogram is ordered from left to right in ascending order of the number of gesture instances for each gesture type. Gesture type is shown on the x-axis, and the y-axis is 'Number of Individuals'. In grey are the number of individuals that only express a gesture type; in white are the number of individuals that only understand a gesture type; and in black are the number of individuals that both express and understand a gesture type. If a gesture type has any combination of 2 or 3 of these colours, it shows that individuals of that sex or age group both express and understand the gesture type.

The dotted black line shows the cut off of ≥3 gesture instances, above which most gesture types are both used and understood by all individuals. The black arrows point out gesture types that are not both used and understood all individuals.

3.4 Discussion

3.4.1 Bonobo gestural communication

When I combined individuals' expressed and understood repertoires into an overall repertoire, their average repertoire size increased from 14.4 gesture types (expressed only) to 18.8 gesture types. It is unsurprising that including the understood alongside the expressed repertoire increases the overall repertoire. However, it is useful for any scientist to be able to maximise the amount of data in their dataset. One of the limitations of fieldwork is that a large amount of effort yields very little in return. Spending the same amount of time studying captive bonobos as I have spent studying wild bonobos would have yielded a much larger quantity of video footage. If a method promises to increase the amount of data for analysis, it can only be a good thing. I am not arguing to merge both, but to report both alongside one another, increasing available data while at the same time analysing potential differences in signaller-recipient roles.

I found that all gesture types were both expressed and understood by both females and males, with the exception of *Leg Flap*, which was expressed but not received and understood by adult males. *Leg Flap* is found in a sexual context; in the following chapter on meaning (Chapter 4), I will discuss possible reasons for this sex difference. All in all, these findings are quite remarkable – a communication system in which the signals are accessible to both sexes as signallers and recipients. As mentioned, in many species, visual displays are produced only by one sex (often male), and directed towards the other (often female). That bonobo gestural communication does not differ greatly by sex suggests that it is a mutually understood communication system. Slightly more gesture types were different by age group: three that adults expressed but did not receive and understand; three that infants and juveniles received and understood but did not express; and one that infants and juveniles expressed but did not receive and understand. Out of 68 gesture types, the differences are very small. And when considering that there are almost no differences in females and males, it means that throughout an individual's lifetime they have the opportunity to use all gesture types.

The gesture type *Present (climb on)* nicely illustrates that differences in repertoire may actually be differences in the *opportunity* to use a gesture, rather than the absence of that gesture from the repertoire. Usually only adult females use *Present (climb on)* directed towards their offspring, but when I observed an adult male carrying a juvenile (Figure 3.7), he used similar gestures to adult females. For ~3 months (~1 month consistently), the adult male carried a juvenile male whose mother, because she has an amputated leg from a snare injury, was unable to carry him. During this time, the adult male used *Present (climb on)*, which is usually expressed only by adult females. This gesture type was therefore already in his repertoire, he just needed the opportunity to use it. It is therefore likely that this gesture type also appears in the actual repertoire of other adult males, but they have just never had the opportunity to use it.

Figure 3.7. Adult male, Daniel, carried a juvenile male, Hideo, for ~3 months.

I chose to use an index of individuals that both used and understood a gesture type over the number of individuals that either used or understood that same gesture type, as a way of determining whether, at an individual level, there was variation in who was a signaller and who was a recipient. These individual differences might have been determined by the sex or age group to which an individual belonged, and were indeed picked up in the group analysis. On an individual level, there were many gesture types with index values close to zero. These gesture types however, were often ones with few gesture instances. Indeed, the index of individuals that both used and understood each gesture type increased as the number of gesture instances increased. Thus, the apparent differences in individual roles as signallers and recipients are liable to have been an artefact of paucity of data. If all gesture types were observed >2000 times, then the index is predicted to asymptote at ~0.9 – that is 90% of individuals both express and understand the gesture type. Why wouldn't it asymptote at 100%? There may be sex and age differences as mentioned earlier. The dataset includes young infants who are just starting to engage in gestural communication. During these early stages, perhaps they only use gestures but don't respond to them, or only respond to gestures but do not use them. Further exploration of the expressed and understood repertoires could shed light on the development of gesture usage.

Also, no matter how many gesture instances are observed for the whole community, some individuals are much more peripheral and do not engage so often in social behaviour. Even for central individuals, their personality may dictate whether they engage socially. For example, Bokuta is the highest ranking and also the oldest female in P Group. She is estimated to be over 60 years old. Although I devoted an equal amount of time focal sampling Bokuta as all the other members of P Group, I never once saw her groom another individual. She was sometimes groomed, and sometimes those individuals requested grooming in return, but she never acquiesced. Probably, at some point in her life, she must have groomed other individuals, but at this late stage, she did not. Another old individual, this time from E1 Group, Tawashi, was also less socially involved, which might explain his smaller repertoire size. Long term studies that follow individuals throughout their entire life, collecting consistent data each year could reveal dynamic changes in an individual's role as signaller and recipient. Also, analyses could include individual identity as a random factor, in order to pick up on individual identity. Finally, social network analysis could detect whether the centrality of an individual within the group affects their opportunity to gesture and therefore their repertoire size.

Finding that most gesture types, given enough data, are indeed mutually understood, makes it hard to reconcile ontogenetic ritualization as the form of acquisition. This harks back to my question in the introduction of whether gesture forms might be phylogenetically or ontogenetically ritualised. Tomasello proposed the following trajectory for Ontogenetic Ritualization (OR), and uses *arm raise* as an example:

> "1. initially one youngster approaches another with rough-and-tumble play in mind, raises his arm in preparation to play-hit the other, and then actually hits, jumps on, and begins playing;
>
> 2. over repeated instances, the recipient learns to anticipate this sequence on the basis of the initial arm-raise alone, and so begins to play upon perceiving this initial step; and
>
> 3. the communicator eventually learns to anticipate this anticipation, and so raises his arm, monitors the recipient, and waits for her to react—expecting this arm-raise to initiate the play" (Tomasello, 2008)

First, the two individuals perform an action, then the recipient starts to anticipate the action, and finally the signaller anticipates that the recipient will anticipate their action. This way of learning would predict that only the specific signaller and recipient dyad recognise the gesture, and that it would be used in one direction unless they reverse roles. In terms of my findings, ontogenetic ritualization would have predicted more gesture types that were one-way, particularly between adult females and their offspring. While I do not rule out the possibility that a handful of gestures may have been learnt through ritualization in this population, given the interchangeability of signaller and recipient shown here, it is highly unlikely that all gestures are acquired that way. It would be necessary to explain gesture acquisition by another form of social learning, or accept that the gestural repertoire is largely biologically inherited. That the bonobo repertoire is species-typical, is a strong pointer towards the argument that these gesture types are biologically inherited.

3.4.2 The bigger picture

First, including the understood alongside the expressed repertoire, significantly increasing repertoire size, is a useful methodological tool. Individual repertoire size is low for most studies on great apes and this may help to remedy that. Although long-term studies of wild populations are ideal, in the shorter term we can better glean an individual's *actual* repertoire by including understood gesture types in their *overall* repertoire. I would suggest though that we report them separately, and can then compare the two repertoires. Moreover, studying the signals that an individual understands brings us closer to the way linguists assess *receptive vocabularies*. If our aim is to understand the evolution of human language, it's important to have more comparable methods to those used in human studies.

Examining expressed and understood repertoires for all species would allow us to check whether, as I suspect, other great apes' gestural repertoires are also mutually understood. Although it is probably also the case that other great apes' repertoires are largely shared across sexes and age-groups, I did find several bonobo gestures that appeared to differ in signaller and recipient identity. There may be differences in great ape social structures that affect who uses and who receives which gestures. One potential interspecies difference between bonobos and chimpanzees may be that bonobo females have more opportunity to use sexual solicitation gestures, because of their female-female sexual behaviour. This will be examined in Chapter 6, where I compare bonobo and chimpanzee gestures. Future research should examine whether female gorillas use similar solicitation gestures for GG-rubbing (Grueter & Stoinski, 2016).

Signaller-recipient interchangeability is a feature in the communication system of our own great ape species, the human. Bonobo gestural communication, it would appear, is a mutually understood communication system, wherein all individuals have the opportunity to be both signaller and recipient for all gesture types. In this regards, it is similar to human language. Humans of both sexes have access to the entire vocabulary of whichever language they speak. This signaller-recipient interchangeability is important for individuals that need to communicate about something that both sexes experience.

While my work does not focus specifically on gesture acquisition, my finding that the bonobo gestural repertoire is species-typical and mutually understood corroborates findings in wild chimpanzees, that there are very few one-way gesture types (Hobaiter & Byrne, 2011b). In that study, the 5 individuals with the largest repertoire size, 17% of the repertoire consisted of one-way gestures, but those individuals also produced 25% more gesture instances than they received, so that the real number of one-way gestures was probably negligible (Hobaiter & Byrne, 2011b). In the wild, the chimpanzee repertoire appeared to be species typical. If it were also to have high signaller-recipient interchangeability, which seems likely, then the claim of idiosyncratic, one-way gestures would be untenable. In my study, the 13 gesture types that were used only by one individual were only observed once (successfully achieving an ASO). After a gesture occurred more than two times, I did not observe any other “idiosyncratic” gestures. Idiosyncrasy, in that case, was caused by lack of observation rather than being a gesture unique to one individual.

Sceptics will argue that there are only so many ways to move your arms about – the bonobos could be waving and shaking and moving in coincidentally similar ways. That is why the next step of analysis is so important – does the same gesture type used by different individuals mean the same for all individuals? There *are* only so many ways to move your arms about, but it would be a huge coincidence if 64 individual bonobos moved their arms about in one of 68 ways to mean the exact same thing. In the next chapter, I explore the meaning of gestures and look at the effects of individual identity on gesture meaning.

3.5 Conclusion

Bonobos use 68 gesture types, but estimates of individual repertoire size are relatively small (mean of 14.4 gesture types). Including the understood with the expressed repertoire gives a significantly larger overall repertoire (mean of 18.8 gesture types). As the number of gesture instances increases, so does the number of individuals who both express and understand them and it therefore appears that the gestural repertoire can be mutually understood by all individuals. Once a gesture type had been observed more than once, there were no idiosyncratic gesture types. Once a gesture type had been observed three or more times, each age or sex group both received and understood that gesture type. Reporting both the expressed and understood repertoires is a useful method for increasing the amount of data for individuals, without misrepresenting their actual repertoire, and is more comparable to human data. It also, more excitingly, indicates that the majority of bonobo gestural communication is a mutually understood communication system, as is human language. In the next chapter, I will examine whether these gesture types, that seem to be used by everyone, mean the same thing for all individuals.

Chapter 4 – Gesture dictionary: Meaning of bonobo gestures

4.1 Background

In the previous chapter, I found that the bonobo gestural repertoire is accessible to all individuals as both recipients and signallers. Here, I examine what the gestures mean. I first look at which gesture types achieve which ASOs, and whether they have specific meanings. I then ask "how does a bonobo get what it wants?", since in Chapter 6, that is how I will compare bonobo with chimpanzee gesture meaning.

4.1.1 Meaning in human language

Language encompasses the ability to attribute meaning to arbitrary symbols. These symbols and their meanings are conventionalized, so that members of the same linguistic community can understand one another. If community members did not agree on the meaning of words (I mean their *fundamental* meaning, not the interpretation of their meaning by specific audiences in particular contexts), then language would be pointless. Such conventionalised symbol-meaning pairings are exactly what Grice meant when he described "non-natural meaning" – where the meaning of a signal is not inherently linked to the form of the signal (Grice, 1957, 1969). "Natural meaning", on the other hand, occurs when a signal is automatically produced under certain conditions and the meaning thereby points towards the conditions that yielded the signal (Grice, 1957, 1969).

Meaning occurs both at the level of the word and at the level of a phrase. In this chapter, I address the former – meaning at the level of an individual unit. We use words to refer to objects, events, actions, people, places, concepts etc. Reference is the way of using words, symbols, or gestures to stand in place of such things (Sebeok, 1996). Some words and hand signs are iconic; they physically resemble the referent. Iconic spoken words are called onomatopoeia, for example, the word "buzz" resembles the sound that it refers to. Many gestures that we use are iconic, and many sign language signs have iconic features, for example, ASL for "tree" physically resembles a tree. Most words however, are somewhat arbitrary – there is no clue in the form of the word to what it refers to. If you did not speak English and heard the word "tree" devoid of any contextual information, you would have no idea what it referred to.

For non-iconic signals, how can a linguist work out the meaning of a word? To use Quine's famous example, a linguist hears someone say the word Gavagai as a rabbit runs past (Quine & Van, 1960). The linguist might infer immediately that Gavagai refers to the rabbit, but does it refer to that specific rabbit, to rabbit-ness, to a collection of rabbit parts, or to any small moving animal? Only through repeated experiences of hearing the word Gavagai is the linguist able to say for certain what object or set of traits this word refers to. Both the context in which the linguist sees "Gavagai" and the reaction that the word receives are important in reconstructing the meaning of the word. Animal communication researchers study the meaning or "function" of animal signals in a similar way.

4.1.2 Function in animal communication

Function comprises what a signal is used for, and can therefore be studied by looking at (a) the context in which the signal occurs and (b) the reaction that it elicits. Our best understanding of the function of animal signals comes from the alarm call literature. Alarm calls are used to alert others to the presence of predators, and can be found across many social species. To categorise alarm calls, one can look at the context in which they occur (is there a specific predator present?) and the response that they receive (do the recipients react in a way that is only appropriate for a certain predator type?). A wide variety of taxa are known to use different call types for different predators or level of threat, and Drongos, for example, even mimic the alarm calls of other species (Putty-nosed monkey: Arnold & Zuberbühler, 2008; Pied babbler, Glossy starling, Crowned plover, Fork-tailed Drongo: Flower, 2011; Meerkat: Manser, 2001; Vervet monkey: Seyfarth et al., 1980b).

This method of studying the function of alarm calls can also be applied to other call types. For example, as well as giving alarm calls, the pied babbler produces contact calls that serve to distribute group members across a foraging area to minimise competition (Radford & Ridley, 2008). In this example, the context is feeding and the reaction to the call is for other individuals to disperse from the signaller. Some members of the mongoose family (*Herpestidae*) also make contact calls that are thought to produce the same effect (Fitch, 2012), and dolphin signature whistles not only act as contact calls, but are stereotypical to identify individuals (Janik, Sayigh, & Wells, 2006). The function of food calls can also be determined by looking at context and reaction – chimpanzees use acoustically different food calls for different food items (Slocombe & Zuberbuhler, 2006). Looking at the context and reaction to signals is a useful way of identifying the signal's function. But, can we ever go beyond analysing function of animal signals, and talk about their *meaning*?

4.1.3 Function or meaning?

Grice's definition of meaning, as described earlier, is central to the debate on whether animal communication only has function or also has meaning. Apparently no-one has said it better than Grice, and so both sides of the debate re-interpret what he stated, moulding the argument to fit their needs rather than putting forward a new definition. The point on which it rests is whether animal signals are produced intentionally. In Chapter 1, I listed Grice's and Dennett's criteria for intentionality, showing that great apes engage in at least first order intentionality, i.e. aiming to change the behaviour of the recipient.

The most parsimonious explanation for most animal communication is that it is zero-order intentional, automatically produced. Without evidence to the contrary, the visual displays that we saw in the previous chapter–lekking bird species (Endler & Thery, 1996), peacock spiders (Girard et al., 2011), smooth newts (Halliday, 1974), and ring-tailed lemurs (Sauther et al., 1999)–are most likely produced in automatic response to a stimulus, for example, the presence of a sexually receptive female. However, there may be more cases of intentional communication in non-human animals than has typically been assumed (Ristau, 1991; Vail, Manica, & Bshary, 2013), and the best evidence comes from great ape gesturing.

In an ongoing call-and-response style series of papers, Thomas Scott-Phillips and Richard Moore argue about whether it is appropriate to talk about meaning in great ape gestural communication. Scott-Phillips argued that intentionality is not adequate for meaning – the intentionality must be *overt*, i.e. ostensive, drawing attention to its own communicative actions (Scott-Phillips, 2015, 2016). Moore responded that eye-gaze marks ostension in human developmental studies – infants gaze into the faces of those with whom they are communicating – which equates to the great ape “audience checking” criterion for intentionality, where a great ape signaller looks and checks the attention of the recipient before signalling (Moore, 2016). While Scott-Phillips and Moore agree that great ape gestural communication is first-order intentional, Scott-Phillips still does not believe that it’s ostensive. I stand with Moore in this debate, that great ape gestures meet criteria for intentionality and ostension as used by developmental psychologists. If the argument is made against meaning in great apes, it must therefore be equally applied to human children. I am not opposed to revising the criteria for good reason, but am uncomfortable with the double standards shown to non-human great apes (and all other non-human animals) and humans. The goal posts for non-human communication are always shifting, and “Language is often defined circularly as whatever aspects of communication are uniquely human” (Gillespie-Lynch, Greenfield, Lyn, & Savage-Rumbaugh, 2014).

4.1.4 Meaning in great ape gestural communication

Research on *function* can inform how we study the *meaning* of great ape gestures, i.e. by looking at context and outcome. Oddly, most studies seem to have focused only on the former, finding that gestures occur in many different contexts and then purporting that they therefore have flexible meanings (Call & Tomasello, 2007; Hobaiter & Byrne, 2011b; Pollick & de Waal, 2007). However, broad contexts, such as affiliative, agonistic, food, groom, play, sex, locomotion, and non-agonistic (Pollick & de Waal, 2007), do not adequately describe the specific meaning of each gesture. For example, within the feeding context one can imagine several specific intended meanings, e.g. "request food", "offer food", "stop begging", and "move away".

To define a gesture's meaning by the outcome also requires that the recipient's reaction was the *intended* outcome. The meaning of a gesture can then be defined by the "Apparently satisfactory outcome" (ASO), the reaction of the recipient that satisfies the signaller as shown by cessation of gesturing (Hobaiter & Byrne, 2014). This way of examining meaning has been used for captive orangutans and wild chimpanzees, finding variation in the rigidity of gesture meanings – gesture types could have *Tight* (achieved >70% of instances by one ASO), *Loose* (achieved 50-70% of instances by one ASO), or *Ambiguous* (not achieved >50% of instances by any one ASO) meanings (Cartmill & Byrne, 2010; Hobaiter & Byrne, 2014).

For orangutans, the apparently satisfactory outcomes grouped into 6 social goals: affiliate/play, stop action, look at/ take object, share food/object, co-locomote, and move away (Cartmill & Byrne, 2010). The orangutan gestural repertoire still exhibits contextual flexibility, but gestures are semantic, made with "specific intentional meaning and functional consequences" (Cartmill & Byrne, 2010). Of the 64 gesture types, 29 had tight meanings, 7 had loose meanings, and 4 had ambiguous meanings (24 were not observed frequently enough for analysis).

For chimpanzees, nineteen ASOs were reported:

> “Acquire object”, “Attend to specific location”, “Change play: increase intensity”, “Change play: decrease intensity”, “Climb on me”, “Climb on you”, “Contact”, “Follow me”, “Initiate grooming”, “Move away”, “Move closer”, “Reposition body”, “Resume play”, “Sexual attention (to female)”, “Sexual attention (to male)”, “Start play”, “Stop that”, “Travel with me (adult)”, “Travel with me (infant)” (Hobaiter & Byrne, 2014).

Each gesture type achieved an average of 2.8 ASOs; of the 36 gesture types that they analysed, 13 had tight meanings, 11 had loose meanings, and 12 had ambiguous meanings (Hobaiter & Byrne, 2014). Natural conditions, as opposed to captive conditions, likely provide more reasons for the apes to gesture, which may explain why there were more chimpanzee than orangutan ASOs, although differences in sociality between the two species may also affect number of ASOs.

In this chapter, I analyse the meaning of bonobo gestures. For each gesture type, I show which ASOs it achieves and in what distribution it achieves them. Conversely, for each ASO, I show the gesture types that achieve it, by proportion of instances. Meaning is at the core of language, allowing us to communicate about external objects, events, and abstract ideas. By looking at meaning in gestural communication, I hope to gain a better idea of how much information is being encoded in bonobo gestures, and what exactly they are communicating about. In looking at the meaning of gestures, I hope to understand the sort of meanings that are adaptive, and the possible selective pressures that could have led to the explosion of meaning in human language.

4.2 Specific Methods

Data collection was described in my general methods chapter, Chapter 2. From that data, I extracted the following coded information: *part of bout, part of sequence, signaller, recipient, signaller age/sex/rank, recipient age/sex/rank, gesture type, check attention, response waiting, recipient response, persistence, goal,* and *goal met* (also described in Chapter 2). I only analysed gestures that were used intentionally (i.e. they met the criteria for audience checking, response waiting, or persistence). Meaning can only be analysed when a gesture is successful, so as not to assume that I intuitively know the meaning. I therefore required that the recipient respond to the gesture (or the sequence in which the gesture occurred) with an ASO.

4.3 Results

4.3.1 Which gesture types are satisfied by which ASOs?

I recorded 4256 intentionally-produced gesture instances, but here I only analyse gesture instances (including those in sequences) that successfully achieved an ASO. There were 2463 intentional gestures that achieved ASOs, after excluding gestures used in play (231 instances); including play data would risk masking the normal meaning of gesture. Of the 1562 gesture instances that did not achieve an ASO, the signaller persisted in 806 instances and was unable to persist in a further 143. I limited the analysis to ASOs that were achieved ≥3 times for a given gesture type, to exclude rare gesture types and reduce observer error. This left 2321 gesture instances and 33 gesture types (Table 4.1). From this starting point, I identified 14 different ASOs: *Acquire object/food, Climb on me, Climb on you, Contact, Follow me, Initiate grooming, Mount me, Move closer, Reposition, Initiate copulation, Initiate GG-rubbing, Travel with me, Move away, Stop behaviour*. The first 12 of these ASOs serve to initiate or develop an activity, and the last 2 to stop an activity.

First, I looked at the number of ASOs that each gesture type achieved: 17/33 gesture types had only a single meaning; 6/33 gesture types had 2 meanings; and 10/33 gesture types had >2 meanings (Figure 4.1). The mean number of ASOs per gesture type is 2.27 ± 1.84 (median=2, range 1-8).

Table 4.1. By gesture type, the ASOs achieved and the number and proportion of instances in which each ASO is achieved, ordered by the proportion for which the primary ASO is achieved (largest to smallest).

Gesture type	Goal (ASO)	# Instances	Proportion
Present (grooming)	Initiate grooming	1063	1.00
Big Loud Scratch	Initiate grooming	67	1.00
Directed push	Climb on me	46	1.00
Present (climb on)	Climb on me	43	1.00
Mouth stroke	Acquire object/food	39	1.00
Embrace	Contact	11	1.00
Leg flap	Initiate copulation	8	1.00
Hand fling	Move away	8	1.00
Bipedal rocking	Initiate GG-rubbing	7	1.00
Push	Move away	7	1.00
Beckon	Climb on me	6	1.00
Hip thrust	Initiate copulation	5	1.00
Stroking	Initiate GG-rubbing	5	1.00
Slap other	Stop behaviour	4	1.00
Tandem walk	Initiate grooming	4	1.00
Head rock	Initiate GG-rubbing	3	1.00
Roll over	Contact	3	1.00
Dangle	Initiate GG-rubbing	15	0.79
	Initiate copulation	4	0.21

Arm up	Contact	16	0.76
	Climb on me	5	0.24
Present (genitals forward)	Initiate GG-rubbing	298	0.64
	Initiate copulation	168	0.36
Leg swing	Initiate copulation	5	0.63
	Initiate GG-rubbing	3	0.38
Present (genitals backward)	Initiate copulation	15	0.58
	Mount me	11	0.42
Reach	Climb on me	19	0.58
	Acquire object/food	7	0.21
	Climb on you	7	0.21
Punch other	Move away	4	0.57
	Stop behaviour	3	0.43
Bipedal stance	Initiate GG-rubbing	16	0.55
	Initiate copulation	10	0.34
	Climb on you	3	0.10
Grab-pull	Follow me	57	0.53
	Reposition	33	0.31
	Climb on me	8	0.07
	Move closer	6	0.06
	Initiate grooming	4	0.03
Rocking	Initiate GG-rubbing	16	0.52
	Initiate copulation	12	0.39
	Contact	3	0.10
Object shake	Initiate GG-rubbing	8	0.44
	Initiate copulation	6	0.33
	Initiate grooming	4	0.22
Arm swing	Initiate copulation	12	0.38
	Initiate GG-rubbing	10	0.31
	Climb on me	7	0.22
	Contact	3	0.09
Hand on	Contact	7	0.35
	Initiate grooming	4	0.20
	Climb on you	3	0.15
	Follow me	3	0.15
	Stop behaviour	3	0.15
Grab	Climb on me	10	0.32
	Reposition	8	0.26
	Initiate grooming	5	0.16
	Stop behaviour	5	0.16
	Contact	3	0.10
Arm raise	Initiate grooming	25	0.31
	Initiate copulation	17	0.21
	Initiate GG-rubbing	16	0.20
	Climb on you	15	0.19
	Climb on me	4	0.05

	Contact	4	0.05
Touch other	Climb on me	19	0.31
	Initiate GG-rubbing	10	0.16
	Initiate grooming	7	0.11
	Move away	7	0.11
	Initiate copulation	6	0.10
	Reposition	5	0.08
	Stop behaviour	5	0.08
	Travel with me	3	0.05

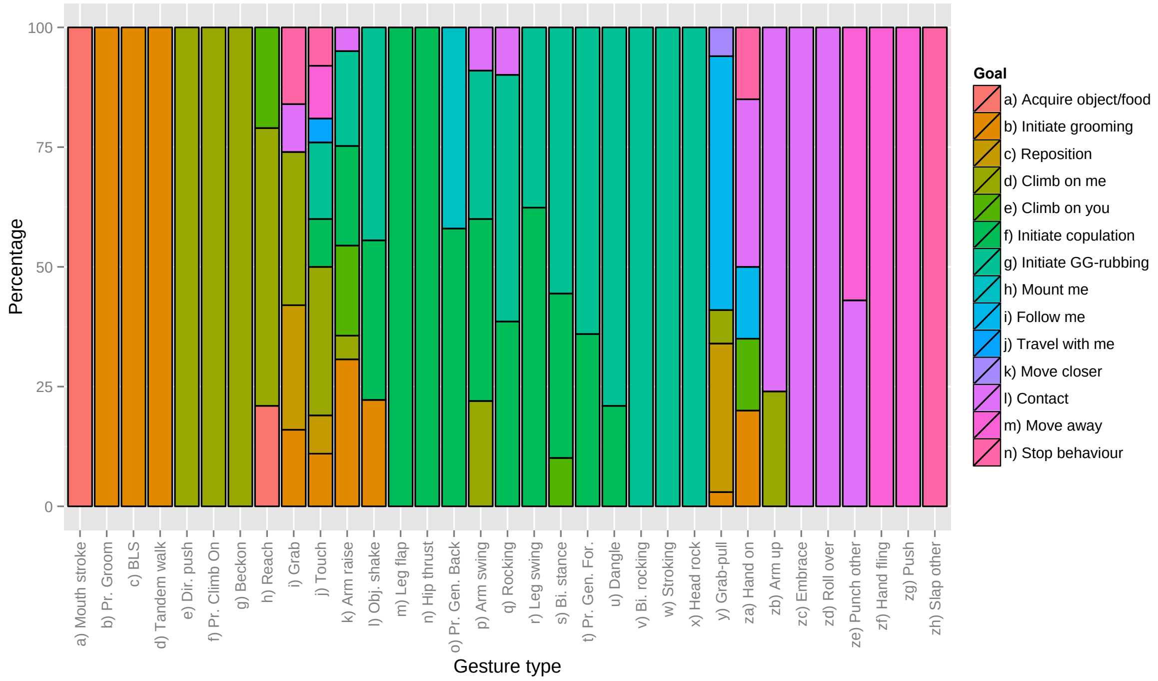


Figure 4.1. Proportional stacked histogram for ASOs achieved by each gesture type. ASOs are coloured in a gradient adjacent to behaviourally similar ASOs, and gesture types are arranged adjacent to those with similar ASO profiles.

There was no correlation between the number of ASOs a gesture type achieved and the number of total instances that the gesture type was observed (Pearson's product-moment correlation r(31)=-0.06, p=0.72). However, *Present (Grooming)* and *Present (Sexual)* were extreme outliers with 1063 and 466 instances respectively (Figure 4.2, left). When these two outliers were removed, there was a significant correlation between number of instances and number of ASOs (r(29)=0.39, p=0.032) (Figure 4.2, right).

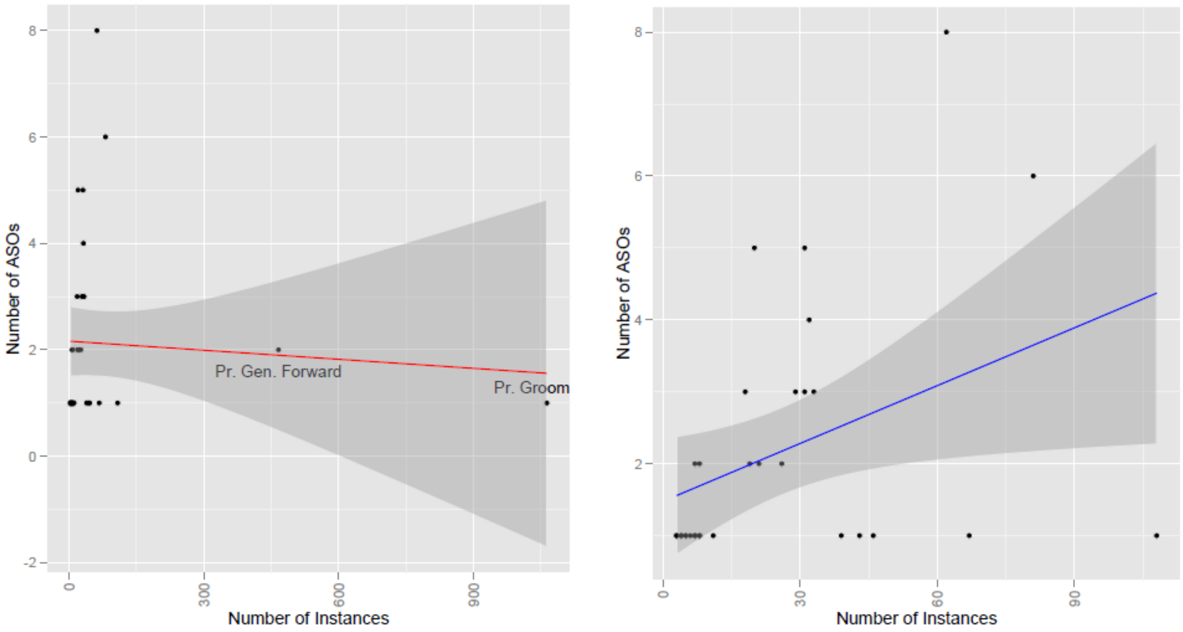


Figure 4.2. Scatterplots with linear regression lines in colour and 95% confidence region in dark grey. The left graph shows the correlation including *Present (genitals forward)* and *Present (grooming)* in analysis, and the right graph shows the correlation excluding these 2 gesture types.

4.3.2 Which ASOs are achieved by which gesture types?

The mean number of gesture types per ASO is 5.29 ± 4.10 (median=4, range 1-12) (Table 4.2). There is a significant correlation between the number of instances an ASO is observed and the number of gesture types that achieve the ASO (Pearson's product-moment correlation, r(12)=0.55, p=0.042) (Figure 4.3, left). "Initiate grooming" appears to be an outlier, and after removing it, the correlation becomes even stronger (Pearson's product-moment correlation, r(11)=0.86, p=0.0002) (Figure 4.3, right).

Table 4.2. By ASO, the gesture types and the number and proportion of instances that each gesture type achieves each ASO, ordered by number of gesture types (smallest to largest) then number of instances (largest to smallest).

Goal	Gesture	# Instances	Proportion	# Gestures
Mount me	Present (genitals backward)	11	1.000	1
Travel with me	Touch other	3	1.000	1
Move closer	Grab-pull	6	1.000	1
Follow me	Grab-pull	57	0.950	2
	Hand on	3	0.050	
Acquire object/food	Mouth stroke	39	0.848	2
	Reach	7	0.152	
Position	Grab-pull	33	0.717	3
	Grab	8	0.174	
	Touch other	5	0.109	
Climb on you	Arm raise	15	0.536	4
	Reach	7	0.250	
	Bipedal stance	3	0.107	
	Hand on	3	0.107	
Move away	Hand fling	8	0.308	4
	Push	7	0.269	
	Touch other	7	0.269	
	Punch other	4	0.154	
Stop behaviour	Grab	5	0.250	5
	Touch other	5	0.250	
	Slap other	4	0.200	
	Hand on	3	0.150	
	Punch other	3	0.150	
Contact	Arm up	16	0.320	8
	Embrace	11	0.220	
	Hand on	7	0.140	
	Arm raise	4	0.080	
	Rocking	3	0.060	
	Arm swing	3	0.060	
	Grab	3	0.060	
	Roll over	3	0.060	
Initiate grooming	Present (grooming)	1063	0.899	9
	Big Loud Scratch	67	0.057	
	Arm raise	25	0.021	
	Touch other	7	0.006	
	Grab	5	0.004	
	Grab-pull	4	0.003	
	Hand on	4	0.003	
	Object shake	4	0.003	
	Tandem walk	4	0.003	
Climb on me	Directed push	46	0.275	10

	Present (climb on)	43	0.257	
	Reach	19	0.114	
	Touch other	19	0.114	
	Grab	10	0.060	
	Grab-pull	8	0.048	
	Arm swing	7	0.042	
	Beckon	6	0.036	
	Arm up	5	0.030	
	Arm raise	4	0.024	
Initiate GG-rubbing	Present (genitals forward)	298	0.732	12
	Bipedal stance	16	0.039	
	Rocking	16	0.039	
	Arm raise	16	0.039	
	Dangle	15	0.037	
	Arm swing	10	0.025	
	Touch other	10	0.025	
	Object shake	8	0.020	
	Bipedal rocking	7	0.017	
	Stroking	5	0.012	
	Head rock	3	0.007	
	Leg swing	3	0.007	
Initiate copulation	Present (genitals forward)	168	0.627	12
	Arm raise	17	0.063	
	Present (genitals backward)	15	0.056	
	Rocking	12	0.045	
	Arm swing	12	0.045	
	Bipedal stance	10	0.037	
	Leg flap	8	0.030	
	Object shake	6	0.022	
	Touch other	6	0.022	
	Hip thrust	5	0.019	
	Leg swing	5	0.019	
	Dangle	4	0.015	

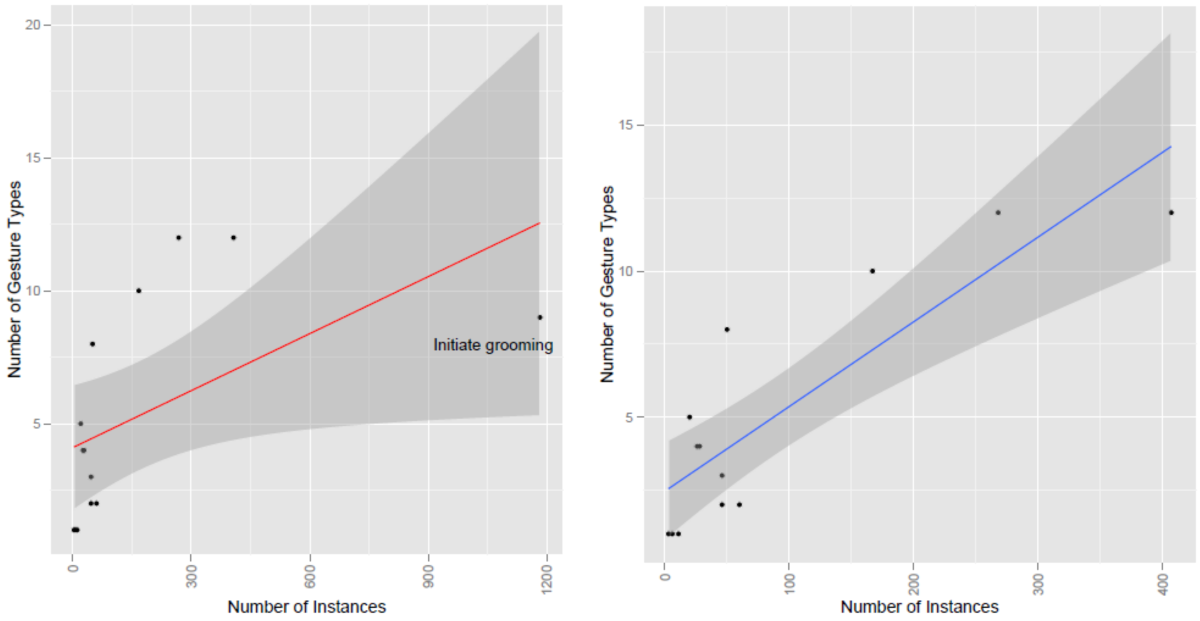
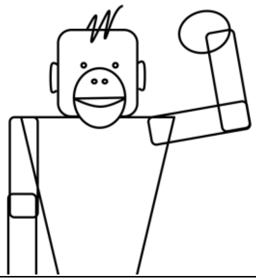
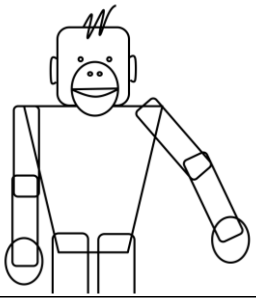


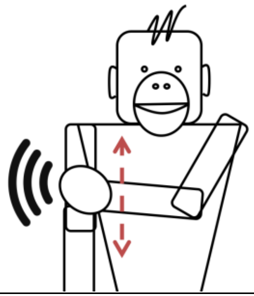
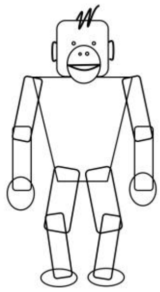
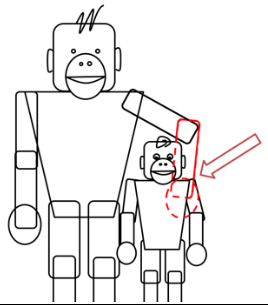
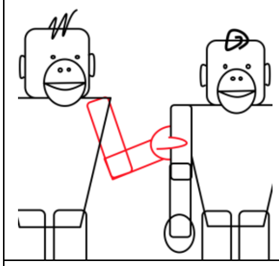
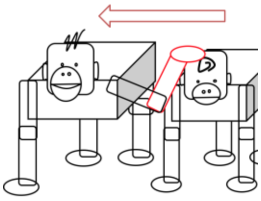
Figure 4.3. Scatterplots with linear regression lines in colour and 95% confidence region in dark grey. The left graph shows the correlation including "Initiate grooming" in analysis, and the right graph shows the correlation excluding this ASO.

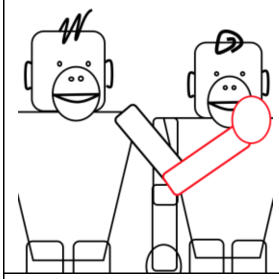
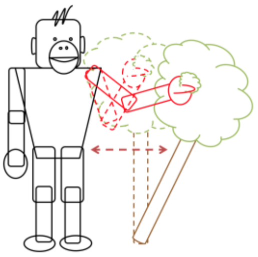
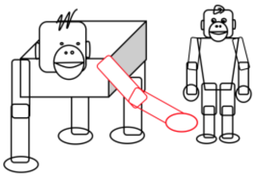
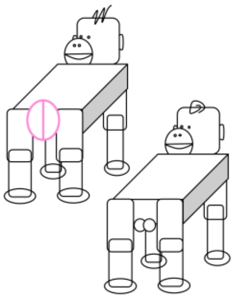
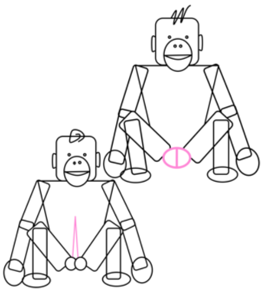
4.3.3 Do different gesture types achieve different ASOs?

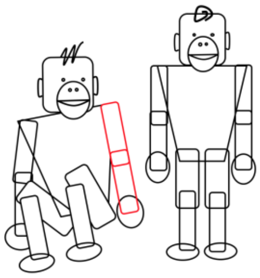
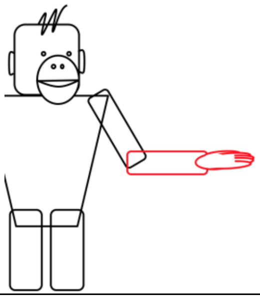
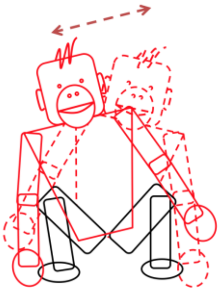
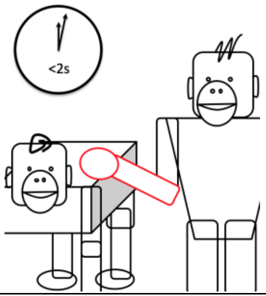
In accordance with Hobaiter & Byrne 2014, I used a series of ANOVAs to analyse whether the specific distribution of ASOs for a gesture type differed from the average distribution (the distribution of ASOs across all gesture instances). To be included in parametric analyses, I required that each gesture type achieve an ASO at least 3 times by at least 3 individuals (I analysed 1896 gesture instances; 15 gesture types were suitable for this analysis, and 51 individuals contributed data). Then I converted the number of instances a gesture type achieved each ASO into a proportion of the total number of gesture instances an individual used that gesture type. I also calculated the average distribution by converting the number of instances *all* gesture instances achieved each ASO into a proportion of the total number of gesture instances. For values of 0 or 1, I converted them in accordance with Snedecor and Cochran (0 → 1/(4N) and 1 → 1-(1/(4N)), where N is the total number of instances for that gesture type) (Snedecor & Cochran, 1989). Finally, to calculate how the specific distribution deviated from the average distribution, I subtracted the average from the specific distribution. I then conducted the ANOVA with this resulting deviation as the dependent variable, ASO as the independent variable, and signaller identity as a random effect. P-values of <0.05 show that the deviation of the specific from the average distribution is significant (See Table 4.3). All but one gesture type (*Object shake*) showed significant deviation from the average distribution.

Table 4.3. Gesture types that were analysed for ASO distribution; primary and secondary ASOs for each gesture type as a percentage of all instances for all ASOs; N as number of individuals and n as number of gesture instances; results for ANOVA, including Bonferroni-Holm adjusted p-values; and primary and secondary ASOs for the same gesture types analysed in chimpanzees. Underlined ASOs are shared by both chimpanzees and bonobos for that gesture type.

Gesture Type	Bonobo ASO (%) all individuals	N(n)	Evidence	Chimpanzee ASO (Hobaiter & Byrne 2014)
Arm raise 	Climb on you 34% (Initiate grooming 22%) *Ambiguous*	9(50)	f=3.13, df=12,96 p=0.0009 (adjusted p=0.002)	Acquire object 38% (Move away 29%) *Ambiguous*
Arm up 	Contact 80% (Climb on me 20%) *Tight*	3(15)	f=85.14, df=12,24 p<0.0001 (adjusted p=0.002)	-

Big loud scratch 	Initiate grooming 100% *Tight*	10(41)	f=893.1, df=12,108 p<0.0001 (adjusted p=0.002)	Initiate grooming 82% (Travel with me (adult) 9%) *Tight*
Bipedal stance 	Initiate copulation 50%, Initiate GG-rubbing 50% *Loose*	4(12)	f=4.46, df=12,36 p=0.0002 (adjusted p=0.002)	-
Directed Push 	Climb on me 100% *Tight*	4(37)	f=1330, df=12,36 p<0.0001 (adjusted p=0.002)	Reposition body 57% (Move closer 15%) *Loose*
Grab 	Climb on me 31% (Reposition 23%, Stop that 23%) *Ambiguous*	4(13)	f=4.55, df=12,36 p=0.0002 (adjusted p=0.002)	Stop that 44% (Climb on me 18%) *Ambiguous*
Grab-pull 	Follow me 58% (Reposition 21%) *Loose*	13(80)	f=48.62, df=12,144 p<0.0001 (adjusted p=0.002)	Move closer 35% (Climb on me 27%) *Ambiguous*

Mouth stroke 	Acquire object 100% *Tight*	5(24)	f=2779, df=12,48 p<0.0001 (adjusted p=0.002)	Acquire object 93% (Move closer 7%) *Tight*
Object Shake 	Initiate GG-rubbing[1] 58% (Initiate grooming 33%) *Loose*	3(12)	f=1.42, df=12,24 p=0.223 (adjusted p=0.223)	Move away 37% (Sexual attention to male[1] 35%) *Ambiguous*
Present (climb on) 	Climb on me 100% *Tight*	7(34)	f=4720, df=12,72 p<0.0001 (adjusted p=0.002)	Climb on me 100% *Tight*
Present (genitals backward) 	-	-	-	*Present (sexual)* in Hobaiter & Byrne, 2014 includes *Present (genitals forward)* and *Present (genitals backward)* Sexual attention to female 49% (Contact 33%) *Ambiguous*
Present (genitals forward) 	Initiate GG-rubbing[1] 64% (Initiate copulation 36%) *Loose*	41(450)	f=64.47, df=12,480 p<0.0001 (adjusted p=0.002)	

Present (grooming) 	Initiate grooming 100% *Tight*	47(1058)	f=7835, df=12,552 p<0.0001 (adjusted p=0.002)	Attend to specific location 99% (Initiate grooming 1%) *Tight*
Reach 	Climb on me 78% (Acquire object 11%, Climb on you 11%) *Tight*	5(18)	f=17.59, df=12,48 p<0.0001 (adjusted p=0.002)	Acquire object 53% (Contact 20%) *Loose*
Rocking 	Initiate copulation 54% (Initiate GG-rubbing 46%) *Loose*	3(13)	f=4.56, df=12,24 p=0.0008 (adjusted p=0.002)	-
Touch other 	Climb on me 41% (Move away 15%, Initiate GG-rubbing 15%) *Ambiguous*	8(41)	f=6.53, df=12,84 p<0.0001 (adjusted p=0.002)	Acquire object 32% (Contact 29%) *Ambiguous*

[1] Initiate GG-rubbing is considered the same as "sexual attention to a female" and "sexual attention to a male" because in the former it is a female recipient and in the latter it is a female signaller, both of which are true of GG-rubbing

It seems that in general, individual gesture types do achieve a different distribution of ASOs to the average distribution across all gesture types. The gesture types that I analysed have specific meanings, although some have loose and ambiguous meanings, with the primary ASO being achieved 50-70% or <50% of instances respectively. In the next chapter (Chapter 5), I explore the possible causes of this apparent ambiguity of meaning.

4.3.4 Are different ASOs achieved by different gesture types?

While the previous section was important for testing our assumptions about the distribution of ASOs per gesture type, the current section addresses the interesting question "How does a bonobo get what it wants?" I recognise that performing this analysis, which is the inverse of the previous analysis, is therefore not entirely independent. However, in order to answer my research question and also to compare to the meaning of chimpanzee gestures in Chapter 6, I felt that it was appropriate to perform the analysis both ways. Also, in the current analysis, I look at whether there is variation in the proportion of gesture types achieving each ASO, *not* the deviation from the average distribution. Thus, I do not subtract the average distribution in this analysis.

I followed a similar procedure as described previously, using a series of ANOVAs to analyse whether there was variation in the proportion of instances that each gesture type achieved an ASO. I required that each ASO was achieved by any gesture type at least 3 times by at least 3 individuals (2130 gesture instances, 9 ASOs, and 53 individuals contributed data). Then, I converted the number of instances an

ASO was achieved by any one gesture type into a proportion of the total number of instances an individual achieved that ASO. I included all gesture types that were suitable for analysis for any of the ASOs, in order to get a picture of which out of the available gesture types were used. For values of 0 or 1, we converted them in accordance with Snedecor and Cochran (0 → 1/(4N) and 1 → 1-(1/(4N)), where N is the total number of instances for that gesture type) (Snedecor & Cochran, 1989). Again, I *did not* subtract the average from the specific distribution for this analysis. I conducted the ANOVA with the corrected proportion as the dependent variable, gesture type as the independent variable, and signaller identity as a random effect (Table 4.4). All ASOs showed significant variation in the proportion of gesture types that achieve them.

Table 4.4. Table showing ASO and the top 3 gesture types that achieve it; N is number of individuals, n is total number of instances; and the ANOVA results from comparing the distribution of gesture types for that ASO, including Bonferroni-Holm adjustment.

Goal	Top 3 Gesture Types	N(n)	Results
Acquire object/food	1. Mouth stroke 86% 2. Reach 14%	6(29)	f=28.67, df=28,140 p<0.0001 (adjusted p=0.0009)
Climb on me	1. Directed push 27% 2. Present (climb on) 25% 3. Touch other 12%	11(157)	f=14.28, df=28,280 p<0.0001 (adjusted p=0.0009)
Climb on you	1. Arm raise 65% 2. Bipedal stance 13% 3. Reach 13%	4(23)	f=3.32, df=28,84 p<0.0001 (adjusted p=0.0009)
Contact	1. Arm up 36% 2. Embrace 21% 3. Hand on 12%	5(33)	f=2.75, df=28,112 p<0.0001 (adjusted p=0.0009)
Follow me	1. Grab-pull 95% 2. Hand on 5%	8(42)	f=724, df=28,196 p<0.0001 (adjusted p=0.0009)
Initiate copulation	1. Present (genitals forward) 62% 2. Arm raise 6% 3. Present (genitals backward) 6%	27(251)	f=50.99, df=28,728 p<0.0001 (adjusted p=0.0009)
Initiate GG-rubbing	1. Present (genitals forward) 73% 2. Bipedal stance 4%	25(397)	f=330.5, df=28,672 p<0.0001

	3. Rocking 4% (and *Arm raise* and *Dangle*, 4%		(adjusted p=0.0009)
Initiate grooming	1. Present (grooming) 90% 2. Big Loud Scratch 6% 3. Arm raise 2%	48(1178)	f=1284, df=28,1316 p<0.0001 (adjusted p=0.0009)
Reposition	1. Grab-pull 70% 2. Touch other 20% 3. Grab 10%	4(20)	f=8.04, df=28,84 p<0.0001 (adjusted p=0.0009)

4.3.5 Is requesting GG-rubbing different from requesting copulation?

GG-rubbing and copulation are both sexual activities, but are they requested in the same way? I took the data as set up in the previous section and extracted "Initiate GG-rubbing" and "Initiate copulation", only including data from females that achieved both ASOs. I then performed the same ANOVA as before, but adding "ASO" as an independent variable to look at the interaction of ASO and gesture type. There was a significant interaction of ASO and gesture type (f=8.20, df=14,203 p<0.0001). I created an interaction plot to qualitatively assess the differences in proportion of instances each gesture type achieves each ASO (Figure 4.4). It seems that *Present (genitals forward)* is used more for GG-rubbing than for copulation, and that *Present (genitals backward)* is used less, but that most other gesture types are used in similar proportions.

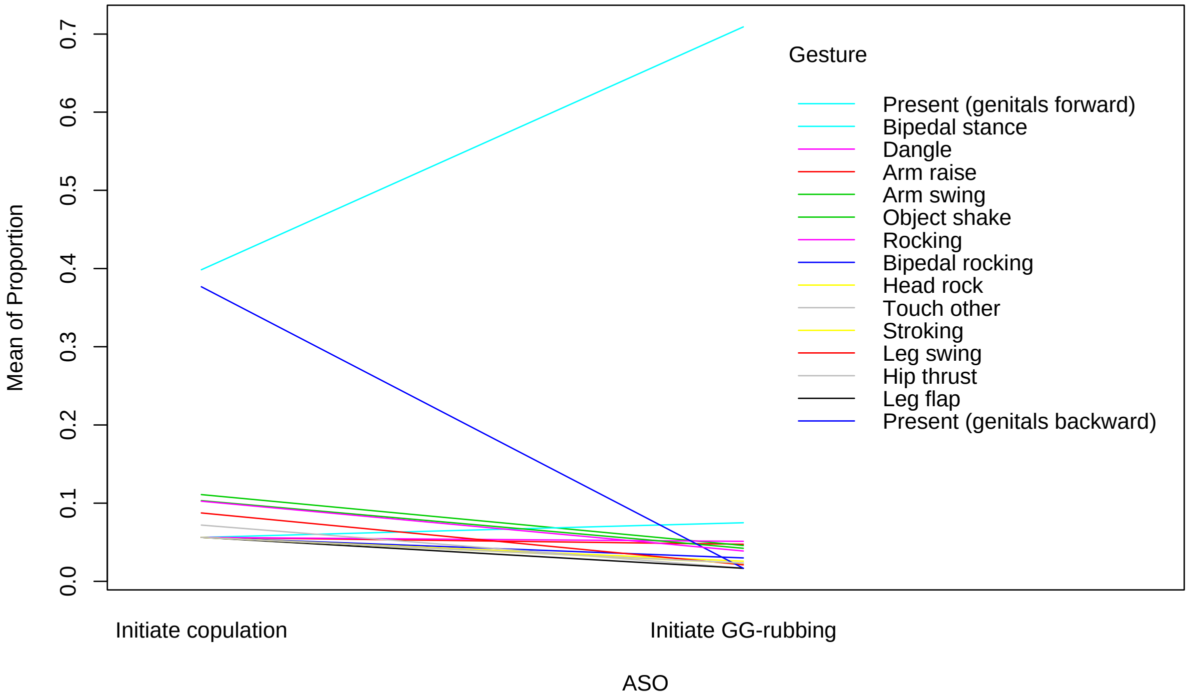


Figure 4.4. Interaction plot illustrating ANOVA results for females who achieved both "Initiate copulation" and "Initiate GG-rubbing", looking at the interaction between ASO and Gesture type in terms of the proportion of total gesture instances that each gesture type achieves each ASO.

4.4 Discussion

4.4.1 Bonobo gestural communication

I assessed the meaning of bonobo gestures by looking at the reaction of the recipient that apparently satisfied the signaller (Apparently Satisfactory Outcome, ASO). I found 14 outcomes (ASOs), and then looked at which gesture types achieve which ASOs. Of the 33 gesture types that I was able to analyse, 17 had a single meaning, only ever achieving a single ASO; 6 had 2 meanings, and 10 had 3 or more meanings. The average number of ASOs per gesture type was 2.27.

I did find a correlation between the number of ASOs and the number of instances for gesture types, after removing 2 outliers. This would suggest that as I observe more gesture instances, gesture types should achieve more and more ASOs. However, the two outliers (at 466 and 1063 instances) may be indicative that with many more instances for all gesture types the correlation would drop away. The same goes for the correlation that I found between the number of gesture types per ASO and the number of instance for an ASO.

Bonobo gestures have specific meanings: each gesture type achieves a different set of ASOs from the average distribution of ASOs across all gesture types. The one exception was *Object shake* and I wonder whether it did not vary significantly because it achieves "Initiate grooming", "Initiate copulation", and "Initiate GG-rubbing", all of which dominate the average distribution of gesture instances. Moreover, it was only observed used by 3 individuals with a total of 12 instances. It remains to be seen whether, given more instances, it continues to mimic the average distribution or whether it is stably only used for these three ASOs.

I also asked "how do bonobos use gestures to get what they want (a single ASO)?" Of the 14 ASOs, three were achieved only by a single gesture type. However, these three ASOs, "Travel with me", "Move closer", and "Mount me", were achieved only on 3, 6, and 11 instances, respectively. Indeed, the number of gesture types that achieve an ASO is significantly correlated with the total number of instances that the ASO was observed. When the two outliers, mentioned earlier, were removed, the correlation became even stronger. Thus, the number of gesture types that achieve an ASO increases with observation of that ASO. Again, I would need to conduct a much longer study to see for how long this correlation holds.

I conducted similar ANOVAs for each ASO as I did earlier for gesture types, and all ASOs varied significantly in their distribution of gesture types. This means that all ASOs are each achieved by a varied distribution of gesture types. I will use this line of questioning when comparing gesture meaning with chimpanzees in Chapter 6, because I want to know whether chimpanzees and bonobos use similar gesture types to achieve the same goal.

Bonobo sexual behaviour is quite unusual – females frequently engage in female-female genito-genital rubbing. To determine whether GG-rubbing and copulation were treated the same in terms of gestures to solicit them, I compared the distribution of gesture types that achieve the two ASOs. There is a significant interaction of gesture type and ASO; females use *Present (genitals backward)* and *Present (genitals forward)* equally often for requesting copulation (~40% of instances), but never use *Present (genitals backward)* for GG-rubbing, while *Present (genitals forward)* increases to ~70% of instances. Although a similar comparison is not possible with chimpanzees, future research on female gorillas could explore whether a similar pattern emerges when they request copulation and GG-rubbing (Grueter & Stoinski, 2016).

4.4.2 The bigger picture

At a first glance, it seems that chimpanzee gestures are more ambiguous than bonobo gestures; bonobos had more gesture types that were used for only a single ASO (17 for bonobos compared to 3 for chimpanzees, after eliminating gestures seen in <3 instances) (Hobaiter & Byrne, 2014). But note that the chimpanzee paper included

“Play” ASOs, which may have inflated the number of ASOs per gesture type. Once those differences in datasets are addressed, any interspecies differences in number of ASOs per gesture type may possibly be explained by the shorter response time and lower rates of persistence in bonobos compared to chimpanzees (Fröhlich et al., 2016). Bonobos respond more quickly to gestures than chimpanzees and persist less frequently (Fröhlich et al., 2016), and so may also be less likely to settle for an ASO that is similar but not exactly what they wanted, having tried and tried without success. Such limitations in the way that we assign ASOs will be expounded in the general discussion chapter.

When looking more closely at the specific ASOs that each gesture type achieves for each species (Table 4.3), eight out of 12 gesture types share a primary or secondary ASO, and these shared gesture types generally have a tight meaning (achieved by one ASO >70% of instances). Notably, there are some ASOs that are very similar, i.e. “Follow me”, “Move closer”, “Travel with me”, and “Climb on me”, all of which require the recipient to move towards the signaller. The only difference is in whether they stay, make contact, or travel. Again, this apparent difference in ASOs may be linked to the quicker response time and lower persistence in bonobos (Fröhlich et al., 2016). Perhaps the bonobos are quickly responding correctly and the chimpanzees are settling for other variations of similar ASOs. I will explore such interspecies differences in Chapter 6, where I carry out a full comparison of the bonobo and chimpanzee repertoires and meanings.

Meaning in ape gestural communication seems to be more or less ambiguous. Ambiguity of meaning is naturally disconcerting; it appears that there is no fixed way of knowing what a gesture is for. But in human languages, many words are polysemous. The word “right”, for example, means both “correct” and “opposite of left”. That the bonobo gestural repertoire has flexible meanings for some gestures and rigid meanings for others is not so different from the meanings of human words. I’m not claiming that bonobos have language – I only found 14 ASOs, not the multitude of meanings in human language, and these ASOs were largely to request activities and objects. As far as this method goes, I was not able to determine whether bonobos use gestures to label abstract concepts; not that I would expect them to (Imagine the males complaining about the female hegemony orchestrated by the sexual power that they exert! (Rousseau, 1754)). But in future research, it will be necessary to consider ways of looking at declarative gestures.

When we think about how a human audience deciphers polysemous words, to return to the “right” example, we have many tools at our disposal. The first that springs to mind is syntax – the cornerstone of language. We can use word order and combinations, punctuation and emphasis to get our meaning across. We also attend to our shared context and can often infer the speaker’s intended meaning merely because of it; the audience is able to pick up from the context (whether the person is talking about an answer or giving directions), which meaning of the word is intended. In the following chapter, I will explore whether bonobos may use similar ways of deciphering the meaning of gestures.

4.5 Conclusion

I found 14 outcomes (ASOs) achieved by bonobo gestures. About half of gesture types only achieved one ASO, and the other half achieved two or more ASOs. I found correlations between the number of ASOs per gesture type and the total number of instances per gesture type; and the number of gesture types per ASO and the total number of instances per ASO (the latter being a stronger correlation). For gesture types that were suitable for ANOVA analysis, all but one showed significant variation between the distribution of ASOs per gesture type and the average distribution. For ASOs that were suitable for ANOVA analysis, all of them showed significant variation in the distribution of gesture types. Although these two tests are not fully independent, I carried out both to (a) make my research comparable to a past study on wild chimpanzees, and (b) to conduct future comparison with a chimpanzee dataset. On a side note, I found that female bonobos use a different distribution of gesture types to request GG-rubbing and copulation – the gesture types are largely the same, but the proportion of usage differs significantly. The next step is to determine how recipients decipher gestures with more ambiguous meanings.

Chapter 5 – Syntax and context: Modifiers of bonobo gestures

5.1 Background

In the previous chapter, I defined the meaning of each gesture type by the outcome that it achieves. Half of gesture types achieved only a single ASO, but the rest had more ambiguous meanings. That a single gesture type can achieve several ASOs is potentially confusing for both signaller and recipient. But in reality the recipient usually does respond successfully with an Apparently Satisfactory Outcome (ASO), suggesting that they somehow have enough information to know what the signaller wants. Where does that information come from? Are the bonobos using syntax-like modifiers to alter the meaning of their gestures? Or are they getting contextual information that helps them to decipher the gesture's intended meaning?

5.1.1 Human syntax & context

Humans not only attribute meanings to individual words; we attribute meaning to composite phrases, and are able to modify the meaning of words and phrases using syntactic devices. Syntax "makes infinite use of finite means" by providing a framework onto which words can be scaffolded to encode more complex meaning (Chomsky, 1965; Palmer, 1984; von Humboldt, 1836). When native English speakers think about syntax or grammar, the first thing likely to spring to mind is word order, where changing the order of words in a series changes the meaning of the series

(Palmer, 1984). For example, a harmless phrase such as “the child eats the chicken” takes on a morbid meaning, just by flipping the order – “the chicken eats the child”. Furthermore, within a series of words, agreement usually occurs between word classes (i.e. nouns, verbs, adjectives) so that the form of each word changes to show, for example, which verb modifies which noun (Palmer, 1984).

But word order isn’t the only way to modify meaning. Punctuation in written language or pausing in speech can also change the meaning of a sentence. If you remove the second comma from the sentence “here are my parents, a dog, and a parrot”, then it sounds as though I come from a rather unusual family. Modifiers such as affixes are also used in both spoken and sign languages to change the meaning of words. For example, in English, the suffix –ed makes a verb past tense, and in ASL the affix for “person” changes “teach” or “learn” into “teacher” or “student” (Aronoff, Meir, & Sandler, 2005). Tonal languages create different meanings for the same word just by changing the pitch (Yip, 2002). Syntax encompasses so much more than word order.

Many sign language grammars rely on modifiers such as directionality, reduplication, and paralinguistic features (E. Cohen, Namir, & Schlesinger, 1977). *Directionality* is the direction in which the sign is given, and can be used, among other things, to say whether I did something to someone or they did something to me. *Reduplication* is the repetition of a sign twice, which does not just mean “two of the same thing” but changes the meaning, for example showing that it’s bigger or faster. Reduplication is also a modifier in spoken languages, for example, in Kiswahili and Lingala. *Paralinguistic features* include intensity, size, amplitude, body posture, and facial expressions (E. Cohen et al., 1977). Sign languages are real languages and are therefore different from gestures, but the modifiers used in sign languages may hold insight into how the meanings of gestures can be changed.

Academics sometimes talk about meaning as if it were always separate from context, but humans *do* pay attention to context in language. If I talk about “drawers” in a cabinet shop, my audience does not think that I’m talking about underwear; if I talk about “drawers” in a lingerie shop, my audience does not think that I’m talking about furniture. This happens automatically; both the signaller and recipient share a context and interpret the signals in regard to that context, without considering other possible meanings. The ability to use shared common ground with one’s communication partner – and thus automatically interpret ambiguous utterances – is considered part of theory of mind (Tomasello et al., 2005).

5.1.2 Animal signal combinations

Syntax is complicated, recursive, and hierarchical. There is very sparse evidence that non-human animals possess anything nearly as complicated. However, there are indications that other species combine signals, often in two-slot combinations, and that some combinations change the meaning of a signal. This is “syntax-like”, but far from the degree to which humans structure language. Nevertheless, a two-slot mould may have been an important step in language evolution for early Hominins (Progovac, 2016), and signal combinations in non-human animals may give insight into this early model.

In the previous chapter, I listed a number of species for which researchers have determined the function of various calls, and several of these species use their calls in combinations. For instance, the chestnut-crowned babbler produces two call types, a flight call (produced during flight) and a prompt call (produced during nestling provisioning), formed of 2 acoustic elements (Engesser, Crane, Savage, Russell, & Townsend, 2015). The flight call is composed of acoustic elements A+B and the prompt call is B+A+B. In playback experiments, the babblers reacted in the same way to natural calls as they did to artificially engineered "cut and paste" calls. The babblers' responses to both call types suggests that they get different information from the combination of acoustic elements; the function of the call is altered by the order of the signals.

Another species of babbler, the pied babbler, combines complete call types. The pied babbler produces an "alert call" for low-urgency threats, and a "recruitment call" for recruiting group members while travelling. When they combine these two call types, the response changes – it becomes a "mobbing call", recruiting group members to assist against a potentially high-urgency threat (Engesser, Ridley, & Townsend, 2016). The resulting meaning of combining two calls is different than those calls separately, though it could be argued that it has the same basic function as the recruitment call but is a higher-urgency version.

Also from the previous chapter, the putty-nosed monkey not only uses individual alarm calls, but uses them in series. A series of "hack" calls are still functionally referential for eagles and a series of "pyow" calls are still functionally referential for leopards and other disturbances. The response for the "hack" call is to inhibit movement, and the response for the "pyow" call to react quickly, move slightly closer, and scan the area. When these calls are combined into "pyow-hack" series (1+ pyows followed by 1+ hacks), the response is different – the monkeys are slower to respond but move much further (Arnold & Zuberbühler, 2008). Combining the 2 call types elicits a different response, or has a different function.

Mongooses also combine call types in 2-slot moulds. One study looked at 3 call types: a “digging call”, which they produce while digging; a “searching call”, produced when searching for food on the ground; and a “moving call”, produced when travelling (Jansen, Cant, & Manser, 2013). The digging call can be combined with the latter two calls, and because it varies acoustically among individuals but is consistent within an individual, the researchers proposed that this is a kind of signature call (Jansen et al., 2013). Unfortunately, this study did not look at the responses of call combination, just simply that they do combine calls. Another study *did* look at the responses to alarm call combinations of dwarf mongoose (Collier, Radford, Manser, & Townsend, 2016). While these findings are preliminary, they suggest that when an “aerial alarm” call and a “terrestrial alarm” call are combined, the response to the combined call differs from the response to the individual calls.

The preliminary mongoose findings appear very similar to those from the titi monkey, which uses different call combinations to signal predator type and location (Cäsar, Zuberbühler, Young, & Byrne, 2013). Of their predators, raptors are usually found in the canopy and oncilla are usually found on the ground, and they use call type A for raptors and call type B for oncilla. But when a raptor is found on the ground, the titi monkey begins the sequence with call type A but ends with call type B (e.g. A+A+A+A+A+B). When an oncilla is found in the canopy, they start with an initial call type A and then continue with the normal call type B (e.g. A+B+B+B+B). The call combinations are therefore changing the function to alert recipients of the unusual location of each predator type.

Divers taxa across the animal kingdom are capable of combining signals in simple but meaningful ways. One might then expect that our closest living relatives also combine signals, and that they can comprehend some level of syntax. In fact, the best evidence may come from the bonobo.

5.1.3 Bonobo syntax

The first evidence that bonobos may comprehend syntax came from ape language studies on Kanzi (but note that similar abilities have been found for a language-trained grey parrot and bottlenose dolphins (Kako, 1999)). Kanzi showed understanding of discrete combinatorics, i.e. when “words combine, their meanings do not blend one into another, as do colours when they are mixed, rather, their meanings also combine, in lawful ways prescribed by syntax” (Kako, 1999). Kanzi could combine symbols for “hug” and “[a specific person]” to signify who he wanted to hug. In experiments testing his comprehension of spoken English, Kanzi understood argument structure, where the ordering of words around a verb gives information about what something does, or who/what it does it to. Kanzi performed best (74% correct) for phrases with a different word order and a different verb, such as “Take the potato outdoors” versus “Go outdoors and get the potato" (Kako, 1999). For phrases with identical word order but a different verb, or different word order and an identical verb, he performed somewhat poorer at 57% accuracy, but still well above chance. It would be amazing to revisit the ape-language studies to see what might be driving differences in syntactic comprehension in these situations.

If bonobos do indeed have some level of syntax-like comprehension, is there any evidence of it in their natural behaviour? It seems that their calls may be used in meaningful combinations. When giving food calls, bonobos use sequences containing various call types, and the construction of sequences is related to the desirability of food items (e.g. kiwi high-desirability, apple low-desirability). In one study at Twycross Zoo, UK, researchers recorded the call sequences that bonobos made when given apples and when given kiwis (Clay & Zuberbühler, 2011), and then trained the bonobos to locate kiwis on one side of the field and apples on the other. When given the playback for either the "apple" sequence or the "kiwi" sequence, the bonobos searched in the "correct place" – the place where they were trained to find the fruit. Thus, the call sequences encode information about the food item. In future, it would be nice to know the function of component call types in these sequences or compare with artificially assembled sequences, so that we can say more about how these sequences encode information.

5.1.4 Great ape gesture sequences

In all of my given examples from other species, researchers looked at two-slot signal combinations, but great ape gestural communication includes longer sequences than that. When complexity moves beyond a combination of two signals, there is a strong compulsion to look at signal order, because word order is such an important syntactic device for humans. Great apes frequently gesture in series, and sequences are defined as gestures occurring in a series in quick succession, although some researchers categorise sequences as consecutive gestures occurring with a <5s interval

(Liebal et al., 2004) and others categorise them with a <1s interval (Hobaiter & Byrne, 2011a). Chimpanzee gesture sequences often occur in play, and are often the repetition of the same gesture type (Liebal et al., 2004). That particular study looked at the function of gestures within a sequence and found no evidence that the first gesture in a sequence is used as an “attention getter” (Liebal et al., 2004). In another study on wild chimpanzees, 70% of gestures were produced within a series of gesturing and sequences contained from 2 to 11 gestures (Hobaiter & Byrne, 2011a). The frequency of using gesture sequences decreased significantly as age increased; younger chimpanzees used more gesture sequences than adult chimpanzees (Hobaiter & Byrne, 2011a). In general, sequences were less successful than single gestures, but the success rate of any given gesture type did not differ with age (Hobaiter & Byrne, 2011a). Therefore, the overall success rate of gesturing increased as age increased, and so success rate was negatively correlated with occurrence of gesture sequences (Hobaiter & Byrne, 2011a). All of this suggests that younger chimpanzees use sequences because they do not yet know which gesture types are more successful, and may go through “repertoire tuning” as they age (Hobaiter & Byrne, 2011a). If sequences are used to add redundancy by younger individuals, there is little reason to imagine that the sequences are syntactic, in terms of signal order (Liebal et al., 2004).

Syntax would be very exciting to find, but another explanation for the ambiguity of gesture meanings may be much simpler. Plooij and Goodall both recognized that gestures could be used in many different contexts, as well as in combinations (Goodall, 1986; Plooij, 1978). Other researchers have also found gestures to be used across a wide range of contexts (Call & Tomasello, 2007; Pollick & de Waal, 2007), but did not consider that they might *mean different things in different contexts*.

These studies used context as a proxy for meaning, without addressing that context might actually affect the meaning. We take for granted that context affects the meaning of our own language, where a rich tapestry of contextual information allows us to understand one another without exhaustive explanation. For great apes, we can observe “behavioural context”, the behaviour of the signaller at the time of gesturing, and “interpersonal context”, the relationship of signaller and recipient, both of which are also important in human communication. Disentangling context and meaning may finally get at how a recipient is able to correctly interpret the meaning of seemingly ambiguous gesture types.

In this chapter, I look for potential modifiers of gesture meaning: gesture combinations and ordering, and behavioural and interpersonal context. I aim to explain the apparent ambiguity of gesture meanings presented in the previous chapter, to understand how a bonobo recipient deciphers the signaller’s message.

5.2 Specific Methods

Data collection was described in my general methods chapter, Chapter 2. From my data, I extracted the following coded information: *part of bout, part of sequence, signaller, recipient, signaller age/sex, recipient age/sex, signaller context prior, gesture type, check attention, response waiting, recipient response, persistence, goal,* and *goal met* (also described in Chapter 2). I only analysed gestures that were used intentionally (meaning that they met the criteria for audience checking, response waiting, or persistence), giving me 4256 gesture instances. I took the results from

Chapter 4, on gesture meaning, and worked from there to look at causes of the apparent ambiguity.

Here, I would like to acknowledge the limitations of my analysis. By the time we get down from gestures, to gestures used in sequences, to gestures used in specific positions in sequences etc. there are too few instances to run parametric analyses. While qualitative assessment of the data shows a nice picture on its own, I still wanted to conduct statistical analyses, and was limited to Chi-square tests and Fisher's exact tests, both of which pool individuals, risking pseudoreplication. The results are still worth presenting, but please bear these limitations in mind.

5.3 Results - Syntax

5.3.1 Do gesture types achieve the same ASOs when they are used singly as when they are used in sequences?

If the purpose of gesture sequences is to modify the meaning of a gesture type, then one would expect the meaning of gestures in sequences to be different to those used singly. To test this, I looked at gesture types that are used both singly and in sequences. I excluded "Play" and "Unknown" ASOs in order to only examine properly identified ASOs. I required that an ASO be achieved at least 5 times for a given gesture type.

Fourteen gesture types were suitable for analysis. I first created a proportional stacked histogram to qualitatively examine the data (Figure 5.1). Most gesture types have a similar profile for single and sequence usage. For 12/14 gesture types, the primary ASO was the same for single gestures and sequences. Only one gesture type, *Grab*, did not share any ASOs between single instances and sequences (Table 5.1).

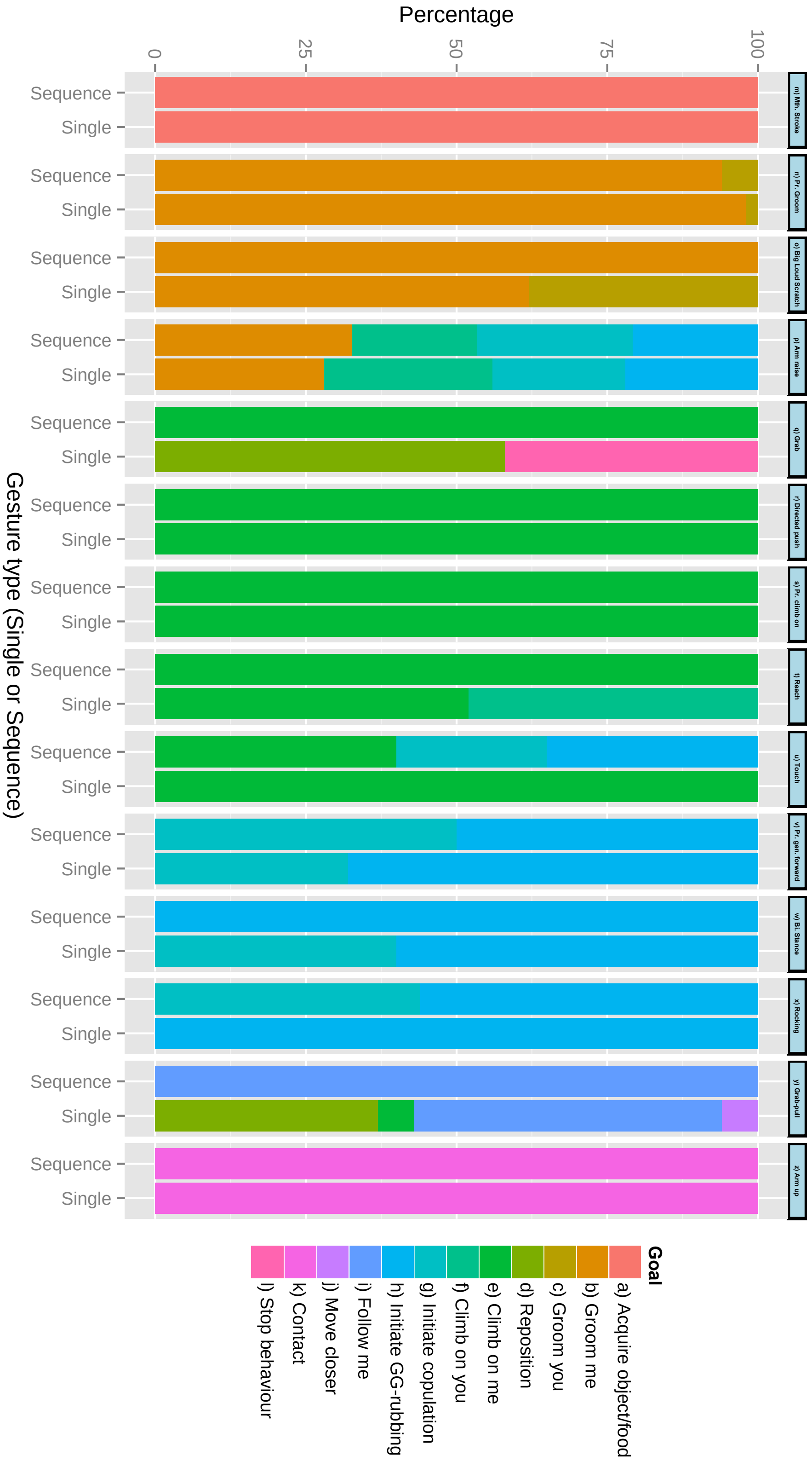


Figure 5.1. Proportional stacked histogram showing the proportion of total instances each single instance or sequence for each gesture type achieved each ASO. The chart is arranged so that similar goals (ASOs) appear in adjacent colour gradients and that gesture types with similar histogram profiles appear in adjacent columns.
Table 5.1. Table showing the gesture type (arranged according to similar histogram profile in Figure 5.1); number of instances in sequences and singly (sequence, single); whether the primary ASO is the same; and the number of shared ASOs over the number of total ASOs.

Gesture Type	**# Instances (sequence, single)**	**Primary ASO same?**	**# Shared ASOs/ Total ASOs**
Mouth stroke	7, 32	Yes	1 / 1
Present (grooming)	90, 975	Yes	2 / 2
Big loud scratch	44, 21	Yes	1 / 2
Arm raise	39, 36	Yes	4 / 4
Grab	8, 12	No	0 / 3
Directed push	18, 28	Yes	1 / 1
Present (climb on)	17, 26	Yes	1 / 1
Reach	7, 21	Yes	1 / 2
Touch	20, 11	Yes	1 / 3
Present (genitals forward)	107, 373	No	2 / 2
Bipedal stance	7, 15	Yes	1 / 2
Rocking	18, 7	Yes	1 / 2
Grab-pull	16, 81	Yes	1 / 4
Arm up	11, 5	Yes	1 / 1

I then examined whether the distribution of ASOs for each gesture type was the same for single gestures and those in sequences. Four gesture types (*Mouth stroke*, *Directed push*, *Present (climb on)*, and *Arm up*) had only 1 ASO and were identical for both single instances and sequences, rendering statistical analysis impossible and unnecessary. For the remaining gesture types, where there were enough data (no more than 20% of cells with <5 expected value and no cells with <1 expected value), I performed Chi-square tests on a table of "single" or "sequence" by ASO (Table 5.2). If there was not adequate data for a Chi-square test and the table was 2x2, I performed Fisher's exact test (Table 5.2). Fisher's exact test can also be used for m x n contingency tables (Freeman & Halton, 1951; Mehta & Patel, 1983), and when I have used this method, I specify the size of the contingency table in Table 5.2. Both analyses risk pseudoreplication, and these results should therefore be considered as preliminary. Four gesture types (*Present (grooming), Arm raise, Bipedal stance*, and *Rocking*) had the same distribution for single and sequence (plus the 4 gesture types of 100% identical ASO), and six gesture types (*Big Loud Scratch, Grab, Reach*, *Touch other, Present (genitals forward),* and *Grab-pull*) had significantly different distributions.

To answer the sub-heading question "do gesture types achieve the same ASOs when they are used singly as when they are used in sequences?": yes, most gesture types (12/14) had the same primary ASO for single gestures and sequences, and most gesture types (8/14) had the same distribution of ASOs for single gestures and sequences. It seems that the simple presence of a gesture type in a sequence is not sufficient for changing the meaning of that gesture type.

Table 5.2. Gesture type arranged according to similar histogram profile in Figure 5.1; whether or not the gesture type had the same distribution of ASOs for single gestures and sequences; and results for Chi-square and Fisher's exact tests.

Gesture Type	Same dist.?	Results
Present (grooming)	Yes	χ^2=2.16, df=1, p-value=0.14 (Yates' continuity correction)
Big loud scratch	No	χ^2=15.75, df=1, p-value<0.0001 (Yates' continuity correction)
Arm raise	Yes	χ^2=0.72, df=3, p-value=0.87
Grab	No	Fisher's exact test, p<0.0001 (2x3 table)
Reach	No	Fisher's exact test, p=0.03 (2x2 table)
Touch other	No	Fisher's exact test, p= 0.003 (2x3 table)
Present (genitals forward)	No	χ^2=12.02, df=1, p-value<0.0001 (Yates' continuity correction)
Bipedal stance	Yes	Fisher's exact test, p=0.12 (2x2 table)

Rocking	Yes, **but close**	Fisher’s exact test, p=0.06 (2x2 table)
Grab-pull	No	Fisher's exact test, p=0.002 (2x4 table)

5.3.2 Should “Groom me” and “Groom you” be combined into one ASO?

In the previous section, *Big loud scratch* shared the same primary ASO, “Groom me”, in single instances and sequences, but had a different distribution; if used singly, it also achieved the ASO “Groom you”. This might be explained by the way in which I have assigned ASOs. If bonobo A performs *Big loud scratch*, then bonobo B performs *Present (grooming)*, and bonobo A begins to groom bonobo B, then both bonobos appear satisfied and the ASO for *Big loud scratch* is “Groom you” and that for *Present (grooming)* is “Groom me”. However, both bonobos may have been requesting “Groom me”, but one of them gave in and began to groom the other, resulting in her ASO being “Groom you”. That scenario is clearly different from requesting to groom the other individual and having your aim fulfilled, but the two appear to be the same in my coding. An alternative scenario could be that to bonobos the meaning is simply “Initiate grooming” without any preference for who grooms whom. This confusion could be overcome by combining the “Groom me” and “Groom you” ASOs into one “Initiate grooming”.

To see how combining “Groom me” and “Groom you” into “Initiate grooming” changed the ASO distributions of each gesture type, I started from the raw data again and combined the ASOs. I then followed the same process as previously: excluding “Play” and “Unknown” ASOs; excluding ASOs with fewer than 5 instances singly or in sequences; colour grading similar ASOs; and arranging gesture types in the graph to be adjacent to gesture types with similar ASO distributions (Figure 5.2).

Four gesture types were affected by combining “Groom me” and “Groom you” into “Initiate grooming” – *Present(grooming), Big loud scratch, Arm raise*, and *Touch other* (Table 5.3). *Present (grooming)* and *Big loud scratch* now have one identical ASO (“Initiate grooming”) for single gestures and sequences, where before the distribution for *Big loud scratch* was significantly different for single and sequence usage. *Arm raise* still has no significant difference in the distribution of ASOs for single gestures and sequences (χ^2=0.86, df=3, p-value =0.84). *Touch other* still has too few values to perform a Chi-square test, but Fisher’s exact test reveals an even stronger significant difference in distribution (p=0.002). The distribution for *Touch other (single)* now more closely resembles the distribution for *Arm raise* and has therefore been repositioned on the histogram (Figure 5.2).

To answer the question “should “Groom me” and “Groom you” be combined into one ASO?”: yes (probably), because when requesting grooming the signaller and recipient may have competing goals and combining the two ASOs corrects for this possibility. Combining the ASOs errs toward the side of “no difference” between meanings, with 4/4 gesture types now with the same primary ASO and 3/4 with a similar distribution of ASOs, and it is best to take this more conservative stance. However, further exploration into gesture usage during grooming interactions could further illuminate requests to groom or be groomed.

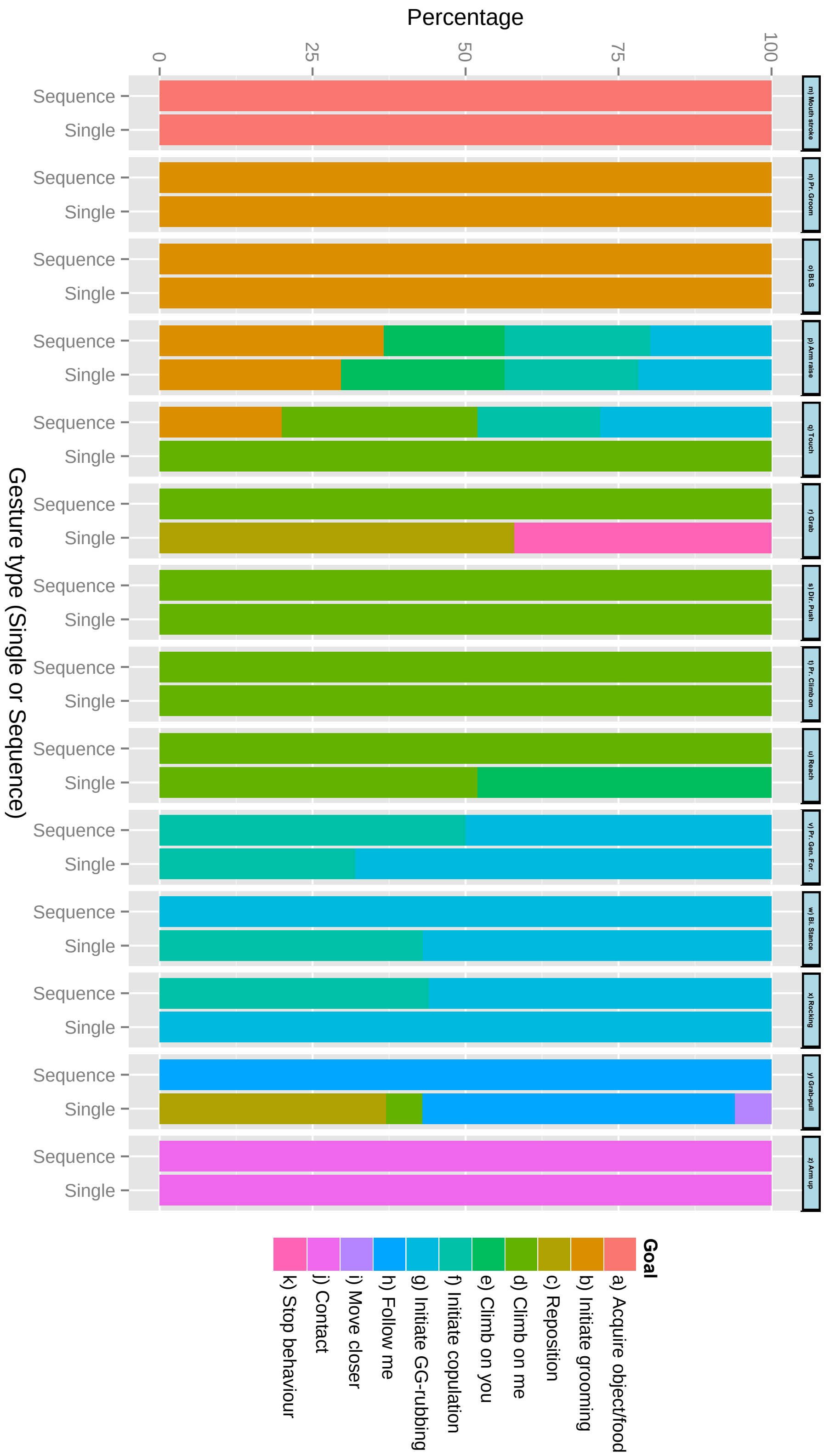


Figure 5.2. After combining "Groom me" and "Groom you" into "Initiate grooming", this proportional stacked histogram shows the proportion of total instances each single instance or sequence for each gesture type achieved each ASO. The chart is arranged so that similar goals (ASOs) appear in adjacent colour gradients and that gesture types with similar histogram profiles appear in adjacent columns.

Table 5.3. Gesture type (for gestures that were affected by combining "Groom me" and "Groom you" into "Initiate grooming"); number of instances in sequences and singly (sequence, single); whether the primary ASO is the same; and the number of shared ASOs over the number of total ASOs.

Gesture Type	**# Instances (sequence, single)**	**Primary ASO same?**	**# Shared ASOs/ Total ASOs**
Present (grooming)	90, 975	Yes	1 / 1
Big loud scratch	47, 21	Yes	1 / 1
Arm raise	41, 37	Yes	4 / 4
Touch other	25, 11	Yes	1 / 4

5.3.3 Are certain gesture types more likely to appear at a specific position in a sequence?

Before seeing whether the position in a sequence affects the meaning of a gesture, I wanted to see whether gesture types are more likely to occur in certain positions in a sequence. To do this, I first took all gesture instances occurring in sequences for which the position in the full sequence is known (sometimes I observed incomplete sequences, due to filming constraints). I labelled the positions as "First", "Middle" (occurring in any position in the middle of a sequence), and "Last". This gave me 291 instances in the "First" position, 291 in the "Last" position, and 101 instances in the "Middle" position (43% First, 15% Middle, 43% Last), with sequences ranging from 2-8 gestures.

I then excluded "Play" and "Unknown" ASOs, as in previous analyses, and excluded all gesture types that achieved any one ASO <5 times. Note that for this analysis, there are some additional gesture types – these gesture types have an ASO ≥5 times in sequences, so they are included here, but they did not achieve an ASO ≥5 times singly and so were excluded for the previous analysis. This left 415 instances in total: 172 "First" position, 58 "Middle" position, and 185 "Last" position (41% First, 14% Middle, 45% Last), again with sequences ranging from 2-8 gestures.

I then tested whether the distribution of positions for each gesture type was different from the distribution of positions across all gesture types (Table 5.4). Where possible, I used a 2x3 Chi-square tests, with "gesture type" and "all gesture types" by "First", "Middle", and "Last". If a Chi-square was not appropriate, I used Fisher's exact test.

Table 5.4. Gesture type (arranged first by total number of instances, and then alphabetically); the frequency of occurring in the first position in a sequence, anywhere in the middle of a sequence, and at the end of a sequence; the total number of instances observed; and the results for Fisher's exact test or Chi-square test, including Bonferroni-Holm adjustment.

Gesture	First	Mid	Last	Total	Results
Arm up	4	0	1	5	-
Leg swing*	2	2	1	5	-
Stroking*	3	2	0	5	-
Grab-pull	3	0	3	6	-
Mouth stroke	1	2	3	6	-
Bipedal stance	6	0	1	7	-
Reach	4	1	2	7	-
Grab	5	2	1	8	-
Leg flap*	0	3	5	8	-
Object shake*	4	3	1	8	-
Arm swing*	4	7	6	17	Fisher's exact test, p= 0.016 (adjusted p=0.128)
Present (climb on)	3	2	12	17	Fisher's exact test, p=0.078 (adjusted p=0.546)
Directed push	5	3	10	18	Fisher's exact test, p=0.48 (adjusted p=1.000)
Rocking	6	3	9	18	Fisher's exact test, p=0.76 (adjusted p=1.000)
Touch other	6	5	9	20	Fisher's exact test, p= 0.29 (adjusted p=1.000)
Arm raise	11	19	6	36	χ^2=1.63, df=2, p-value=0.44 (adjusted p=1.000)
Big Loud Scratch	14	9	21	44	χ^2=2.14, df=2, p-value=0.34 (adjusted p=1.000)

Present (grooming)	43	0	44	87	χ^2=13.80, df=2, p-value=0.001 (adjusted p=0.009)
Present (genitals forward)	48	8	37	93	χ^2=3.90, df=2, p-value=0.14 (adjusted p=1.000)
TOTAL	**172**	**58**	**185**		

*Gestures that are included in this analysis, but not in the previous analyses, because they achieve an ASO ≥5 times in a sequence but not singly.

Four gesture types were suitable for Chi-square analysis, comparing the distribution of positions (first, middle, last) for each gesture type to the distribution of positions across all gesture types. Of these, only one gesture type, *Present (grooming)*, had a significantly different distribution, possibly owing to the fact that it never occurred in the middle position. I did not analyse gesture types that were observed <10 times, but *did* perform Fisher's exact test on those that were observed >10 times but not enough times for a Chi-square test. Of the 5 gesture types analysed with a Fisher's exact test, one (*Arm swing*) was significantly different, and one (*Present (climb on)*) was tending towards significance. Of the 9 gesture types that I analysed, only 2 had a significantly different distribution of positions to the average distribution.

To answer the question "are certain gesture types more likely to appear at a specific position in a sequence?": no, most gesture types (7/9) appear in a similar distribution across positions to the average distribution of all gestures across all positions. I already found that there is no difference of meaning for a gesture type used singly or in sequence, and now there is no difference in the position of a gesture type in the sequence. The next question is whether the meaning of each gesture type is affected by the position in which it occurs in a gesture sequence.

5.3.4 Does the position of a gesture in a sequence affect the meaning?

I began with the 9 gesture types for which there had been adequate data for Chi-square and Fisher's exact tests in the previous section, and calculated the proportion of instances for which a gesture in each position achieved each ASO. Like in the analysis comparing single gestures and sequences of gestures, I created a proportional stacked histogram to qualitatively examine the data (Figure 5.3). Most gesture types appear to have a similar profile for all three positions. I then assessed whether the primary ASO was shared for all three positions (first, middle, last): 4 gesture types (*Big Loud Scratch*, *Present (grooming)*, *Directed push*, and *Present (climb on)*) shared the primary ASO across all positions; 4 gesture types (*Touch other, Arm swing, Present (genitals forward)*, and *Rocking*) shared the primary ASO in 2 positions; and one gesture type (*Arm raise*) did not share a primary ASO in any position (Table 5.5). All gesture types, except *Rocking,* shared all ASOs across positions. *Rocking* shared "Initiate copulation" across all positions, but "Initiate GG-rubbing" was only achieved in the first and last position.

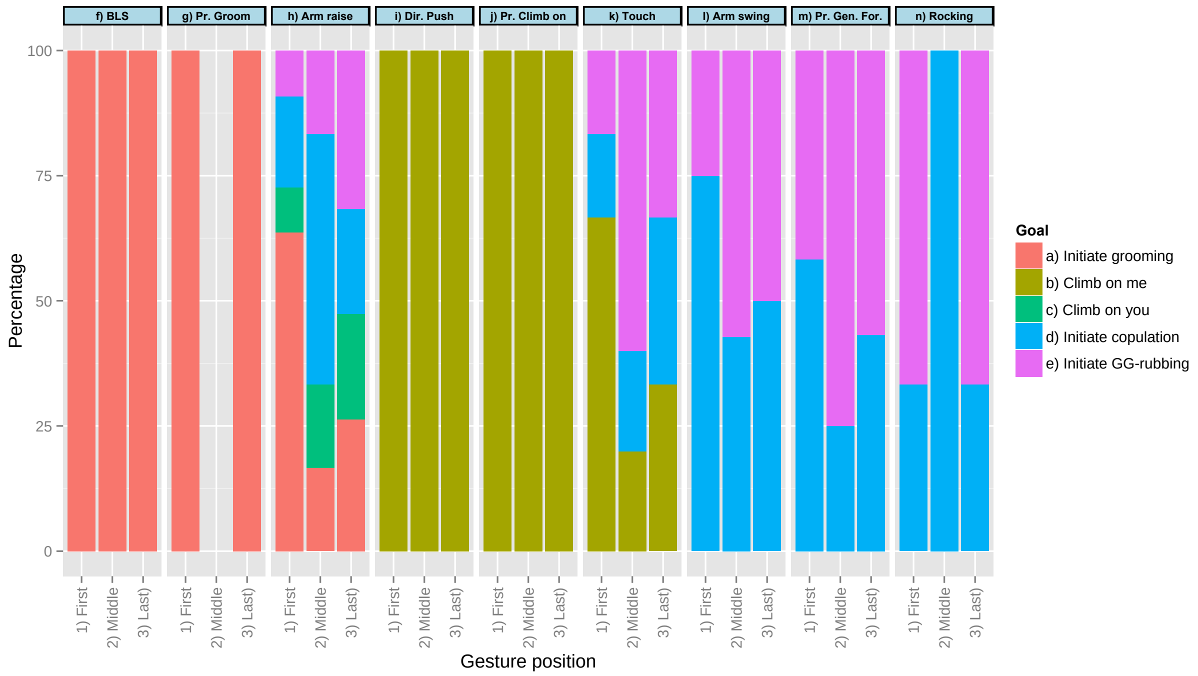


Figure 5.3. Proportional stacked histogram showing the proportion of total instances each position (first, middle, last) for each gesture type achieved each ASO. The chart is arranged so that similar goals (ASOs) appear in adjacent colour gradients and that gesture types with similar histogram profiles appear in adjacent columns.

Table 5.5. Table showing gesture types (arranged according to similar histogram profile in Figure 5.3); the primary ASO achieved in each position (first, middle, last); whether the primary ASO was shared by all gesture types ("Yes" or "No") or by 2 of the gesture types ("Part"); and the number of total ASOs across the gesture types that were shared.

Gesture	**Primary ASO - First**	**Primary ASO - Middle**	**Primary ASO - Last**	**Shared Primary**	**Shared ASOs**
Big loud scratch	Initiate grooming	Initiate grooming	Initiate grooming	Yes	1/1
Present (grooming)	Initiate grooming	-	Initiate grooming	Yes	1/1
Arm raise	Initiate grooming	Initiate copulation	Initiate GG-rubbing	No	4/4
Directed push	Climb on me	Climb on me	Climb on me	Yes	1/1
Present (climb on)	Climb on me	Climb on me	Climb on me	Yes	1/1
Touch other	Climb on me	Climb on me & Initiate copulation & Initiate GG-rubbing	Initiate GG-rubbing	Part	3/3
Arm swing	Initiate	Initiate GG-	Initiate	Part	2/2

	copulation	rubbing	copulation & Initiate GG-rubbing		
Present (genitals forward)	Initiate copulation	Initiate GG-rubbing	Initiate GG-rubbing	Part	2/2
Rocking	Initiate GG-rubbing	Initiate copulation	Initiate GG-rubbing	Part	1/2

Big loud scratch, Present (Grooming), Directed Push, and *Present (climb on)*, all achieve only one identical ASO for each position, making statistical analysis unnecessary. For the remaining 5 gesture types, the counts for each cell are too low for Chi-square analysis. I have therefore performed m x n Fisher's exact test (Freeman & Halton, 1951; Mehta & Patel, 1983), but would like to acknowledge that these results should be approached with caution due to low number of observations (Table 5.6). None of the 9 gesture types, those that are 100% identical and those that were tested, had a significantly different distribution of ASOs depending on the position in which the gesture occurred.

To answer the question "does the position of a gesture in a sequence affect the meaning?": no, all gesture types (9/9) had a similar distribution of ASOs in each position. All in all, gestures used singly versus in sequences do not have different meanings, they do not occur in a distribution of positions different from the average distribution, and their position in the sequence does not affect their meaning.

Table 5.6. Table showing the gesture type (arranged according to similar histogram profile); whether or not the gesture type had the same distribution of ASOs for all positions (first, middle, last); and results for Fisher's exact test.

Gesture Type	**Same dist.?**	**Results**
Arm raise	Yes	Fisher's exact test, p=0.34 (3x4 table)
Touch other	Yes	Fisher's exact test, p=0.57 (3x3 table)

Arm swing	Yes	Fisher's exact test, p=0.70 (3x2 table)
Present (genitals forward)	Yes	Fisher's exact test, p=0.14 (3x2 table)
Rocking	Yes	Fisher’s exact test, p=0.14 (3x2 table)

5.4 Results – Context

5.4.1 Can behavioural context explain the ambiguity of gesture meanings?

My evidence all supports the hypothesis that bonobo gestural communication does not use sequence-order syntax, at least not in the sense that sequences of gestures have different meanings depending on the position of each gesture type. Here, I examine whether the “behavioural context”, defined as the behaviour of an individual immediately prior to gesturing, predicts the ASO. To look at behavioural context, I started with all gesture instances (single and in sequences together) that achieved an ASO. Then I limited to ASOs that occur ≥5 times for a given gesture type, to maintain consistency with the previous syntax analysis. I calculated the proportion of instances for achieving each ASO by the total number of instances for that gesture type (Table 5.7). Fifteen gesture types achieved one ASO in 100% of instances. Analysis will continue with the remaining 13 gesture types, which have <1.00 proportion for each ASO.

Table 5.7. All gesture types that achieve at least one ASO ≥5 times, arranged by decreasing proportion achieved by the primary ASO; ASOs achieved by each gesture type in decreasing proportion; number of instances that each ASO is achieved; and the proportion of instances for each ASO by the total instances of all ASOs for that gesture type. Gesture types above the double line achieve one ASO in 100% of instances, and those below the line will be included in context analysis.

Gesture	ASO	# Instances	Proportion
Present (grooming)	Initiate grooming	1065	1.00
Big Loud Scratch	Initiate grooming	68	1.00
Directed push	Climb on me	46	1.00
Present (climb on)	Climb on me	43	1.00
Mouth stroke	Acquire object/food	39	1.00
Dangle	Initiate GG-rubbing	18	1.00
Embrace	Contact	11	1.00
Beckon	Climb on me	8	1.00
Hand fling	Move away	8	1.00
Leg flap	Initiate copulation	8	1.00
Bipedal rocking	Initiate GG-rubbing	7	1.00
Push	Move away	7	1.00
Hip thrust	Initiate copulation	5	1.00
Leg swing	Initiate copulation	5	1.00
Stroking	Initiate GG-rubbing	5	1.00
Arm up	Contact	16	0.76
	Climb on me	5	0.24
Arm swing	Initiate copulation	12	0.68
	Initiate GG-rubbing	12	0.39
	Climb on me	7	0.23
Present (genitals forward)	Initiate GG-rubbing	308	0.64
	Initiate copulation	172	0.36
Bipedal stance	Initiate GG-rubbing	16	0.62
	Initiate copulation	10	0.38
Hand on	Contact	8	0.62
	Initiate grooming	5	0.38
Object shake	Initiate GG-rubbing	9	0.60
	Initiate copulation	6	0.40
Rocking	Initiate GG-rubbing	17	0.59
	Initiate copulation	12	0.41
Present (genitals backward)	Initiate copulation	15	0.58
	Mount me	11	0.42
Grab-pull	Follow me	57	0.55
	Climb on me	8	0.08
	Move closer	6	0.06
Reach	Climb on me	18	0.49
	Climb on you	12	0.32
	Acquire object/food	7	0.19

Grab	Climb on me	10	0.34
	Reposition	8	0.28
	Stop behaviour	6	0.21
	Initiate grooming	5	0.17
Touch other	Climb on - me	19	0.32
	Initiate GG-rubbing	10	0.17
	Initiate grooming	7	0.12
	Move away	7	0.12
	Initiate copulation	6	0.10
	Reposition	5	0.08
	Stop behaviour	5	0.08
Arm raise	Initiate grooming	23	0.31
	Climb on you	18	0.24
	Initiate copulation	18	0.24
	Initiate GG-rubbing	16	0.21

For the 13 gesture types that had more than one ASO, I then cut down the dataset to exclude any ASO seen for a context <5 times. This eliminated *Hand on* from analysis, but left 12 gesture types. I then created a proportional stacked histogram of the ASOs achieved by these 12 gesture types (Figure 5.4). With the stronger criteria of requiring any one context to achieve any one ASO ≥5 times, *Arm up* achieved the ASO “Contact” in 100% of instances (for the behavioural context “Affiliating”), and was therefore excluded from future analyses.

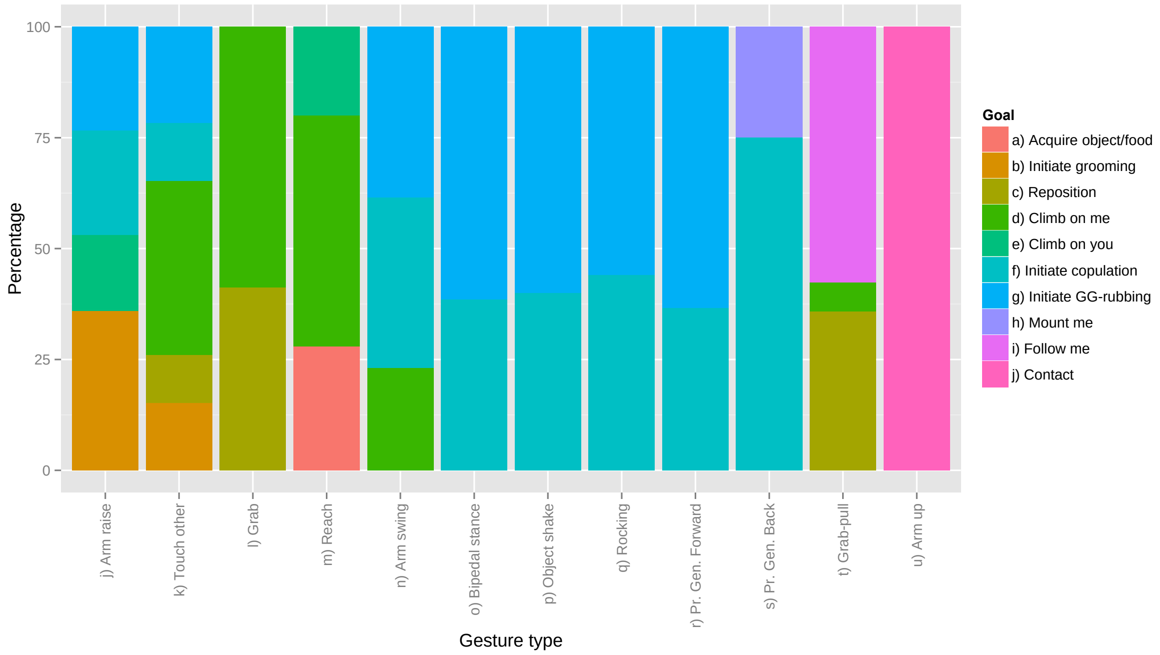


Figure 5.4. Proportional stacked histogram of ASOs achieved by each gesture type. ASOs are arranged in a colour gradient with similar ASOs adjacent to one another, and gesture types are likewise arranged adjacent to gestures with similar profiles.

I then took the gesture types split by behavioural context, which is the behaviour of the signaller immediately prior to gesturing. I used similar categories of behaviour as for the focal individual sampling (see Appendix 1). I created a proportional stacked histogram of ASOs achieved in each context by each gesture type (Figure 5.5). Three gesture types, *Bipedal stance, Object Shake*, and *Rocking*, only occurred in a sexual context and so are not shown on the histogram (see Figure 5.4 for proportions). The meaning of *Grab* and *Present (genitals backward)* became completely disambiguated when split by context (*Grab* achieved “Reposition” in the Grooming context and “Climb on me” in the Travelling context, *Present (genitals backward)* achieved “Mount me” in the Agonistic context and “Initiate copulation” in the Sexual context); *Arm-raise* was disambiguated in 2/3 contexts (achieving “Initiate grooming” in the Grooming context and “Climb on you” in the Vocalisation context);

Reach, Arm swing and *Grab-pull* in 1/2 contexts (*Reach* achieved “Acquire food” in the Feeding context, and *Arm swing* and *Grab-pull* achieved “Climb on me” in the Travelling context); and *Touch other* and *Present (genitals forward)* in 1/3 contexts (*Touch other* achieved “Climb on me” in the Travelling context, and *Present (genitals forward)* achieved “Initiate GG-rubbing” in the Agonistic context). One noticeable effect is that in all gesture types occurring in a sexual context (except *Present (genitals backward)*), the ASO can be used to initiate both copulation and GG-rubbing. It is therefore unsurprising that *Present (genitals backward)* is the exception as it is not physically conducive to GG-rubbing.

For all gesture types occurring in multiple contexts, I performed Fisher’s exact tests of ASO by Context (Table 5.8). All gesture types had significantly different distributions of ASOs compared across contexts.

To answer the question “can behavioural context help to explain the ambiguity of gesture meanings?”: yes, all gesture types (8/8) became disambiguated in one or more contexts – that is, they achieved only one ASO in that context. This supports the hypothesis that gestures achieve different ASOs in different behavioural contexts; the behaviour of the signaller immediately prior to the gesture provides additional information so that the ASO achieved by the gesture differs depending on the behavioural context. The remaining ambiguity is largely for gestures that achieve “Initiate copulation” and “Initiate GG-rubbing”, and so the *interpersonal* context may also have some bearing upon the ASO.

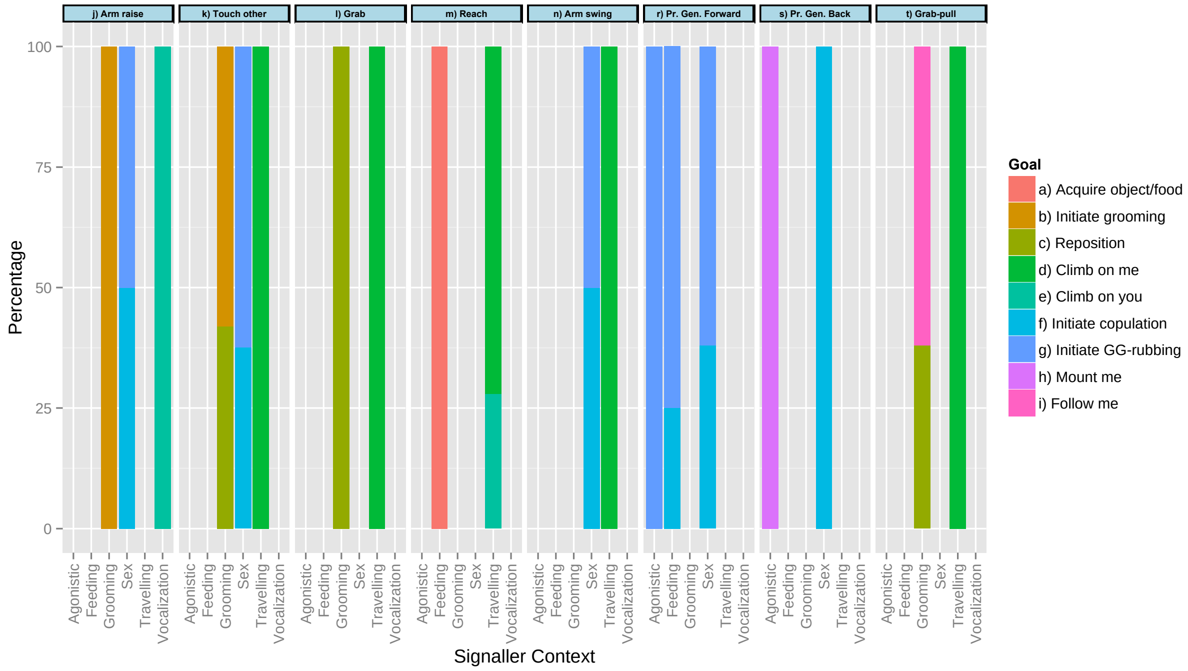


Figure 5.5. Proportional stacked histogram showing the proportion of instances that each ASO is achieved in each context for each gesture type. ASOs are arranged in a colour gradient with similar ASOs adjacent to one another, and gesture types are arranged adjacent to gestures that had similar profiles in Figure 5.4.

Table 5.8. Gesture types divided by context divided by ASO, giving the proportion of instances for which each ASO is achieved in each context for that gesture type. In the right column, the results of Fisher's exact test comparing the distribution of ASOs across contexts for each gesture type.

Gesture	Context	Goal	Proportion	Test Distribution
Arm raise	Grooming	Initiate grooming	1	Fisher's exact test, p<0.0001 (3x4 table)
	Sex	Initiate copulation	0.5	
		Initiate GG-rubbing	0.5	
	Vocalization	Climb on you	1	
Touch other	Grooming	Reposition	0.42	Fisher's exact test, p<0.0001 (3x5 table)
		Initiate grooming	0.58	
	Sex	Initiate copulation	0.38	
		Initiate GG-rubbing	0.63	
	Travelling	Climb on me	1	
Grab	Grooming	Reposition	1	Fisher's exact test, p<0.0001 (2x2 table)
	Travelling	Climb on me	1	
Reach	Feeding	Acquire object/food	1	Fisher's exact test, p<0.0001 (2x3 table)
	Travelling	Climb on you	0.28	
		Climb on me	0.72	

Arm swing	Sex	Initiate copulation	0.5	Fisher's exact test, p<0.0001 (2x3 table)
		Initiate GG-rubbing	0.5	
	Travelling	Climb on me	1	
Bipedal Stance	Sex	Initiate copulation	0.38	-
		Initiate GG-rubbing	0.62	
Object shake	Sex	Initiate copulation	0.4	-
		Initiate GG-rubbing	0.6	
Rocking	Sex	Initiate copulation	0.44	-
		Initiate GG-rubbing	0.56	
Present (genitals forward)	Agonistic	Initiate GG-rubbing	1	Fisher’s exact test, p=0.047 (3x2 table)
	Feeding	Initiate copulation	0.25	
		Initiate GG-rubbing	0.75	
	Sex	Initiate copulation	0.38	
		Initiate GG-rubbing	0.62	
Present (genitals backward)	Agonistic	Mount me	1	Fisher's exact test, p<0.0001 (2x2 table)
	Sex	Initiate copulation	1	
Grab-pull	Grooming	Reposition	0.38	Fisher's exact test, p<0.0001 (2x3 table)
		Follow me	0.62	
	Travelling	Climb on me	1	

5.4.2 Does interpersonal context further disambiguate gesture meaning?

To determine whether interpersonal context, specifically the age and sex of signaller and recipient, affects the ASO, I analysed gestures where the behavioural context failed to disambiguate meaning. Seven gesture types, *Arm raise, Arm swing, Bipedal Stance, Object Shake, Present (genitals forward), Rocking,* and *Touch other,* achieved both “Initiate copulation” and “Initiate GG-rubbing” in a sexual context. *Reach* achieved both “Climb on me” and “Climb on you” in a travelling context. Here I took these 5 gesture types across all contexts (except “Play” and “Unknown” contexts) for the specific aforementioned ASOs. I first looked at the proportion for which they achieved the selected ASOs by creating a proportional stacked histogram (Figure 5.6).

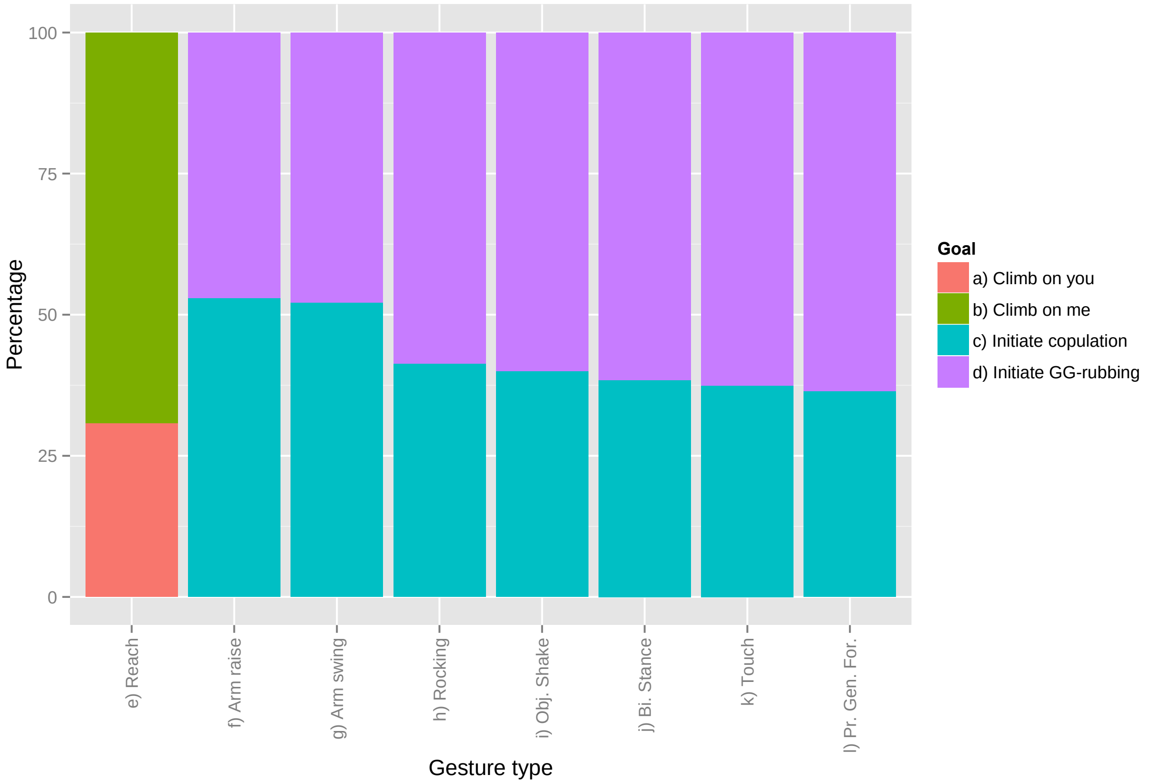


Figure 5.6. Proportional stacked histogram for which each gesture type achieves the selected ASOs. ASOs are arranged on a colour gradient adjacent to similar ASOs, and gesture types are arranged to be adjacent to gesture types with similar profiles.

For the sexual ASOs, I then categorised the sex of both recipient and signaller as *Female-Male* or *Female-Female*, ignoring the direction of the gesture, i.e. male to female or female to male. For the "Climb on" ASOs, I categorised the age *and* direction of signaller and recipient as *Adult* → *Young* or *Young* → *Adult*. I required that each age or sex category achieve an ASO at least 5 times for inclusion in analysis. Splitting into age and sex categories completely disambiguated the ASOs for almost all gesture types (Table 5.9). The only gesture type that is not totally disambiguated is *Present (genitals forward*), which for Female-Male achieves "Initiate copulation" 97% of the time and "Initiate GG-rubbing" only 3% of the time. Upon closer examination, all of the female-male GG-rubbing instances are between young individuals and adults not between sexually mature individuals. Even so, the distribution of ASOs for *Present (genitals* *forward)* between sex categories is significantly different (χ^2=443.67, df=1, p-value<0.0001). Finally, I created a proportional stacked histogram to visually present my results (Figure 5.7).

To answer the question "does interpersonal context further disambiguate gesture meaning?", yes, interpersonal context (the age and sex of signaller and recipient) entirely disambiguates meaning in 4/5 gesture types. The remaining ambiguous gesture type, *Present (genitals forward)*, achieved "Initiate GG-rubbing" in 100% of instances for the Female-Female context and "Initiate copulation" in 97% of instances for the Female-Male context – with the 3% to "Initiate GG-rubbing" involving sub-adult individuals. Behaviour and interpersonal context together disambiguate the meaning of bonobo gestures.

Table 5.9. Gesture type; Relationship is the interpersonal context, split by age or sex relationship of signaller and recipient; Goal is the ASO; Number of instances that the ASO was achieved; and the proportion of instances the ASO was achieved by the total instances that the Relationship used the Gesture Type to achieve that ASO.

Gesture Type	**Relationship**	**Goal**	**# Instances**	**Proportion**
Reach	Young → Adult	Climb on you	7	1.00
	Adult → Young	Climb on me	19	1.00
Arm raise	Female-Male	Initiate copulation	17	1.00
	Female-Female	Initiate GG-rubbing	16	1.00
Arm swing	Female-Male	Initiate copulation	12	1.00
	Female-Female	Initiate GG-rubbing	11	1.00
Rocking	Female-Male	Initiate copulation	12	1.00
	Female-Female	Initiate GG-rubbing	17	1.00
Object shake	Female-Male	Initiate copulation	6	1.00
	Female-Female	Initiate GG-rubbing	9	1.00
Bipedal stance	Female-Male	Initiate copulation	19	1.00
	Female-Female	Initiate GG-rubbing	16	1.00
Touch	Female-Male	Initiate copulation	6	1.00
	Female-Female	Initiate GG-rubbing	9	1.00
Present (genitals forward)	Female-Male	Initiate copulation	168	0.97
		Initiate GG-rubbing	5	0.03
	Female-Female	Initiate GG-rubbing	296	1.00

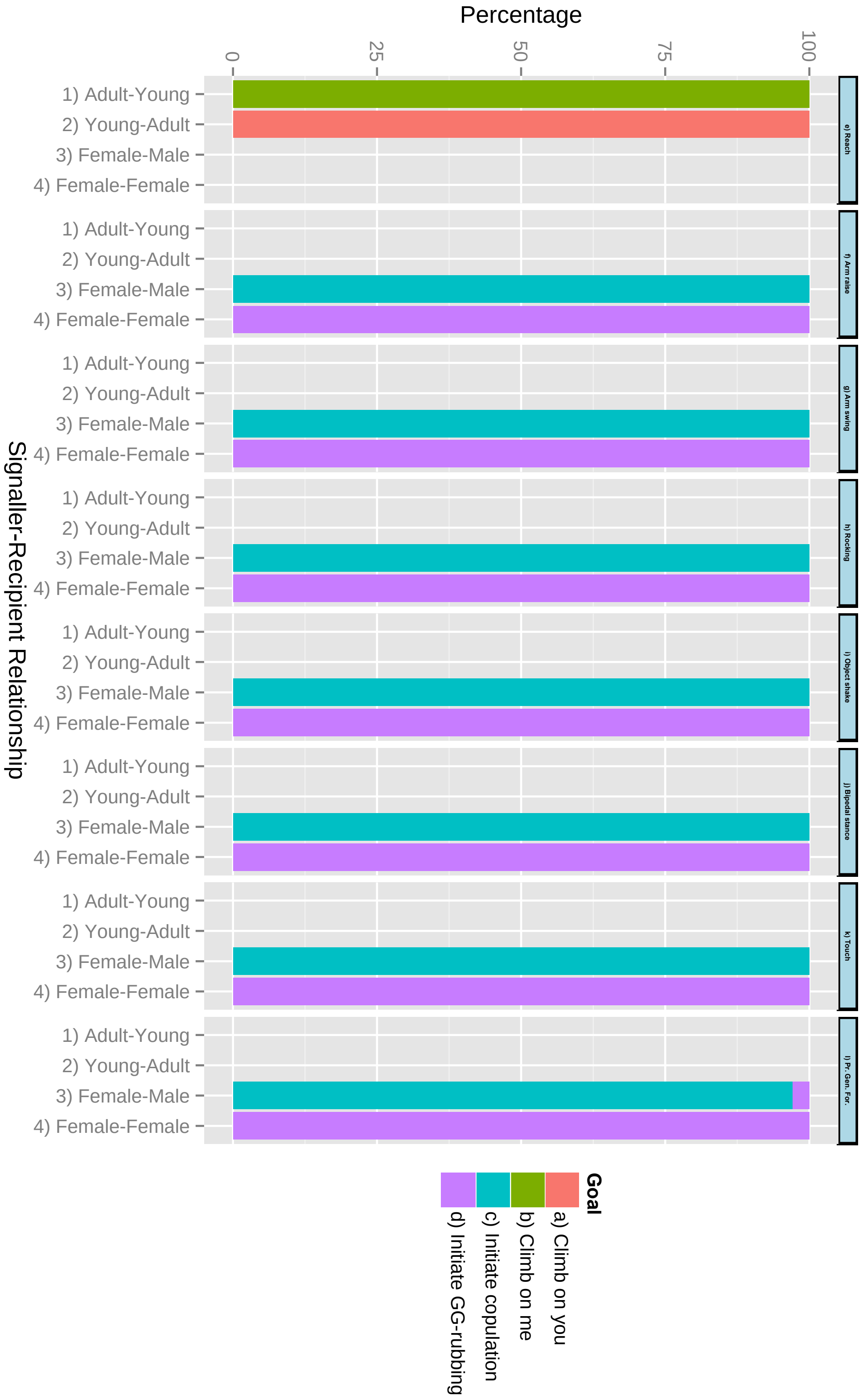


Figure 5.7. Proportional stacked histogram showing the proportion of instances for which each gesture type in each age or sex relationship category achieves each ASO. ASOs are arranged on a colour gradient adjacent to similar ASOs, and gesture types are arranged to be adjacent to gesture types that had similar profiles in Figure 5.6.

5.5 Discussion

5.5.1 Bonobo gestural communication

Bonobo gestural communication clearly does not have syntax in the complex, recursive way that human language does. But it now seems that it does not even use syntax-like meaningful signal combinations. In general, gestures in sequences do not achieve different ASOs to the same gestures used singly, and the position that gestures are in in a sequence does not affect their meaning either.

Of the gesture types suitable for analysis, 12/14 had the same primary ASO and 8/12 gesture types had the same distribution of ASOs, singly and in sequences. Both gesture types that do not share the same primary ASO, *Present (genitals forward)* and *Grab*, had significantly different distributions of ASOs for single and sequence usage. However, *Present (genitals forward)* only achieved 2 ASOs and these ASOs were both achieved by single gestures *and* in sequences. These two ASOs were "Initiate copulation" and "Initiate GG-rubbing" – both requests for sexual contact, not drastically different ASOs. *Grab*, on the other hand, did not share any ASOs – singly it achieved "Climb on me" and in sequences it achieved "Reposition" and "Stop behaviour". It seems that the difference in distribution for *Grab* singly and in sequences may be explained by context, because the meaning is different in different contexts. If I had more data for *Grab* in different contexts for single gestures and gesture sequences, perhaps the distribution would look more similar.

Four gesture types, *Big Loud Scratch, Reach, Touch other*, and *Grab-pull,* shared the same primary ASO for single gestures and in sequences, but the distribution of ASOs was different. Three of these achieve the same ASOs but in different proportions and the ASOs were fairly similar ("Groom me" and "Groom you"; "Initiate copulation" and "Initiate GG-rubbing"). The grooming ASOs are complicated, because in an exchange where two individuals are presumably requesting "Groom me", the one who "wins" has the ASO "Groom me", but so does the other who (in my opinion) didn't get what they actually wanted. Or perhaps I, as the observer, was misinterpreting the ASO and the real desired goal was simply to "Initiate grooming" regardless of who groomed whom. I therefore decided to combine those ASOs into "Initiate grooming", which I have to do anyway for my comparison with chimpanzees in the next chapter. With these ASOs combined, *Big Loud Scratch* and *Present (grooming)* now have an identical distribution (100%) for both single and sequence use.

I then wanted to see if the position of a gesture in a sequence affected its meaning. First, I looked at whether gestures were more likely to occur in a certain position in a sequence. I tested whether the distribution for each gesture type in all positions was different from the distribution of positions across all gesture types, and found that only 2/9 gesture types differed significantly, with *Arm swing* being found more often in the middle position, and *Present (grooming)* never being found in the middle position. Then, I found that the position of a gesture in a sequence did not affect the meaning; of 9 gesture types, 4 had an identical (100%) ASO for first, middle, and last positions, and the remaining 5 did not have a significantly different distribution of ASOs depending on the position in which the gesture occurred. Sequence does not disambiguate gesture meaning as I had hoped it would. Although bonobos may attend to call sequences (Clay & Zuberbühler, 2009), they do not seem to attend to the order of gesture sequences.

Behavioural context, defined as the behaviour in which the signaller was engaged immediately before gesturing, almost entirely disambiguates the meaning of bonobo gestures. The remaining ambiguity is then explained by interpersonal context – whether it's a female-female dyad or female-male dyad, or whether it's an adult → young or young → adult (Table 5.10). After that, *Touch other* and *Grab-pull* in the grooming context are the only ambiguous ASOs. Perhaps here, important tactile information is missing – how hard is the pressure being applied? Is the pressure being directed? I cannot deduce these things from video and it is possible that this missing information on my part is obvious and important for the bonobos. Overall, bonobos seem able to retrieve enough information from behavioural and interpersonal contexts to accurately interpret ambiguous gestures.

Table 5.10. These gesture types achieve these ASOs in this specific context.

Gesture Type	ASO	Behavioural Context	Interpersonal Context
Arm raise	Climb on you	Vocalization	-
	Initiate copulation	Sexual	Female-Male
	Initiate GG-rubbing		Female-Female
	Initiate grooming	Grooming	-
Arm swing	Climb on me	Travelling	-
	Initiate copulation	Sexual	Female-Male
	Initiate GG-rubbing		Female-Female
Bipedal Stance	Initiate copulation	Sexual	Female-Male
	Initiate GG-rubbing		Female-Female
Grab	Climb on me	Travelling	-
	Initiate grooming	Grooming	-
Grab-pull	Climb on me	Travelling	-
	Follow me (62%)	Grooming	-
	Reposition (38%)		-

Object Shake	Initiate copulation	Sexual	Female-Male
	Initiate GG-rubbing		Female-Female
Present (genitals backward)	Initiate copulation	Sexual	-
	Mount me	Agonistic	-
Present (genitals forward)	Initiate copulation (97%)	Sexual, Feeding	Female-Male
	Initiate GG-rubbing (3%)		
	Initiate GG-rubbing		Female-Female
Reach	Acquire object/food	Feeding	
	Climb on me	Travelling	Adult → Young
	Climb on you		Young → Adult
Rocking	Initiate copulation	Sexual	Female-Male
	Initiate GG-rubbing		Female-Female
Touch other	Climb on me	Travelling	
	Initiate copulation	Sexual	Female-Male
	Initiate GG-rubbing		Female-Female
	Initiate grooming (58%)	Grooming	-
	Reposition (42%)		

In the past, researchers have looked at the context in which a gesture occurs as a way of looking at meaning, and then saying that the meaning is flexible because it occurs in multiple contexts. My findings show that context can *not* be used as a proxy for meaning, because the meaning of a signal is affected by the context. It would be circular and confounding to define the meaning by something that changes it. It is invaluable to still look at context, but to look at the interaction of context and meaning rather than define one by the other.

5.5.2 The bigger picture

In their study on wild chimpanzee gesture meaning, Hobaiter and Byrne also found many gesture types with loose and ambiguous meanings (Hobaiter & Byrne, 2014). I suggest that with the same analysis of syntax and context, they would find similar results to mine: that the "ambiguous" gestures actually have specific meanings in specific contexts. In another paper looking at the use of gesture sequences, they did not look at specific meanings, but rather at the success of gesturing singly and in sequences (Hobaiter & Byrne, 2011a). Younger individuals used sequences more frequently than older individuals, as though sequences are used for throwing everything out there and figuring out what works. Then as individuals get older, they work out which gestures are most successful and use them singly. There is no evidence that the young chimpanzees alter the meaning of gestures by changing their position in sequences.

In future, there are other syntactic devices that we should look at. Syntax in gestural communication may possibly be found in modifiers such as those employed by sign languages: affixes, directionality, intensity, amplitude, and facial expressions (Aronoff et al., 2005; E. Cohen et al., 1977). No study on great ape gestural communication has yet examined such features. Future studies should look for these modifiers by noting the direction of the gesture relative to the recipient, the force with which the gesture is executed, the size of the gesture, and whether the gesture is accompanied by facial expressions. The possibility that bonobos use affixes is of particular interest: if they do, an affix would look like a gesture type that, when applied to other gesture types, always modifies the meaning in a similar way (Aronoff et al., 2005).

In the next chapter, I compare the gestural repertoire and meanings of the bonobo to that of the chimpanzee, but I do not systematically look at context. However, if chimpanzee gestural communication undergoes the same effect of context on meaning, then it may help to explain potential interspecies differences. There are striking differences in social behaviour between the two species, such as high frequency of bonobo GG-rubbing and centrality of females to the group, that may impact upon the ASOs that we observe for each species. We may then address whether differences in gesture meaning come down to experiencing behavioural contexts in different proportions, rather than differences in underlying gesture meanings.

That context affects meaning in bonobo gestures is not so different from how context affects human language. Humans attend to our shared context when we are talking to one another, and can infer the meaning of polysemous words based on that shared context. If I talk about “bark” in a dog kennel you don’t assume I’m talking about trees, and if I talk about “bark” in a logging camp you don’t assume I’m talking about dogs. Being able to recognise and act upon our shared context has been accredited to human mentalising abilities, but it seems that bonobos are also attending to one another’s behaviour and relationship when communicating. The interplay of signaller and recipient in communication not only informs us on the evolution of language, but also on cognition and the mental representation of others.

5.6 Conclusion

Most gestures used singly have the same primary ASO and same distribution of ASOs as the same gesture used in a sequence (10/12, 8/12 respectively). When looking at the position of a gesture in a sequence (first, anywhere in the middle, last), only 2/9 gesture types had a significantly different distribution from the average distribution of position across all gesture types. Moreover, all of the gestures had the same meaning regardless of position in the sequence. It seems that bonobos do not attend to sequence when deciphering gesture meaning. However, a combination of behavioural and interpersonal context completely disambiguates gesture meaning – gestures mean different things in different behavioural contexts and between different dyadic compositions. Bonobos must attend to contextual information (behaviour and interpersonal relationship) when they are deciphering the meaning of a gesture. In the next chapter I will look at how the findings in these last three chapters compare to findings for wild chimpanzees.

Chapter 6 – Comparing bonobo and chimpanzee gestures

6.1 Background

In the last three chapters, I described the bonobo gestural repertoire, the meanings of the gestures, and the way that context disambiguates meanings. In this chapter, I take those results for wild bonobos and compare them to published findings and raw data for wild chimpanzees, provided by Dr Catherine Hobaiter from her work at Budongo, Uganda. I will first compare the gestural repertoire, then determine whether gestures mean the same things for chimpanzees and bonobos, and finally discuss how a future comparison of context may explain some of the apparent inter-species differences.

6.1.1 Bonobo and chimpanzee geography, evolution, and physiology

Bonobos and chimpanzees are equally related to humans. The *Pan* and Hominin lineages diverged ~5 million years ago (Chen & Li, 2001), and subsequently, bonobos and chimpanzees diverged ~1 million years ago (Becquet & Przeworski, 2007; Fischer et al., 2011; Won & Hey, 2005). In comparative psychology, however, the emphasis has always been put on the chimpanzee. In fairness, it was not until 1933 that bonobos were recognised as a separate species, the 'pigmy chimpanzee' (Coolidge, 1933), when they had previously been considered a sub-species (Schwarz, 1929). Until then, bonobos and chimpanzees had been housed together and studied together in zoos, so that some early descriptions of chimpanzees may in fact be describing bonobos (de Waal, 1997).

Bonobos and chimpanzees currently live in similar habitats in Africa. Bonobos are distributed in a small area south of the Congo River, a geographic barrier that cuts them off from chimpanzees to the north (Caldecott & Miles, 2005). Chimpanzees have a wider distribution, from Senegal to Tanzania (Caldecott & Miles, 2005), and are divided into 4 subspecies: central (P. t. troglodytes) (Blumenbach, 1799), western (P. t. verus) (Schwarz, 1934), eastern (P, t. schweinfurthii) (Giglioli, 1872), and Nigeria-Cameroon (P. t. vellerosus) (Gray, 1862). Both chimpanzees and bonobos live mainly in forest habitats. The climate and habitat in the bonobo range is comparable to that of rainforest chimpanzee populations, whose behaviour is known to differ from savannah chimpanzees. Both bonobos and chimpanzees are omnivorous, with a diet consisting mainly of fruit and leaves (Hohmann, Robbins, & Boesch, 2012).

On an evolutionary timescale, the areas in which bonobos and chimpanzees range are thought to have presented different selective pressures. Bonobo-chimpanzee speciation may be the result of a bottleneck effect on a small population of chimpanzees separated by the Congo River (Eriksson, Hohmann, Boesch, & Vigilant, 2004; Thompson, 2003). For many years, primatologists thought that the formation of the Congo River had separated bonobos and chimpanzees. However, new geological information suggests that the Congo River formed much earlier than previously thought – 30 mya rather than 4mya (Colyn, Gautier-Hion, & Verheyen, 1991; Thompson, 2003; Takemoto et al., 2015). Our best estimates show the chimpanzee-bonobo divergence at roughly 1 MYA (Becquet & Przeworski, 2007; Fischer et al., 2011; Won & Hey, 2005). The current best explanation for speciation is that a small founder population of the bonobo-chimpanzee LCA crossed the Congo River during a period of low water levels (Takemoto et al, 2015).

Overall, chimpanzees seem to be more genetically diverse than bonobos, which is unsurprising given the founder effect. Genetically, chimpanzees have retained more polymorphisms, making bonobos by comparison look highly monophyletic (Fischer et al., 2011). Chimpanzees, consistent with their more expansive distribution, have a much wider gene pool, and bonobos fall within the genetic variation of the chimpanzee (Fischer et al., 2011). That being said, bonobos *do* exhibit genetic variability between populations (Kawamoto et al., 2013); indeed, bonobos actually have higher diversity estimates than humans and eastern chimpanzees, but similar to western and central chimpanzees (Eriksson et al., 2004). Opinion is divided over whether bonobos are derived from a chimpanzee-like ancestor that became isolated and changed dramatically (Furuichi, 2011; Hare, Wobber, & Wrangham, 2012), or conversely bonobos are most like our last common ancestor, and chimpanzees are the ones that have undergone harsh selection pressures (de Waal, 2009). Only through a combination of genetic research, paleo-primatology, and geology will we solve that debate.

There are some morphological differences between the two species, but not as extreme as is often portrayed. The name ‘pigmy chimpanzee’ suggests a dwarfed version of the common chimpanzee, but bonobos are of comparable size to eastern chimpanzees: medians of 39kg for males and 31kg for females compared to 41.15 kg for males and 34.1kg for females, respectively (Caldecott & Miles, 2005; Rowe, 1996). Bonobos are somewhat more gracile, with proportionally longer and more slender limbs, and smaller teeth (Zihlman & Cramer, 1978). Bonobo infants have black hands and faces, whereas chimpanzee infants have pink skin in those areas (Kano, 1992). Bonobos retain pink lips and a small tuft of white tail into adulthood, leading some researchers to invoke paedomorphosis, suggesting that bonobos stop developing at a stage equal to adolescent chimpanzees (Hare et al., 2012).

Of most interest to cognitive researchers, bonobos have a smaller cranial capacity than chimpanzees: 350 cm^3 compared to 390 cm^3 (Zihlman & Cramer, 1978). Smaller absolute brain size might predict lower capacity for cognitive abilities (Reader & Laland, 2002), though other factors such as the relative proportions of different brain structure should also be considered (Rilling, 2014). Preliminary evidence suggests that bonobos and chimpanzees perform similarly on cognitive tasks (Herrmann, Hare, Call, & Tomasello, 2010). Bonobos may have smaller absolute brain size, but neuroimaging shows that they have more grey matter in regions of the limbic system implicated in stress and aggression control (Rilling et al., 2012). Conversely, chimpanzees have more grey matter in parietal and occipital lobe regions (Rilling et al., 2012). Both chimpanzees and bonobos have asymmetric areas analogous to Broca's and Wernicke's areas in humans (Cantalupo & Hopkins, 2001; Gannon, Holloway, Broadfield, & Braun, 1998; Hopkins et al., 1998), areas that play an important role in language production and comprehension. However, all of these differences in brain morphology have yet to be convincingly tied to differences in cognitive performance.

6.1.2 Bonobo and chimpanzee behaviour

It seems right to begin this section with a caveat acknowledging the tendency to overstate the behavioural differences between bonobos and chimpanzees. The two species are often presented as opposing models of human behaviour (de Waal, 1997), leading one landmark paper to warn against the danger of dichotomizing bonobos and chimpanzees (Stanford, 1998). It is dangerous to use one species to represent the dark side of human nature and another to represent the good. Here, I attempt to present a balanced report that does not oversell the differences, but at the same time does not ignore them completely.

There are many similarities in bonobo and chimpanzee societies. Both form fission-fusion groups, large semi-permanent living groups that fraction into smaller parties (Furuichi et al., 1998; Kano, 1980; Nishida, 1979). Males are philopatric; they stay with their natal group, while females emigrate at adolescence (Kano, 1980; Nishida, 1979; Pusey & Packer, 1987). Despite this, chimpanzee males within a group are no more genetically related than the females (Vigilant, Hofreiter, Siedel, & Boesch, 2001), and with new genetic analysis on bonobos at Wamba, the same may prove true for bonobos. For both species, females take the largest role in raising offspring, although males sometimes play with young infants and juveniles. Both groom socially; social grooming is one way to strengthen social ties, for chimpanzee males in particular, who sit in chains or groups grooming one another (Foster et al., 2009; Nakamura, 2003; Sakamaki, 2013). Females of both species have genital swellings that advertise fertility, although the co-occurrence of ovulation and the maximal swelling period in female bonobos is unusually variable (Douglas, Hohmann, Murtagh, Thiessen-Bock, & Deschner, 2016; Wallis, 1992). Finally, their life span in the wild is roughly similar at 50 years for chimpanzees (but with a life expectancy at birth of 15 years) and 52.5 years for bonobos (Caldecott & Miles, 2005; Furuichi et al., 1998; Hill et al., 2001).

Despite these similarities, the social positions of adult females and adult males within the group structure differs between the two species. Female bonobos occupy higher social positions than do female chimpanzees. Chimpanzee society is male-dominated: all males outrank all females (the highest ranking female is lower than the lowest ranking male) (Nishida, 1979). The attendance ratio of males within a party is higher than females, possibly because lower-ranking individuals, i.e. females, range peripherally to avoid stressful, aggressive interactions (Wrangham, 1979, 2000). The male hierarchy is maintained by intrasexual competition through aggressive interactions and coalition formation (de Waal, 1982; Nishida, 1983), but also by reconciliation and social grooming (de Waal, 1982; Nishida, 1983). Unlike chimpanzees, male bonobos are not known to form coalitions with other males (Hashimoto et al., 2008; Tokuyama & Furuichi, 2016). The rank of a bonobo male is influenced by the rank of his mother, and having his mother in the group allows a male to range more centrally (Furuichi, 1997; Surbeck et al., 2011). But like chimpanzees, it is possible to calculate the rank of male bonobos by looking at the outcome of aggressive interactions, whereas this method does not reveal rank order in female bonobos.

Bonobo society is female-centred, and has been described as egalitarian. Bonobo parties have much higher female attendance ratios than chimpanzees; indeed the attendance ratio of bonobo females in a party is higher than males (Furuichi, 2009; Furuichi et al., 2008; Mulavwa et al., 2008). Female bonobos thus form the central core of the group, while males range on the peripheries (Kitamura, 1983). Females are usually the highest ranking individuals, and the hierarchy is formed of interspersed males and females. Determining the female hierarchy is difficult, because aggression among females is rare. Instead, a female's rank is instead determined by factors like feeding priority, leadership in travelling, and grooming reciprocity. But female-male aggression does occur, and in instances of agonistic interactions for male-female dyads at Wamba, females were equal to males, winning half of male-female agonistic interactions (Furuichi, 1997). Remarkably, when female bonobos form female-female coalitions against one or more males, they win in 100% of cases (Tokuyama & Furuichi, 2016). Female bonobo coalition formation may therefore be important in maintaining the centrality of females in a group.

Many researchers have hypothesised that bonobo sexual behaviour is key for maintaining the female social position. While bonobo and chimpanzee females both immigrate at adolescence and therefore enter into a group of unrelated individuals, bonobo females form social bonds with females in their new group by using (among other pro-social behaviour) genito-genital rubbing (GG-rubbing) (Furuichi, 2011; Idani, 1991). To GG-rub, two females embrace ventro-ventrally and wiggle, rubbing their genitals together. GG-rubbing, as well as maintaining social bonds, seems to be important for tension release: when female bonobos reach a feeding patch that could potentially be monopolised by an individual, and tensions are high, they GG-rub and then begin feeding next to one another (Furuichi, 2011; Hohmann & Fruth, 2000). If GG-rubbing is an important social bonding mechanism, one might expect coalition formation to be based around females who frequently GG-rub together. However, new evidence on coalition formation in female bonobos shows that factors such as GG-rubbing partners, grooming partners, and proximity, do *not* predict who forms coalitions with whom – that is entirely predicted by age, with older females supporting younger females (Tokuyama & Furuichi, 2016). Social bonding may therefore be a result of the centrality of females, who once they find themselves living and competing more closely then benefit from activities that promote tolerance.

Heterosexual copulation is not dissimilar between the two species, despite pop-culture claims of bonobo sexuality. When females approach the fertile phase of their menstrual cycle, their genital area swells and becomes pink, and ovulation occurs towards the end of maximal swelling (Wallis, 1992). Bonobo females have a prolonged swelling period that is highly variable, where the maximal swelling period does not necessarily overlap with ovulation (Douglas et al., 2016). Chimpanzee females are in the swelling phase for 40% of their menstrual cycle and 6% of their interbirth interval, whereas female bonobos are in the swelling phase for 35% of their menstrual cycle but 27% of their interbirth interval (Furuichi & Hashimoto, 2002). This is because, although there is no difference in interbirth interval between the two species, female chimpanzees are anoestrus until their infant is 4 or 5 years old (Wrangham, 1993), while female bonobos resume their swelling cycle and become receptive around one year after giving birth (Furuichi & Hashimoto, 2002). It is thought that prolonged swelling for bonobos helps to mitigate male harassment and competition (Douglas et al., 2016; Furuichi & Hashimoto, 2002). For chimpanzees, the alpha male has preferential access to fertile females, though younger, low-ranking males still sire offspring (Wroblewski et al., 2009). This is possibly also true of bonobos, where the highest ranking male (because of his high-ranking mother) ranges more centrally and may have more mating opportunities (Furuichi, 2011; Surbeck, Mundry, & Hohmann, 2011).

Chimpanzees have three mating strategies: opportunistic, possessiveness, and consortship (Tutin, 1979). In an opportunistic setting, many males mate with the receptive female (Tutin, 1979), and sperm competition plays a vital role in conception (Anderson et al., 2007; Hasegawa & Hiraiwa-Hasegawa, 1990). Possessive males guard females and may coerce them into copulation (B. B. Smuts & Smuts, 1993; Tutin, 1979). In consortships, a male (likely, but not necessarily, low-ranking) and female leave the group and sneak-mate, avoiding competition from other males (Muller, Kahlenberg, Emery Thompson, & Wrangham, 2007; Tutin, 1979). Chimpanzee males can gain access to females through male-male competition, but also by engaging in pro-social behaviour towards the desired female (Tutin, 1979). Bonobos are not known to engage in consortships, with most mating happening in proximity to the group (Furuichi & Hashimoto, 2002). Possessiveness is not widely reported in bonobos, but anecdotally seems to occur in certain individuals, possibly as a personality difference (Heungjin Ryu, personal communication).

Finally, intergroup encounters are famously different for bonobos and for chimpanzees. Neighbouring groups of chimpanzees have hostile relationships (Mitani, Watts, & Amsler, 2010; Watts, Muller, Amsler, Mbabsi, & Mitani, 2006; Wilson & Wrangham, 2003). Encounters are male-driven, with males forming lethal border patrols that pick off and kill individual male intruders along their border with neighbouring groups (Mitani et al., 2010; Nishida, 1985; Watts et al., 2006; Wilson & Wrangham, 2003; Wrangham & Peterson, 1996; Wrangham, 1999). They kill lone individuals, but encounters between large groups are not lethal, consisting of loud auditory exchanges (Wilson & Wrangham, 2003). At both Gombe and Mahale, one group totally and systematically eradicated the neighbouring group, in what has controversially been termed “genocide” (Diamond, 2014; Goodall, 1986; Nishida, 1985). Similarly, at Ngogo, the study group has expanded its territory by killing members of neighbouring groups (Mitani et al., 2010). Bonobo intergroup encounters, on the other hand, appear to be non-fatal – there has not yet been a recorded fatality during an intergroup encounter (but note that overall observation time of bonobos has been much shorter than for chimpanzees). However, there is debate over how stressful it is for the bonobos; during encounters, there are a lot of vocalisations, and some aggressive interactions. Nevertheless, neighbouring groups do come together, and at the beginning of such encounters, the females tend to lead the encounter, going ahead, making first contact, and often GG-rubbing with females of the other group (Furuichi, 2011). At Wamba, four groups have bordering ranges, and two or more groups can encounter and range together for several days, eating in the same trees and grooming one another.

6.1.3 Bonobo and chimpanzee communication

Given that bonobos and chimpanzees are physiologically similar, they should be capable of producing the same physical gestures, but their differences in social behaviour brings to question whether they might need to use different communicative signals. In a short-term captive study, bonobos used 28 gestures and chimpanzees used 29 gestures, and of these physical gesture forms three were unique to chimpanzees and two were unique to bonobos (Pollick & de Waal, 2007). In a study on wild chimpanzees, the estimated overlap with the gorilla and orangutan repertoires was 60% and 80%, respectively, but at the time there was no comparison with the bonobo repertoire (Hobaiter & Byrne, 2011b). However, all of these studies only looked at the physical form of the gesture types, and it is possible that while the forms resemble each other the meanings do not. An important aspect of language is that a word should have roughly the same meaning for all members of a linguistic community, and so for gestures we should also examine whether the same "words" mean the same things.

Moreover, the behavioural differences between bonobos and chimpanzees are not fully represented in a captive environment. In captivity, apes are provided with food without having to forage; they don't have to travel long distances; group sizes are generally smaller than in the wild; not all individuals in a group are allowed to reproduce; and there is more time to play. Part of the reason that researchers find more gesture types in wild than captive chimpanzees is that the apes are exhibiting a wider range of behaviour for which gestures are used. And if social behaviour affects the gestures that an individual uses, one might therefore expect bonobos and chimpanzees to use some different gestures, or for some of their gestures to have different meanings.

Of course, it is possible that the repertoire overlap reported in Pollick and de Waal's captive study is exaggerated because of the level of 'lumping' gesture types (Pollick & de Waal, 2007). Opinion is still divided on how best to categorize gestures into types, so differences in reported repertoire size may be an artefact of analysis rather than true difference in communicative behaviour. Realistic estimates of repertoire size will likely come from describing gesture types by first finely splitting gesture types by physical differences, then lumping according to whether physically similar gesture types achieve the same satisfactory reaction from the recipient. I am perfectly positioned to compare my bonobo data to that of the wild chimpanzee, because I used comparable criteria for categorization.

In this chapter, I take some of my findings from the previous chapters and compare them with what is known for the chimpanzee. I first compare the gestural repertoires, i.e. the physical forms of the gesture types used, for the bonobo and the chimpanzee. I then compare the meaning for each gesture type, to determine whether the gesture types that bonobos and chimpanzees share also share the same meaning. I have yet to systematically examine context for the chimpanzee dataset, but present in the discussion a preliminary look at how context may explain the differences in chimpanzee and bonobo gesture meanings.

6.2 Specific Methods

I described my general methods in Chapter 2. The bonobo data is taken from results on the community repertoire from Chapter 3 and from the meaning of gestures in Chapter 4. Comparison with the chimpanzee gestural repertoire (the physical form of gesture types) was possible using published data (Hobaiter & Byrne, 2011b). However, to analyse meaning required using the original data, which Dr Catherine Hobaiter (CH) kindly gave me access to.

CH collected data on one community of wild chimpanzees (Sonso community) at Budongo Conservation Field Station, Uganda (1°35'–1°55'N, 31°18'– 31°42'E). CH's fieldwork ran from October 2007 to March 2008, June 2008 to January 2009, and May to August 2009, following chimpanzees daily from ~07:30 to ~16:30, with a weekly schedule of three days on, one day off, three days on, two days off. Observation time amounted to 266 days. Habituation began for the Sonso community (n=92) in 1990. At the beginning of this study, in 2007, the total sample size was 81 individuals, with 32 adults, 16 sub-adults, 15 juveniles, and 18 infants. From 2007 to 2009, there were 10 deaths (or disappearances), 6 immigrations, and 5 births. Chimpanzee age groups are divided into infant (≤4 years), juvenile (5-9 years), sub-adult (male: 10-15 years, female: 10-14 years), and adult (male: 16+ years, female: 15+ years) (Reynolds, 2005).

Like me, CH filmed social interactions using focal behaviour sampling, where the focal behaviour was whenever two or more individuals approached within 5m of each other. CH recorded video footage using a miniDV tape using a Sony Handycam (DCR-HC-55). CH also imported video footage each day, labelled it, and entered it into a clip directory in FileMaker Pro. CH coded her gestures with FileMaker Pro, using similar fields to me. For analysis here, I pulled out the following coded information: *part of bout, part of sequence, signaller, recipient, signaller age/sex/rank, recipient age/sex/rank, gesture type, check attention, response waiting, recipient response, persistence, goal*, and *goal met* (described in Chapter 2). I only analysed gestures that were used intentionally (meaning that they met the criteria for audience checking, response waiting, or persistence).

As mentioned in Chapter 2, CH acted as a second coder for inter-observer reliability for the bonobo video footage. CH coded 100 gesture instances for the following information: gesture type, audience checking, persistence, and signaller apparently satisfied. Again, the Cohen's Kappa values for these respective variables was 0.87 (almost perfect), 0.56 (moderate), 0.70 (substantial), and 0.63 (substantial) (Altman, 1991). I am therefore satisfied that any comparison between our research is comparing the same gestures with the same criteria.

6.3 Results

6.3.1 Do bonobos and chimpanzees use the same gestures?

I found 68 gesture types in wild bonobos, compared to 66 gesture types for wild chimpanzees (Hobaiter & Byrne, 2011b). However, my categorization of two gesture types was more finely split than CH's, and to be comparable with the bonobo repertoire I needed to split the chimpanzee gesture types (*Touch other* to *Touch other* and *Stroking*; and *Present (sexual)* to *Present (genitals forward)* and *Present (genitals backward)*). The resulting chimpanzee repertoire was 68 gesture types. Of the 68 bonobo gestures 60 were shared with chimpanzees: an 88% overlap (see Figure 6.1). Several gesture types not reported by Hobaiter and Byrne (*Bipedal rocking, Bipedal stance, Hip thrust, Rocking*), have since been seen in chimpanzees at Budongo, and one gesture type (*Arm up*) has been seen but not reported at Bossou, Guinea (Catherine Hobaiter, personal communication). Including these gesture types raises the total to 65 gesture types shared with chimpanzees: a 96% overlap. That leaves 3 gesture types (*Bounce, Leaf drop, and Leg flap*) as apparently bonobo exclusive gesture types. All three of these gesture types are used in a sexual context.

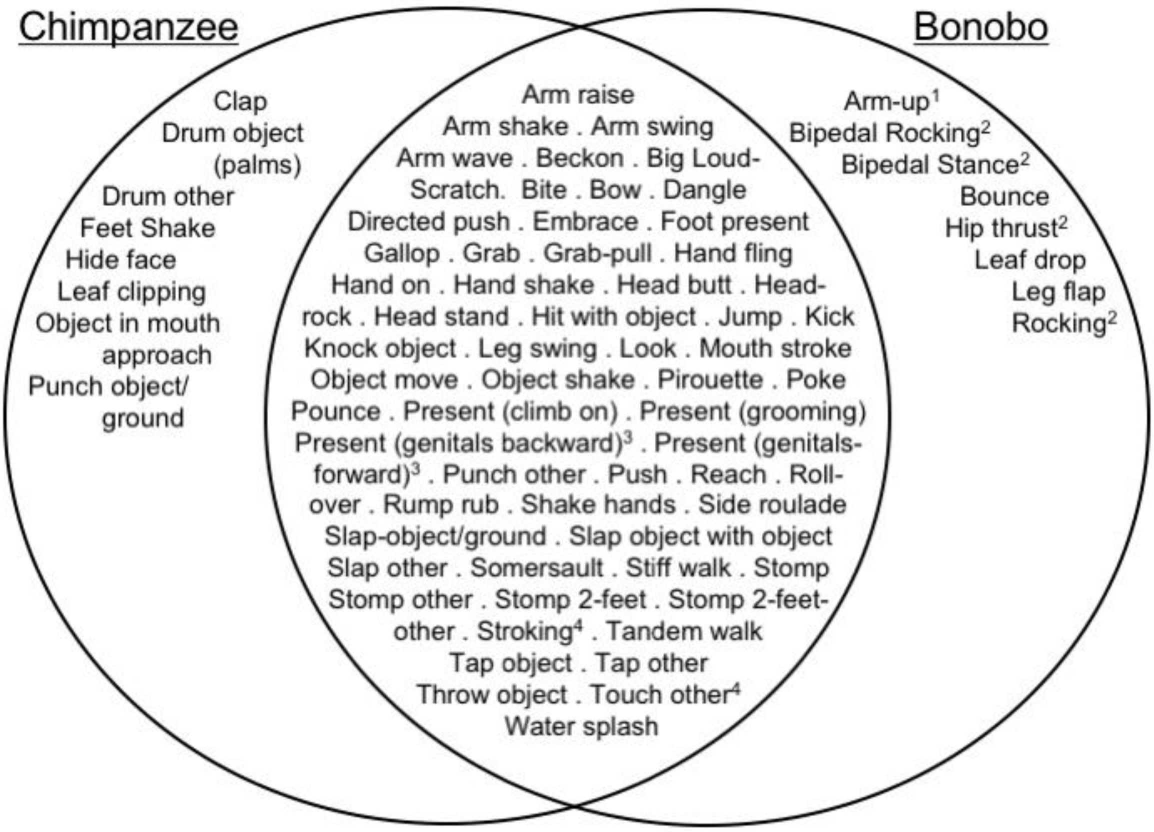


Figure 6.1. This Venn diagram shows the gesture types used by chimpanzees and bonobos, with the portion of the overlapping circles showing the gesture types that the two species share. Eighty-eight percent of the gesture types overlap.

[1] These gesture types have been seen in chimpanzees at Bossou, not reported at Budongo (Catherine Hobaiter, personal communication).

[2] These gesture types have been seen in chimpanzees at Budongo, subsequent to Hobaiter & Byrne, 2011 (Catherine Hobaiter, personal communication)

[3] These gesture types were split from *Present (sexual)* in Hobaiter & Byrne, 2011

[4] These gesture types were split from *Touch other* in Hobaiter & Byrne, 2011

6.3.2 Do bonobos and chimpanzees use the same gestures for the same ASOs?

To compare meanings in the bonobo and chimpanzee gestural repertoire, myself, Catherine Hobaiter, and Richard Byrne collaborated with James Ounsley (School of Biology, University of St Andrews) for assistance with statistical analyses. In this section, I have set up the data for analysis and James has conducted the analyses.

We compared the meanings of bonobo gestures and the meaning of chimpanzee gestures compare to randomised iterations with various levels of constraints.

First, we set up the bonobo and chimpanzee matrices for comparison, with the complete repertoire of gesture types against all possible ASOs. A “1” in this gesture matrix indicated that the gesture type had achieved the given ASO at least two times and by a minimum of two individuals, i.e. individual A uses it once, individual B uses it once. A “0” in the matrix indicated that the gesture type did not achieve that ASO for the minimum number of instances. We then matched the bonobo and chimpanzee matrices to only include gesture types that achieved any ASO in both species (n=22), and ASOs that were achieved by any gesture type in both species (m=11), giving the same matrix dimensions for both species. We defined the similarity between two gesture matrices as the sum of all matching corresponding matrix entries, be they 0 or 1. We graphically represented the similarity between the bonobo and chimpanzee matrices (Figure 6.2).

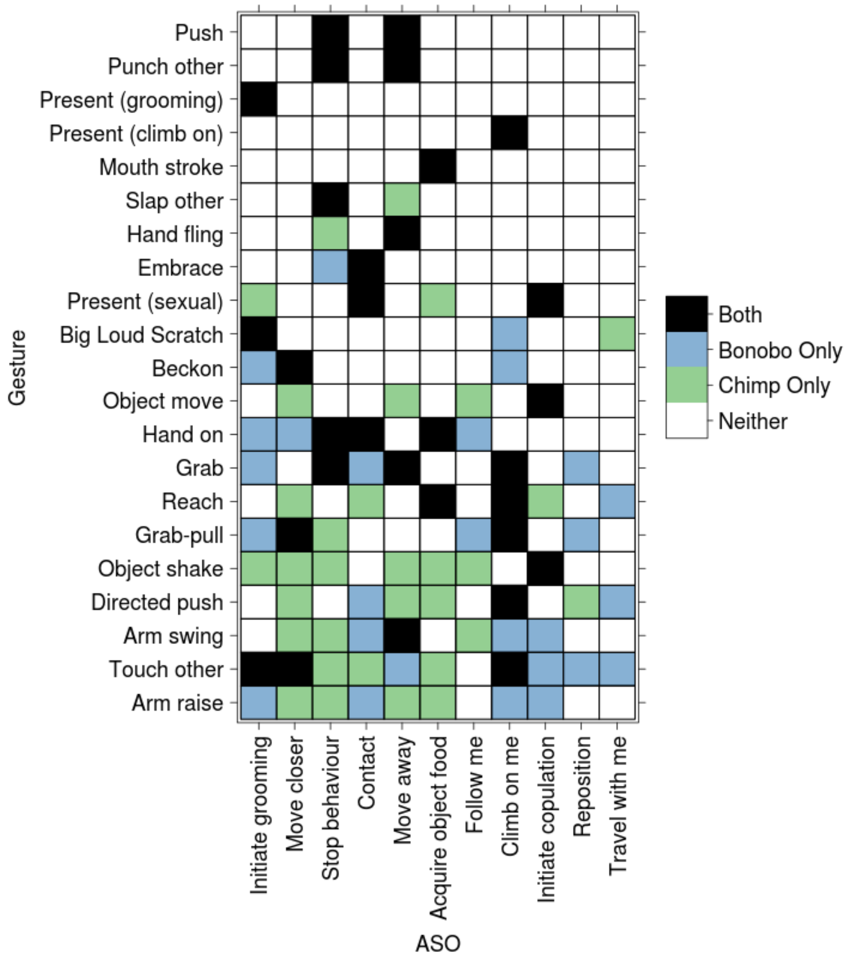


Figure 6.2. The overlap in gesture type to ASO assignment between chimpanzees and bonobos. White cells correspond to gesture-ASO assignments absent in both species, green cells correspond to gesture-ASO assignments only present in chimpanzees, blue cells correspond to gesture-ASO assignments only present in bonobos and black cells correspond to gesture-ASO assignments present in both species.

Using a randomisation procedure, we tested the null hypothesis that the similarity between the two species would be the same under a random assignment of gestures to ASOs for each species. we compared four different methods of matrix permutation: (a) no constraints (least conservative); (b) constraints on the column sums; (c) constraint on the row sums; and (d) constraint on both column and row sums (most conservative, conducted using the “tswap” algorithm in the vegan package in R). None of these models produced a pair of matrices that were more similar than the original bonobo and chimpanzee data (Figure 6.3). The similarity of the gesture matrices for the two species is greater than expected by chance assignment of gestures to ASOs, as defined by the randomisation procedure.

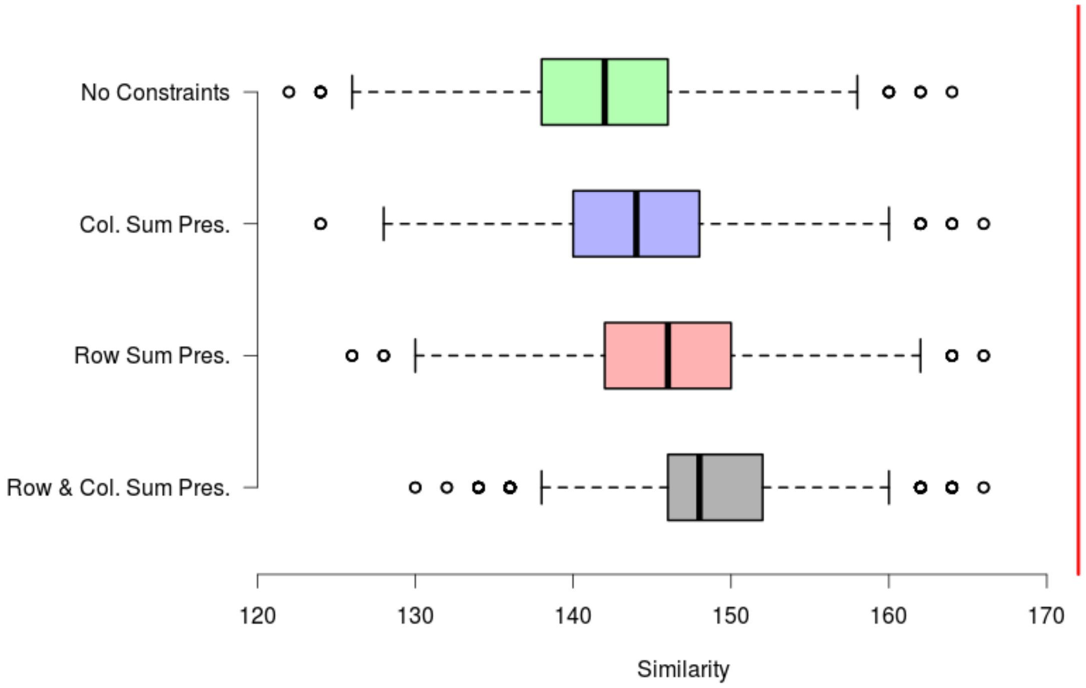


Figure 6.3. The distribution of similarities between gesture matrices generated under the randomisation procedure using four different methods. From bottom to top: Row & Column Sum Preservation, black; Row Sum Preservation, red; Column Sum Preservation, blue; No Constraints, green. The red vertical line gives the similarity of the original gesture matrices.

We showed that the bonobo and chimpanzee gestures do achieve the same ASOs, i.e. bonobo and chimpanzee gestures share the same meanings. Even compared to 10,000 randomised matrices with the strictest constraints on row *and* column sums, none of the random matrices were more similar to the actual bonobo and chimpanzee matrices than the ape matrices were to one another. This is very convincing evidence that not only do bonobos and chimpanzees share the forms of gestures, but also share their meanings.

6.3.3 Do bonobo and chimpanzee gestures share meanings in the same proportions?

Knowing that bonobo and chimpanzee gestures mean the same thing, I wanted to push it to see whether they achieve the same ASOs in the same proportions. To compare the bonobo and chimpanzee data, I required that a minimum of 3 individuals achieve an ASO a minimum of 3 times for both species. For bonobos, 51 individuals contributed data totalling 1714 gesture instances; for chimpanzees, 50 individuals contributed data totalling 1422 gesture instances. Seven ASOs provided sufficient data for comparison. I first looked at, for each ASO, how many gestures are common to bonobos and chimpanzees (Table 6.1). Only one ASO, *Follow me*, did not show any gesture types in common; the other 6 ASOs all shared 2 or more gesture types. To represent the data graphically, I created a stacked histogram of the percentage each gesture type achieved each ASO for both species (Figure 6.4).

Table 6.1. Gesture types (in alphabetical order) that each species uses to achieve each ASO, with shared gestures bold and underlined.

ASO	Gestures used by bonobos	Gestures used by chimpanzees
Acquire object/food *(2 shared/15)*	**Mouth stroke**, **Reach**	Arm raise, Arm shake, Arm swing, Dangle, Directed push, Hand on, Leg swing, **Mouth stroke**, Object move, Object shake, Present (sexual), Punch other, **Reach**, Slap object, Touch other
Climb on me *(6 shared/12)*	Arm raise, Arm swing, Arm up*, Beckon, **Directed push**, **Grab**, **Grab-pull**, **Present (climb on)**, **Reach**, **Touch other**	Big Loud Scratch, **Directed push**, Foot present, **Grab**, **Grab-pull**, **Present (climb on)**, **Reach**, **Touch other**
Contact	Arm raise, Arm up*, **Embrace**, Grab, **Hand on**, **Present**	Bite, **Embrace**, Grab-pull, **Hand on**, Pounce, **Present (sexual)**,

(3 shared/16)	**(sexual)**, Rocking*, Roll over	Reach, Rump rub, Shake hands, Tap other, Touch other
Follow me *(0 shared/22)*	Grab-pull, Hand on	Arm shake, Arm swing, Arm wave, Big Loud Scratch, Directed push, Embrace, Head rock, Jump, Knock object, Leg swing, Object move, Object shake, Present (sexual), Punch object/ground, Rump tub, Slap object, Slap object with object, Stomp, Stomp 2-feet, Throw object
Initiate copulation *(3 shared/21)*	Arm raise, Arm swing, Bipedal stance*, Dangle, Hip thrust*, Leg flap, Leg swing, **Object move**, **Object shake**, **Present (sexual)**, Rocking*, Touch other	Directed push, Drum object (palms), Leaf clipping, **Object move**, **Object shake**, **Present (sexual)**, Punch object/ground, Reach, Slap object, Slap object with object, Stomp
Initiate grooming *(5 shared/15)*	Arm raise, **Big Loud Scratch**, **Grab**, Grab-pull, Hand on, **Object shake**, **Present (grooming)**, Tandem walk, **Touch other**	**Big Loud Scratch**, Bite, Directed push, Embrace, **Grab,** Head nod, **Object shake**, **Present (grooming)**, Present (sexual), Reach, **Touch other**
Reposition *(2 shared/6)*	**Directed push**, **Grab**, Grab-pull	Beckon, **Directed push**, **Grab**, Slap object, Tap object

* Gesture types that were not coded in the chimpanzee data, but have been seen at Budongo or Bossou. Although these gesture types are only reported for bonobos, they may also have the same meaning for chimpanzees.

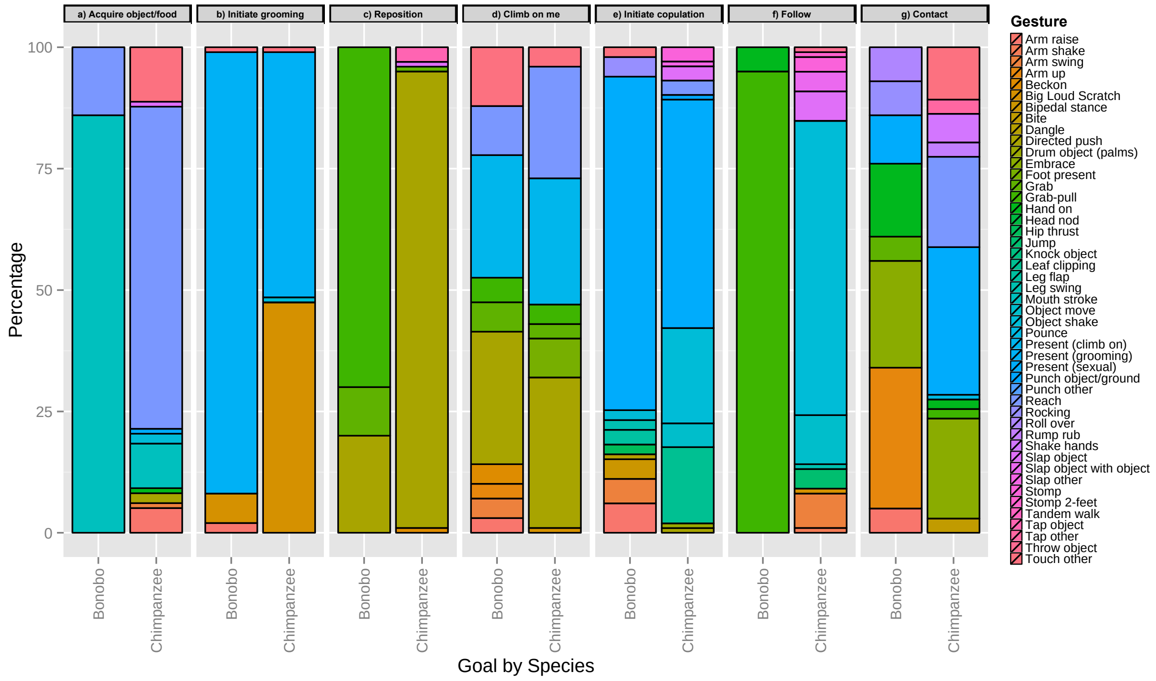


Figure 6.4. Stacked histogram showing the percentage of instances that each gesture type (arranged alphabetically) achieves each ASO (arranged adjacent to similar ASOs) divided by species (bonobo and chimpanzee). To make the bonobo and chimpanzee datasets directly comparable: For bonobos, I lumped gesture types *Present (genitals forward)* and *Present (genitals backward)* into *Present (sexual)*; I lumped the gesture type *Stroking* in with *Touch other*; and I lumped the ASO “Mount” in with “Contact”. For chimpanzees, I lumped the ASOs “Initiate copulation (male)” and “Initiate copulation (female)” into “Initiate copulation”; and I lumped “Direct attention” with “Initiate grooming”.

I then used a series of ANOVAs to determine whether there was variation in the proportion of instances that each gesture type achieved an ASO, as an interaction between gesture type and species. I converted the number of instances an ASO was achieved by any one gesture type into a proportion of the total number of instances an individual achieved that ASO. I included only gesture types that were achieved by one or both species for that ASO, in order to see whether, out of the gesture types they use, there is variation in the distribution between species. As in Chapter 4, I converted values of 0 or 1 in accordance with Snedecor and Cochran (0 → 1/(4N) and 1 → 1-

(1/(4N)), where N is the total number of instances for that ASO) (Snedecor & Cochran, 1989). I conducted the ANOVA with the corrected proportion as the dependent variable, species and gesture type as independent variables, and signaller identity as a random effect (Table 6.2). All of the ASOs had a significant interaction of species and gesture type.

Table 6.2. Table showing ASO and the top 3 gesture types that achieve it, with N(n) in square brackets [N is number of individuals, n is total number of instances]; and the ANOVA results from the interaction between species and gesture type. Underlined gestures are shared by bonobos and chimpanzees in any of the top three positions.

Goal	Bonobo, Top 3 Gesture Types	Chimpanzee, Top 3 Gesture Types	Results
Acquire object/food	1. Mouth stroke 86% 2. Reach 14% [6(29)]	1. Reach 65% 2. Touch other 11% 3. Mouth stroke 9% [22(256)]	f=18.54, df=14,364 p<0.0001
Climb on me	1. Directed push 27% 2. Present (climb on) 25% 3. Touch other 12% [11(157)]	1. Directed push 31% 2. Present (climb on) 27% 3. Reach 23% [7(74)]	f=2.28, df=11,176 p=0.0126
Contact	1. Arm up 29% 2. Embrace 22% 3. Hand on 15% [7(41)]	1. Present (sexual) 31% 2. Embrace 21% 3. Reach 19% [20(107)]	f=3.97, df=15,375 p<0.0001
Follow me	1. Grab-pull 95% 2. Hand on 5% [8(42)]	1. Object shake 60% 2. Object move 10% 3. Arm swing 7% [4(367)]	f=21.59, df=21,210 p<0.0001
Initiate copulation	1. Present (sexual) 68% 2. Arm raise 6% 3. Arm swing 5% [27(250)]	1. Present (sexual) 48% 2. Object shake 20% 3. Leaf clipping 16% [24(197)]	f=5.86, df=19,931 p<0.0001
Initiate grooming	1. Present (grooming) 90% 2. Big Loud Scratch 6% 3. Arm raise 2%	1. Present (grooming) 50% 2. Big Loud Scratch 47% 3. Object shake & Touch	f=42.15, df=12,948 p<0.0001

	[48(1175)]	other 1% [33(299)]	
Reposition	1. Grab-pull 70% 2. Directed push 20% 3. Grab 10% [4(20)]	1. Directed push 94% 2. Tap object 3% 3. Beckon 1% [13(80)]	f=35.75, df=5,75 p<0.0001

In the previous section, I found that overall the bonobo and chimpanzee repertoires use similar gesture types to achieve the same ASOs. However, in this section, I found that bonobo and chimpanzee gesture types achieve ASOs in different distributions. Given that, in Chapter 5, I found that context affects the meaning of gestures, finding that bonobos and chimpanzees use the same gestures types for the same meanings but in different proportions is not so surprising.

6.4 Discussion

If gestures were all learned or ritualised through ontogenetic ritualization, it would remarkable if the bonobo gestural repertoire (the physical form of the gestures) overlapped by 88% or more with that of the chimpanzee. However, given that the chimpanzee repertoire has been shown to be species-typical in the wild (Hobaiter & Byrne, 2011b), perhaps it is not surprising that the repertoire should also be largely shared with their closest living relative, the bonobo. In fact, personal communication with Catherine Hobaiter revealed that several "bonobo typical gestures" (*Bipedal rocking, Bipedal stance, Hip thrust, Rocking, Arm up*) have been seen at Budongo, Uganda, and Bossou, Guinea, subsequent to their publication. This large overlap of gesture types supports the hypothesis that great ape gestural repertoires are biologically inherited – there is a genetic predisposition towards acquiring gesture types, although experience and environmental effects are likely to modify their development and use. I am not claiming that bonobos and chimpanzees are incapable of learning gestures, but that the most parsimonious explanation for such a large overlap in the repertoire is biological inheritance. Phylogenetic ritualization, where actions become ritualized into communicative signals over an evolutionary timescale (Lorenz, 1966), may explain why so many gesture forms resemble the actions that would physically achieve the same result.

The remaining three gesture types that seem to be “bonobo exclusive” (*Bounce*, *Leaf drop*, and *Leg flap*) are all used in a sexual context. Given that bonobo females are sexually proceptive and that they also engage in GG-rubbing, they may have more gestures for sexual solicitation. However, chimpanzee consortships are notoriously difficult to follow and it is possible that these gesture types will eventually be observed in the chimpanzee, after enough data on consortships have been collected, just as gesture types *Hip thrust* and *Rocking* were observed later at Budongo, by a researcher looking specifically at sexual solicitation (Brittany Fallon, personal communication). The prevalence of consortships in chimpanzee but not bonobo behaviour, means that chimpanzees are exposed to a unique *behavioural context*, which, as we saw in the previous chapter, may affect the meaning of gesture types, and I will come back to that later.

Although clearly not the same gesture type, both bonobos and chimpanzees audibly manipulate leaves in a sexual context – the bonobo *Leaf drop* and the chimpanzee *Leaf clip*. Within the chimpanzee, *Leaf clip* takes different forms – ripping a leaf with hands, biting a leaf with teeth – and so *Leaf drop* may represent a cultural variant. Both *Leaf drop* at Wamba and *Leaf clip* at Budongo are used in a sexual context. Unfortunately, in my study there were not enough successful sequences including *Leaf drop* to analyse its meaning, but all occurred in a sexual context; and *Leaf drop* did occur in communication events where later bouts ended in copulation. Expanding our scope to look at the success of entire communication events would allow us to examine the meaning of *Leaf drop* and to make use of many gesture examples that we currently discard (Cartmill, 2016).

The bonobo and chimpanzee gestural repertoires, that is the *physical form* of the gestures, overlap by 88-96% but until now we did not know whether the meanings also overlap. To know whether the gesture meanings are shared by both species first required examining what bonobo gesture types mean (in Chapter 5), as that work has already been done for the chimpanzee (Hobaiter & Byrne, 2014). Comparing the chimpanzee and bonobo repertoires showed that their gesture meanings across the repertoires are more similar than would be expected by chance. Bonobos and chimpanzees use similar gesture types to achieve the same ASOs.

Then I went further and asked "do bonobos and chimpanzees use similar gesture types in similar proportions to achieve the same ASO?" I compared the distribution of gesture types that achieve each of seven ASOs (that had sufficient data for parametric analysis in both species), and found significant variation for all of them. Bonobos and chimpanzees use similar gesture types to achieve the same ASO, but in significantly different proportions.

One explanation for the different distributions is that bonobos and chimpanzees respond differently to gestures. Bonobos respond more quickly than chimpanzees, often starting to respond before the signaller has stopped gesturing

(Fröhlich et al., 2016). In addition, chimpanzees persist and elaborate using gesture sequences more often than bonobos (Fröhlich et al., 2016). Where a chimpanzee uses more sequences and bouts, a bonobo can get away with fewer gestures. The repertoire tuning hypothesis proposes that young chimpanzees use more sequences because they do not yet know the most successful gesture types. Although I have not looked specifically at the development of gestures, one could imagine that if bonobo mothers are quicker to respond to their infants' gestures than chimpanzee mothers, then bonobos would use fewer gesture types per ASO, quickly picking up on the appropriate usage. Persistence and use of sequences in young chimpanzees may explain the apparent "messiness" of chimpanzee gesture meaning compared to the bonobo. Of course, this idea would require a different methodological approach, and so is currently merely postulation.

But a simpler explanation for why bonobo and chimpanzee gestures have the same meanings but use them in different proportions harks back to the previous chapter on context. Take "Follow me" for example, which is the ASO that is most strikingly different for the bonobo and the chimpanzee. In the bonobo, this ASO most often occurs in the grooming context, whereas for the chimpanzee it occurs most often in consortships. The difference in distribution comes down to the context in which the gesture occurs. Although the ASO is to follow the signaller, it seems to depend whether the recipient should follow the signaller to be groomed or to follow the signaller for copulation. It may be that other differences in the distribution of gesture types for ASOs are also to do with the varying frequency of encountering a certain behavioural or interpersonal context in each species. But this scenario also raises questions about immediate and final goals – an ASO shows the immediate or “proximate” goal, e.g. “Follow me”, whereas for consortship gestures, the chimpanzee may be signalling towards the final or “ultimate” goal, “follow me so that we can go have sex”. There is no obvious way to objectively assign the ultimate goal, and no clear cut-off point: is the chimpanzee gesturing for the female to follow him to have sex to sire offspring etc.? Looking at ASOs in conjunction with context is currently the closest we can get.

In future, examination of the role of context in meaning for the chimpanzee might explain the apparent interspecies differences in gesture meanings. We can then make predictions about where the gesture meanings may differ, based on our knowledge of social behaviour for the two species. Once we have enough data, we can break down our comparison by sex, and see whether female bonobos use a wider variety of gesture types to request sexual solicitation, as may be expected given their female-female sexual behaviour. However, perhaps we need to keep GG-rubbing separate from copulation solicitation, because of the other functions that it serves. It might be possible to look at GG-rubbing solicitation in gorillas, who we now know to also engage in this behaviour (Grueter & Stoinski, 2016), and to see if they use similar gesture types to solicit it. Agonistic interactions are infrequent in bonobos and are difficult to film clearly, but with enough clear video footage, it would be possible to look at recruitment or appeasement gestures and to see whether certain gesture types *are* used for these purposes in bonobos, and are just un-reported because of low occurrence and observation limitations.

We should also work towards collecting comparable data for wild gorillas and wild orangutans. We can then have a more accurate idea of the overlap of their natural gestural repertoires, that is the physical form of the gestures. Taking our current estimates of 60% overlap for gorilla-chimpanzee and 80% overlap for orangutan-chimpanzee, we still know next to nothing about whether these overlapping gesture types achieve a similar set of ASOs. And finally, once we have a picture for all of the gesture meanings for all great ape species, we need to fill in the human-shaped gap. Have we retained the great ape gestural repertoire (Byrne & Cochet, 2016)? If not, where has it gone? And if so, how can we study it?

6.5 Conclusion

The bonobo gestural repertoire overlaps by 88-96% with the chimpanzee gestural repertoire. This large overlap points towards a genetically channelled repertoire, but hypothetically, bonobos and chimpanzees could just be moving their bodies and limbs in coincidentally similar ways. And so my next question was "do bonobos and chimpanzees' gestures achieve the same ASOs?" I found that bonobos and chimpanzees use similar gesture types to achieve the same ASOs (using the randomisation), but that they use them in significantly different proportions (using ANOVAs). The differences may come down to the differences in behavioural and interpersonal contexts that successfully disambiguated bonobo gesture meanings in the previous chapter. Given the differences in social behaviour of the bonobo and the chimpanzee, it would not be surprising if the frequency at which they experience different contexts correlates with the apparent differences in meaning. In future, we need to consider the overlap in gesture form and gesture meaning in the repertoire of all great apes, including humans.

Chapter 7 – General Discussion

7.1 Gestural repertoires

I began this thesis by talking about the importance of gesturing for humans; we use gestures to accompany speech and to help us think. We use deictic, iconic, and conventionalised gestures. But then, in Chapter 3, when I talk about the bonobo gestural repertoire, bonobo gestures sound totally foreign. I did not talk about bonobos pointing (deictic), gestures that resemble the referent (iconic), or gestures that have come to stand for a referent in a specific culture and must be learned by all members (conventionalised). Rather, I introduced the concept of a biologically inherited repertoire, gestures that bonobos all use, but that may be shaped by experience. Bonobos use just under 70 gesture types, and most gestures are used by multiple members of the community. In an ideal study, we could track individuals throughout their lifetimes, and I predict that we would find that all individuals use all gesture types, Currently, the individuals with the smallest repertoire sizes are older, less socially active individuals. While it may appear that they don’t share the same gesture types as others, this is probably a matter of opportunity rather than that they are lacking the gesture types. Overall, the bonobo repertoire seems to be species-typical.

In Figure 3.4, thirteen gestures appear to be idiosyncratic – only used by one individual. This is misleading. First, this figure only includes gestures that were expressed *and* understood. If we take the conventional way of looking only at the expressed repertoire, then the number of gesture types used by only one individual drops to 7 (*Arm shake, Bow, Hand shake, Knock object, Stiff walk, Tape object, Water splash*), but none of these would actually be included in the individuals' repertoires, since they only appeared once. All "idiosyncratic" gestures in this study are probably just rare gesture types. As the number of gesture instances increases so does the number of individuals that both express and understand those gesture types, and as soon as I observed two instances of a gesture type there are no "idiosyncratic" gestures. All of this points towards a gestural repertoire that is biologically inherited – so how does this compare to other great apes, including humans?

When compared to the chimpanzee, 88-96% of gesture types were shared, strengthening the case for a biologically inherited repertoire. We already knew that the chimpanzee gestural repertoire was species-typical (Hobaiter & Byrne, 2011b), and it now seems that it may be genus-typical. Moreover, the overlap for orangutans with chimpanzees and gorillas with chimpanzees currently stands at 80% and 60%, respectively (Hobaiter & Byrne, 2011b). I imagine that with time, as more studies are conducted with comparable methods, we will have a better map of shared gestures. Such a large overlap across species suggests a biological element to the repertoire, possibly beginning with an innate phylogenetically ritualised repertoire that is tuned and shaped by experience. We might therefore expect that humans share this great ape gestural repertoire (Byrne & Cochet, 2016). The challenge comes in how to study innate gestures amid the myriad of socially learned gestures that humans possess. It is possible to use similar observational methods with humans as I have with bonobos, but how can we distinguish learned from inherited gesture types (well, the same argument could also be made for other great apes)? An elegant solution could come from my methods in Chapter 3, where I looked at the understood, as well as expressed, repertoire. Understanding of a gesture type may show that that gesture type is in an individual’s overall repertoire. So to test the human gestural repertoire, one could study whether humans understand the bonobo repertoire better than would be predicted by chance. Such a study would, of course, rely on first knowing what bonobos mean by their gestures.

7.2. Gesture meanings

To assess the meaning of bonobo gestures, I used Apparently Satisfactory Outcomes (ASOs) (Hobaiter & Byrne, 2014). I found 14 ASOs in total, and the average number of ASOs per gesture type was 2.27 ± 1.84. Seventeen gesture types achieved a single ASO, and 16 achieved two or more ASOs. I chose to exclude gestures that occurred in play, to avoid misinterpreting their meanings, and as such am missing a few ASOs that were assigned for chimpanzee gestures (Hobaiter & Byrne, 2014). Otherwise, the ASOs for bonobos are largely the same as for chimpanzees.

While ASO is currently the best behavioural indicator of meaning, the method does have limitations. Firstly, it requires a change in the behaviour of the recipient, so I could not have known if a gesture meant “keep doing exactly what you’re doing right now”. One would also not expect a recipient to react to a declarative gesture, e.g. “this is a tree” or “you look lovely this evening”. So the ASO method might miss out on meanings without an observable behavioural change in the recipient. The second worry is that we define a signaller as satisfied when they stop gesturing. This assumes that (a) the signaller would have persisted if not satisfied, and (b) the signaller will only accept the response that they originally intended. In my dataset, of the gesture instances (or gesture sequences) that did not receive a reaction, the signaller persisted in 806 out of 1562 instances, and in a further 143 was unable to persist (e.g. the signaller was an infant communicating with another individual, and her mother came and picked her, the signaller, up preventing any further interaction). Bonobos persist frequently, but not all of the time. Rates of persistence may represent a species difference between bonobos and chimpanzees, with bonobos responding more quickly and thus allowing less persistence (Frohlich et al., 2016). Persistence in the face of non-reactions should be specifically addressed in future, and changes made to the ASO criteria, but it currently offers our most conservative way of assigning meaning.

In terms of settling for a response, I would not be surprised if occasionally the bonobos did settle for a response other than the one that they originally intended, but most likely one that is somehow similar to their intended goal. Bonobos are unlikely to settle for just any ASO all the time, and so with my extensive dataset, the primary ASO probably *is* the intended outcome, and maybe the very infrequent ASOs indicate when a signaller settled for less. If I ask for a cappuccino and you give me a latte, I will probably accept it. If Bonobo A asks Bonobo B to move away, but Bonobo B just stops pestering Bonobo A, Bonobo A will likely be satisfied. Actually, in these last two examples, one can imagine that there is a lot of individual variation in who settles and who persists, and I would like to examine that more in the future. The relationship between myself and the coffee-bringer could also affect the likelihood of me accepting or rejecting the latte. The scope of future research questions is seemingly endless.

When we compared the bonobo and chimpanzee repertoire, we found that the bonobo meanings and repertoire overlap more than would be expected by chance. None of the 10,000 randomised iterations matched better than the actual bonobo and chimpanzee gesture meanings. It seems as though bonobos and chimpanzees use the same gesture types to elicit the same responses. This supports the idea that not only are the gesture forms biologically inherited, but so are their meanings. We might then predict that since bonobos and chimpanzees inherently understand gestures, humans also have this latent ability.

As I alluded to earlier, we could test whether humans still possess a biologically inherited gestural repertoire by assessing their understanding of bonobo and chimpanzee gestures. One could run participants through an online survey, showing them videos of the most common gesture types and asking them to choose which outcome they think the signaller desires. One could examine whether humans (a) assign the same meanings to the same gesture types (as analysed for bonobos and chimpanzees compared to randomised iterations), (b) assign the same meaning in the same proportions, or (c) assign the same meaning to that specific instance of a gesture. I suspect that humans will perform above chance at assigning meanings to gestures, as measured in the randomised iterations. If so, then testing human understanding of other apes' gestures may be a useful tool in future for trying to separate inherited gestures from learned gestures; in the latter case, one would expect no understanding outside of the individuals or group in which the gesture was innovated and learned.

7.3 Context affects meaning

Around half of gesture types achieved multiple outcomes, i.e. had ambiguous meaning. I first looked for syntax, but neither presence in a sequence nor position in a sequence affected the meanings of ambiguous gesture types. Instead, some gesture types mean different things in different contexts. Bonobo recipients correctly interpret the meaning of gestures by accounting for the behavioural context of the signaller (the behaviour of the signaller immediately prior to gesturing) and the interpersonal context of their respective sexes and ages (female-female, female-male, young → old, old → young). We already knew that great apes use the same gesture type across a range of contexts (Call & Tomasello, 2007; Goodall, 1986; Plooij, 1978; Pollick & de Waal, 2007), and now we know that they achieve different ASOs in different contexts. But what does this mean for gestural communication – are gestures essentially meaningless and all of the meaning comes from context? Not necessarily.

First, not all gesture types are ambiguous –I found that about half of bonobo gesture types achieve only one ASO (Table 7.1). These gesture types have a very specific meaning, and there was no need for me to analyse context to try to disambiguate them. Taking a glance at my data, some of these gesture types, with only one meaning, do only occur in one context, but others occur in multiple contexts, maintaining the same meaning (see Table 5.7, Chapter 5). In the table, I reported gestures seen ≥5 times to match the context analysis, but many of the gestures were seen in other contexts <5 times. Overall, gesture types seem to maintain their specific meaning regardless of context, although this should be confirmed quantitatively in future, with additional data. Context therefore does not appear to impact upon the

ASO achieved by these gesture types, and so these gestures are indeed meaningful on their own.

If we look within a context, there can be multiple potential ASOs – the ratio of Context:ASO is not 1:1. For example, the Grooming context includes ASOs “Initiate grooming”, “Reposition”, and “Follow me”. Different gesture types are used to elicit “Initiate grooming” (*Present (grooming), Big loud scratch, Arm raise, Grab*) than “Reposition” and “Follow me” (*Grab-pull*). Therefore [Context + Any gesture] does not achieve the same ASO. If Bonobo A is grooming herself (Context = Grooming) and uses a random gesture to Bonobo B, that does not always lead to the same ASO. One ambiguous gesture type used in a specific context can achieve a different ASO to a different ambiguous gesture type used in the same context. It would then seem that ambiguous gesture types still have a degree of specificity, achieving a small cluster of ASOs, not merely all achieving the same thing in different contexts. Ambiguous gesture types could be thought of as “polysemous”, rather than meaningless.

Context is important for deciphering ambiguous gesture types (which still have a specific range of ASOs) by providing the recipient with additional information. It is more complex than a signal being linked 1:1 to a response; rather, the recipient must also take into account the behaviour of the signaller and their relationship to one another. In my analyses, I chose to look at behavioural context (the behaviour of the signaller immediately prior to gesturing) and interpersonal context (the relationship of age and sex between signaller and recipient). When I looked at both of these context types, the information provided was adequate to almost entirely disambiguate the meaning of gesture types (see Table 5.10, Chapter 5). Each gesture type achieved each ASO only in a specific behavioural or interpersonal context. The notable exceptions, *Grab-pull* and *Touch other*, are both contact gestures, and there could be additional information in the amount of pressure applied or the duration of the gesture that was not picked up in context analysis. This is probably an artefact of the difficulty of categorising contact gestures (we cannot perceive the amount of force exerted), rather than a failing of separating by context.

All in all, for polysemous gestures, context is necessary but not sufficient (without a specific gesture type) for achieving an ASO. No gestures are meaningless without context, but rather context helps the recipient to correctly interpret the signaller's intended goal. This is not unlike human language, where we are able to navigate the potential confusion of polysemous words by an (unconscious) understanding of our shared context. If you and I are in a kennel and I say the word "bark" I do not need to overtly specify that I am talking about dogs, you would assume that from our shared context. Likewise, if I said "bark" at a conference on forestry, I would not need to overtly specify that I am talking about trees. In the case of human language, we would probably attribute the correct interpretation of polysemous words to our "superior" mentalizing abilities. One would probably say that we are able to subconsciously account for the fact that we share a context with the "other" and we know that they know that we are sharing a context. There is a reticence to ascribing such mentalizing abilities to non-human great apes, but the fact that signallers and recipients communicate within a shared context recognised by both parties does beg the question – how do non-human great apes mentally represent one another during gestural communication?

While my study would suggest that context is important for deciphering the signaller's intended message, it is possible that it does so just by adding another layer to a stimulus-response scenario – where the signaller's stimulus is their physical desire plus the presence of another individual who can satisfy that desire and the signaller's response is to gesture. Then the recipient's stimulus is witnessing the gesture plus the behavioural and interpersonal contexts and the recipient's response is the ASO. But at a certain point one has to wonder whether the stimulus-response is actually the most parsimonious explanation (Byrne & Bates, 2006). Alternatively, if we do settle for gestures being a response to a rich set of stimuli, we would seriously have to question whether much human action is also a response to a rich set of stimuli.

Although I found that bonobos and chimpanzees achieve the same outcomes for the same gesture types, they do so in different proportions. The most likely reason may be tied to context – if ambiguous gestures mean different things in different contexts, and bonobos and chimpanzees experience contexts at different frequencies, then it would look like bonobos and chimpanzees are using gestures for a different proportion of ASOs. Considering all of the known differences in social behaviour that I outlined in Chapter 6, one would expect the frequency of a gesture achieving a certain ASO to be affected by inter-species differences in the frequency of encountering certain contexts. I'm currently talking with Catherine Hobaiter about the possibility of analysing context in her chimpanzee data, and am hopeful that I'll be able to answer this question shortly.

In an experiment to test human understanding of great ape gestures, I wonder how much contextual information would be needed for humans to assign the correct meaning for a specific gesture instance. Can humans also decipher gesture meanings based on the bonobo's context? One could manipulate the conditions, like the length of time a participant watches the video before the gesture, or give them information about the sex of the communicating bonobos. However, at that point, I think you would have to feed too much information to participants for it to be a good measure of understanding gestures in different contexts.

To make a big, opinionated leap (which I'm told I'm allowed to do in a PhD General Discussion chapter), the importance of context in meaning could prove relevant for the evolution of human language. Gestures can mean different things in different contexts, and so bonobos and chimpanzees are able to communicate about the same desires that they experience at different frequencies. As the Homo and Pan lineages diverged, what different contexts were early hominins experiencing? All of the gesture meanings that I found were to request actions from a recipient, but clearly at some point a need for declarative and informative communication arose. Was the ability for a gesture to mean something different in a different context useful as early humans encountered new contexts? At what point was the available biological repertoire inadequate under the pressure for an expansive vocabulary and a proto-syntactic organisation?

I think the future lies in looking comprehensively at all types of communication under a similar framework. Studies on multi-modal communication go part of the way towards this, but should not limit themselves to only look at the simultaneous production of signals in different modalities. Studying the production and outcomes of gestures, vocalisations, and facial expressions, in directly comparable terms will allow us to determine the situations in which each form of communication is most useful. We can then ask the same questions of all forms of communication as for gestures: Are they intentionally produced? What are the signals' meanings? Are the functions of vocalisations and facial expressions also affected by context?

7.4 The BIG Conclusion

I have finally answered the question “why on earth anyone would want to study how ~~monkeys~~ great apes move their arms?” Studying bonobo gestural communication has revealed that bonobos deploy gestures with more or less specific meanings; the meanings of ambiguous gestures become disambiguated by context; the bonobo gesture repertoire overlaps by 88-96% with that of the chimpanzee; and the meaning of bonobo and chimpanzee gestures also seem to be shared, but occur at different frequencies. These findings are interesting in their own right – studying the animal for the sake of learning more about that species. But it would be dishonest to say that I’m not also interested in the importance of studying other species of great ape to learn more about ourselves.

The similarity of bonobo and chimpanzee gestural communication, when taken alongside gorilla and orangutan findings, probably means that *Pan* gesturing resembles the gesture use of our last common ancestor. Gestural communication is just one piece when trying to assemble the puzzle of language evolution, but my findings on the importance of context will hopefully influence future research directions. When considering the evolution of language and of the diverse forms of communication in the animal kingdom, it is hard not to think of Darwin: “from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved" (Darwin, 1859).

References

Anderson, M. J., Chapman, S. J., Videan, E. N., Evans, E., Fritz, J., Stoinski, T. S., Dixson, A. F., & Gagneux, P. (2007). Functional evidence for differences in sperm competition in humans and chimpanzees. *American Journal of Physical Anthropology*, *134*, 274–280.

Arnold, K., & Zuberbühler, K. (2008). Meaningful call combinations in a non-human primate. *Current Biology*, *18*(5), 202–203.

Aronoff, M., Meir, I., & Sandler, W. (2005). The paradox of sign language morphology. *Language*, *81*(95), 301–344.

Bates, E. (1976). *Language and context: The acquisition of pragmatics*. New York: Academic Press.

Becquet, C., & Przeworski, M. (2007). A new approach to estimate parameters of speciation models with application to apes. *Genome Research*, *17*(10), 1505–19.

Bloom, P. (2002). *How Children Learn the Meanings of Words*. Cambridge, MA: MIT Press.

Bradley, B. J. (2008). Reconstructing phylogenies and phenotypes: A molecular view of human evolution. *Journal of Anatomy*, *212*, 337–353.

Bryan, A. L. (1963). The essential morphological basis for human culture. *Current Anthropology*, *4*(3), 297–306.

Butterworth, G. (1998). What is special about pointing in babies. In F. Simion & G. Butterworth (Eds.), *The development of sensory, motor and cognitive capacities in early infancy: From perception to cognition* (pp. 171–190). Hove, UK: Psychology Press Ltd.

Byrne, R. W., & Bates, L. A. (2006). Why are animals cognitive? *Current Biology*, *16*(12), 445–448.

Byrne, R. W., & Cochet, H. (2016). Where have all the (ape) gestures gone? *Psychonomic Bulletin & Review*.

Caldecott, J., & Miles, L. (2005). *World atlas of great apes and their conservation*. Berkeley, CA: University of California Press.

Call, J., & Tomasello, M. (2007). *The Gestural Communication of Apes and Monkeys*. Manhaw, NJ: Lawrence Erlbaum Associates.

Cantalupo, C., & Hopkins, W. D. (2001). Asymmetric Broca's area in great apes: A region of the ape brain is uncannily similar to one linked with speech in humans. *Nature*, *414*(6863), 44–46.

Carpenter, M., Nagell, K., Tomasello, M., Butterworth, G., & Moore, C. (1998). Social Cognition, Joint attention, and Communicative Competence from 9 to 15 Months of Age. *Monographs of the Society for Research in Child Development*, *63*(4), 1–174.

Cartmill, E. A. (2016). Lasting Impacts of the Code Model on Primate. In S. G. Roberts, C. Cuskley, L. McCrohon, L. Barceló-Coblijn, O. Feher, & T. Verhoef (Eds.), *The Evolution of Language: Proceedings of the 11th International Conference (EVOLANG11)*.

Cartmill, E. A., & Byrne, R. W. (2007). Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology*, *17*(15), 1345–8.

Cartmill, E. A., & Byrne, R. W. (2010). Semantics of primate gestures: intentional meanings of orangutan gestures. *Animal Cognition*, *13*(6), 793–804.

Cäsar, C., Zuberbühler, K., Young, R. J., & Byrne, R. W. (2013). Titi monkey call sequences vary with predator location and type. *Biology Letters*, *9*, 20130535.

Chapman, C. A., White, F. J., & Wrangham, R. W. (1993). Defining subgroup size in fission-fusion societies. *Folia Primatologica*, *61*, 31–34.

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

Chen, F.-C., & Li, W.-H. (2001). Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees. *American Journal of Human Genetics*, *68*, 444–56.

Chomsky, N. (1965). *Aspects of the Theory of Syntax*. Cambridge, MA: MIT Press.

Chomsky, N. (1972). *Language and mind*. New York: Harcourt Brace Jovanovich.

Clay, Z., & Zuberbühler, K. (2009). Food-associated calling sequences in bonobos. *Animal Behaviour*, *77*(6), 1387–1396.

Clay, Z., & Zuberbühler, K. (2011). Bonobos extract meaning from call sequences. *PloS One*, *6*(4), e18786.

Cohen, E., Namir, L., & Schlesinger, I. M. (1977). *A new dictionary of sign language*. The Hague, Paris: Mouton.

Collier, K., Radford, A. N., Manser, M. B., & Townsend, S. W. (2016). Dwarf mongooses combine meaningful alarm calls. In S. G. Roberts, C. Cuskley, L. McCrohon, L. Barceló-Coblijn, O. Fehér, & T. Verhoef (Eds.), *The Evolution of Language: Proceedings of the 11th International Conference (EVOLANG11)*.

Colyn, M., Gautier-Hion, A., & Verheyen, W. (1991). A re-appraisal of palaeoenvironmental history in Central Africa: evidence for a major fluvial refuge in the Zaire Basin. *Journal of Biogeography*, *18*(4), 403–407.

Coolidge, H. J. (1933). Pan paniscus. Pigmy chimpanzee from south of the Congo river. *American Journal of Physical Anthropology*, *18*(1), 1–59. doi:10.1002/ajpa.1330180113

Corballis, M. C. (2009). Language as gesture. *Human Movement Science*, *28*(5), 556–65.

Darwin, C. (1859). *On the Origin of Species* (1st ed.). Down, Bromley, Kent: John Murray, Albemarle Street.

de Waal, F. B. M. (1982). *Chimpanzee politics: Power and sex among apes*. New York: Harper & Row.

de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (Pan paniscus), compared to that of chimpanzees. *Behaviour*, *106*(3/4), 183–251.

de Waal, F. B. M. (1997). *Bonobo: The forgotten ape*. Berkeley, CA: University of California Press.

de Waal, F. B. M. (Ed.). (2009). *Tree of Origin: What Primate Behavior Can Tell Us about Human Social Evolution*. Cambridge, MA: Harvard University Press.

Dennett, D. C. (1983). Intentional systems in cognitive ethology: The "Panglossian paradigm" defended. *Behavioral and Brain Sciences*, *6*, 343–90.

Diamond, J. (2014). *The Third Chimpanzee: On the Evolution and Future of the Human Animal*. London: Oneworld Publications.

Doran, D. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology*, *18*, 183–206.

Douglas, P. H., Hohmann, G., Murtagh, R., Thiessen-Bock, R., & Deschner, T. (2016). Mixed messages: wild female bonobos show high variability in the timing of ovulation in relation to sexual swelling patterns. *BMC Evolutionary Biology*, *16*(140), 1–17.

Douglas, P. H., & Moscovice, L. R. (2015). Pointing and pantomime in wild apes?

Female bonobos use referential and iconic gestures to request genito-genital rubbing. *Scientific Reports*, *5*(August), 13999.

Dronkers, N. F., Plaisant, O., Iba-Zizen, M. T., & Cabanis, E. A. (2007). Paul Broca's historic cases: High resolution MR imaging of the brains of Leborgne and Lelong. *Brain*, *130*(5), 1432–1441.

Endler, J. A., & Thery, M. (1996). Interacting Effects of Lek Placement, Display Behavior, Ambient Light, and Color Patterns in Three Neotropical Forest-Dwelling Birds. *The American Naturalist*, *148*(3), 421–452.

Engesser, S., Crane, J. M. S., Savage, J. L., Russell, A. F., & Townsend, S. W. (2015). Experimental evidence for phonemic contrasts in a nonhuman vocal system. *PLoS Biology*, *13*(6), 1–16.

Engesser, S., Ridley, A. R., & Townsend, S. W. (2016). Meaningful call combinations and compositional processing in the southern pied babbler. *Proceedings of the National Academy of Sciences*, *113*(21), 5976–5981.

Eriksson, J., Hohmann, G., Boesch, C., & Vigilant, L. (2004). Rivers influence the population genetic structure of bonobos (Pan paniscus). *Molecular Ecology*, *13*, 3425–35.

Farkas, G., & Beron, K. (2004). The detailed age trajectory of oral vocabulary knowledge: Differences by class and race. *Social Science Research*, *33*, 464–497.

Fenson, L., Dale, P. S., Reznick, J. S., Bates, E., Thal, D. J., Pethick, S. J., Tomasello, M., Mervis, C.B., & Stiles, J. (1994). Variability in Early Communicative Development. *Monographs of the Society for Research in Child Development,* 59(5), 1-185.

Fischer, A., Prüfer, K., Good, J. M., Halbwax, M., Wiebe, V., André, C., … Pääbo, S. (2011). Bonobos fall within the genomic variation of chimpanzees. *PloS One*, *6*(6), e21605.

Fitch, W. T. (2012). Segmental structure in banded mongoose calls. *BMC Biology*, *10*(98).

Flower, T. (2011). Fork-tailed drongos use deceptive mimicked alarm calls to steal food. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1711), 1548–1555.

Foley, R. (2005). The adaptive legacy of human evolution: A search for the environment of evolutionary adaptedness. *Evolutionary Anthropology: Issues,* *News, and Reviews*, *4*(6), 194–203.

Foster, M. W., Gilby, I. C., Murray, C. M., Johnson, A., Wroblewski, E. E., & Pusey, A. E. (2009). Alpha male chimpanzee grooming patterns: implications for dominance “style”. *American Journal of Primatology, 71*, 136–44.

Freeman, G. H., & Halton, J. H. (1951). Note on an Exact Treatment of Contingency, Goodness of Fit and other Problems of Significance. *Biometrika*, *38*(1/2), 141–149.

Frishberg, N. (1987). Home sign. *Gallaudet Encyclopedia of Deaf People and Deafness*, *3*, 128–131.

Fröhlich, M., Kuchenbuch, P., Müller, G., Fruth, B., Furuichi, T., Wittig, R. M., & Pika, S. (2016). Unpeeling the layers of language: Bonobos and chimpanzees engage in cooperative turn-taking sequences. *Scientific Reports, 6*, 25887.

Furuichi, T. (1997). Agonistic interactions and matrifocal dominance rank of wild bonobos (Pan paniscus) at Wamba. *International Journal of Primatology*, *18*(6), 855–875.

Furuichi, T. (2009). Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. *Primates, 50*, 197–209.

Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology*, *20*(4), 131–42.

Furuichi, T., & Hashimoto, C. (2002). Why female bonobos have a lower copulation rate during estrus than chimpanzees. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos* (pp. 156–167). New York: Cambridge University Press.

Furuichi, T., Idani, G., Ihobe, H., Kuroda, S., Kitamura, K., Mori, A., Enemoto, T., Okayasu, N., Hashimoto, C., & Kano, T. (1998). Population dynamics of wild bonobos (Pan paniscus) at Wamba. *International Journal of Primatology*, *19*(6), 1029–1043.

Furuichi, T., Mulavwa, M. N., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Idani, G., Ihobe, H., Hashimoto, C., Tashiro, Y., & Mwanza, N. (2008). Relationships among fruit abundance, ranging rate, and party size and composition of bonobos at Wamba. In T. Furuichi & J. A. M. Thompson (Eds.), *The bonobos: behavior, ecology, and conser- vation* (pp. 135–149). New York: Springer.

Furuichi, T., & Thompson, J. A. M. (2008). *The bonobos: behavior, ecology, and conservation*. New York: Springer.

Gannon, P. J., Holloway, R. L., Broadfield, D. C., & Braun, A. R. (1998). Asymmetry of chimpanzee planum temporale: humanlike pattern of Wernicke's brain language area homolog. *Science*, *279*, 220–222.

Gardner, R. A., & Gardner, B. T. (1969). Teaching sign language to a chimpanzee. *Science*, *165*, 664–72.

Gelman, S. A. (2005). *The Essential Child: Origins of Essentialism in Everyday Thought*. Oxford: Oxford University Press.

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the gorilla (Gorilla gorilla): repertoire, intentionality and possible origins. *Animal Cognition*, *12*(3), 527–46.

Genty, E., Clay, Z., Hobaiter, C., & Zuberbühler, K. (2014). Multi-modal use of a socially directed call in bonobos. *PloS One*, *9*(1), 1–12.

Genty, E., Neumann, C., & Zuberbühler, K. (2015). Complex patterns of signalling to convey different social goals of sex in bonobos, Pan paniscus. *Scientific Reports*, *5*, 16135.

Genty, E., & Zuberbühler, K. (2014). Spatial Reference in a Bonobo Gesture. *Current Biology*, *24*, 1–5.

Gillespie-Lynch, K., Greenfield, P., Lyn, H., & Savage-Rumbaugh, S. (2014). Gestural and Symbolic Development among Apes and Humans: Support for a Multimodal Theory of Language Evolution. *Frontiers in Psychology*, *5*(1228).

Girard, M. B., Kasumovic, M. M., & Elias, D. O. (2011). Multi-modal courtship in the peacock spider, Maratus volans (O.P.-Cambridge, 1874). *PloS One*, *6*(9), e25390.

Gomez, J. C. (1994). The emergence of intentional communication as a problem-solving strategy in the gorilla. In S. T. Parker & K. R. Gibson (Eds.), *'Language' and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives* (pp. 333-355). Cambridge: Cambridge University Press.

Goodall, J. (1971). *In the Shadow of Man*. New York: Mariner Books.

Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Cambridge, MA: Belknap Press of Harvard University Press.

Goulden, R., Nation, P., & Read, J. (1990). How large can a receptive vocabulary be?

Applied Linguistics, *11*(4), 341–363.

Grice, H. P. (1957). Meaning. *The Philosophical Review*, *66*(3), 377–388.

Grice, H. P. (1969). Utterer’s meaning and intention. *The Philosophical Review*, *78*(2), 147–177.

Grueter, C. C., & Stoinski, T. S. (2016). Homosexual Behavior in Female Mountain Gorillas: Reflection of Dominance, Affiliation, Reconciliation or Arousal? *Plos One*, *11*(5), e0154185.

Gunderson, E. A., Spaepen, E., Gibson, D., Goldin-Meadow, S., & Levine, S. C. (2015). Gesture as a window onto children’s number knowledge. *Cognition*, *144*, 14–28.

Halliday, T. R. (1974). Sexual Behaviour of the Smooth Newt, Triturus vulgaris (Urodela, Salamandridae). *Journal of Herpetology*, *8*(4), 277–292.

Hare, B., Wobber, V., & Wrangham, R. W. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), 573–585.

Hasegawa, T., & Hiraiwa-Hasegawa, M. (1990). Sperm competition and mating behavior. In T. Nishida (Ed.), *The chimpanzees of the Mahale mountains: Sexual and Life History Strategies* (pp. 115–132). Tokyo: University of Tokyo Press.

Hashimoto, C. (1997). Context and development of sexual behavior of wild bonobos (Pan paniscus) at Wamba, Zaire. *International Journal of Primatology*, *18*(1), 1–21.

Hashimoto, C., Furuichi, T., & Tashiro, Y. (2001). What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. *International Journal of Primatology*, *22*(6), 947–959.

Hashimoto, C., Tashiro, Y., Hibino, E., Mulavwa, M. N., Yangozene, K., Furuichi, T., Idani, G., & Takenaka, O. (2008). Longitudinal structure of a unit-group of bonobos: male philopatry and possible fusion of unit-groups. In T. Furuichi & J. A. M. Thompson (Eds.), *The Bonobos: Behavior, Ecology, and Conservation* (pp. 157–170). New York: Springer.

Hashimoto, C., Tashiro, Y., & Kimura, D. (1998). Habitat use and ranging of wild bonobos (Pan paniscus) at Wamba. *International Journal of Primatology*, *19*(6), 1045–1060.

Hayes, K. J., & Hayes, C. (1951). The intellectual development of a home-raised chimpanzee. *Proceedings of the American Philosophical Society*, *95*(2), 105–109.

Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PloS One*, *5*(8), e12438.

Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J., & Wrangham, R. (2001). Mortality rates among wild chimpanzees. *Journal of Human Evolution*, *40*, 437–450.

Hobaiter, C., & Byrne, R. W. (2011a). Serial gesturing by wild chimpanzees: its nature and function for communication. *Animal Cognition*, *14*(6), 827–38.

Hobaiter, C., & Byrne, R. W. (2011b). The gestural repertoire of the wild chimpanzee. *Animal Cognition*, *14*(5), 745–67.

Hobaiter, C., & Byrne, R. W. (2014). The Meanings of Chimpanzee Gestures. *Current Biology*, *24*, 1–5.

Hobaiter, C., Leavens, D. A., & Byrne, R. W. (2014). Deictic gesturing in wild chimpanzees, (Pan troglodytes)? some possible cases. *Journal of Comparative Psychology*, *128*(1), 82–87.

Hoetjes, M., Krahmer, E., & Swerts, M. (2015). On what happens in gesture when communication is unsuccessful. *Speech Communication*, *72*, 160–175.

Hoff, E. (2006). How social contexts support and shape language development. *Developmental Review*.

Hohmann, G., & Fruth, B. (2000). Use and function of genital contacts among female bonobos. *Animal Behaviour*, *60*(1), 107–120.

Hohmann, G., Robbins, M. M., & Boesch, C. (Eds.). (2012). *Feeding Ecology in Apes and Other Primates*. New York: Cambridge University Press.

Hopkins, W. D., Marino, L., Rilling, J. K., & MacGregor, L. A. (1998). Planum temporale asymmetries in great apes as revealed by magnetic resonance imaging (MRI). *NeuroReport*, *9*, 2913–2918.

Idani, G. (1991). Social relationships between immigrant and resident bonobo (Pan paniscus) females at Wamba. *Folia Primatologica*, *57*, 83–95.

Idani, G., Mwanza, N., Ihobe, H., Hashimoto, C., Tashiro, Y., & Furuichi, T. (2008). Changes in the status of bonobos, their habitat, and the situation of humans at Wamba in the Luo Scientific Reserve, Democratic Republic of Congo. In T. Furuichi & J. A. M. Thompson (Eds.), *The Bonobos: Behavior, Ecology, and*

Conservation (pp. 427–444). New York: Springer.

Janik, V. M., Sayigh, L. S., & Wells, R. S. (2006). Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences*, *103*(21), 8293–7.

Jansen, D. A., Cant, M. a, & Manser, M. B. (2013). Segmental concatenation of individual signatures and context cues in banded mongoose (Mungos mungo) close calls. *BMC Biology*, *10*(97).

Kako, E. (1999). Elements of syntax in the systems of three language-trained animals. *Animal Learning & Behavior*, *27*(1), 1–14.

Kano, T. (1980). Social behavior of wild pygmy chimpanzees (Pan paniscus) of Wamba: A preliminary report. *Journal of Human Evolution*, *9*, 243–260.

Kano, T. (1992). *The last ape: Behavior and ecology of pygmy chimpanzees*. Stanford: Stanford University Press.

Kano, T., & Nishida, T. (1999). Bilia as an authentic vernacular name for Pan paniscus. *Pan Africa News*, *6*(1), 1–3.

Kawamoto, Y., Takemoto, H., Higuchi, S., Sakamaki, T., Hart, J. A., Hart, T. B., … Furuichi, T. (2013). Genetic structure of wild bonobo populations: diversity of mitochondrial DNA and geographical distribution. *PloS One*, *8*(3), e59660.

Kellogg, W., & Kellogg, L. (1933). *The ape and the child: a study of environmental influence upon early behavior*. New York: Hafner Publishing Company.

Kendon, A. (1997). Gesture. *Annual Review of Anthropology*, *26*, 109–28.

Kitamura, K. (1983). Pygmy chimpanzee association patterns in ranging. *Primates*, *24*(1), 1–12.

Kortlandt, A. (1995). A survey of the geographical range, habitats and conservation of the pygmy chimpanzee (Pan paniscus): an ecological perspective. *Primate Conservation*, *16*, 21–36.

Kuroda, S. (1979). Grouping of the pygmy chimpanzees. *Primates*, *20*(2), 161–183.

Ladd, P. (2003). *Understanding Deaf Culture: In Search of Deafhood*. Clevedon: Multilingual Matters Ltd.

Ladygina-Kots, N. N. (2002). *Infant chimpanzee and human child: a classic 1935 comparative study of ape emotions and intelligence*. (F. B. M. de Waal, Ed.). Oxford: Oxford University Press.

Lander, E. S., Reich, D., Gnerre, S., Patterson, N., & Richter, D. J. (2006). Genetic evidence for complex speciation of humans and chimpanzees. *Nature*, *441*(7097), 1103–1108.

Leavens, D. A., & Hopkins, W. D. (1999). The whole-hand point: the structure and function of pointing from a comparative perspective. *Journal of Comparative Psychology*, *113*(4), 417–425.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *110*(4), 346–353.

Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005). Intentionality as Measured in the Persistence and Elaboration of Communication by Chimpanzees (Pan troglodytes). *Child Development*, *76*(1), 291–306.

Lewis, S. M., & Cratsley, C. K. (2008). Flash Signal Evolution, Mate Choice, and Predation in Fireflies. *Annual Review of Entomology*, *53*, 293–321.

Liebal, K., Call, J., & Tomasello, M. (2004). Use of gesture sequences in chimpanzees. *American Journal of Primatology*, *64*, 377–396.

Liebal, K., Pika, S., Call, J., Tomasello, M. (2004). To move or not to move: How apes adjust to the attentional state of others. *Interaction Studies*, 5(2), 199–219.

Lorenz, K. Z. (1966). Evolution of Ritualization in the Biological and Cultural Spheres. *Philosophical Transactions of the Royal Society B*, *251*(772), 273–284.

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1483), 2315–24.

Mehta, C. R., & Patel, N. R. (1983). A Network Algorithm for Performing Fisher Exact Test in r X c Contingency-Tables. *Journal of the American Statistical Association*, *78*(382), 427–434.

Millikan, R. G. (1984). *Language, Thought, and Other Biological Categories: New Foundations for Realism*. Cambridge, MA: MIT Press.

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, *20*(12), R507–8.

Moore, R. (2016). Meaning and ostension in great ape gestural communication. *Animal Cognition*, *19*, 223–231.

Mulavwa, M. N., Furuichi, T., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Idani, G., Ihobe, H., Hashimoto, C., Tashiro, Y., & Mwanza, N. (2008). Seasonal changes in fruit production and party size of bonobos at Wamba. In T. Furuichi & J. A. M. Thompson (Eds.), *The Bonobos: Behavior, Ecology, and Conservation* (pp. 121–134). New York: Springer.

Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 1009–14.

Nakamura, M. (2003). “Gathering” of social grooming among wild chimpanzees: implications for evolution of sociality. *Journal of Human Evolution*, *44*, 59–71.

Nation, P., & Waring, R. (1997). Vocabulary size, text coverage and word lists. In N. Schmitt & M. McCarthy (Eds.), *Vocabulary: Description, Acquisition and Pedagogy* (pp. 6–19). Cambridge: Cambridge University Press.

Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. *The Great Apes*, *5*, 73–121.

Nishida, T. (1983). Alpha status and agonistic alliance in wild chimpanzees (Pan troglodytes schweinfurthii). *Primates*, *24*, 318–336.

Nishida, T. (1985). Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. *Zeitschrift Für Psychologie*, *67*, 284–301.

Orr, E. (2014). *Meaning , sociality and dialog in bonobo (Pan paniscus) gestural communication: an observational study at the Milwaukee County Zoo* (Doctoral Thesis).

Palmer, F. R. (1984). *Grammar*. New York: Penguin.

Patterson, F. G. (1978). The gestures of a gorilla: Language acquisition in another pongid. *Brain and Language*, *5*, 72–97.

Pepperberg, I. M. (1983). Cognition in the African Grey parrot: Preliminary evidence for auditory/vocal comprehension of the class concept. *Animal Learning & Behavior*, *11*(2), 179–185.

Pika, S. (2007). Gestures in subadult bonobos (Pan paniscus). In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys.* (pp. 41–68). New Jersey: Lawrence Erlbaum Associates.

Pika, S., Liebal, K., & Tomasello, M. (2005). Gestural communication in subadult bonobos (Pan paniscus): repertoire and use. *American Journal of Primatology*, *65*(1), 39–61.

Pika, S., Mitani, J. (2006). Referential gestural communication in wild chimpanzees (Pan troglodytes). *Current Biology*, 16(6), 191–2.

Pinker, S. (1994). *The Language Instinct: How the Mind Creates Language*. New York: William Morrow and Company.

Plooij, F. X. (1978). Some basic traits of language in wild chimpanzees? In A. Lock (Ed.), *Action gesture and symbol* (pp. 111–131). London: Academic Press.

Pollick, A. S., & de Waal, F. B. M. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences*, *104*(19), 8184–9.

Pollick, A. S., Jeneson, A., & de Waal, F. B. M. (2008). Gestures and multimodal signaling in bonobos. In T. Furuichi & J. A. M. Thompson (Eds.), *The Bonobos: Behavior, Ecology, and Conservation* (pp. 75–94). New York: Springer.

Price, C. J. (2000). The anatomy of language: contributions from functional neuroimaging. *Journal of Anatomy*, *197*, 335–359.

Progovac, L. (2016). What kind of grammar did early humans (and Neanderthals) command? A linguistic reconstruction. In S. G. Roberts, C. Cuskley, L. McCrohon, L. Barceló-Coblijn, O. Fehér, & T. Verhoef (Eds.), *The Evolution of Language: Proceedings of the 11th International Conference*.

Progress & Plans. (2016). Retrieved from http://www.koko.org/progress-plans

Pusey, A. E., & Packer, C. (1987). Dispersal and philopatry. In B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. Struhsaker (Eds.), *Primate Societies* (pp. 250–266). Chicago: University of Chicago Press.

Pyers, J. E., Shusterman, A., Senghas, A., Spelke, E. S., & Emmorey, K. (2010). Evidence from an emerging sign language reveals that language supports spatial cognition. *Proceedings of the National Academy of Sciences*, *107*(27), 12116–20.

Quine, W., & Van, O. (1960). *Word and object: An inquiry into the linguistic mechanisms of objective reference.* New York: Wiley.

Radford, A. N., & Ridley, A. R. (2008). Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Animal Behaviour*, *75*(2), 519–527.

Raffaele, P. (2006). Speaking Bonobo. Retrieved from http://www.smithsonianmag.com/science-nature/speakingbonobo.html

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, *99*(7), 4436–41.

Reynolds, V. (2005). *The Chimpanzees of the Budongo Forest*. Oxford: Oxford University Press.

Rilling, J. K. (2014). Comparative primate neuroimaging: insights into human brain evolution. *Trends in Cognitive Sciences*, *18*(1), 46–55.

Rilling, J. K., Scholz, J., Preuss, T. M., Glasser, M. F., Errangi, B. K., & Behrens, T. E. (2012). Differences between chimpanzees and bonobos in neural systems supporting social cognition. *Social Cognitive and Affective Neuroscience*, *7*(4), 369–79.

Ristau, C. A. (1991). Aspect of the cognitive ethology of an injury-feigning bird, the Piping Plover. In C. A. Ristau (Ed.), *Cognitive ethology. The minds of other animals* (pp. 91–126). Hillsdale: Lawrence Erlbaum Associates.

Roberts, A. I., Vick, S.-J., & Buchanan-Smith, H. M. (2012). Usage and comprehension of manual gestures in wild chimpanzees. *Animal Behaviour*, 84(2), 459–70.

Rousseau, J. J. (1754). *Discourse on Inequality*.

Rowe, N. (1996). *The pictorial guide to the living primates*. East Hampton: Pogonia Pr.

Sakamaki, T. (2013). Social grooming among wild bonobos (Pan paniscus) at Wamba in the Luo Scientific Reserve, DR Congo, with special reference to the formation of grooming gatherings. *Primates*, *54*(4), 349–59.

Sandler, W., Meir, I., Padden, C., & Aronoff, M. (2005). The emergence of grammar: systematic structure in a new language. *Proceedings of the National Academy of Sciences*, *102*(7), 2661–2665.

Sauther, M. L., Sussman, R. W., & Gould, L. (1999). The Socioecology of the Ringtailed Lemur: Thirty-Five Years of Research. *Evolutionary Anthropology*, *8*(4), 120–132.

Savage-Rumbaugh, E. S. (1986). *Ape language: From conditioned response to symbol*. New York: Columbia University Press.

Savage-Rumbaugh, E. S., & Lewin, R. (1994). *Kanzi: The Ape at the Brink of the Human Mind*. New York: Wiley.

Savage-Rumbaugh, E. S., McDonald, K., Sevcik, R. A., Hopkins, W. D., & Rubert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (Pan paniscus). *Journal of Experimental Psychology*, *115*(3), 211–35.

Savage-Rumbaugh, E. S., Murphy, J., Sevcik, R. A., Brakke, K. E., Williams, S. L., & Rumbaugh, D. M. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child Development*, *58*(3-4), 1–222.

Schwarz, E. (1929). Das Vorkommen des Schimpansen auf den linken Kongo-Ufer. *Revue de Zoologie et de Botanique Africaines*, *16*, 425–426.

Scott-Phillips, T. C. (2015). Meaning in animal and human communication. *Animal Cognition*, *18*(3), 801–805.

Scott-Phillips, T. C. (2016). Meaning in great ape communication: summarising the debate. *Animal Cognition*, *19*(1), 233–238.

Sebeok, T. A. (1996). *Signs: An introduction to semiotics*. *Journal of Pragmatics*. Toronto: University of Toronto Press.

Senghas, A. (2005). Language Emergence: Clues from a New Bedouin Sign Language. *Current Biology*, *15*(12), 463–465.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, *28*, 1070–1094.

Slocombe, K. E., & Zuberbühler, K. (2006). Food-associated calls in chimpanzees: responses to food types or food preferences?. *Animal Behaviour*, *72*(5), 989-999.

Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior*, *22*, 1–63.

Snedecor, G. W., & Cochran, W. G. (1989). *Statistical methods 7th edition* (7th ed.). Iowa: Iowa State University Press.

Stanford, C. B. (1998). The Social Behavior of Chimpanzees and Bonobos: Empirical Evidence and Shifting Assumptions. *Current Anthropology*, *39*(4), 399–420.

Surbeck, M., Mundry, R., & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (Pan paniscus). *Proceedings of the Royal Society B: Biological Sciences*, *278*, 590–8.

Taglialatela, J. P., Cantalupo, C., & Hopkins, W. D. (2006). Gesture handedness predicts asymmetry in the chimpanzee inferior frontal gyrus. *Neuroreport*, *17*(9), 923–927.

Tanner, J. E., & Byrne, R. W. (1996). Representation of Action through Iconic Gesture in a Captive Lowland Gorilla '. *Current Anthropology*, *37*(1), 162–173.

Tashiro, Y., Idani, G., Kimura, D., & Bongori, L. (2007). Habitat changes and decreases in the bonobo population in Wamba , Demoratic Republic of the Congo. *African Study Monographs*, *28*(2), 99–106.

Teichroew, F. J. M. (1982). Receptive versus productive vocabulary: A survey. *Interlanguage Studies Bulletin*, *6*(2), 5–33.

Terrace, H. S., Petitto, L. A., Sanders, R. J., & Bever, T. G. (1979). Can an ape create a sentence? *Science*, *206*(4421), 891–902.

Thompson, J. A. M. (2003). A model of the biogeographical journey from Proto-pan to Pan paniscus. *Primates*, *44*, 191–7.

Tokuyama, N., & Furuichi, T. (2016). Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Animal Behaviour*, *119*, 27–35.

Tomasello, M. (2008). *Origins of human communication*. *The Jean Nicod lectures 2008*. Cambridge, MA: MIT Press.

Tomasello, M. (2009). *Constructing a Language: A Usage-Based Theory of Language Acquisition*. Cambridge, MA: Harvard University Press.

Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: a trans-generational study. *Primates*, *35*(2), 137–154.

Tomasello, M., Call, J., Warren, J., Frost, G. T., Carpenter, M., & Nagell, K. (1997). The Ontogeny of Chimpanzee Gestural Signals: A Comparison Across Groups and Generations. *Evolution of Communication*, *1*(2), 223–259.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and brain sciences*, *28*(05), 675-691.

Tomasello, M., Carpenter, M., & Liszkowski, U. (2007). A New Look at Infant Pointing. *Child Development*, *78*(3), 705–722.

Tomasello, M., Gust, D., & Frost, G. T. (1989). A longitudinal investigation of gestural communication in young chimpanzees. *Primates*, *30*(1), 35–50.

Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., … Manser, M. B. (2016). Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals. *Biological Reviews*.

Tutin, C. E. G. (1979). Mating Patterns and Reproductive Strategies in a Community of Wild Chimpanzees (Pan troglodytes schweinfirthii). *Behavioral Ecology and Sociobiology, 6*(1), 29–38.

Umiker-Sebeok, J., & Sebeok, T. A. (1981). Clever Hans and smart simians: the self-fulfilling prophecy and kindred methodological pitfalls. *Anthropos*, *76*(1/2), 89–165.

Vail, A. L., Manica, A., & Bshary, R. (2013). Referential gestures in fish collaborative hunting. *Nature Communications*, *4*, 1765.

Vea, J., & Sabater Pi, J. (1998). Spontaneous pointing behaviour in the wild pygmy chimpanzee (Pan paniscus). *Folia Primatologica, 69*, 289–290.

Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences*, *98*(23), 12890–5.

von Humboldt, C. W. F. (1836). *Ueber die Verschiedenheit des menschlichen Sprachbaues*. Berlin: Druckerei der Königlichen Akademie der Wissenschaften.

Wallis, J. (1992). Chimpanzee genital swelling and its role in the pattern of sociosexual behavior. *American Journal of Primatology*, *28*, 101–13.

Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., … Slocombe, K. E. (2015). Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees. *Current Biology*, *25*(4), 495–499.

Watts, D. P., Muller, M. N., Amsler, S. J., Mbabsi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology*, *68*, 161–180.

Wernicke, C. (1969). The symptom complex of aphasia: a psychological study on an anatomical basis. In R. S. Cohen & M. W. Wartofsky (Eds.), *Proceedings of the Boston Colloquium for the Philosophy of Science 1966/1968* (Vol. 4, pp. 34–97). Dordrecht: Springer Netherlands.

West, M. J., & King, A. P. (1988a). Female visual displays affect the development of male song in the cowbird. *Nature*, *334*, 244–246.

West, M. J., & King, A. P. (1988b). Female visual displays affect the development of male song in the cowbird. *Nature*, *334*, 244–246.

Wilkins, D. (2003). Why Pointing With the Index Finger Is Not a Universal (in Sociocultural and Semiotic Terms). In S. Kita (Ed.), *Pointing: Where Language, Culture, and Cognition Meet* (pp. 171–215). Mahwah, NJ: Lawrence Erlbaum Associates.

Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology*, *32*, 363–392.

Witmer, L. (1909). A monkey with a mind. *Psychological Clinic*.

Won, Y.-J., & Hey, J. (2005). Divergence population genetics of chimpanzees. *Molecular Biology and Evolution*, *22*(2), 297–307.

Wrangham, R. W. (1979). Sex differences in chimpanzee dispersion. In D. Hamburg & E. McCown (Eds.), *The great apes* (pp. 481–489). Menlo Park: Benjamin/Cummings.

Wrangham, R. W. (1993). The evolution of sexuality in chimpanzees and bonobos. *Human Nature*.

Wrangham, R. W. (1999). Evolution of coalitionary killing. *American Journal of Physical Anthropology*, *42*, 1–30.

Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In P. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 248–258). Cambridge: Cambridge University Press.

Wrangham, R. W., & Peterson, D. E. (1996). *Demonic males: Apes and the origins of human violence*. Boston: Houghton Miffli.

Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, Pan troglodytes schweinfurthii. *Animal Behaviour*, *77*(4), 873–885.

Yamamoto, S. (2015). Non-reciprocal but peaceful fruit sharing in wild bonobos in Wamba. *Behaviour*, *152*(3-4), 335–357.

Yip, M. (2002). *Tone*. Cambridge: Cambridge University Press.

Zihlman, A. L., & Cramer, D. L. (1978). Skeletal differences between pygmy (Pan paniscus) and common chimpanzees (Pan troglodytes). *Folia Primatologica*, *29*, 86–94.

Appendices

Appendix 1. Focal behaviour and individual sampling categories for "behaviour"

Agonistic: includes acts of aggression, attack, threat, display, submission, defence, reassurance, and appeasement

Drag branch: broken branch dragged along ground during locomotion, display

Explore: locomotion staying in same area, not travelling between locations

Feed: includes feeding, foraging, digging for food, food sharing, and food processing

Groom: focal individual grooming other individual

Being groomed: focal individual being groomed by other individual

Groom/being groomed: mutual grooming between two individuals, or focal individual grooming one individual while being groomed by another individual (polyadic grooming)

Groom self: focal individual grooming self

Nest: resting in day nest or in night nest

Nurse: [for mother] to feed infant at breast, [for infant] to feed at breast

Other: unusual behaviour not under listed category, described in comments section

Out of sight: focal individual is not visible

Rest: in stationary position, remaining immobile and not engaging in any other activity

Sexual: includes copulation, genito-genital rubbing, and solicitation

Social play: play between multiple individuals

Social play with object: play between multiple individuals involving an object

Solitary play: one individual play by self

Solitary play with object: one individual play by self with an object

Travel: locomotion between locations over long or short distances by walking, running or climbing

Unknown: location of individual was clear, but behaviour was not

Appendix 2. Focal behaviour and individual sampling categories for "posture"

Climb: locomotion in trees including vertical ascending and descending, and walking quadrupedally along branches

Cling: stationary, gripping tree trunk using all four limbs

Cling (belly): for infant or juvenile, holding on to adult's front

Cling (back): for infant or juvenile, holding on to adult's back

Dorso-ventral: during copulation, female's back faces male's front

Hang: suspended from branch usually by one or two limbs

Lie: stationary, on ground or in tree, lying in horizontal position on back or on front

Roll: rolling on ground, often in play, includes somersault

Run bipedal: locomotion, rapid gait with two feet touching ground

Run quadrupedal: locomotion, rapid gait with four feet touching ground

Sit: stationary, on ground or in tree, sit on rear with torso upright

Stand bipedal: stationary, stand upright on two feet

Stand bipedal with support: stationary, stand on two feet while holding onto object or other individual for support

Stand quadrupedal: stationary, stand on four feet

Unknown: location of individual was clear, but posture was not

Ventro-ventral: during copulation or genito-genital rubbing, both individuals face towards one another

Walk bipedal: locomotion, walking upright with two feet touching ground

Walk quadrupedal: locomotion, walking quadrupedally with four feet touching ground

Appendix 3. Focal behaviour and individual sampling categories for “general context”

Agonistic: includes act of aggression, attack, threat, display, submission, defence, reassurance, and appeasement

Encounter: Inter-group encounter

Feed: includes feeding, foraging, digging for food, food sharing, and food processing

Groom: includes grooming, mutual grooming, polyadic grooming, and self-grooming

Nest: resting in day nest or in night nest

Other: unusual behaviour not under listed category, described in comments section

Play: includes social play, social play with object, solitary play, and solitary play with object

Rest: in stationary position, remaining immobile and not engaging in any other activity

Sexual: includes copulation, genito-genital rubbing, and solicitation

Travel: locomotion over long or short distances by walking, running or climbing, includes exploration

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

22 November 2013

Project Title:	Gestural communication in wild bonobos (*Pan paniscus*)
Researcher's Name:	Kirsty Graham
Supervisor:	Professor Richard Byrne

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 20th November 2013. The following documents were reviewed:

1. Animal Ethics Form	20/11/2013
2. External Permissions (Kyoto University)	20/11/2013

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

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

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

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

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

Yours sincerely

Convenor of the School Ethics Committee

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