A field study on communication in wild *Pongo pygmaeus wurmbii* mother-offspring dyads

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Summary

Human communication consists of unique linguistic symbols which are not used by any other animal species . The evolution of human language has therefore been studied by focussing on non-human great apes as they represent the most recent divergence from the human lineage. What properties of communication do they posses and how are they used? Gestural communication, a means of communicating through ineffective body movements signalling particular messages, seems more similar in use then is vocalization of primates and is therefore studied. Did human language evolve from gestures?

The non-captive field of primate gesture research is understudied and comparisons between captive and wild living conspecifics can not easily be made due to differing environmental factors. For orangutans, the most arboreal and solitary great-ape species, no systematic communication study had been carried out yet. When focussing on wild orangutans, the mother-offspring dyad is most likely to perform communicative interactions as they have a strong bond. The duration of the offsprings dependence lasts 5-8 years and communicative interaction related to this dependence are present in e.g. locomotion and food sharing. Aditionally, vocalizations within the dyad can be studied as they might reflect communicative messages related to dependence.

By videotaping commucative interactions between mother-offspring orangutan dyads, analyses were carried out to obtain a repertoire of both forms of communication and comparisons have been made related to other great-ape species and age of offspring. Twelve intentional gestures were identified consisting of four different types: ‘Hit’, ‘Grab/Grasp’, ‘Touch’ and ‘Reach’. All gestures were found for captive orangutans and wild chimpanzees and gorillas too. No gestures were recorded in dyads with offspring of 2 and 50 months old, which represented the oldest and the youngest offspring within this study. However, vocal communication by means of ‘soft hoots & whimpers’ was already present in the 2 month old infant but this decreased for the oldest two infants of 47 and 50 months old. As proximity within a dyad increases with age, less communicative interaction were found for the older offspring. When being carried, mother initiate carries by means of gestures (‘Grab’) but mostly by means of actions (‘Gather’ or ‘Pull) as they might be more effective. Offspring, on the other hand, initiate carries only by actions (‘Climb on’). Food sharing takes place by initiation by the infant and consists of gestures (‘Reach’) and actions whereas actions were more successful. The highest number of carry initiations and food share attempts were found for the 21 month old infant and a decreas was observed for older offspring. Thus, a peak might be present in the occurance of orangutan mother-offspring communicative interactions.

By adopting the method for selecting on intentional gestures, from a captive orangutan gesture study, cases of possible intentional communication had te be excluded. For this reason, criteria have been altered and oppurtunities have been created for further research.

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1. Introduction

1.1 The study of communication in primates

Human communication consists of unique linguistic symbols which are not used by any other animal species (Pika, Liebal, Tomasello, & Call, 2005; Hobaiter & Byrne, 2011). The evolution of human language aroused the interest of paleoanthropologists studying the rise and evolution of the genus *Homo* (Cartmill, 2008). Research has focused on non-human apes as they represent the most recent divergence from the human lineage (Stauffer, Walker, Ryder, Lyons-Weiler, & Hedges, 2001; Cartmill, 2008). What properties of communication are present in non-human apes and how they are used is questioned (Cartmill, 2008). Studying primate vocalization led to the conclusion that it seems biologically fixed (innate), unintentional and in general is unlearnt (Pika et al., 2005; Hobaiter & Byrne, 2011; Slocombe, Waller, & Liebal, 2011). Any other form of communication is gestural: a means of communicating through ineffective body movements signalling particular messages, e.g. pointing (Liebal & Call, 2011). Gestural communication, opposed to vocal communication in non-human apes, appears to be more flexible, voluntary and intentional, like human language. It may reveal information about the precursor of speech (Pika et al., 2005; Cartmill & Maestripieri, 2011; Tempelmann & Liebal**,** 2012; Halina, Rossano, & Tomasello, 2013). Did human language evolve from gestures?

Slocombe et al. (2011) concluded that out of 553 primate communication studies only 9% (n=51) had focused on the gestural modality, where only 7,8% (n=4) was carried out in the wild. Out of all gestural studies 78,4% focused on great-apes. As environmental factors in captive settings differ from the wild (e.g. animals being forced to live within a certain area with conspecifics or being able to interact with humans), gestural repertoires found in captive studies possibly differ from those of wild conspecifics (Call & Tomasello, 1996; Tomasello & Call, 2011; Tempelmann & Liebal**,** 2012;). Nevertheless, the majority of gestures identified in a captive orangutan study by Liebal et al. (2006) were also found among wild and other captive individuals. In accordance, recent studies tend to designate inheritance as the main contributor of gestures in great-apes (Hobaiter & Byrne, 2011; Genty, Breuer, Hobaiter & Byrne, 2009) As the non-captive field is understudied, there appears to be a need for non-captive gestural communication research (Slocombe et al., 2011).

Among non-human great-apes, orangutans are the most solitary and arboreal suggesting that their communication may differ from the other great-ape species (van Schaik, 1999; Pika et al., 2005). An orangutans arboreal and solitary lifestyle presents many challenges when conducting research on orangutan communication, e.g. poor visibility and a limited number of communicative interaction

occurrences. Perhaps for these reasons, few studies have been carried out to date (Mackinnon, 1974; Rijksen, 1977; Bard, 1992).

Orangutans have a slow life-history including females having their first offspring at an mean age of 15.5 years and an interbith interval of 7.7 years (van Noordwijk, Sauren, Nuzuar, Abulani, Morrogh-Bernard, Atmoko, & van Schaik, 2009). The period of immaturity in orangutans has a duration of approximately 5-8 years and has therefore the longest duration of any ape species (Wich, de Vries, Ancrenaz, Perkins, Schumaker, Suzuku, & van Schaik, 2009). As the bond of mothers and offspring is the only strong bond in orangutans, the majority of gesture occurrences among wild oranguts are expected to be found within this dyad (Maestripirie, 1999 as cited in Liebal et al., 2006) . Immature orangutans below 8 years are (totally) dependent on their mothers for nutrition and transportion, thus communicative interactions within the context of 'feeding' and 'locomotion' are expected (van Adrichem, Utami, Wich, van Hooff & Sterck, 2006; Wich et al., 2009).

Offspring are dependent on their mother for locomotion, e.g. when being carried and when crossing gaps between trees. Communicative interactions are likely to happen at the initiation of the offspring being carried as this involves individuals coming into direct contact with each other. Communicative interactions in the context of 'feeding' occur when food is shared, something common in dyads with infants of a few years old (van Noordwijk et al., 2009). In comparison with other great-ape species, less communicative interactions are expected in the contexts of 'social play' and 'social grooming' as these behaviours are seldomly expressed within orangutan mother-infant dyads (van Noordwijk, 2009). In general, it is expected that communivative interactions will involve gestures, actions and vocalizations. Possible gestures include: 'Reach' within the food context and 'Touch' within the context of locomotion. The main vocalization type given by infants, the 'soft hoot & whimper', reflects the infants dependence on the mother as it is emitted in stressful situations when frightened and in feeding context (Wich et al., 2009). As dependence on the mother gradually decreases with age, variation in occurrance of communicative interaction and thus possibly gestures and vocalizations might be present.

To date, no systematic communication research has been carried out on wild orangutan mother-offspring dyads. This study therefore fills in a gap within this field. As the period of infancy in great-apes in general is understudied, this study might reveal important information about the acquisition of gestures (Schneider, Call & Liebal, 2011). How gestures are acquired is a subject of much debate (e.g. Hobaiter and Byrne 2011; Liebal and Call 2011; Doktorin, 2012, Halina et al., 2013; Bard et al., 2014).

1.2. Objectives

The aim of this observational behavioural research is to gain knowledge about gestural and vocal communication in wild mother-offspring orangutan (*Pongo pygmaeus wurmbii*) dyads.

Specific objectives are to:

1. Identify and describe the gestural repertoire of wild mother-offspring dyads.
2. Compare the gestural repertoire of wild orangutans with the repertoire reported for captive populations and other great-ape species.
3. Compare the gestural repertoire of mother-offspring dyads with regards to offspring age.
4. Compare vocal communication of mother-offspring dyads with regards to offspring age.
5. Compare gestural communication versus vocal communication.

2. Materials & Methods

2.1 Study site

The study took place in the Sabangau peat-swamp forest in Borneo, Indonesia (Figure 1; Indonesia–Malaysia confrontation, n.d.). It was carried out as part of the OuTrop multi-disciplinary research project in collaboration with CIMTROP (Figure 1). This forest consists of deep peatland which was subjected to illegal logging until 2004 (Morrogh-Bernard, 2009).

Figure 1: Borneo, divided among Brunei, Malaysia and Indonesia. This study took place in Central Kalimantan.

The study site is located within The Natural Laboratory for the Study of Peat Swamp Forest (NLPSF); an 500 km2 area within the Sabangau forest (Figure 2; Morrogh-Bernard, 2009). A research station is located 20 km south-west of Palangkaraya (2° 19'S and 114° 00'E). Within the study site, a grid system within a mixed-swamp forest sub-type was established. The grid system is a cut and marked trail system and contains trails every 250m running north-south and east-west (Appendix I).

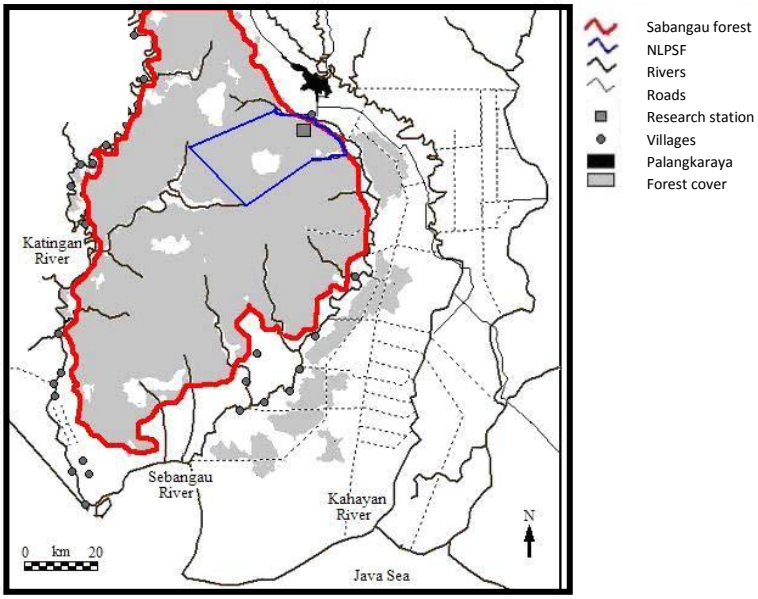

Figure 2: The Sabangau forest, containing the Natural Laboratory for the Study of Peat Swamp Forest (NLPSF) and the research station.

2.2 Study subjects and data collection

Data were collected on six habituated orangutan (*Pongo pygmaeus wurmbii*) mother-offspring dyads which have their home ranges (partially) within the grid system (Table 1). Following orangutans took place using the 'Sabangau Orangutan Behaviour Project Field Protocol' (ESM 1). Age classes are classified following Rijksen (1974). Data were ideally collected for a full active period (i.e. the moment an orangutan sits up in her nest, until the end of their active period when the orangutan has finished building its night nest and lays down). If a dyad was not followed for the entire active period, the follow was coded as a partial follow.

Table 1: Details on subjects

Dyad identification number	Individual	Sex	Age offspring (months) at first data collection	Age class
1	Cleo	Female		Adult female
	Chuck	Male	23	Infant
2	Feb	Female		Adult female
	Fio	Male	50	Juvenile
3	Gracia	Female		Adult female
	Gretel	Female	47	Juvenile
4	Indy	Female		Adult female
	Icarus	Male	21	Infant
5	Teresia	Female		Adult female
	Trevor	Male	31	Juvenile
6	Indah	Female		Adult femle
	Infant	-	2	Infant

Orangutans were followed in a team ranging from two to four observers. Ad libitum sampling was applied to video tape as much interaction between mothers and infant, including gestures and vocalizations (Altman, 1974). The same observer recorded the video footages on every follow. A Canon Powershot sx50 video camera was used in combination with a Velbon up-400 monopod.

The 'primary' data collector, as described in the 'Sabangau Orangutan Behaviour Project Field Protocol', collected data on estimated proximity between mothers and infants. This was carried out using instantaneous sampling on a 5 minute interval. Proximity was categorized as: 0=0m (contact), 1=<2m, 2=2-5m, 3=6-10m, 4=11-20m, 5=21-50m, 6=>50m, u=unknown (Appendix II).

The occurrence and number of vocalizations emitted by either the mother or infant were noted and, if possible, recorded on video. For 'soft hoot & whimper' vocalizations the duration was categorized and noted as: 1=1-10s, 2=11-30s, 3=31-60s, 4=61-300s, 5=>300s.

2.3 Analyses

2.3.1. Gestural repertoire

All videos were analysed for the presence of intentional gestures, defined according to the criteria used by Cartmill (2008) and Cartmill & Byrne (2010) to enable a direct comparison with their captive orangutan gesture study (Appendix III). Contrary to their method, no facial expressions were included in this research. A coding scheme was established to enable data analysis (Appendix IV). Gestural ethograms included in previous ape gestural studies were used to compare and identify gestural definitions and descriptions (i.e. varying criteria were used across the following studies: orangutan: Liebal et al., 2006, Cartmill, 2008, Cartmill & Byrne, 2011; Tempelmann & Liebal**,** 2012, chimpanzee: Hobait & Byrne, 2011, gorilla: Genty et al., 2009). Additionally, a focus was made on behaviours in the contexts of 'locomotion' and 'feeding' as it was expected that they could be involved in communicative interactions to a great extent due to an orangutan offspring's dependence on the mother.

2.3.1.1. Gesture use in the context of locomotion

Following the method of Halina et al. (2013), a carry was defined as '' the infant becoming somehow attached to his or her mother for the purpose of joint travel'' (p. 655). This could be by means of an action or a gesture initiated by mother or infant. Gestures were defined as described (refer 2.3.1). An carry initiation action was defined as ''any behaviour that succeeded in initiating a carry through direct physical force—that is, through the manipulation of another's body or the movement of one's own body into a carry position'' (p.655).

A coding scheme was established for data analysis on the following variables: 'Initiator', 'Means of carry initiation' and 'Definition' (Appendix V). Only videos where it was clear which individual initiated the carry were included in the analyses.

2.3.1.2. Gesture use in the context of feeding

Food sharing was defined according to the method of Feistner & McGew (1989; as cited in Jaeggi et al. 2008) as ''the transfer of a defendable food item from one food-motivated individual to another'' (p.535). Subsequently, a food item was defined as: ''different plant parts—fruits, flowers, mature leaves, young leaves, pith, inner bark (including phloem and cambium) and vegetative plant parts—of the same species'' (p. 535). Food share attempts could occur by means of an action or a gesture. Gestures were defined as described (refer 2.3.1). Food share actions were defined as: any behaviour that succeeded in the transfer of a defendable food item from one food-motivated individual to another through direct physical force—that is, through the manipulation of another's body or the movement of one's own body.

A coding scheme was established for data analysis including the following variables: 'Initiator', 'Means of food share attempt', 'Definition' and 'Successfulness' (Appendix VI). Only videos in which it was clear which individual initiated the food share attempt were included in the analyses.

2.4. Statistical analyses

Statistical analyses were performed using SPSS Statistics 22. Paramatric tests were two-tailed and were significant at an alpha level of 0.05.

Descriptive statistics were carried out on all objectives. A repeated measures-ANOVA was carried out to analyse the influence of the offspring's age on proximity. For this analysis, proximity data were re-categorized as follows: 0=0m, 1=1-10m and 2=>10m. For carry initiations, but also for food share attempts and vocalizations, the number of occurrences on every follow was converted to a 661 minute follow (mean active period in this study)([number of occurrence *661]/duration of the follow in minutes)) as not all follows were full day follows. The converted numbers per 661 minute during follow were then averaged per individual to a mean carry initiation rate per follow. This enables making a clear comparison between dyads.

3.Results

A total of 193 hours and 35 minutes was spent collecting data on six different orangutan mother-infant dyads (Table 2).

Table 2: Observation times divided over 6 different mother-infant dyads.

Dyad	Full day follows (n)	Partial follows (n)	Hours [u]:mm
1	1	1	20:22
2	5	2	61:38
3	1	1	19:01
4	3	1	39:21
5	3	-	31:34
6	2	-	21:39
Total	**15**	**5**	**193:35**

3.1. Gestural repertoire

In total 1059 videos were collected ranging in duration from a few seconds to > 16 minutes each. All videos were analysed on presence of intentional gestures. Twelve intentional gestures occurrences were identified. Three gesture types were performed by mothers and included 'Hit' (n=1), 'Grab/Grasp' (n=2) and 'Touch' (n=3)(Table 3). Two different gesture types were performed by the offspring: 'Reach' (n=5) and 'Hit' (n=1;)(Table 3). 'Reach' could have either the modality 'contact' or 'silent' as the hand could come in contact with the recipient, however, both modalities served the same goal (i.e. food sharing) and contact was not made in a distinct intentional manner. All other gesture types were of the modality 'contact'. The repertoires of the dyads are ranked according to the age of the offspring (youngest-oldest)(Table 4). No gestures were identified for those dyads containing the youngest and the oldest offspring.

Table 3: Definitions of gestures displayed by mothers and offspring.

Individual	Gesture type	Definition
Mother	Hit	*Hand touches recipient quickly and with force*
	Grab/Grasp	*Hand closes on recipient's body part*
	Touch	*Hand (palm and/or fingers) gently come in contact with recipient*
Offspring	Hit	*Hand touches recipient quickly and with force*
	Reach	*Arm extends to the recipient with hand in an open position (contact/visual)*

Table 4: Gestural repertoires ranked on age of the offspring (low-high). A 'X' represents the presence of a gesture type within the dyad's repertoire with N being the number of identified intentional occurances of that gesture type.

Age offspring (months)	Dyad	Gesture type			
		Hit	Grab/Grasp	Touch	Reach
2	6				
21	4		X (N=1)		X (N=5)
23	1	X (N=1)	X (N=1)	X (N=1)	
31	5	X (N=1)		X (N=1)	
47	3			X (N=1)	
50	2				

3.1.1. Gesture use in the context of locomotion

In total, proximity data were collected on 2364 5-minute intervals. There were 367 cases which had to be excluded as they were coded unknown. A repeated measures ANOVA highlighted that there was a significant, positive relationship between age and proximity (p=0,00). The two month old offspring was carried for 100% of the observed time and gradually this decreases to less then 1,8% of the observed time in a 50 month old offspring (Figure 3). The proximity never exceeded 50 meters in any of the dyads observed.

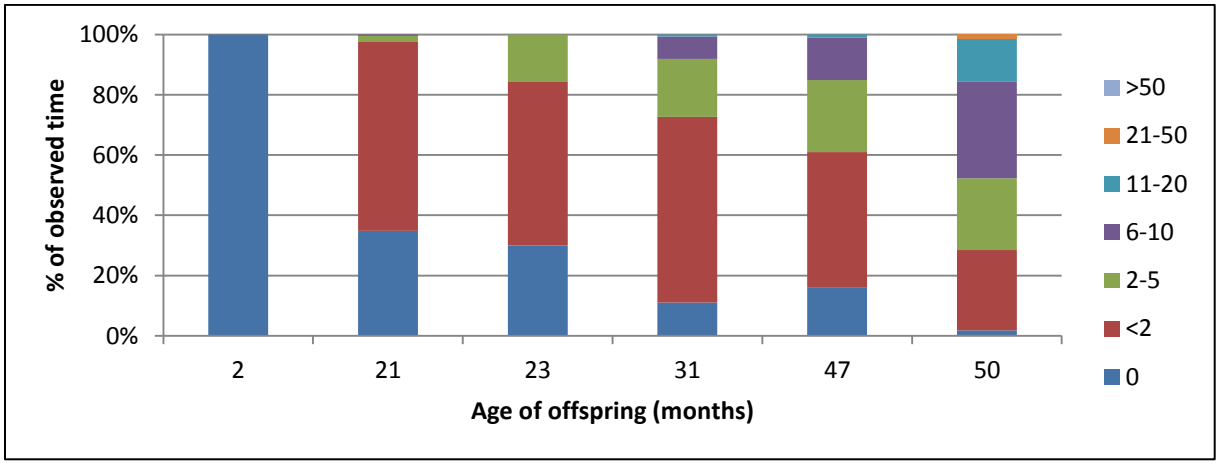

Figure 3: The relationship between an individual's age and proximity between mother and offspring (m), expressed as the percentage of time a proximity category was recorded within the entire observational period.

In total 72 carry initiations could be identified. A converted mean number of carries per follow was calculated for every dyad to enable comparison with each other (Table 5). No carry initiations were observed for dyad 6 as the 2 month old infant was never observed out of carry position. The highest mean number of carry initiations per follow was observed among dyad 4 (21 month old infant). A gradual decrease to 0,1 carry initiations per follow was found between the ages 21 and 50 months.

Table 5: Converted mean carry initiation number/follow ranked on age of the offspring (low-high).

Age offspring (months)	Dyad	Converted mean carry initiation number/ follow
2	6	0,0
21	4	13,7
23	1	6,5
31	5	2,7
47	3	1,5
50	2	0,1

Out of all 72 identified carries, 41 were initiated by the mother. Of all mother initiated carries, 26 took place by means of an action: 'Gather '(n=16) and 'Pull' (n=10) (Table 6). Two mother initiated carries were gestures and were identified as 'Grab'. From the 13 remaining mother initiated carries, the modality was unclear. All infant initiated carries (31) took place by means of an action. Carry initiation behaviour definition were adopted from Halina et al., (2013), except for the definition for the action 'Climb on'.

Table 6: Definitions of carry initiation behaviours displayed by mothers and offspring

Initiator	Behaviour	Type	Definition
Mother	Action	Gather	*Bring hand, arm, foot, or leg around the recipient's body; gather or turn the recipient toward on applying pressure to the body*
		Pull	*Grab the recipient's hair, skin, or body and exert a force (pull) so as to move the recipient toward*
	Gesture	Grab	*Grab the recipient's hair, skin or body. Exert either no force or a pulling force that is mechanical*
Offspring	Action	Climb on	*Climb onto the recipient's back or side-venter*

3.1.2. Gesture use in the context of feeding

In total 67 food share attempts were recorded where the initiator could be identified. All food share attempts were initiated by the offspring. It includes 5 gestures of the type 'Reach' (Table 3), 29 actions and 13 cases where it was unclear what the modality was. Gestures resulted in a succesrate of 40% whereas for action a succesrate of 90% was found. In total, 68% of all food share initiations resulted in a successful transfer of a food item (15% not successful, 17 unclear outcome).

A converted mean number of food share attempts per follow was calculated for every dyad to enable direct comparisons with each other (Table 7). No food share attempts were initiated by the 2 month old infant (dyad 6). The 21 month old infant (dyad 4) was found to initiate the highest number of food share attempts. For all other dyads, the mean number of food share attempts per follow was between 2.0 and 4.6.

Table 7: Converted mean food share attempt number/follow ranked on age of the offspring (low-high)

Age	Dyad	Converted mean food share attempt number/ follow
2	6	0,0
21	4	9,6
23	1	2,0
31	5	1,9
47	3	4,6
50	2	3,5

3.2. Vocalizations

The vocalization type which occurred within the mother-offspring dyads, being directed towards the other, was the 'soft hoot & whimper' emitted by the offspring as defined by Wich et al. (2009). These vocalisations were given by each offspring studied. In total 121 bouts were noted. A converted mean number of vocalization bouts per follow was calculated for every dyad to enable direct comparisons with each other (Table 8). The two oldest offspring had a reduced number of mean vocalization bouts per follow in comparison to the other 4 offspring.

Table 8: Converted mean vocalization bout number/follow ranked on age of the offspring (low-high)

Age	Dyad	Mean vocalization bout number/follow
2	6	11,8
21	4	7,8
23	1	10,5
31	5	13,7
47	3	0,5
50	2	2,4

The duration of each vocalisation bout was categorised (1=1-10s, 2=11-30s, 3=31-60s, 4=61-300s, 5=>300s) and the number of vocalization bouts per category were expressed as a percentage of the total number of vocalization bouts emitted by an individual. For each offspring, the majority of emitted 'soft hoot & whimpers' had a duration of 0-10 seconds (Figure 4).

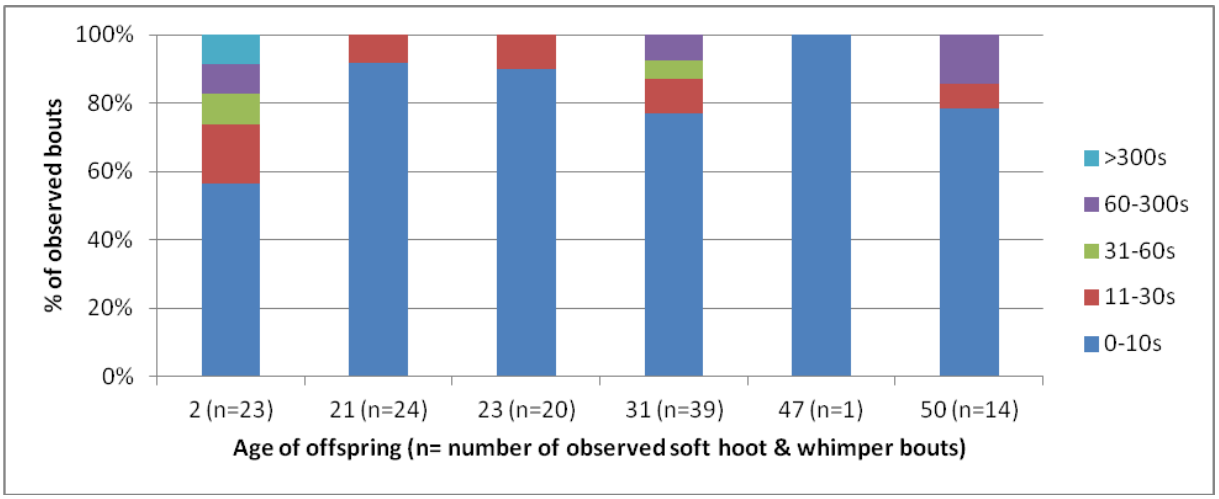

Figure 4: The relationship between an individual's age and occurance of 'soft hoot & whimper' bouts categorized based on duration, expressed as a percentage of the total number of observed vocalization bouts per individual.

4. Discussion

The aim of this study was to gain knowledge about gestural and vocal communication in wild mother-offspring orangutan (*Pongo pygmaeus wurmbii*) dyads with the objectives to:

1. Identify and describe the gestural repertoire of wild mother-offspring dyads.
2. Compare the gestural repertoire of wild orangutans with the repertoire reported for captive populations and other great-ape species.
3. Compare the gestural repertoire of mother-offspring dyads with regards to offspring age.
4. Compare vocal communication of mother-offspring dyads with regards to offspring age.
5. Comparing gestural communication versus vocal communication.

4.1. A comparison of communicative repertoires

Twelve intentional gestures were identified consisting of four different gesture types: 'Hit' (n=2), 'Grab/Grasp' (n=2), 'Touch' (n=3), and 'Reach' (n=5). Criteria used to identify intentional gestures were adopted from the method of a captive study on orangutans to enable a direct comparison (Cartmill, 2008; Cartmill & Byrne, 2011). All four gesture types were also found in the captive study. However, the gesture 'Reach' within this study could have either the modality 'contact' or 'silent' whereas it is identified as a 'silent' (visual) gesture in the captive study. Studies by Liebal at el. (2006) and Tempelmann & Liebal (2012), using similar but not the same criteria, included 'Gentle touch' and 'Hold hand in front of mouth' in a captive orangutan's repertoire. 'Gentle touch' was defined by Liebal et al. (2006) as: 'Sender touches the social partner gently with hand or foot on any body part (p. 11)' and 'Hold hand in front of mouth' was defined as: 'Sender puts its extended arm with the palm directed upwards in front of the mouth of another individual (p.11)'. Gestures observed in this study have therefore been previously reported for captive orangutan populations. In addition, the gestures 'Grab/grasp', 'Touch' and 'Reach' have been reported for wild chimpanzees (Hobaiter & Byrne, 2011), and the gestures ''Reach' and 'Touch' have been reported for wild gorillas too (Genty et al., 2009).

Captive studies focusing on gestural communication in orangutans were never focused on the mother-offspring dyad but found high numbers of gestural occurrences. Cartmill (2008) found 1334 intentional gestures of 64 different types, Liebal et al. (2006) found 2112 communicative signals (gestures, facial expressions and action) and Liebal et al. (2012) recorded 1128 gestures of 27 types. When making a comparison between captive and wild, various explanations for this difference can be found, independent of the duration of the study. One of the most obvious differences is that captive

orangutans were kept in groups whereas the natural social organization of orangutans is more solitary. As socio-cognitive skills are correlated with social complexity, more gestures may occur in group-living orangutans (Whiten & Byrne, 1997 as cited in Liebal et al., 2006). Differences in diet, environmental construction, activity budget and close association with humans may also have had an influence on the gestural communication of orangutans in captivity.
Also, the use of different intentional gesture selection criteria makes findings incomparable.

No gestures were observed in those dyads containing the youngest (2 month old) and the oldest offspring (50 month old). In accordance, Schneider (2012) reported the onset of gestural communication of captive orangutans at a mean age of 15 months. Liebal et al. (2006) found a negative correlation in age and number of communicative interaction signals observed (gestures, facial expressions and actions). An increase in number was observed within the infants and juveniles period but a decrease followed for subadults and adults. For wild orangutans, a decrease in communicative interactions in correlation with age might be supported by the increasing proximity through the development of independence. When proximity increases, the number of communicative interactions are likely to decrease.

The 2 month old infant was carried for 100% of the observed time this is because an orangutan infant is in need of constant body contact for the first months of his/her life. No carry initiations could be identified for this dyad (Wich et al., 2009). For the second youngest infant, the proximity and the number of Carry initiations increased accordingly but the number of carry initiations dropped for older offspring. Two gestures were used by the mother to initiate a carry whereas all infant initiated carries took place by actions. Within carry initiation, infants are thus more likely to use a action (i.e. Climb on) to become attached to his or her mother. This might be due to the offspring's tendency to stay in close proximity when the mother starts moving. Mothers however, have been recorded to use gestures but use more action. This might be due to the mothers being or become inpatient when waiting for the offspring. By performing an action, the offspring is more likely to become attached to the mother as performing a gesture is motorically ineffective and the infant still has to climb onto the mother and thus also has the chance not to do so.

For food sharing a similar pattern was observed. The youngest offspring was still dependent on mother milk and no food share attempts were recorded, whereas for the second youngest offspring the highest number of food share attempts was recorded. The number of food share attempts were lowest for all older individuals. Transfer of food from mother to infant is common in primates and may occur as means of 'nutritional transfer', e.g. leading to a increased grow rate and reduce

dependent period, or as means of 'information transfer', e.g. gaining knowledge about diet or food-processing skills (Brown, Almond & van Bergen, 2004). As offspring made all food transfer attempts and the number of attempts decreased with age, it is more likely that the informational hypotheses suggested by Brown et al. (2004) is an explanation for food sharing within orangutan mothers and offspring. Food share attempts included the gesture type 'Reach' on 5 occasions, but more sharings took place by means of an action. By means of an action, the changes of success might be enhanced in comparison with the use of a motorically ineffective gesture. This appears to be true for gestures asa success rate of 40% was found, whereas for actions a success rate of 90% was found. The number of successful attempts, either being an action or gesture, resulting in the transfer of a food item, was relatively high (68%).

The other form of communication, vocalization, included 'soft hoot & whimpers' emitted by the offspring. Bouts were recorded on 121 occasions. The two oldest offspring had a reduced number of mean vocalization bouts per follow in comparison to the other 4 youngest offspring. When comparing this vocal form of communication with the gestural form, differences can be found regarding to age. While the youngest offspring was not observed performing gestures, vocalization occurrences were present. Additionally, where younger offspring had more carry initiations then food share attempts, the two eldest offspring showed opposite results . Offspring therefore seem to be more dependent on the mother for food then for locomotion. With regards to age, gesture and vocalization occurrences seem to rise simultaneously, but eventually decrease when the offspring becomes more independent.

4.2 Limitations and recommendations

Due to the small number of subjects in this study, age effects have to be interpreted with caution. For a study looking at developmental behaviours in orangutans, longitudinal studies with ideally numerous similar aged subjects are needed as the orangutan development of independence has a duration of approximately 8 years. However, this study was a short term study but can be seen as a pilot study in a very promising new field. Limitations were found during this gestural pilot study and will be described here.

a) Visibility: an orangutan's arboreal lifestyle does not lend itselfs easily for a study on communication between conspecifics. To enhance data analysis, videos were taped so behaviours could be replayed numerous times for analysis. Also, only a limited number of videos could be included in the analyses because in many cases not all criteria were be fullfilled.

b) Gestural criteria: when defining intentional gestures many different criteria can be used. In this study, criteria applied to captive orangutan behaviours were adopted as no wild studies with the same focus had been carried out yet in the wild to date. These criteria limited the number of gestures but also gesture types identified. The wild orangutans' solitary lifestyle and environmental factors differ from those in captivity, and could have caused the criteria to not be as applicable as they were in other studies. Based on the obtained experience from this study, the suggestion is made to alter the criteria With the altered criteria more intentional gestures could be identiefied in future studies. Observed behaviours which might fullfill the altered criteria, but not the adopted criteria, are listed (Appendix VII). The altered criteria will be suggested for future research (Appendix VIII).

5. Conclusion

To date, this was the ever first study focusing on communication within wild orangutan mother-infant dyads. By making an inventory of the gestural and vocal repertoire, and comparing these repertoires among different aged offspring and other great-ape species, an attempt was made to gain knowledge about the use of these forms of communication. Gestures observed have been reported for other great-apes in previous research. Differences based on age seem present, in which vocal communication is present in young infants, whereas gestural communication is not. Proximity within a dyad was found to be positively influenced by the offsprings' age. Accordingly, the number of carry initiations and food share attempts peaked for the 21 month old infant and decreased later. Within carry initiations, mothers used gestures, but mainly actions, whereas infant's only used actions. Also for food share attempts, which were all initiated by the offspring, gestures and actions were used but actions appeared to be more successful and possibly thus preferred by the signaller. 'Soft hoot & whimper' bouts had a duration of 0-10s for the majority of occurrences and the number of bouts seems to decline with age. This is in accordance with becoming more independent. As the mean number of food share initiations for the two older infants was higher than the number of carry initiations, offspring seem to be more dependent on the mother for food then for locomotion. In general, as offspring become more independent with age, less communicative interactions will take place.

Due to criteria used for selection on gestures, the number of gestures identified was limited. Therefore, criteria have been altered to suit the orangutan's solitary and arboreal lifestyle better. When applying these criteria, the identified gestural repertoire will only expand. As this short-term study was a pilot, future oppurtunities have been created for further research.

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7. Appendices

Appendix I: Study site map

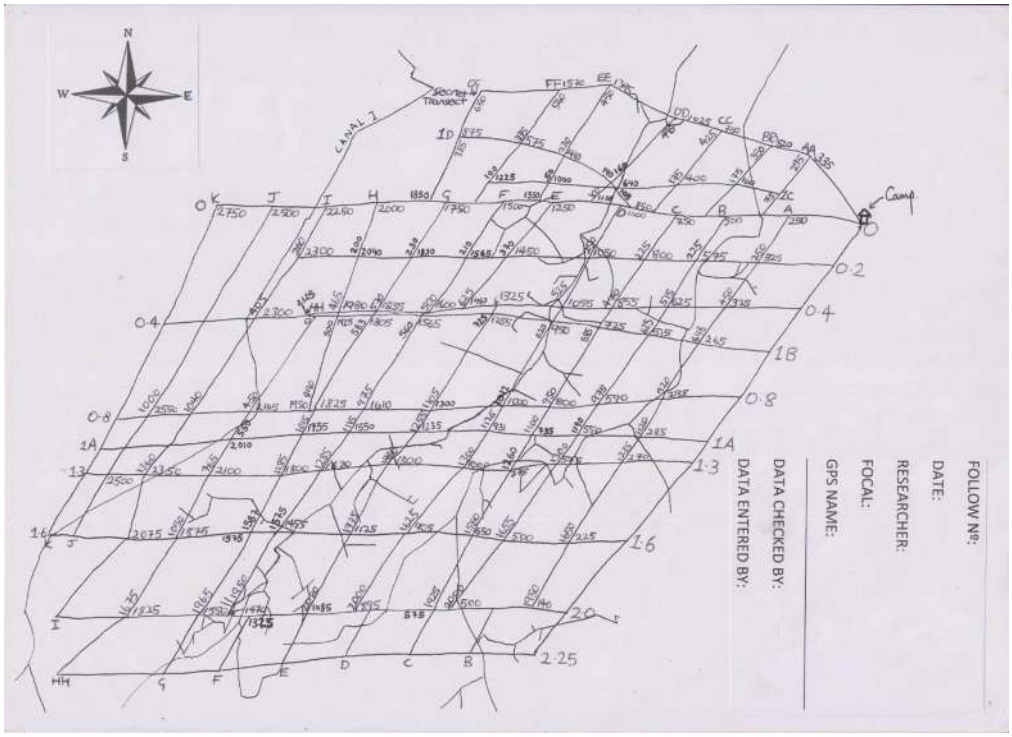

Figure 5: The west side of the grid system in which this research was out, containing trails every 250m running north-south and east-west.

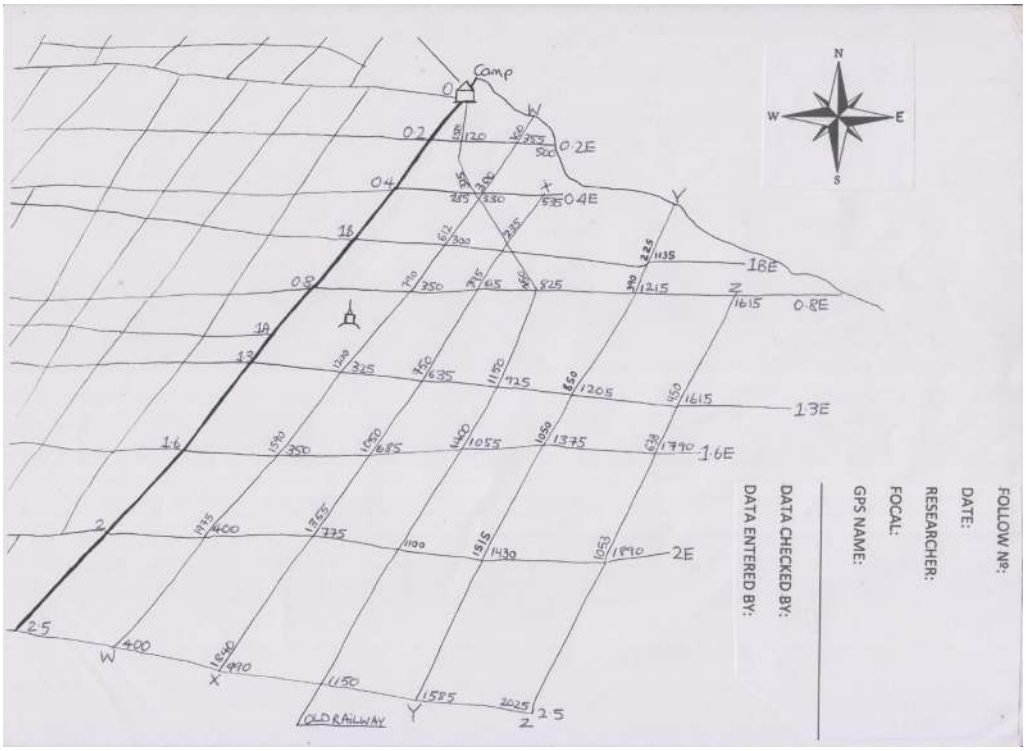

Figure 6: The east side of the grid system in which this research was out, containing trails every 250m running north-south and east-west

Appendix II: Proximity coding scheme

Table 9: Proximity coding scheme.

Dyad	Age infant (months)	Date	Time (u:mm)	Proximity
			5:00	
			5:05 etc.	

Coding as following:

Dyad: 1, 2, 3, 4, 5 or 6 (Tabel 1)

Age infant (months): Chuck=23, Fio =50, Gretel=47, Icarus=21, Trevor =31, Infant=2 (Table 1)

Date: dd.mm.yy

Time: 5 minute intervals

Proximity: 0=0, 1=<2, 2=2-5, 3=6-10, 4=11-20, 5=21-50, 6=>50, u=unknown

Appendix III: Gestural criteria

Potential gesture were defined according to the method of Cartmill & Byrne (2010):

> Movements of the face, head, limbs, or body when ‘‘motorically ineffective’’ ... and directed towards another individual. Gestures were considered to be motorically ineffective if they did not directly perform a practical act such as scratching or picking up an object. Potential tactile [contact] gestures were considered to be motorically ineffective if the recipient did not move immediately (as if by force) after contact, or the degree of the actual movement was considered to be greater than justified by the force of the gesture... Determining whether a movement was directed towards another individual was straightforward when the movement was tactile. Visual [silent] movements were defined as directed only if the gesturing individual performed the act while oriented towards and apparently looking at another individual. We did not require that visual [silent] gestures be potentially detectable by the individuals towards whom they were directed (as did Genty et al. 2009), because this would have excluded cases of ineffective signal use and ruled out the possibility of analysing the frequency of ineffective signal use.
>
> We coded all potential gestures that occurred during a social interaction unless the interaction involved continuous active contact between the individuals. Coding was thus stopped at the onset of physical play (such as wrestling), cuddling, nursing or carrying an infant, or mating. If continuous interaction ceased for at least 10 s, any gestures following the pause were again coded and included in the analysis. We included facial expressions in our list of potential gestures, provided they met the criteria of directedness and were performed on their own rather than accompanying a manual potential gesture (when they accompanied a manual potential gesture, they were recorded as an aspect of that potential gesture). (p. 796-797)

Contrary to what is cited above, no facial expressions were included in this study. Intentionality was defined as (Carmtill & Byrne, 2010):

> An act is deemed to be intentionally communicative if it is: (1) directed towards another (part of our criteria for potential gestures), with (2) the apparent objective of obtaining a goal, and (3) employed flexibly rather than as an automatic response to a stimulus... In order to establish whether the signaller had an intended goal, we looked for evidence that the signaller ‘‘expected’’ a reaction from the recipient, rather than signalling in an automatic response to some environmental stimulus; measures of expected reaction included remaining oriented towards the recipient without performing any additional act as if waiting for a reaction, alternating gaze between the recipient and an object or location, persisting, and using modalities appropriate to the attentional state of the recipient (e.g. using silent visual gestures only when the recipient is looking). Use of potential gestures in varying combinations with other potential gestures was also considered evidence of flexible, goal-directed behaviour. (p. 797)

‘Response waiting/waiting for a reaction’ was defined as: ‘’ Signaller pauses after gesture, remains oriented towards recipient for at least 5 seconds’’ (Cartmill, 2008, p. 43) and persistence was defined as ‘‘repeating the same gesture, using another gesture, or holding the final position of the gesture for more than 2s.’’ (Cartmill & Byrne, 2010, p. 800).

Appendix IV: Intentional gesture coding scheme

Table 10: Intentional gesture coding scheme

Date	Dyad	Video	Individual	Visibility on potential gesture	Definition	Motorically effective	Directed to other individual	Goal directed	Flexibly employed	Intentional gesture	Note

Coding as following:

Date: dd.mm.yy

Dyad: 1, 2, 3, 4, 5 or 6 (Table 1)

Video: video number as coded on camera. If more potential gestures occurred in one video, they were separated and coded as separate clips, e.g. '10.1' and 10.2'.

Individual: 1=mother, 2=infant

Visibility on potential gesture: 1=clear, 2=unclear (e.g. not in complete good sight)

Definition: gestural definition

Motorically effective: 1=yes, 2=no, 3=unclear

Directed to other individual: 1=yes, 2=no, 3=unclear

Flexibly employed: 1=yes, 2=no, 3=unclear

Intentional gesture: Sums codings of the following colums: 'Motorically effective, 'Directedness', 'Goal directed'and 'Flexibly employed'. If the calculated number equals 4, then all criteria have been fulfilled and the 'Intentional gesture' collum was coded with 1=intentional gesture. If not, the collum was coded with 2= not intentional gesture

Note: notes were made about time of potential gesture occurrence in video and what movements were observed

Appendix V: Carry initiation coding scheme

Table 11: Carry initiation coding scheme

Date	Dyad	Video	Initiator	Means of carry initiation	Definition	Note

Coding as following:

Date: dd.mm.yy

Dyad: 1, 2, 3, 4, 5 or 6 (Table 1)

Video: video number as coded on camera. If more potential gestures occurred in one video, they were separated and coded as separate clips, e.g. '10.1' and 10.2'.

Initiator: 1=mother, 2=infant, 3=unclear

Means of carry initiation: 1=gesture, 2=action

Definition: gesture/action defenition

Appendix VI: Food sharing coding scheme

Table 12: Food sharin coding scheme.

Date	Dyad	Video	Initiator	Means of food share attempt	Definition	Successfulness	Note

Coding as following:

Date: dd.mm.yy

Dyad: 1, 2, 3, 4, 5 or 6 (Table 1)

Video: video number as coded on camera. If more potential gestures occurred in one video, they were separated and coded as separate clips, e.g. '10.1' and 10.2'.

Initiator: 1=mother, 2=infant

Means of food share attempt: 1=gesture, 2=action

Definition: gesture/action definition

Succesfulness: 1=successful, not successful, 3= unclear

Appendix VII: Explanation for altering of gestural criteria

Criteria used in the method of Cartmill (2008) and Cartmill & Byrne (2010) on captive orangutans were adopted but did not seem to fit the more arboreal and solitary life style of wild orangutan mother-infant dyads. Why part of the criteria did not seem to fit, will be described here.

- Motorically ineffectiveness

Determing wether a movement is motorically ineffective can be difficult for contact gestures. If the recipient does not moves (as if by force) or if the degree of the actual movement is greater than justified by the force of the gestures, can be doubted. Making the division between gestures and actions here is a problem and this can not be solved by no other means than excluding these ambiguous cases.

- Directedness towards an other individual

For silent gestures, the criteria for directedness were as following: 'the gesturing individual performed the act while oriented towards and apparently looking at another individual'. The study using this criterium included settings in which great-apes were likely to communicate with more than one social partner and subjects were more likely to be visible. However, for wild orangutan mother-offspring dyad, a third social partner is absent for the majority of time and vegetation limits visibility to a great extent. For example, a infant is not in sight but the mother is. The infant extends his/her arm and hand (open) to the mothers mouth, by which the infants limb becomes partially visible (no contact). As one is not able to determine if the infant is oriented towards and apparently looking at another individual due to visibility, this case can not be included as a potential gesture eventhough all criteria for intentional gesture may be fullfilled (e.g. response waiting and employed flexibly rather than an autonomic response). In addtion, as no other social partner is present for the majority of time, the only conspecific to which the gesture can be directed to is the other individual in the dyad.

- Inclusion or exclusion of continuous active contact interactions

Wheter to include or exclude interactions which involve continuous active contact between individuals , e.g. play, can be doubted. In this study, play interactions were excluded for analyses unless they ceased for 10 seconds and an other gesture was displayed. When an ongoing interaction was interrupted by 5 seconds and a next signal was expressed, Liebal et al. (2006) included the latter gesture again within the research whereas Genty et al. (2009) focused only on play initiations and Hobaiter & Byrne included all play gestures if they fullfilled all criteria. Eventhough play interactions

do not take place often within mother-offspring dyads, gestures still might occur and thus might have been missed in this study.

- Goal-directedness

Criteria were for goal directedness were: the signaller remained oriented towards recipient without performing any additional act as if waiting for a reaction, alternating gaze between the recipient and an object or location, persisitng and using modalities appropriate to the attentional state of the recipient. Response waiting/waiting for a reaction was defined as: Signaller pasuses after gesture, remains oriented towards recipient for at least 5 seconds. If a signaller remained oriented was not always possible to see eventhough. Persisting was defined as: repeating the same gesture, using antoher gesture, or holding the final position of the gesture for more than 2s. Use of a particular duration wil unneccesary exclude cases of intentional gestures.

Appendix VIII: Altered gestural criteria.

Potential gesture:

- Movement of the face, head, limbs or body when motorically ineffecive
- Deliberately targeted to a particular recipient
- Aim of influencing their behaviour in a particular way (including interactions which involve continuous active contact between individuals).

Intentional gesture:

- Goal directed: signaller expects a reaction: holds position or remains oriented as if in waiting, alternates gaze between the recipient and anobject or location, persists or elaborates,
- Employed flexibly rather than as an automatic re sponse to a stimulus

Appendix IX: Observed behaviours with intentional gesture potential

Tabel 1: Behaviours observed with potential of being a intental gesture, pending on the criteria used: Cartmill (2008)/Cartmill & Byrne (2010)[1], Hobaiter & Byrne (2011) [2], Liebal et al. (2006)[3].

Behaviour	Desciption
Beckon	Arm, hand or finger is extended towards recipient and then swept in an arc towards recipient[1]
Bite	Open mouth is pressed against recipient and then partially-closed[1]
Brush	Hand/fingers lightly drag(s) along recipient[1]
Dangle	Signaller hangs upside down from structure (usually in front or above recipient)[1]
Duck lips closed	Lips are pursed together, fully extended and flexed outward to creata a trumpet shape[1]
Extend arm	Sender extends its arm towards the recipient: the palm of the hand is not directed upwards[3]
Frog lips	Lips flattened and broadened into a straight horizontal line[2]
Grab	Hand closes quickly on recipient's body part[1]
Grasp	Hand closes slowly on recipient's body part[1]
Mouth stroke	Signallers palm and finger are repeatedly run over the mouth area of the recipient[2]
Nudge	Body part is placed in contact with recipient and directional force is applied/Part of the body other than the handgently pushes recipient[1]

Object in mouth approach	Signaller approaches recipient while carrying an object in the mouth (e.g. a small branch) [2]
Offer	Object is extended towards recipient[1]
Play face	Corners of mouth are pulled back, mouth is opened wide and teeth are shown[1]
Pout	Lips are pursed together and extended [1]
Present body part	Part of the torso or upper part of the limb is extended o rangled towards recipient/Part of the body is extended or angled towards recipient and held[1]
Present climb on me	Arm or leg is extended to young recipient in order to facilitate them climbing onto the signallers body (normally other to infant)[2]
Pull	Hand closes on recipient and retracts towards signaller[1]
Pull away appendage	Hand closes on recipients appendage and extends away from signaller/Hand grasps hand or foor of recipient and extends away from signaller[1]
Pull hair	Hand closes on recipient's hair and retracts towards signaller/Hand grasps clump of recipients hair and retracts towards signaller [1]
Push	Hand grips or rests on recipient and moderate or hard force is applied away from signaller[1]
Raise arm/limb	Arm is extended from body and raised[1]
Raspberry-face	Mouth forms shape of raspberry vocalizastion but without vocalization/ (movement is often repeated several times)[1]

Reach	Arm and hand are both extended towards recipient[1]/Arm extends to the recipient with hand in an open, upwards position (no contact)[2]
Restrain	Hand grips recipient and restricts recipients movement/ Hand grips recipient's appendage and holds it tightly[1]
Seize	Hand grabs or grasps object held by recipient[1]
Shake	Object is held out from body and waved quickly[1]
Shoo	Back of hand facing recipiënt, arm or hand extendedquickly in arc towards recipient/ Arm or hand extended quickly in arc towards recipient with back of hand facing recipient[1]
Shrug	Shoulder is raised quickly against recipient/ Shoulder is raised and lowered quickly in contact with recipient[1]
Simultaneous hit	Signaller and recipient 'hit' eacht other at the same time/Signaller and recipient strike each other with an extended arm at the same time (usually preceded by a slow coordinated arm raise)[1]
Swing	Body suspended from structure and moved through an arc /back and forth (often repeated/usually in front of or above recipient)[1]
Tap	Fingertips lightly and quickly 'hit'/touch recipient (and retracts)[1]
Teeth bared	Lips retracted fully revealing parted teeth[1]
Whistle face	Lips are shaped into a tight 'o' shape and extended forward[1]