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Sex and communication in bonobo (*Pan paniscus* Schwartz, 1929). The role of gestures and facial expressions

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Aim of the study

We tested the following hypothesis:

Hierarchy and dominance relationships

a) Recent studies on bonobo dominance showed a society characterized by *non-linear* hierarchy with *co-dominance* of males and females. We expect comparable results.

b) Asymmetries in the performance of *genital contacts* between bonobos were abundantly reported. If sexual interactions are conditioned by rank, we expect that our results, in agreement with the hypothesis of Hohmann and Fruth (2000), show *high-ranking* individuals more frequently in the *upper positions*.

2) **Possible factors influencing sexual contacts**

a) If *sex* represents an important resource for the homeostasis of bonobo group, we expect that distribution of sexual contacts is not random, but shaped by different variables (anatomical and social).

b) Considering that females, with the appearance of *sexual swelling,* are characterized by an increase in proceptivity, receptivity and attractiveness to males, we expect that frequency of reproductive heterosexual contacts increase when females experience *maximum degree of tumescence* (swelling).

c) *Sexual swelling* subsequently evolved as attractive signal to other females. Following this hypothesis we expect that frequency of female homosexual contacts (genito-genital rubbing) increase when at least one female experiences *maximum degree of tumescence*.

3) Communicative strategies

a) In the investigation of communicative strategies used to persuade an individual to engage in sexual contacts, we can find many communicative forms lead by different cognitive level. Following the hypothesis of Pollick and de Waal (2007), we expect that gestures are the most flexible communicative signals used in several social contexts.

b) Assuming that sex is essential in bonobo sociality, we suppose to find that communication before sexual contacts (sexual invitations) is managed by intentional component (gestures). Could it be an evidence of intentionality and an indicator of motivation in communication?

c) If sex is a resource, and sexual invitations are guided by *intentions*, can we observe an evidence of *communicative effort* to gain *sexual resources* in terms of signal optimization*?* We expect that transmission of important messages is entrusted to *communicative complex signals,* to increase their efficiency and gain one of the most important resources, sex.

CHAPTER I

INTRODUCTION

1 - Many way to communicate

Communication can be defined, in behavioural ecology, as the process through sender individuals called *actor* uses specifically structured signals or display to modify behaviour of *receiver* (*Krebs & Davies*, 2002) . This definition includes only those signals and displays that *specifically evolved* for having a communicative function and therefore, explains their ultimate causation (*Mayr 1961*; *Tinbergen*, 1963).

Animals can use different sensorial channels to exchange information: chemical, acoustic, tactile and visual. Egalitarian species living in complex social systems, show the highest communicative complexity.

Natural selection had facilitate, and continue to encourage, communicative signals with high efficiency in term of costs-benefits, within the environmental opportunities scenario. Considering that signal's effectiveness depends by the *answer* of receivers, we can glimpse the essential role played by receiver in the evolutionary origin of signals and in the evolution of communication and its complexity.

Despite the unquestionable importance of establishing the ultimate causation of primate communicative signals, the current debate on primate communication is mainly focused on their proximate causation. More in detail, scientists applying a more psychological approach are particularly interested in establishing whether a communicative signal is the outcome of intentional or emotional processes (*Liebal et al.*, 2013).

1.1 – Between intentionality and emotionality

Before speaking about communication, it's important to underline the mode that found it. Modification in the use of a given communicative signal, according to environmental and social factors, entails some degree of *intentionality* and it is of particular importance for establishing the proximate factors leading to its emission. Therefore *intentional* communicative signals are produced under voluntary control and they are the product of complex cognitive capacities, in comparison to *emotional* signals produced by emotional states.

So far, almost all the available findings on primate *intentional* signals concerned the *gestural* communication in the great apes (*Call & Tomasello*, 2007). Although a certain degree of voluntary control has been highlighted also for primate *facial expressions* and *vocalizations* (Arbib et al. 2008; Sherwood et al. 2004, 2005;), these signals are predominantly classified as *emotional signals* (*Ekman* 1993, 1997; *Parr et al.* 2005).

Criteria used to identify intentional communications are:

- signals are voluntarily produced (*Call & Tomasello,* 2007; *Arbib et al,.* 2008)
- signals are socially used (*Leavens et al.,* 2005)
- realization of signals is affected by degree of receiver's attention (*Bakeman & Adamson 1986*; *O'Neill 1996*).
- persistence or behaviour processing when signals reach no one (*Genty & Zuberbühler, 2014*)

All of these characteristics were detected in the gestural communication of great apes (*Call & Tomasello,* 1994; *Hare et al.*, 2000; *Hostetter et al.*, 2001; *Pika et al.*, 2003; *Liebal et al.*, 2004; *Poss et al.*, 2006; *Pollick & de Waal*, 2007; *Leavens et al.*, 1996, 2004a,b).

The most studied non-physiological communicative signals are: *vocalizations*, *facial expressions* and *gestures*. Originally, researchers definitely divided *gestural communication* from *vocalizations* and *facial expressions* meaning only gestures as intentional signals while vocalizations and facial expression as belonging to emotional sphere. Parr and colleagues (2005*)* instead had proven that also facial expressions can be intentionally produced and today growing evidence suggests that this dichotomy should be revisited as the degree at which *intentional* and *emotional* processes intermingle is nowadays impossible to ascertain (*Cattaneo & Pavesi*, 2014). Moreover some authors argue that intentionality and emotionality are not mutually exclusive in the signal-production process but, rather, may represent two mechanisms that interact during signal production (*Demuru et al.,* 2014; *Liebal et al*., 2014).

The issue of intentionality becomes central when we consider that intentionality is the key feature of human communication. Therefore, the study of intentional communication in primates could help us to shed light on the evolutionary pathway that led to the emergence of human language.

1.1.1 – Vocal communication

Primates exhibit a genetically preconditioned repertoire of vocalizations and they can't create new signals (*Snowdon & Hausberger, 1997*). Generally vocalizations are considered fixed and not flexible because they directly depend by specific context (*Arbib et al. 2008*; *Genty et al. 2009*) and are strictly linked to it, for example predator avoid, food discovered and group movement coordination (*Tomasello & Zuberbühler, 2002)*. Clearly primates has a certain freedom degree and can modulate and modify its vocal repertoire, it is demonstrated by vocal signal differences in different social situations, better known as "*audience effect*" (*Tomasello & Zuberbühler, 2002*).

The *audience effect* reveal that an individual can strategically modify vocal signals regarding individuals which listen and it was observed in many primates species (*Caine et al. 1995*; *Cheney & Seyfarth 1985*; *Mitani & Nishida 1993*; *Slocombe & Zuberbühler 2007*; *Slocombe et al. 2010*), and other taxa (*Owings & Virginia 1978*; *Gyger et al. 1987*). In non-human primates and *Homo sapiens*, neural bases of vocalization are different: Ploog (2002) find that in non-human primates, vocalization are grounded in a very archaic neural path which include limbic regions (brains zone which regulate emotions) canalized in mesencephalic periaqueductal gray.

While in humans vocalizations are regulated by neocortical path, most recent, and which take part in the pyramidal tract, essential for voluntary voice control.

1.1.2 – Facial expressions

For a long time, facial expressions are been considered deeply linked to specific internal states (*Darwin*, 1872) and now researchers strongly agree upon power of facial expressions in underline emotional states but also intention of *emitter* (*Ekman*, 1997; *Hess & Blairy* 2001; *Palagi et al.,* 2015). Evidences explain that facial expressions are mutually coevolved with the encephalon capability of decode it (*Schyns et al.*, 2009), increasing in complexity together with social organizations complexity and concurrently with inter-individual relationships (*Parr et al.,* 2005). So facial expressions facilitate group cohesion and coordination in many social interactions (**Figure 1.1**) obtaining a fundamental role as evolutionary adaptation (*Schmidt & Cohn*, 2001). Today the debate upon the communicative category that include facial expressions are still opened, indeed Maestripieri consider it as a *gesture* (1997) and someone else as oro-facial movement or action (*Ferrari et al.*, 2003), but for many others instead, facial expression can be arranged as a category a part from this. They believe that facial expressions complete the context of communicative signals together with gestures, vocalizations, body postures and locomotory pattern (*Liebal*, 2006; *van Hoof,* 1962;

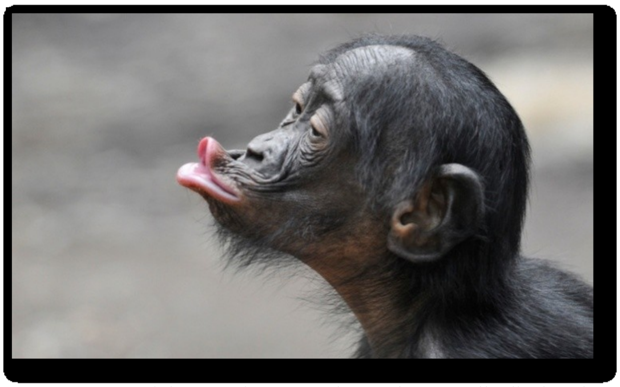


Figure 1.1 – Facial expressions named *Pout face*, usually displayed by juveniles to express a request.
Source: http://feelgrafix.com/data_images/out/19/926599-bonobo.jpg

Fridlund, 1994). Additional complication in facial expression study is represented by its association with vocalization because today still remain unappreciated the independence degree between these different signals.

Sherwood and colleagues (2004, 2005) demonstrated the presence of two different neuro-anatomical routes determining the emission of facial expressions: an involuntary "emotional" path (through the facial nucleus in the pons of the brainstem) and a voluntary "intentional" path (through activity in the facial representation area of the motor cortex). However recent neurobiological studies have underlined a strictly connection between intentional and emotional communicative systems (*Cattaneo & Pavesi, 2014*), but the interconnection degree remain unclear, unclear as the ontogenetic mechanisms of facial expressions same. There are evidences that infants of *Macaca mulatta* grown in social isolation conditions present facial expression typical of the same species (*Brandt et al.*, 1971) and that homologous facial expression produced by phylogenetically related species can transmit different information because it depends by social organization (*Parr & Waller*, 2006).

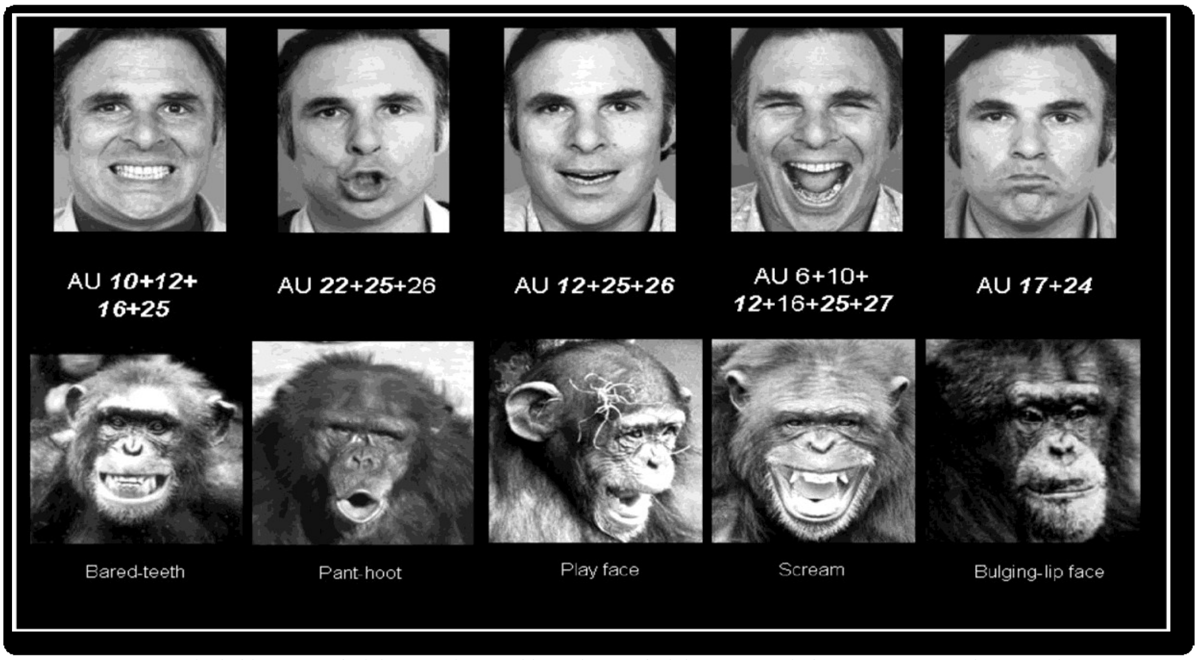


Figure 1.2 – Prototypical chimpanzee facial expressions and homologous facial movement in human; Sources: Ekman et al., 2002

A recent and interesting approach to describe and classify facial expressions in primates, especially in chimpanzee is the creation of "*Chimp*anzee *F*acial *A*ction *C*oding *S*ystem" better known as ChimpFACS (*Vick et al.*, 2007; *Parr et al.*, 2008 - **Figure 1.2**). It is been created to objectively describe chimps facial expression and to compare with the human FACS (*Ekman & Friesen*, 1978).

Ekman work was indeed an inspiration for primatologist which create a comparative system in primates, guided by evidence that human and chimps facial musculature are highly comparable (*Burrows et al.*, 2006; *Waller et al.*, 2006) .

The issue of intentionality becomes central when we consider that intentionality is the key feature of human communication. Therefore, study of intentional communication in primates could help us to shed light on the evolutionary pathway that led to the emergence of human language.

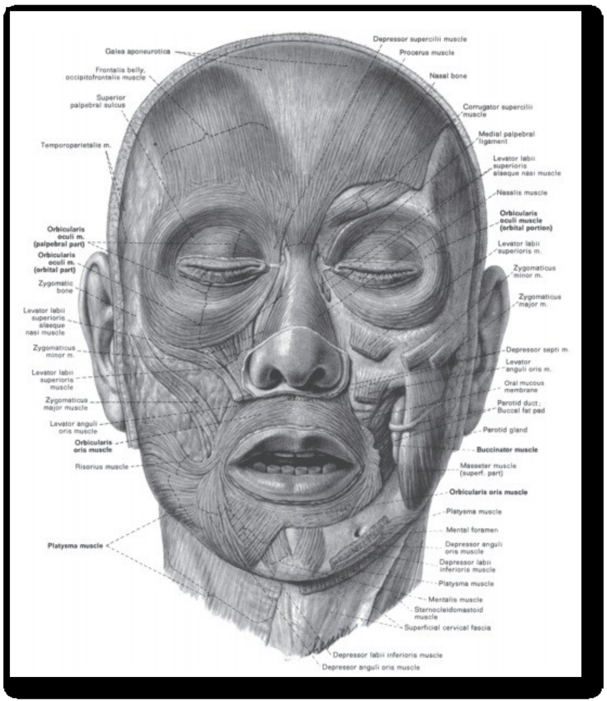


Figure 1.3 – Human facial musculature

Source: Clemente, 1997

From a neurobiological perspective, the discovery of mirror neurons (*Di Pellegrino* et al. 1992) has represented a veritable turning point for the comprehension of different social phenomena, including communication (*Rizzolatti & Arbib* 1998). Mirror neurons fires when the subject either performs a motor action or observes the same action performed by another subject (*Gallese* et al. 1996; *Ferrari* et al. 2003). Mirror neurons has particular relevance in the communicative sphere and can be viewed as the means by which individuals "*experience*" other's behaviours and emotions (*Gallese,* 2001) considering that emotions and intentions are expressed through motor actions.

Empathy phenomenon, the ability to share emotional states, relies on a perception-action mechanism and is essential for successful social interactions (*Preston & de Waal* 2002).

During the observation of a facial expression, the observer re-enacts the same motor pattern in a involuntary way by recruiting neural mechanisms that concurrently activate the same affective state associated with that specific facial expression (Perception-Action Model - *Preston & de Waal* 2002; *Gallese,* 2003; *Gallese et al.* 2004). Perceiving and sharing others' emotions, the so called "*affective empathy*", is a phylogenetically old capacity and is very likely linked to a mechanism in which mirror neurons may be implicated (*de Waal* 2008; *Iacoboni* 2009; *Ferrari* 2014).

Discovery of mirror neurons allowed us to unveil the invisible line connecting primate bodies and minds (de Waal and Ferrari 2012) and gave rise to new lines of research investigating the many ways in which primates communicate.

1.1.3 – Gestural communication

Primates regularly communicate their emotions through facial expressions and vocalizations (Ekman 1993, 1997; Parr et al. 2005), but gestures are mainly restricted to humans and apes where they are very frequent during play (*Liebal* et al. 2006; *Pollick* and de Waal 2007; *Genty* et al. 2009; *Hobaiter & Byrne* 2011a). Gestures (**Figure 1.4**) are conventionally classified as "intentional" signals (*Leavens* et al. 2005), because they are linked to less evolutionary urgent functions, are produced voluntarily by the sender (*Call & Tomasello* 2007; *Arbib* et al. 2008) and are under cortical control.

Although gestural communication in the great apes has been studied for a long time (*Call & Tomasello,* 2007), a universally accepted operational definition of gesture is still lacking.

There are many definitions for *gesture* in scientific field:

- Tanner & Byrne (1999) – gesture refers to a nonlocomotory movement with communicative value of the forearm, leg, hand, foot, wrist, fingers, head. Movement has to be intentionally direct towards a *receiver* that can detect throughout sight (visual signals), hearing (acoustic signals), touch (tactile signals)

- Pollick and colleagues (2008) – exclude head movement
- Tomasello and colleagues (1997) – include facial expression, body postures and some locomotory pattern

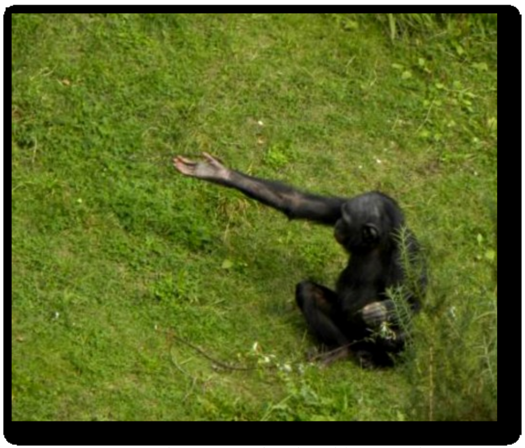


Figure 1.4 – Reach out up – free brachiomanual gesture
Source: Elisa Demuru

Rizzolatti et ali (1996) reports neurological evidence that head and limbs movements produced by the *actor* are perceived in cerebral areas that differs by those area activated by body movements, so gestures can be parsimonious defined as communicative movements of hands, feet, fingers, limbs and head. An important feature that differentiates gestures from other signals is the broad flexibility of their use and their disentanglement from specific behavioural contexts (*Pollick* & *de Waal* 2007; *de Waal* & *van Hooff* 1981). This flexibility is demonstrated by the possibility of using multiple gestures for the same communicative aim by an *actor* (*Tomasello et al. 1985, 1989, 1994, 1997*; *Pollick & de Waal 2007*) resulting that meaning of gestures have to be interpreted by the receiver throughout valuation of social and environmental variables.

Currently seems that free brachiomanual movements, that is no contact between two individuals or between an individual and an object, were mainly evolved in the *Hominoidea* family (*Pollick* & de *Waal*, 2007), but could be the product of an insufficient knowledge about gestural communication in primates. However an high variety of gestural signals is reported for ape in nature and in captivity and this range initially increase with the age, reach the climax between the age of three and six years and finally decrease again with adult age (*Tomasello et al.*, 1997; *Call* & *Tomasello*, 2007; Hobaiter & Byrne, 2011*b*).

Gestural repertoire change also with sex and bonding level and can be very different even between the individuals of the same colony (*Tomasello et al.*, 1994).

Gestural repertoire conformity between same colony individuals broadly depends by social organization system of a species indeed studies in captivity have shown that gestural repertoire conformity is high in more stable social group (gibbon, gorilla) than in species with more fluid social systems (bonobo, chimp, orangutan) (*Call* & *Tomasello*, 2007). So high social complexity is correlated with complex communicative forms.

Intentional nature of gestures was interpreted in *Hominoidea* family (therefore in man also) thanks to the dissociation between gesture and context observed in every apes (*Call* & *Tomasello*, 2007; *Liebal*, 2007; *Pika*, 2007 a, b) and in child also (*Bates et al.*, 1979; *Bruner*, 1972).

Figure 1.5 – Reach out up – free brachiomanual gesture

Source: Elisa Demuru

The communicative context were we usually find more gestures is *play* for every apes except orangutan (*Call* & *Tomasello*, 2007). Gestures are mainly based on cognitive capacities and experience differently from other forms of communication more strictly linked to emotional components (i.e. vocalizations and facial expressions) and in the great apes, one of the proposed learning processes for improvement of the gestural repertoire is the *"ontogenetic ritualization"*.

This process represent the capacity to create or invent new communicative signals by modifying pre-existing behavioural patterns (*Tomasello & Call,* 1997), so that a non-communicative pattern becomes communicative (*Palagi et al.*, 2015). Although most evidence of ontogenetic ritualization is reported for immature subjects, it also appears plausible that adult apes are able to understand the cause–effect of a gesture, anticipate its function and, consequently, use a modified version of that gesture as a communicative signal (*Palagi*, 2008; 2015). Recent studies demonstrated that apes have the capacity to invent new gestures (*Pika, Liebal & Tomasello*, 2003, 2005; *Liebal, Pika & Tomasello*, 2006; *Palagi et al.*, 2015) that later may spread to the rest of the colony through social learning processes (*Whiten*, 2000). The invention of new gestures has been reported also in some monkey species although these have less cortical control over manual movements than do apes (*Perry & Manson*, 2003; *Laidre,* 2008).

However, understanding the way apes and other primates communicate through gestures and how this capacity develops, becomes central when considering that it has been proposed that our ancestors' first linguistic expressions were in the gestural domain more than in the vocal domain (*Corballis,* 2002; *Palagi et al.,* 2015). This hypothesis also seems to be supported by some neurological findings suggesting that human language probably developed from gestural communication (*Cantalupo & Hopkins,* 2001; *Hopkins, Russell & Cantalupo,* 2007).

1.1.4 – Multimodal communication

Due to methodological reasons, communicative signals categories have usually been investigated separately. Nowadays the challenge for researchers interested in animal communication is represented by the study of multimodal communication, defined as communication via composite signals received through more than one sensory channel (*Partan & Marler*, 1999; *Liebal at al.* 2013; *Demuru,* 2015).

The hardest problem studying the multimodal communication is defection of shared criteria, starting by definition of single communicative components and then by the methods of data collection. Multimodal signals have been described in various animals during courtship (spiders, birds), agonistic interactions (frogs) or anti-predator displays (insects, squirrels). However, even in human communication, speech signals are routinely combined with (paralinguistic) vocal and visual signals to convey and modify the speaker's intended meaning (Genty et al., 2015; Slocombe et al., 2011, Uetz et al., 2009; Fusani et al., 1997; de Luna et al., 2010; Rowe et al., 2006; Partan et al., 2009; Pollick & de Waal, 2007; Morris, 1997). Even without any particularly statistical analysis we can glimpse the power and the efficiency of multimodal communication in term of answer of signals receiver (Rowe, 1999; Slocombe *et al.*, 2011) simply considering that more signals get more attention than just one.

Apart from the "*classical*" signal categories mentioned above, primates also communicate by means of behaviours that did not evolve for having a specific communicative function but acquired it only secondarily in highly complex social groups, as it occurred in humans. For instance, body postures and movements (King and Shanker 2003; Pereira and Preisser 1998; Thompson 1998), gaze orientation (Kobayashi and Kohshima 2001), haptics and proxemics (Robinson 1981; Hertenstein et al. 2009) belong to this category of "*communicative clues*" that can be read by group members but did not evolve specifically to serve a precise communicative function. Bonobos, usually combine this kind of communicative *clues* with other classical signals like vocals calls or tactile brachiomanual movement increasing the signal reception probability of any social goals. So we gather the importance of multimodal signals inside communicative scenario where communication of the most important social goals can't be entrust to an unreliable mode.

Also research on *Homo sapiens* require detailed studies on this kind of communication: human language clearly present integration of different communicative signals (Morris, 1999).

1.2 – The bonobo (*Schwarz*, 1929)

The bonobo is the last ape described by scientists and its identifications was made by Ernst Schwarz in the 1929. On December 6, 1927, the Congo Museum (now Royal Museum for Central Africa, Tervuren, Belgium) received the skull and the skin of an adult female chimpanzee collected in the Congo River basin, more or less 30 km south of Befalé. This female chimpanzee skull, registered as #9338, was first classified as the type of *Pan satyrus paniscus*, a subspecies of the eastern chimpanzee (Schwarz, 1929) meanwhile Harold J. Coolidge elevated it to the species rank in the 1933 with the name of *Pan paniscus* (Coolidge, 1933).

The bonobos live exclusively in Democratic Republic of Congo, in a range delimited by the Congo and Lualaba rivers and by the lakes Tumba and Mai-Ndombe (*Fruth et al.*, 2008) (**Figure 1.5**). Natural habitat of bonobos is composed by dry, mixed and mature primary forests (*Mohneke et Fruth*, 2008) especially for nesting activity. Habitat avoid for nesting but also important are: secondary forests, non-mixed forests, swamp forests and liana underhood (*Mohneke et Fruth*, 2008; Reinartz et al., 2008).

Figure 1.6 – Distribution of bonobo
Sources: http://maps.iucnredlist.org/map.html?id=15932

While separation between *Homo sapiens* and *Pan* genus occurred about 4.5 millions of years ago (*Takahata & Satta 1997; Prüfer et al. 2012*), divergence between bonobo and chimpanzee seems occurred 1 million of years ago (*Prüfer et al., 2012*) (**Figure 1.6**).

The Rift Valley formation could be the allopatric speciation event that originated the *Homo-Pan* divergence, producing two different ecosystems. Rainforest became predominant in the west, were *Pan* genus evolved, whereas savannah, the place of *hominids* origins, spread in the east (*Coppens, 1994*). The origin of *bonobo-chimpanzee* divergence was another allopatric speciation event: the Congo river formation (*Yu et al., 2003; Prüfer et al., 2012*). In this evolutionary scenario, the formation of arid and wide open habitat produced chimpanzee speciation in the north of the Congo river, contrary to the south where bonobo can evolved in protected habitat as forests (*de Waal, 1995*).

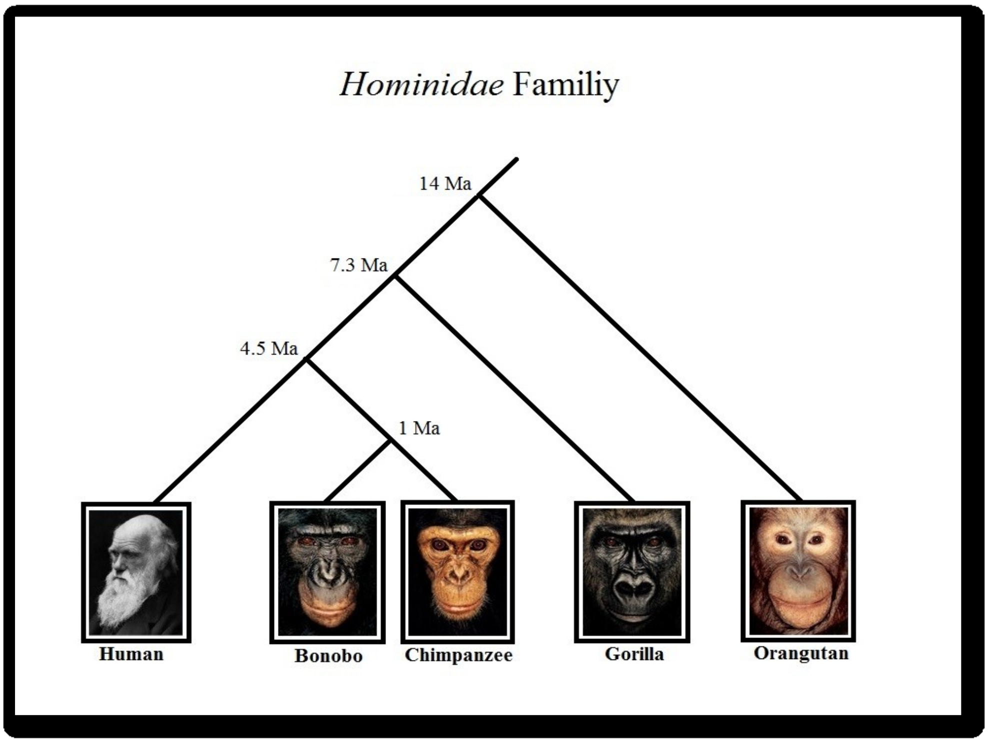


Figure 1.6 – Phylogenetic illustration of the currently existing great ape species
Pictures of ape from: http://cdn.theatlantic.com/static/mt/assets/science/Picture%201000.png

According to DNA findings (*Bradley* et *Vigilant*, 2002; *Kaessman et Pääbo*, 2002), the bonobo, together with the chimpanzee (*Pan troglodytes*), is the most closest living relative to humans (*Fleagle*, 2013) (*Figure 1.2)*. The analysis of non repetitive genome portions underlined that human and bonobo share the 1.6% of genome while human and chimpanzee the 1.7%. Even if bonobo and chimpanzee seem to be very similar, they differ for many morphological features: bonobo is smaller and thinner, it shows a dark face with pink lips and less sexual dimorphisms of chimpanzee.

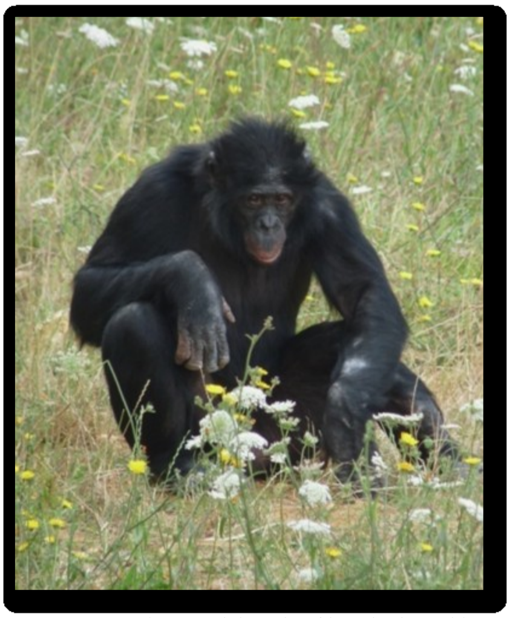


Figure 1.7 – Diwanì, adult male of bonobo hosted in La valléè des Singes. Author: Elisabetta Palagi

Moreover, bonobos are defined by the majority of authors as a highly prosocial and egalitarian species (Kano 1992; de Waal and Lanting 1997; Palagi et al. 2004; Palagi et al. 2006; Furuichi 2011; Hare et al. 2012), in which the hierarchical roles of individuals play a minor role in shaping the social dynamics. They show a vast repertoire of social behaviours such as play (Palagi et al. 2006), socio-sexual interactions (Furuichi 2011), and consolation (Clay and de Waal 2013; Palagi and Norscia 2013), aimed at increasing the cohesiveness among group members, especially among females (female-bonded society) (Kano 1992; de Waal and Lanting 1997). Moreover, in a recent study comparing the neural circuitry implicated in social cognition in the two *Pan* species, Rilling et al. (2011) found that bonobos, compared to chimpanzees, have more developed cortical brain areas involved in perceiving distress in both oneself and others, an emotional state underpinning empathic abilities, prosociality and reduced aggressiveness. Therefore, given that bonobos live in an egalitarian society characterized by high levels of social and cognitive complexity, the *Pan paniscus* is a good model species for carrying out researches on communication.

1.2.1 – Social system

Three main factors shape the social system of a species: social organization, mating system and social structure (*Kappeler & van Schaik,* 2002). According to its social organization a species can be classified as solitary, pair-living or group-living. Mating systems describe the inter-sex dynamics and can be distinguished as monogamous or polygamous. Finally, social structure refers to the relationships existing between the individuals of a group, evaluated through the study of affiliative (positive) and agonistic (negative) interactions. The strict interconnection of these three factors is responsible for the high variability of the social systems in primates. As a whole, five different social systems can be described: noyau, one-male/one-female, one-female group, one-male group, multi-male/multi-female group (Fleagle, 2013).

The most fluid multi-male/multi-female social system is called "fission-fusion" in which individuals belong to a single large group but temporarily form smaller sub-groups that frequently change in size and compositions (Aureli et al. 2008). These five social systems are characterized by an increasing degree of social complexity. Freeberg and colleagues (2012) defined complex social systems as *"those in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time"* (p. 1787). These authors suggested that groups with complex social systems require more complex communicative skills to regulate interactions and relations among group members. Therefore, the linkage between social complexity and communicative complexity could be described as a positive feedback that has evolutionarily led to the sophisticate communicative systems of highly social non-human and human primates.

Bonobo lives in *fission-fusion* social system where communities are composed by 20-120 individuals. Species of *Pan* genus shows males philopatry and females dispersions, therefore males stay in the natal group for the whole life while females migrate in another group when they reach sexual maturity. The presence of bonobo females in community parties is 2/3 of total amount against 1/10 of chimpanzee and this difference is extremely important to understand the social system of bonobo. Indeed, even thought bonobo females migrate for their natal group, they establish strong female-female interactions and long term affiliations, key event for the leadership of society.

1.2.2 – Females dominance

Individuals which feed together in big parties, quickly consume the resources and therefore need to frequently move to another foraging site. In this way females and especially females with infants, which are the slowest, will feed with difficulty (*Furuichi et al., 2008*). Contrary to chimpanzee females, females of bonobo are subject to minor competition for food resources (*Chapman et al., 1994*). Primary forests of Congo offer a high density of foraging site that are influenced by less seasonal variation and present more terrestrial herbaceous vegetations always available. The continuous source of food, for males and females (*Wrangham, 1986; Badrian & Badrian 1984; White 1986; Malenky, 1990*) reduce foraging distance, time of march and so female foraging costs.

Figure 1.8 – A parties caught by a camera traps in the bush
Source: www.bonoboincongo.com

The result is an interesting decrease in resource costs which allow bonobo females to join in bigger parties (*Wrangham 1979, 2000; Janson & Goldsmith 1995; Furuichi, 2011*).

Generally speaking philopatry, kinship and strength of social bonds coincide in non-human primate groups (*Rodseth et al., 1991*). Following the kinship selection theory, is more probable that individuals offer help and support to their related in order to promote transmission of his lineage (*Hamilton, 1964*) therefore the philopatric sex usually shows the strongest bonds because is the sex that stay in his natal group and the exogamic sex shows instead weak bonds. In this scenario, the bonobo represent an interesting exception.

The males of chimpanzee form coalitions, cooperate and regularly undertake affiliative behaviours because their kinship while female-female interactions (excepted *mother-daughter*) are usually temporary, *neutrals* or characterized by *avoid* behaviours (*Goodall 1968, 1986; Nishida 1979, 1990; Wrangham & Smuts 1980*).

Figure 1.9 – Two no-related females reinforcing their relationship during *grooming* activity. Author: Elisabetta Palagi

In bonobo society, amazingly, females establish the strongest social bonds in spite of they represent the exogamic sex (*de Waal, 1995*). Thanks to lesser food competition of chimpanzee, females of bonobo establish strong and long-lasting affiliative bonds (*Furuichi, 2011*) therefore typical coalitions are grounded not in kinship but in affiliation pattern (*Stanford, 1998*). The bonobo females show no interest in interactions with males and usually prefer other females as social partners (*Kano 1992; Idani 1991; White 1988*) for foraging or for stay in body contact, but also in affiliative behaviours as *grooming* (**Figure 1.9)** or in the play (*Parish, 1996*). At the same time, male-male relationships seem to be weak and for a male the best bond in a social group is that one with his mother, it indeed corroborate rank of its mother with maturity (*White*, 1996; *Stanford, 1998*). Thanks to different nature and strength of social bonds, hierarchy relationships are structured in different way in *Pan* genus. The two African apes differ dramatically in pattern of sexuality, dominance, same-sex social bonds and frequency of intensity of both intragroup and intergroup aggressions: chimpanzees have long been described in term of male dominance over females and intercommunity warfare (*Goodall, 1986; Nishida, 1990*), while bonobo society is best characterized as female centered and egalitarian, with sex substituting for aggression. "*Females occupy prominent, often ruling positions in society, and the high points of bonobo intellectual life are found not in cooperative hunting or strategies to achieve dominance but in conflict resolution and sensitivity to others"*(*de Waal,* 1997)

Figure 1.10 – The colony of La Vallée des Singes during feeding: on the center Ukela, the dominant female;

However we cannot speak about *exclusive* female dominance because not every females are dominant on males considering size and physical strength differences.

The immediate advantage of females alliances is food control, fundamental resource that influence reproductive success (*Parish, 1996)* and its possible observe males make away from foraging sites when females is late (*White & Wood, 2007*).

There are virtually no anthropoid primate species where the routine pattern of aggression is female to male and where the dominance rank of all adult females exceeds that of group males but in bonobo, females can and do form coalitions to attack males (*Parish, 1996)*. When conflicts happened in foraging site, allied females charge males and make the force of the group upon the physical strength of the single.

In chimpanzee society, females usually cannot refuse male invitation to sexual interactions and alpha-male and his allied has the priority access on females (*Muller et al., 2007)*. Males usually attack females in ovulation probably to intimidate and scare them, in order to make them obedient and submissive to future copulation invitations (*Goodall, 1986*). In bonobos, females alliances is a deterrent against sexual coercion carried out by males (*Smuts & Smuts, 1991*) and males don't monopolize females in oestrus and also they don't interrupt others copulations (*Furuichi 1997; Hohmann & Fruth 2003a, b*). Females choice of reproductive partners is therefore significant and the best way to obtain reproductive contacts for a male is not domination of other males but is become the first choice of females (*Hohmann & Fruth 2003a, b; Muller et al. 2011; Surbeck et al. 2011*; *Furuichi, 2011*).

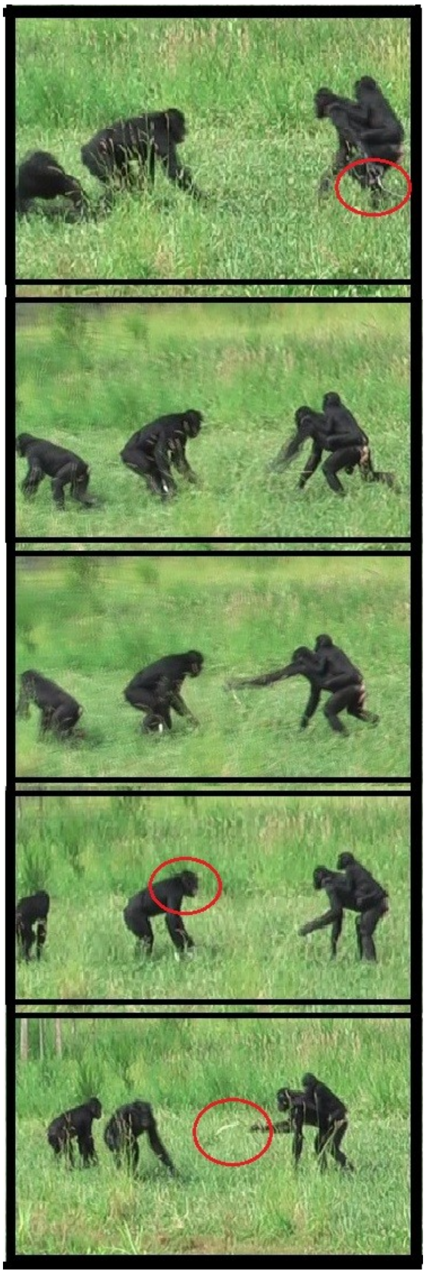


Figure 1.11 – A display made by a female with branch against two males. The first on the left (low rank) hide behind the second (high rank). The second move backwards showing a facial expression of tension named *Beared teeth.*

1.2.3 – Pacific society and neoteny

Frequency and intensity of aggressions between bonobos are certainly lesser then chimpanzee moreover rarely display of males against others group members end with real aggressive contacts (*Wrangham & Peterson 1997; Doran et al. 2002; Furuichi 2011*; *Mori 1983; Kano 1992*). Inter-group interactions are usually social events in bonobos where members sit in contact, play or have sexual contacts (*Itani 1990; Idani 1991; Furuichi 2011*). As chimpanzee, they patrol territory boundary but no lethal aggressions are been reported (*Wrangham 1999; Furuichi 2011*) but clearly this doesn't mean that bonobo is a species without hostility: female groups can attack and seriously injure males (*Parish 1996; Stevens et al. 2006; Hohmann & Fruth 2011*) and it has been explained by the same mechanism of male attacks against females in chimpanzee (*Goodall, 1986*; *Parish, 1996*).

As artificial selection lead the creation of tame domestic animals by wild animals, in the same way females of bonobo could be selected not aggressive males in a process named "*self domestication*" (*Hare et al., 2012*). In evolutionary term, we can think that attempts of aggressive males to dominate females was blocked by female coalitions producing a fitness decrease. The females carried out selective pressure and therefore a sort of *down-regulation* of aggressive behaviours, both intraspecific and interspecific, both offensive and defensive (*Hare et al., 2012*).

Studies on domesticated species show that selection processes which act on physiological system responsible of reduced aggressiveness can conduce to neoteny of some features as *by-product* (*Gould, 1977*). In bonobo we can find many neotenic features that are not shown in chimpanzee:

- *anatomic*: reduced cranial capacity (*Coolidge, 1933*); small size of mandible and teeth (*Cramer, 1977*);

- *behavioural*: increase in play sessions number, adults who play vigorous among them and with more *play faces* (*Palagi, 2006*)
- *behavioural*: while juvenile bonobos and chimpanzees were both found to be highly tolerant, chimpanzees became increasingly intolerant with age but adult bonobos maintained juvenile levels of cofeeding. (*Hare & Kwetuenda, 2010*)

- *physiological*: increase in cortisol level before food competition, in chimpanzee we can see increase in testosterone
- *physiological*: brain of bonobo and chimpanzee differs in others emotional perception area, making the bonobo more responsive (*Rilling et al., 2011*).

- *cognitive*: more stable and less competitive feeding conditions experienced by bonobos are expected to have lowered the benefits of taking risky foraging decisions. Bonobos have indeed been found to be relatively averse to risky outcomes and to prefer immediate rather than delayed rewards when presented with foraging decisions, whereas chimpanzees are relatively risk prone, willing to wait for delayed rewards that are larger or of higher quality (*Rosati et al., 2007*; *Heilbronner et al., 2008*; *Hare 2009; Rosati & Hare unpublished data*).
- *cognitive*: bonobos show delayed development relative to chimpanzees in social situations requiring them to inhibit begging for food from certain social partners but not from others (*Wobber et al., 2010*).
- *cognitive*: when tested for social skills related to reading the behavioural intentions of others, bonobos are more responsive to human gaze direction than are chimpanzees (*Herrmann et al., 2010*).

- *cognitive*: when bonobos and chimpanzees were compared for their ability to spontaneously cooperate on a novel instrumental task, chimpanzees were highly constrained by intolerance while experimentally naïve bonobos outperformed even the most skilled chimpanzees (*Melis et al., 2006; Hare et al., 2007*).

Eye contact plays a foundational role in the development of behaviour and cognition in humans (*Senju et al.,* 2009). Humans orient to others' eyes from birth (*Farroni et al.,* 2002*)* and eye contact facilitates the brain network related to social communication (*Senju et al.,* 2009). Preverbal infants later diagnosed with autistic spectrum disorder (ASD) show a decreased level of eye contact compared to typically-developing (TD) infants as early as 2–6 months of age (*Jones et al., 2013*). The decreased level of eye contact is correlated with the increased level of ASD (*Klin et al., 2002*). Importantly, despite the lack of social skills, some people with ASD show outstanding cognitive abilities in some physical domains (*Happé et al.*, 1999; *Baron-Cohen*, 2009), suggesting a degree of trade-off between socio-emotional and physical cognition in human development.

In humans, eye contact is related to the level of affiliation among individuals, and thus it reflects an individual's temperament and the interpersonal relationships (*Argyle et al.*, 1965; *Kleinke et al.*, 1986). People facing each other tend to reach an equilibrium in both physical distance and eye contact that depends on their affiliative motivation and the approach-avoidance conflict; people with a more relaxed relationship with their partners and with a higher need for affiliation show a closer physical distance and an increased level of eye contact. The level of eye contact is also modulated by social parameters such as cultural background and clinical condition (*Kano et al., 2015*).

Non-human primates have much in common with humans in terms of the pattern and function of eye contact (*Gomez et al.,* 1996). From an early age, humans and chimpanzees preferentially orient to faces looking at vs. looking away from observers (*Farroni et al.,* 2002;

Myowa-Yamakoshi et al., 2003). Visual search experiments have shown that humans and chimpanzees are able to detect such direct gaze faster than averted gaze (*Conty et al.,* 2006; *Tomonaga et al*., 2010) and eye-tracking experiments have shown that humans and several species of nonhuman primates predominantly fixate eyes among facial features (*Guo et al., 2003*; *Gothard et al., 2004*; Keating *et al., 1982*; *Kano et al.,* 2012, 2015). Observational studies have found that, although prolonged eye contact is not commonly observed among adults in nonhuman primates as it serves as a threat to the conspecifics (*Gomez et al.,* 1996), eye contact plays an important role in affiliative contexts. Mothers and infants in macaques and chimpanzees exchange frequent eye contact and facial expressions (*Bard et al.,* 2004; *Ferrari et al.,* 2009). When chimpanzees and gorillas make an attempt to reconcile with conspecifics after fighting, they first establish eye contact before approaching their counterparts (*Yamagiwa et al.,* 1992; *de Waal*, 1990). We thus need to consider the possibility that, as in humans, attentional and motivational biases constitute a proximal cause for cognitive differences also in non-human primates (*Kano et al., 2015*).

Herrmann et al. (2010) conducted a broad range of cognitive tests covering both social and physical domains in bonobos and chimpanzees. Bonobos outperformed chimpanzees in tasks related to theory-of-mind, especially gaze-following (*Kano et al.,* 2014), while chimpanzees outperformed bonobos in tool-using and physical causality tasks. Consistent with these results, previous studies reported that bonobos cooperated better with conspecifics in obtaining food due to their higher tolerance levels compared to chimpanzees (*Rosati et al.,* 2012). Other studies have reported that chimpanzees outperform bonobos in spatial-memory and wait longer for larger foods in temporal-discounting task (*Rosati et al.,* 2007; *Rosati et al.,* 2012). In addition, chimpanzees are well-known for their complex extractive-foraging and tool-using techniques, and the social transmission of those techniques in both captive and wild populations (*Whiten et al.,* 1999; *Matsuzawaet al.,* 2006), while extractive-foraging is relatively infrequent and tool-using in feeding contexts is virtually inexistent in wild bonobos (*van Schaik et al.,* 1999; *Hohmann et al.,* 2006; *Kano et al.,* 1982).

It is noteworthy that such potential cognitive differences between bonobos and chimpanzees may depend on the attentional and motivational differences of the two species, rather than on their cognitive abilities per se. On the one hand, when tested in the laboratory, some bonobo participants showed equivalent or even superior abilities in extractive-foraging and tool-using techniques compared to chimpanzees (*Jordan et al.*, 1982; *Gruber et al.*, 2010; *Kano et al.*, 2015). Chimpanzees possess a remarkable ability to solve a variety of theory-of-mind tasks, especially in competitive contexts (*Hare et al.*, 2000). On the other hand, a recent study has reported that object-play among juveniles was more frequent in chimpanzees than bonobos, while social-play was equally frequent in the two species of juveniles (*Kano et al.,* 2015) but another study reported that social-play among adults was more frequent in bonobos than chimpanzees (*Palagi et al.*, 2006).

Currently lacking is the experimental comparison of the two species' "interest"; how bonobos and chimpanzees spontaneously attend to social stimuli without any task demands (*Kano et al. 2015*). A recent study using the eye-tracking method found that the degree of eye-fixation while viewing naturalistic images could reliably predict the degree of socio-emotional development in human infants (*Jones et al.*, 2013). Using a similar approach, Kano et al. (2015) elucidate the differences between bonobos and chimpanzees in social attention (see **Figure 1.12**). They report that: "*bonobos viewed the face and eyes longer than chimpanzees. Instead of viewing the eyes, chimpanzees viewed the action target objects and ano-genital parts longer than bonobos. These species differences were partly due to a time trade-off, i.e. the longer viewing of faces led to the shorter viewing of the other attractive elements and* vice versa*. Yet, bonobos viewed the face longer than chimpanzees even though the pictures included the two different kinds of attractive elements, action target objects and ano-genital areas of other individuals, suggesting that bonobos actively maintained their* *attention to the face and eyes. Bonobos fixated the eyes rapidly, even immediately after the picture presentation, and chimpanzees showed an opposite pattern; fixating the mouth rather than the eyes. In addition, bonobos viewed the eyes longer than chimpanzees independently of whether the presented stimulus was a conspecific face or an allospecific chimpanzee's face*". These results suggest that bonobos' eye fixation was a well-automated response. A similar, rapid eye-fixation has been reported in humans (*Hershler et al.,* 2005; *Fletcher-Watson et al.,* 2008), from the early age (*Farroni et al.,* 2002), and also in several species of nonhuman primates as monkeys, gorillas and orangutans (*Guo et al.*, 2007; *Kano et al.* 2012, 2015).

Figure 1.12 – Eye-tracking method applied on bonobo and chimpanzee. Source: *Kano et al.*, 2015

Taken together these results suggest that the viewing pattern of each individual depended on a species-specific predisposition rather than on environmental or familiarity factors. In humans, the individual variation of eye contact is also generally stable across contexts and different counterparts (*Farroni et al.* 2002). Kano et al. moreover confirmed the hypothesis that chimpanzees pay more attention to action target objects than bonobos. This attentional difference may be related to the cognitive differences between chimpanzees and bonobos (*Herrmann et al.* 2010). In particular, bonobos' increased performance in the test related to theory-of-mind, especially gaze-following, may partly depend on their increased attention to the experimenter's face and eyes. Also, chimpanzees' increased performance in the test requiring tool-using or an understanding of physical causality may partly depend on their increased attention to the experimenter' action and the target objects, relative to bonobos (or the bonobos' inattentiveness to the action target objects).

One study comparing the local gray matter between bonobos and chimpanzees found differences in the regions involved in the brain network related to social communication (*Rilling et al.*, 2012), which, in humans, is activated when making eye contact (*Senju et al.*, 2009). Further cross-species studies focusing on the neural and cognitive mechanisms of social attention should enhance our understanding of the evolutionary origin of eye contact and the basic social motivation underlying complex social behaviours and cognition.

The data from this and other studies suggest that there may be common neural, hormonal, and genetic mechanisms underlying eye contact and affiliation in human and nonhuman primates (*Kano et al., 2015*). As mentioned above, eye-fixation differences between bonobos and chimpanzees study may resemble the differences that have been previously reported between TD and ASD infants using the same eye-tracking method (*Jones et al., 2013*; *Kano et al., 2015*).

In conclusion, bonobos and chimpanzees differs in their attention to social and physical elements (*Kano et al., 2015*) suggesting that, if such attentional or motivational differences have emerged between bonobos and chimpanzees in a relatively short period of time (1–2 million years), those changes could have influenced the development and evolution of behaviours and cognition of these species in important ways (*Kano et al., 2015*). Finally, just as it may have happened to *Pan* species, the evolutionary shift in attentional and motivational systems may have partly contributed to shaping the species-unique behaviours and cognition of humans even in a relatively short period of evolutionary time (*Kano et al., 2015*).

1.2.4 – Sexual behaviour

Sex is the key to understand sociality of bonobo. Sex is pervasive and represent a social binding agent that link individuals each other and decrease tension caused by potential competition. Whereas in most other species sexual behaviour is a fairly distinct category, in the bonobo it is part and parcel of social relations, and not just between males and females. Bonobos engage in sex in virtually every partner combination (although such contact among close family members may be suppressed) (*de Waal*, 1995). And sexual interactions occur more often among bonobos than among other primates. Despite the frequency of sex, the bonobo rate of reproduction in the wild is about the same as that of the chimpanzee (*de Waal*, 1995).

Bonobos become sexually aroused remarkably easily, and they express this excitement in a variety of mounting positions and genital contacts. Before studying bonobo *face-to-face* copulation was considered uniquely human, a sort of cultural innovation that needed to be taught to preliterate people (hence the term "missionary position") (*de Waal*, 1995) and primatologists Eduard Tratz and Heinz Heck in 1954 was surprised in reporting that the chimpanzees mated *more canum* (like dogs) while bonobos *more hominum* (like people). Although chimpanzees virtually never adopt face-to-face positions, bonobos do so in one out of three copulations in the wild (*Kano, 1992*) and females usually impose this position to males (*Blount 1990; Kano 1992*) and other females. Furthermore, the frontal orientation of the bonobo vulva and clitoris strongly suggest that the female genitalia are adapted for this position (*de Waal*, 1995).

Another similarity with humans is increased female sexual receptivity. The tumescent phase of the female's genitals, resulting in a pink swelling that signals willingness to mate, covers a much longer part of estrus in bonobos than in chimpanzees. Instead of a few days out of her cycle, the female bonobo is almost continuously sexually attractive and active.

Considering that bonobo take part in intercourse for other reason including conflict resolution, affection, social status, erotic game, reconciliation, excitement and stress reduction we can glimpse the social importance of sexual contacts in bonobo society. Frans de Wall excellently synthesized the comparison between bonobo and chimpanzee: "*the chimpanzee resolves sexual issues with power while the bonobo resolves power issues with sex"* (2008) therefore it is believable that *Sex* represent a set of essential social interactions in bonobo so much that it is impossible conceive this species without intercourses.

Figure 1.13 – A male and a female of bonobo during a copulation
Author: Elisabetta Palagi

1.2.4.1 – Reproductive sexual behaviour and sexual swelling

As for others Old World monkeys, females of *Pan* genus experience oestrous cycle: physiologic changes that are induced by reproductive hormones. In the oestrous cycle it is named "oestrous" the periovulatory phase and it is displayed by both physiological/morphological signals and changing in behaviour that announce ovulation to males. The most powerful signal of oestrous is the appearance of *sexual swelling* (**Figure 1.13**), a sort of tumescence of perineal skin produced by water retention that strongly attract males (*Bielert & Girolami, 1986*). During the periovulatory phase, females are characterized by an increase in proceptivity (start, maintain or intensify intercourse), receptivity (accept invitation to copulations) and attractiveness to males (*Beach, 1976*).

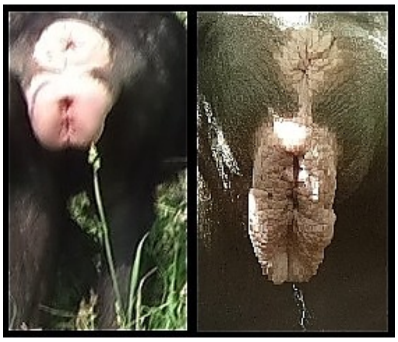


Figure 1.13 – Comparison of perineal skin of bonobo female showing *sexual swelling* (left) and not (right).
Author: Elisabetta Palagi

Many functional meaning are been hypothesized for *sexual swelling* of Old World monkeys and today we have a wide panorama of explanations that can mutually exclude or not.

The two most simple functional meanings recognize the sexual swelling as an informative signal on female quality (reliable quality indicator hypothesis: *Pagel, 1994*) and as honest signal of ovulation increasing paternity certainty (the obvious-ovulation hypothesis: *Hamilton, 1984*). This strong signal induce competition between male to access the best females increasing the probability of take part in intercourse with superior males (the best male hypothesis: *Clutton-Brock & Harvey, 1976*). Contrary to Hamilton, Hrdy thought that by signaling receptivity prominently, a female is able to attract multiple males as mating partners (Hrdy 1981; Hrdy & Whitten 1987) and by mating with multiple males, a female can confuse paternity, which is thought to reduce the risk of infanticide because males are less likely to kill infants they might have sired (the many-male hypothesis: Hardy, 1979). Martin instead suggested that sexual swelling are a graded signals that allows females to follow a mixed strategy of biasing and confusing paternity by mating with the dominant male at peak swelling and with multiple males outside peak swelling (bias and confuse hypothesis: Nunn 1999; van Schaik et al. 2000). Sexual swellings, as reported by Turke, conceal ovulation and force males into long-lasting consortships (concealed ovulation hypothesis: *Turke,* 1984). Another interesting functional meaning supposed for *sexual swellings* is to serve as a social passport during inter-group transfer (social passport hypothesis: Pusey 1979; Nishida et al. 1985; Goodall 1986,) facilitating interactions female-female (*Paoli et al., 2006b*).

Bonobo females experience the first swelling at the age of seven years, but a real and complete swelling usually appear at the age of nine. Instead chimpanzee females experience the first swelling at the age of eight-ten years while a complete swelling appear at the age of ten-twelve (*Wrangham, 1993*). The proportion of oestrous days between bonobo and chimpanzee females is not different as show in the **Table 1.1** but a real difference can be

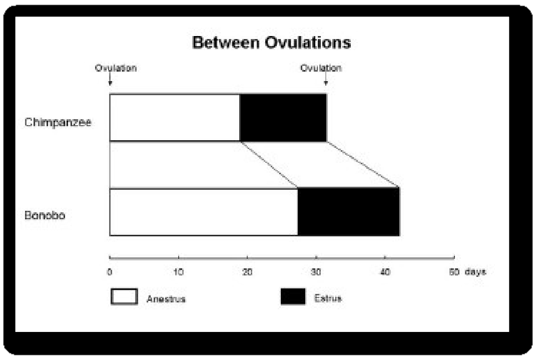


Table 1.1 – Oestrous days of chimpanzee and bonobo. Source: Furuichi, 2011

observed analyzing time of *sexual swelling* showed between two deliver events (**Table 1.2**) in bonobo and chimpanzee. Bonobo show tumescence of perineal region and therefore *swelling* even during infertile periods producing the so called *pseudo-oestrous* (*Furuichi, 2011*). Considering that bonobo females show pseudo-oestrous during pregnancy until one month before delivery and then restart to show it in one year (*Kano, 1992*), contrary to chimpanzees that stop to show visible signals of oestrous 2.6 months after the conception (*Takahata et al., 1996*), don't show pseudo-oestrous during post-partum amenorrhea and restart to show oestrous 55.5 months after the delivery (*Nishida et al., 1990*)., the results of these differences is an interesting variation in the total time of pseudo-oestrous/oestrous showed by females of *Pan* genus (*Furuichi, 2011*). Broadly speaking a female of chimpanzee shows oestrous or pseudo-oestrous only for the 5% of his adult life time contrary to bonobo female which shows oestrous or pseudo-oestrous for the 27% of his adult life time (*Furuichi, 2011*).

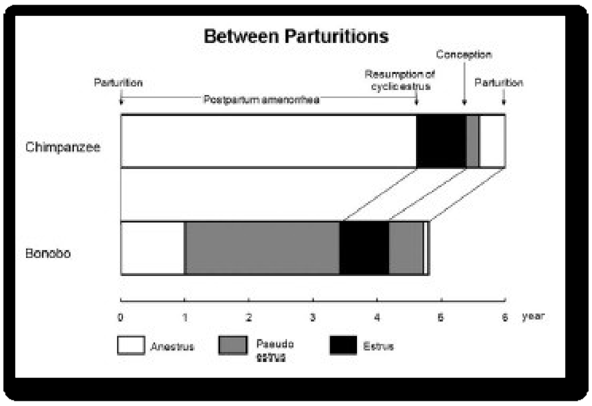


Table 1.2 – Oestrous time of chimpanzee and bonobo between two delivery. Source: Furuichi, 2011

This data, matched with the marked difference in the *parties* sex ratio between chimpanzee and bonobo as previously mentioned, underline another interesting aspect: in chimpanzee there is more sexual competitions of males produced by a higher number of males for a lower number of females in fertile condition. For this reason it is very difficult for a single male of bonobo to monopolize a fertile female (the number of fertile females is too high). Hence thanks to prolonged pseudo-oestrous periods, females of bonobo had reduced both competition of males and male sexual coercion (*Furuichi, 2011*).

1.2.4.2 – Hypothesis on non reproductive sexual behaviour

Two fundamental hypothesis explain the evolution and the meaning of non reproductive sexual behaviour considering the costs and the health risks of sexual contacts: the "*Big brain hypothesis*" (*Beach, 1976*) and the "*Mating system hypothesis*" (*Wrangham, 1993*)

Following the *Big brain hypothesis* sexual activities can be released by hormonal control in species with a sufficiently big brain that permit neural control of sexual activity (*Beach 1976, 1977*).

A complex sexuality was been observed in tree of Mammals species with the biggest brain in proportion with body size: in common bottlenose dolphin (*Tursiops truncatus*), in bonobo and in human (*Homo sapiens*). In comparison with other animals every species of *Hominoidea* (gibbon, orangutan, gorilla, chimpanzee, bonobo and human) has a big brain but sexuality is highly variable among them. Unfortunately *Big brain hypothesis* says us that sexuality was released by hormonal control but says us nothing about interspecific variation of this phenomenon and how it happened (*Wrangham, 1993*). *Mating system hypothesis* says us instead that sexual behaviour is conditioned by social organization, but at the same time it reward reproductive success. It means that species which evolved complex sociality, can count on complex sexuality as social communicative instrument.

1.2.4.3 – Non reproductive sexual behaviour

Sex has many social function in bonobo society and individuals usually take part in intercourse for many different causes. Through copulations between mature males and infertile females who act as fertile, it is generated paternity confusion. This can happen just when ovulation is concealed and make the sexual swelling a deceptive signal of ovulation represent a possible way to generate paternity confusion (*Wrangham, 1993*).

Typically, the majority of *catarrhine* shows start of *perineal tumescence,* called sexual swelling, with the beginning of follicular phase, showing the highest degree of tumescence during the ovulation (*Dixson 1983; Hrdy & Whitten 1986; Girolami & Bielert 1987*) and making the sexual swelling a honest signal of female fertility (*Hamilton, 1984*). When we compare bonobo and chimpanzee, we can see an interesting interspecific variability in the honesty of sexual swelling: females of chimpanzee usually show ovulation in the second part of the maximum tumescence phase while bonobo females show that 1/3 of ovulations happened outside the maximum tumescence phase and also that ovulations can occasionally happened even 10 days after the detumescence phase (*Reichert et al., 2002*). Ovulation in chimpanzee is more strictly linked to swelling pattern than bonobo and is a more honest signal of fertility (*Deschner et al., 2003*).

Figure 1.14 – Ukela and her offspring. Today is unknown the identity of the father even for the zoo keepers. Author: Elisabetta Palagi

The main benefit gained by females by paternity confusion is the inhibition of male aggressiveness against their offspring, making very hardly the infanticide (*Wrangham, 1993*).

Paternity confusion acts as well in bonobo that it is never been observed in nature infanticide cases (*Fowler & Hohmann 2010; Furuichi 2011*) contrary to chimpanzee (*Arcadi & Wrangham 1999; Townsend et al. 2007, Pusey et al. 2008*).

Another functional meaning of non reproductive sexual behaviour is sex as *exchange.*
It is performed by females that obtain non reproductive benefits, usually an immediate benefit in the form of food, while the male obtains chance for copulation (*Wrangham, 1993*). We can see the same pattern of *exchange* in bonobo and chimpanzee: female begging for food to the male, having intercourse with him and finally obtaining food (*de Waal 1990; Goodall 1986; Kuroda 1984*).
But the female can gain also a temporary benefits in form of social support: it usually happened when a young female arrived in a new *community (Wrangham, 1993).*

Non reproductive sexual behaviour can be also explained as practice to improve juvenile skills and expertise of future and complete copulations. Certainly this functional category concern especially immature individuals involving heterosexual contacts but also homosexuals contacts with other juveniles or adults (*Wrangham, 1993*).

1.2.4.4 – Socio-sexual behaviour

When sexual behaviour are adapted for social communications we can talking about socio-sexual behaviour. Following the Wickler's definition, socio-sexual behaviour are structured as normal sexual behaviours but the motivation is not typically sexual, and therefore are defined as adaptative behaviours (*Wickler, 1967*). Socio-sexual contacts are thought to help regulate stress in bonobos, acting as a kind of 'social grease', to alleviate tension and to facilitate peaceful co-existence between group members, who generally lack close genetic ties (de Waal, 1987; Hohmann & Fruth, 2000; Fruth & Hohmann, 2006; *Clay & de Waal*, 2014). Consistent with Hanby's (1977) prediction about the stress relieving function of primate socio-sexual contacts, most non-conceptive sexual behaviours in bonobos occur within socially tense periods, such as feeding, anticipation of feeding, inter-group interactions and following aggressive conflicts (Mori, 1983; de Waal, 1987; Manson et al., 1997; Hohmann & Fruth, 2000; Paoli et al., 2006; Hohmann et al., 2009). Following aggressive conflicts, former opponents often engage in various forms of affiliative contacts, a reparative process known as reconciliation (de Waal & van Roosmalen, 1979; de Waal & Aureli, 1996; Arnold et al., 2001). In bonobos, these contacts are more often sexual in nature (de Waal, 1987, 1992; Manson et al., 1997; Hohmann & Fruth, 2000; Palagi et al., 2004), although various post-conflict behaviours are used in primates and other animals (e.g., de Waal, 1989; Fraser et al., 2008). For instance, chimpanzees reconcile primarily using embrace, kissing, "finger in mouth" and touching (Fraser et al., 2008). In addition to reconciliation, uninvolved bystanders sometimes initiate affiliative contacts with one of the contestants, typically the former victim (de Waal & Roosmalen, 1979; de Waal & Aureli, 1996). Bystanders can accrue various direct benefits by doing so, such as protection from redirected aggression (e.g., Fraser et al., 2009). In a select number of species, however, the offering of friendly contacts appears to be more driven by a motivation to reduce the distress of a close social partner or kin-member, based on an apparent absence of purely self-serving benefits (chimpanzees: e.g., *de Waal & van Roosmalen,* 1979; *Koski & Sterck,* 2007; *Fraser & Aureli*, 2008; *Romero et al.,* 2011; bonobos: *Palagi et al.*, 2004; *Clay & de Waal*, 2013a; gorillas: *Cordoni et al.,* 2006; crows, C. corax: *Fraser & Bugnyar*, 2010: dogs: *Cools et al.,* 2008; wolves: *Palagi & Cordoni*, 2009: African elephants: *Byrne et al.,* 2008; praire vole: *Burkett et al.,* 2016).

Figure 1.14 – Consolation in bonobo: a female embrace another one. Note the facial expressions, manifestation of intense emotional status. Author: Elisabetta Palagi

This type of affiliative act, known as "*consolation"* (**Figure 1.14**), has been shown to be effective in reducing the recipient distress (*Palagi et al.*, 2004, *Fraser et al.*, 2008; *Clay & de Waal,* 2013a). With a shift towards the other, consolation is considered an important bridge between expressions of empathy in animals and humans, as it suggests that the consoler can recognize as well as respond appropriately to alleviate anothers' distress (e.g., *Preston & de Waal*, 2002; *Romero et al.*, 2010; *Clay & de Waal*, 2014).

Reconciliation or peace-making, defined as the first affinitive contact between former opponents occurring within few minutes after the conflict, is one of the main mechanisms to manage conflicts (*Palagi et Norscia*, 2015). By restoring the relationship between former opponents, reducing the probability of further fights, and/or reducing anxiety in the victim, reconciliation is crucial to preserving social unity from the disruption caused by uncontrolled conflict spreading in the group.

Therefore, reconciliation is expected to be present any time that it is valuable for the group members (including dominants) to preserve the alliances that facilitate group survival, thus preserving the benefits of group living (*Palagi et Norscia*, 2015).

Figure 1.15 – A female and a male in a *rump-rump rubbing* sexual contact.
Author: Elisabetta Palagi

Following aggressive conflict, bonobos use a suite of *sexual* and *non-sexual* behaviours to *reconcile* with former opponents and, as bystanders, to console distressed victims.

Reconciliation and consolation were marked by pronounced increases in sexual behaviours, which included *genito-genital* contacts (**Figure 1.15**), *mounting*, *genital touch* (**Figure 1.16**) and, to a lesser extent, *copulation*. Reconciliation was almost exclusively characterized by sexual contacts (*Clay & de Waal*, 2014). While sexual contacts were also the most frequently occurring consolatory behaviour, consolation included a rise in other behaviours as embrace, touch, contact peering and holding (*Palagi et al.*, 2004; *Clay & de Waal*, 2014).

Adults were more likely to engage in post-conflict sexual behaviours than adolescents and juveniles, indicating that the sexual nature of conflict resolution strengthens with age in bonobos and that the mechanisms underlying post-conflict behaviours are likely to vary across development (*Clay & de Waal*, 2014). In accordance with the tension regulation hypothesis, victims receiving sexual contact showed significantly lower rates of self-scratching compared to receiving non-sexual consolatory contact (*Clay & de Waal*, 2014). While receiving any form of consolatory contact appears to be calming, as indicated by reduced self-scratching (*Clay & de Waal*, 2013a, b), the results further specify that sexual contacts are the most effective in doing so.

Figure 1.16 – A *Genital contact* of a female preceded by a visual gesture. Author: Elisabetta Palagi

When reconciliation took place, consolation generally preceded it, suggesting that consolation may be a substitutive behaviour. Palagi (2004) and colleagues suggest that even if reconciliation remains the best option, consolation may be an alternative substitute for reconciliation that is used to buffer the tension originating from an unresolved conflict.

Genito-genital contacts were the most frequently offered form of sexual contact (de Waal, 1987; Hohmann & Fruth, 2000; Paoli et al., 2006). Mounting and genital touches were also frequently observed for both consolation and reconciliation. While, bonobos exhibit a particularly heightened level of sexuality compared to other primates, their use of genial touching and mounting during post-conflict periods appears to reflect a broader relationship for primates between sex and social tension (*Hanby,* 1977). In several species of macaques, for example, female–female mounting and other forms of genital touching occur frequently during post-conflict interactions (*Oi,* 1991; *Flack & de Waal*, 2007; *Call et al.*, 1999, 2002; *Dixson*, 1977). Chimpanzees frequently engage in post-conflict mounting and genital touching (i.e., testicle shakes: Arnold et al., 2001; Romero et al., 2011), as well as during other tense periods, such as during predator or inter-group encounters (Goodall et al., 1979; Herbinger et al., 2009).

Analyzing post-conflict sexual contacts, Clay and de Waal (2014) did not find support for the hypothesis that post-conflict sexual contacts are part of a reproductive strategy. Consolatory copulations were very rare, with only 6% of all sexual contacts potentially resulting in conception and was absent during reconciliation events (*Clay & de Waal*, 2014). This is consistent with a previous study showing an increase in non-conceptive but not conceptive sexual behaviours during periods of short-term crowding and feeding (*Palagi et al.,* 2006). Although feeding and the anticipation of feeding are associated with socio-sexual behaviours in bonobos (*Kuroda,* 1984; *Thompson-Handler et al.*, 1984; *de Waal,* 1987; *Kano,* 1992; *Hohmann et al.,* 2009), Clay and de Waal found no evidence that socio-sexual behaviours were used to resolve conflicts arising over food per se (*Clay & de Waal*, 2014). Post-conflict sexual contacts were not targeted towards valuable social partners and they did not confer obvious reproductive benefits; nor were they used to mediate food-related conflicts. Overall, results highlight the role of sex in regulating tension and social conflicts in bonobos (*Clay & de Waal*, 2014).

Another form of communication based on sexual contacts is the expression of social dominance relationships. High-ranked females assert their social position, develop new alliances and control the formation of others' social bond throughout genital contacts while in the same way low-ranked females create association and alliances with more dominant females and strengthen their social position within the group (*Clay & Zuberbühler*, 2012).

1.2.4.5 – Female homosexual contacts

Genito-genital contacts are a hallmark of socio-sexual behaviour, during which two individuals, most commonly females, embrace ventro-ventrally, swing their hips laterally while keeping their vulva in contact (*Kuroda*, 1980; *Hohmann & Fruth,* 2000) where the clitorises protrude (*Kano*, 1992). This behaviour is named *genito-genital rubbing* (see **Ethogram** for GGR, **Figure 1.17 and 1.18**).

Some studies in the wild and captivity found that females were more likely to perform GG-rubbing during maximum tumescence of perineal skin (*Kuroda*, 1980; *Kano*, 1992; *Hohmann & Fruth*, 2000; *Paoli*, 2006); however, Furuichi (1992) stated that there was no correlation between frequency of GG-rubbing and swelling phase in the same wild bonobo population.

In bonobos the *maximum swelling* may also be used as a means of attractivity among females (i.e., a "*social passport*" tool) in order to enhance social integration. Dahl (1986) observed that the occurrence of swelling shifts the location of the clitoris to a more ventral position, and this finding is consistent with the hypothesis of Takahata et al. (1996) that female bonobos may show maximal swelling in order to exchange GG-rubbing with other

Figure 1.17 – Two females in a *genito-genital rubbing*. Note the presence of maximum swellng in both individuals.
Author: Elisabetta Palagi

females, rather than to copulate with males and that female at the sexual maturity migrate to neighboring groups when they experience a maximum swelling (*Furuichi*, 1989; *Idani*, 1991). As previously mentioned, socio-sexual contacts are thought to help regulate stress in bonobos, acting as a kind of "*social grease*", to alleviate tension and to facilitate peaceful co-existence between group members, who generally lack close genetic ties (*de Waal,* 1987; *Hohmann & Fruth*, 2000; *Fruth & Hohmann*, 2006). GG-rubbing represent an excellent example of stress regulation and reconciliation between females. In support of this statement it was observed an increase in GG-rubbing frequency after agonistic encounters (*Hohmann & Fruth*, 2000; Paoli, 2006) moreover GG-rubbing seem not to be correlated to kin-ship or social bonding (*Hohmann & Fruth, 2000*) contrary to reconciliation phenomena that seems to be correlated to kin-ship and strengthen of social bonding of opponents (*Hohmann et al.,* 2009). Therefore reconciliation it is not enough to explain GG-rubbing. Wrangham (1993) proposed that bonobo use socio-sexual behaviour in order to communicate their social relationship with other members: e.g. to females in GG-rubbing can communicate to males that they are developed a new alliance in a way to inhibit male aggressiveness. Moreover Furuichi (1989) has instead hypothesized that females in a new group use GG-rubbing to establish bonds with the resident females. At this time, *stress reduction* is probably the best answer to the question about functional meaning of GG-rubbing but when we talking about stress reduction we have to interpret GGR as a global phenomenon that take place in many and different situations (post conflict consolation and reconciliation, social passport, replacement of aggression, and relationships management).


Figure 1.18 – Two females in a *genito-genital rubbing*. Author: Elisabetta Palagi

A recent study underlined the relationship between GG-rubbing frequency and cortisol level during food competition (*Hohmann et al., 2009*). It has been proved that cortisol level and

GG-rubbing frequency increase when females of bonobo expect food competition but even if cortisol level decrease quickly during the competition, the GG-rubbing frequency stay high. This lack of relationship between socio-sexual behaviour and hormonal responds suggest us that stress regulation is diversified mechanisms based on physiological and behavioural process.

A low social status can be expressed through submission signal to dominant individuals, whether as response of agonistic display or without them (*East et al., 1993*). Submission signals can include genital display or/and *sexual pattern* (*Kummer et al. 1974; Fox & Cohen 1977*) and asymmetry in sexual contacts can reflects differences in partner status (*Rowell 1966; Bygott 1979; Colmenares 1990*). Different studies on bonobos suggest an asymmetry rank-correlated in sexual invitations, in performance of intercourse and in sexual vocalization consistently with the hypothesis of GG-rubbing as rank-indicator (*Clay & Züberbuhler, 2012*). Concerning with sexual invitations data are discordant. Any studies report that low-ranking females usually ask more for a GG-rubbing contrary to high-ranking (*Hohmann & Fruth 2000; Parish 1994, 1996*); but others instead reveal total absence of rank asymmetry in invitations (*Paoli et al., 2006b; Clay & Züberbuhler, 2012*).

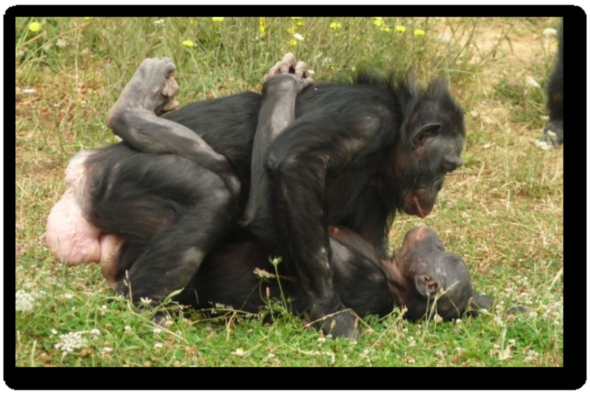


Figure 1.19 – Two females in a *ventro-ventral genito-genital rubbing*. Author: Elisabetta Palagi

Furthermore following the assumption that mount is dominance expressions (*Wickler 1967; Maestripieri 1996*), Hohmann and Fruth verified that high-ranking females usually engage the GG-rubbing in the upper position than low-ranking (*Hohmann & Fruth, 2000*). At this time is not clear if GG-rubbing is rank-correlated but these data, together with the assumption that sexual vocalization during GG-rubbing **are** correlated with rank (*Clay & Züberbuhler, 2012*) suggest us that we need more investigations.

CHAPTER 2

MATERIALS AND METHODS

2 – The colonies

All the observations were performed in two primatological parks: *La Vallée des Singes* (La Gureau, Romagne, France) and *Apenheul Primate Park* (Apeldoorn, The Netherlands) .

2.1 - La vallée des Singes

The park hosts in seminatural conditions the largest group of bonobos in the world (**Figure 2.1**). The colony was founded in 2011 with a starter group of 9 individuals – 4 males and 5 females – from European zoo and since 2012 the park introduced many individuals from America and Europe (**Table 2.1**). Today the colony is composed by 18 individuals.

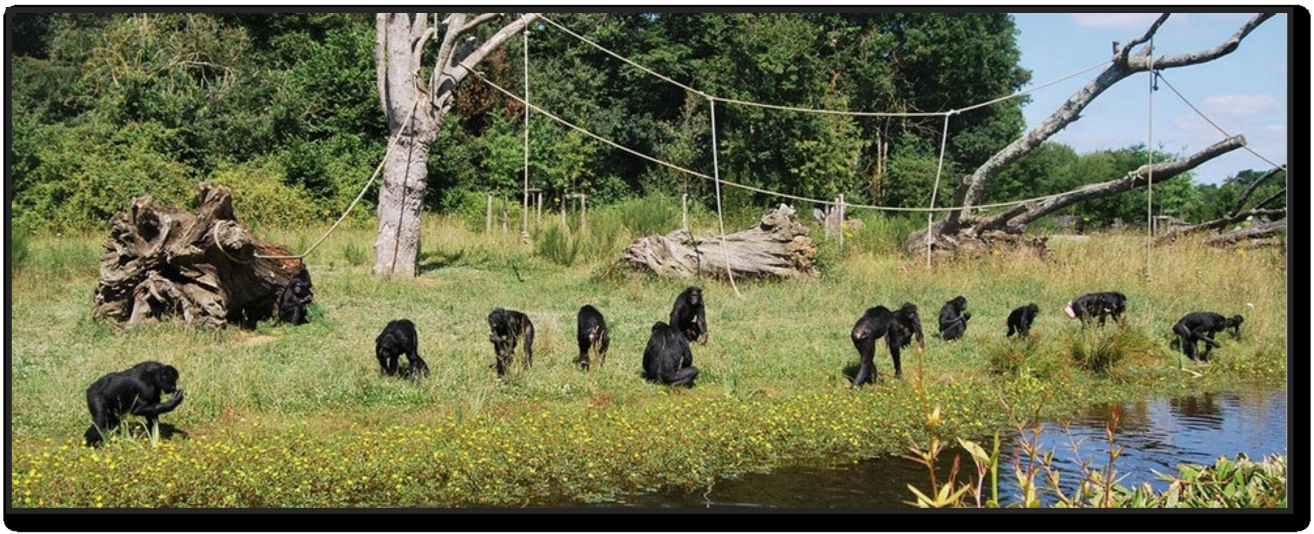


Figure 2.1 – The colony of *La vallée des singes* in the outdoor enclosure during a feeding period

The animals were housed in an enclosure with an indoor and an outdoor facility (900 m^2 split in many different room and 10.000 m^2 respectively) and could move freely from the indoor to the outdoor enclosure after the 10.00.

The outdoor enclosure is represented by an island with a little wood and a grassland portion delimited by an artificial river that act as a natural barrier (**Figure 2.2** and **Figure 2.3**).

Figure 2.2 – Aerial view of bonobos zone
Red circle – Indoor enclosure
Yellow circle – Outdoor enclosure

Figure 2.3 – The outdoor enclosure

Indoor and outdoor enclosures are full of many different kind of environmental enrichments like cords, trunks, swatches, coconuts, pneumatics, bottles of yogurt and exclusively in the indoor enclosure, animals can find hammocks to rest and play. Bonobos spend the night inside the indoor enclosure, at the 9.00 they usually go out and start to search the food which keepers regularly have left and spread before to encourage foraging activity. Furthermore keepers distribute food five times a day whereas water is accessible *ad libitum*. Today the colony is composed by 5 adult males, 7 adult females, 3 juveniles and 3 infants (see **Table 2.2** for details).

2.2 - Apenheul Primate Park

The park host 12 individuals (see **Table 2.3** for colony composition) in an area of interconnected multiple indoor enclosures of about 230 m^2 (**Figure 2.4** and **Figure 2.5**) overall and an outdoor naturalistic island of about 5000 m2, among which the animals could freely move after the first feeding session (9.00) until the last feeding session (17.30). Just before the last feeding session bonobos were separated into two groups with variable composition to spend the night in the indoor facilities and they were reunited the next morning just before the first feeding session. Water was available *ad libitum* and several environmental enrichments were provided. No stereotypic or aberrant behaviour characterized the study group.

Figure 2.4 – *Apenheul primate park* internal enclosures of bonobos; Author: Elisa Demuru

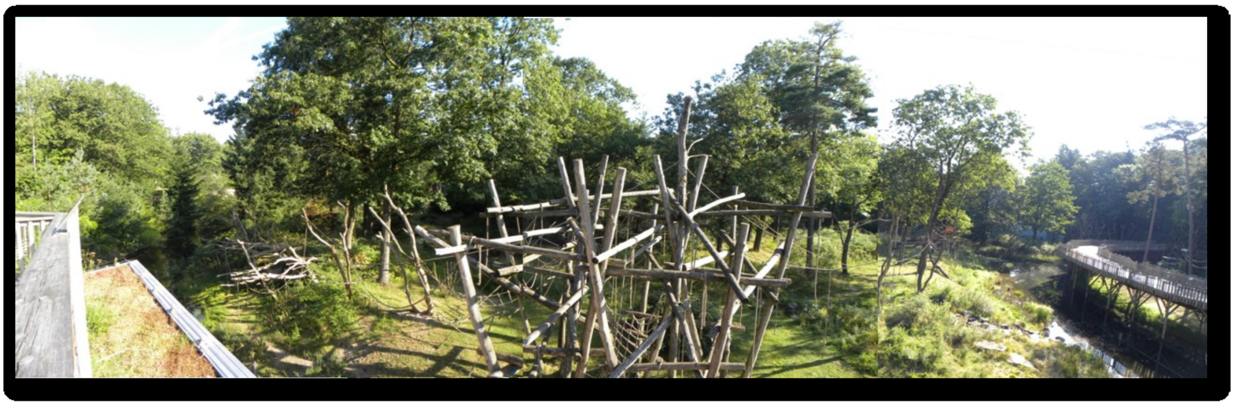


Figure 2.5 – *Apenheul primate park* enclosure of bonobos; Author: Elisa Demuru

NAME	KINSHIP	SEX	AGE CLASS	YEAR OF BIRTH
Daniela (Dn)	Diwani and David’s mother	F	Adult	1968
Diwani (Dw)	Daniela’s son	M	Adult	1996
David (Dv)	Daniela’s son	M	Adult	2001
Kirembo (Kr)	David’s father	M	Adult	1992
Ukela (Uk)	Nakala’s mother	F	Adult	1985
Nakala (Nk)	Ukela’s daughter	F	Juvenile	2007
Moko (Mk)	Ukela’s son	M	Infant	2012
Ulindi (Ul)	Ukela’s sister Loto’s mother	F	Adult	1993
Loto (Lt)	Ulindi’s son	M	Juvenile	2009
Lingala (Ln)	-------------------	F	Adult	2003
Lucy (Lc)	Yuli’s mother	F	Adult	2003
Yuli (Y)	Lucy’s doughter	F	Infant	2014
Kelele (Kl)	------------------	M	Adult	2004
Khaya (Ky)	Khalessi’s mother	F	Adult	2001
Khalessi (Kh)	Khaya’s daughter	F	Infant	2012
Lisala (Ls)	Luebo and Bondo’s mother	F	Adult	1982
Bondo (Bd)	Lisala’s son and Luebo’s brother	M	Adult	1991
Luebo (Lb)	Lisala’s son and Bondo’s brother	M	Juvenile	2006

Table 2.1 – The colony of *La Vallée des Singes* in the summer of

NAME	KINSHIP	SEX	AGE CLASS	YEAR OF BIRTH
Daniela (Dn)	Diwani and David’s mother	F	Adult	1968
Diwani (Dw)	Daniela’s son	M	Adult	1996
David (Dv)	Daniela’s son	M	Adult	2001
Kirembo (Kr)	David’s father	M	Adult	1992
Ukela (Uk)	Nakala’s mother	F	Adult	1985
Nakala (Nk)	Ukela’s daughter	F	Juvenile	2007
Moko (Mk)	Ukela’s son	M	Infant	2012
Lingala (Ln)	-------------------	F	Adult	2003
Lucy (Lc)	Yuli’s mother	F	Adult	2003
Kelele (Kl)	------------------	M	Adult	2004
Khaya (Ky)	Khalessi’s mother	F	Adult	2001
Khalessi (Kh)	Khaya’s daughter	F	Infant	2012

Table 2.2 – The colony of *La Vallée des Singes* in the 2012

NAME	KINSHIP	SEX	AGE CLASS	YEAR OF BIRTH
Jill (J)	Lingala's mother	F	Adult	1985
Lingala (Ln)	Jill's daughter	F	Adult	2003
Zuani (Z)	Liboso's mother; Nayembi's grandomother	F	Adult	~ 1990
Makasi (Mk)	Zuani's son; Liboso's brother; Nayembi's oncle	M	Infant	2009
Liboso (Li)	Zuani's daughter; Nayembi's mother; Makasi's sister	F	Adult	1997
Nayembi (N)	Zuani's granddaughter: Makasi's niece	F	Infant	2006
Hortense (H)	Zamba's mother; Hongo's mother	F	Adult	~ 1978
Zamba (Za)	Hortense's son; Hongo's brother	M	Adult	1998
Hongo (Ho)	Hortense's son; Zamba's brother	M	Juvenile	2006
Mobikisi (M)	-----------------	M	Adult	~ 1980
Kumbuka (K)	-----------------	F	Adult	1999
Yahimba (Y)	Kumbuka's daughter	F	Infant	2009

Table 2.3 – The colony of *Apenheul Primate Park* in the 2009

2.2 – Data collection

The study was conducted with no manipulation of animals and behavioural data were collected during three different periods:

- Apenheul 2009
- La vallée 2012
- La vallée 2014

2.2.1 – Apenheul data collection

Data were collected by two observers during three months of observations (August-October 2009) which were made over a 7 hours period, encompassing morning and afternoon, 6 days a week. The observer used a voice-recorder and the records were then computer transcribed on database sheets. For the data collection a rigorous and repeatable observation protocol was developed by Elisabetta Palagi before commencing systematic data collection. The two observers underwent a training period (the trainer was E.P.) during which they followed the same focal animals simultaneously and then compared data. The training was considered completed when the observations of the two observers matched in 95% of cases (Martin and Bateson 1986).

2.2.2 – La vallée des Singes 2014 and 2012

The observations of 2014 were performed for one month (22/06/2014- 18/07/2014). Two shooting operators observed and filmed bonobos from 9.00 to 18.00 in the indoor and outdoor enclosure every day. The presence of several shooting operators on the field allow us to follow the social activities that take place in different areas to obtain a larger pattern dataset. Shooting operators used HD videocameras and binoculars to observe and record the animals. *Feeding periods* are important moments in data collection because it is easy to observe an increase of tension inside the colony, a climax of social dynamics expression which reflects an increase in recorded data (see **Table 2.4** for feeding schedule details). For this reason, only during the feeding periods, the operators used three cameras instead of two to have a wider angle scenario of the shooting format.

June	July
11.30	11.30
14.30	14.30
15.30we	15.30
17.00	17.00
-	18.00

Table 2.4 – Feeding schedule of La Vallée des Singes 2014

Thanks to the open source video-analysis software "*KINOVEA*" we unified different but simultaneous shootings of feeding period and thanks to "*VLC*" software we have taken note of recorded behavioural data. For the data collection was developed an observation protocol by Elisabetta Palagi and Elisa Demuru before commencing systematic data collection.

The video-analysis operators or "*observers*" underwent a training period (Elisa Demuru was the trainer) during which they learned to distinguish or identify individuals, followed the same focal animals of the trainer and then compared data. A wide array of data regarding various social behaviours and contexts was collected according to a blind coding protocol, in which shooting operators and *observers* were not aware of the hypotheses and predictions that would have been tested. Data collection of 2012, was performed from 25/06/2012 to 31/07/2012 for a total amount of 28 days of observations. The colony was composed by 5 females and 4 males with the introduction of a new individual from an American zoo on July 12th of the same year (see **Table 2.2** for the composition of the colony in 2012). The collection of data was carried out with the same logistic and operational research parameters of 2014. In the colony food was distributed by keepers six times a day: 11.15, 12.30, 14.00, 15.00, 16.00, and 17.00 and water was accessible *ad libitum.* Shooting operators recorded for six days a week for a total amount of 166 hours.

2.2.3 – Operational definitions

Observation of behavioural data was performed using *Focal animal sampling* (Altmann*,* 1974) and *All occurrences sampling* (Altmann, 1974), while social behaviours were investigated using different ethograms. Moreover, via 3-min *scan sampling* we registered the presence of each individual in each video to quantify the total amount of shooting per individual. It's considered *Ethogram* a register of behaviours made through direct or indirect observation of a species. We used a general social ethogram, based on the ethograms formulated by Kano (1980), Enomoto (1990) and de Waal (1988) and developed by Elisabetta Palagi on the basis of previous observations performed on several bonobo colonies but also a *Facial expression ethogram* and a *Gesture ethogram*. For gestures, we adopted the ethogram published by Pollick and de Waal (2007), integrated with the work of Pika et al. (2005) and developed by Elisabetta Palagi and Elisa Demuru. For the facial expressions we adopted an ethogram developed by Elisabetta Palagi and Elisa Demuru.

2.2.3.1 – *Focal animal* and *All occurrences sampling*

We used *Focal animal sampling* technique provided by Altmann (1974) and defined as the observation of an individual for a predetermined period with the recording of all behavioural *states* (S) and *events* (E) described in a ethogram. Behavioural *states* have appreciable durations in time while *events* are instantaneous (e.g. grooming is a state, play slap is a event). In our case time duration was determined by exposure or visibility of the single animal.

Under some conditions, it is possible to record all occurrences of certain classes of behaviours in all members of a group during every observation period. Such records are generally possible when observational conditions are excellent, the behaviours are sufficiently ‘attentionattracting’, and the behavioural events never occur too frequently. As in our case all these conditions were met, it was possible to use the *All occurrences sampling* technique (Altmann, 1974), to collected following behavioural data:

- Aggressions
- Sexual contacts
- Gesture and Facial Expression
- Play
- Yawn
- Food division

2.2.3.2 –Sexual behaviour description

For each sexual behaviour we recorded:

- *Video Title*
- *Date*
- *Actor of sexual invitation*
- *Kind of invitation (pattern used)*
- *Actor of sexual behaviour (individual in the upper position during sexual contact)*
- *Sexual behaviour*
- *Receiver of sexual behaviour (individual in the lower position during sexual contact)*
- *Duration of sexual interactions*
- *Any kind of disturbance by third party during sexual interaction*
- *Union, replacement or interruption by third party during sexual interaction*
- *Food exchange during sexual interaction*
- *Place (indoor or outdoor)*
- *Context*
- *Animals in the group*
- *Note*

2.2.3.3 – Ethogram of sexual behaviour

For convenience, is reported as follow just sexual component of the general ethogram (see **Attached** for complete ethogram):

DVCO, Dorso-Ventral Copulation (event): penetration, thrusting and ejaculation. Female is in crouching position and male is *tergum*.

DVMO, Dorso-Ventral Mounting (event): male is behind female, no penetration. Mounting can be made by a male on another one.

ER, Erection (event): erection.

SBITE, Sexual Bite: bite during sexual contact.

GGR, Genito-Genital Rubbing (event): between two females in ventro-ventral, dorso-dorsal or ventro-dorsal position. Females rub their genital each other with lateral movements (only *Pan paniscus*). - VVGGR, DVGGR, DDGGR, GGRRR (male in sexc, females rub from behind).

IN, Inspecting (event): an animal get closer to another one and inspect its genital area touching it or/and sniffing it.

INV, Invitation (event): different in male and female. Male sit and slap the fet on the ground. The legs are opened. He oscillates and shows its erect penis (identical in *Pan paniscus* e *Pan troglodytes*.

Female walk in front of male watching it, then she stop and restart. In *Pan paniscus* female can lying down or crouching in front of the male .

MA, Masturbation (event): genital manipulation.

MMA, Mouth Masturbation (event): genital manipulation made with mouth

RRR, Rump-Rump Rubbing (event): common between males, two males rub their genital each other with their rump in contact.

RRGGR, Rump-Rump Genito-Genital Rubbing (event): female lying down with open legs, another individual get closer and rub its rump/genital.

BT, Sexual Bared Teeth (event): facial expression, arch are exposed. It state intense emotional state (only *Pan paniscus*).

SEXC, Sexual Crouching (event): crouching position used during sexual contacts.

SPR, Sexual Presenting (event): an individual get closer to another one showing its genital area from behind.

VVCO, Ventro-Ventral Copulation (event): penetration, thrusting and ejaculation. Individuals are in ventro-ventral contact.

VVMO, Ventro-Ventral Mounting (event): male is upon female in ventro-ventral position. No penetration.

2.2.3.3 – Preliminary worksheet for data analysis

Each sexual interaction was integrated in a dyadic system where for the creation of the **AB** individual's dyad it was considered just interactions of individual **A** to **B** but not sexual interactions of **B** to **A** also, considering it a different dyad **BA,** in a way to investigate even the directionality of sexual interactions. However sexual behaviours per dyad was analyzed in term of:

1) Numbers of invitations and frequency of total refused invitations (number of refused invitations/total amount of invitations);

2) Total amount of sexual contacts (copulations and mounts; see **Ethogram**)
3) Total amount of genito-genital contact (*genito-genital rubbing*, *rump-rump rubbing*, *genito-genital rump rump rubbing*, *rump-rump genito-genital rubbing*, *ventro-ventral mounting*, *dorso-ventral mounting*, *ventro-ventral copulation* e *dorso-ventral copulation*).

While social bonds were determined on two levels: kinship and affiliation. Kinship was based on maternal lineages, and only mother-offspring were considered to be related individuals. The affiliation levels between dyads components were categorized using grooming behaviours and calculating the quartile points of dyadic scores for each focal individual.

In a way to test just *quality* of non-kinship social bonds, grooming interactions was integrated in a dyadic system where the **AB** dyad was created by grooming integration of **A** to **B** and **B** to **A** also.

Therefore frequency of grooming for each dyad was get from the total amount of **A** to **B** grooming duration plus **B** to **A** and then, it was divided for the highest observation duration value among individuals of the dyad. After that, dyads were organized in decreasing order using the *frequency of grooming* and only dyads with scores in the top quartile were considered to have a strong affinitive relationship (friends). All the other dyads were labeled as weakly bonded.

Individuals' ranking position was assessed by entering decided conflicts into a winner/loser socio-matrix. Such socio-matrix was reordered via software *Steepness 1.0 by Leiva and de Vries* in a way to assign the Normalized David's Score value, a hierarchical indicator (see **2.3.1** for details).

We categorized our observations into two different social contexts: social tension and relax. The social tension context included post-conflict periods (10 min after an agonistic interaction), captive management activities (from the beginning of the operations till 20 min after the keepers left the enclosure), prefeeding (10 min before food distribution), and feeding (10 min after the food distribution). The relax condition included all the remaining periods of observation time.

2.3 – Statistical analyses

2.3.1 – Dominance relationship

In order to study dominance hierarchies and to establish potential linearity of a hierarchy we devised a socio-matrix of *agonistic encounters*. Hierarchical linearity depends by number of established relationship and by the entity of their transitivity inside the matrix of data (*Landau 1951*; *Kendall 1962*; *Appleby 1983*; *de Vries 1995*). For example, a triad transitive is a set of three interconnected individuals within relationship of transitive asymmetry (if A>B and B>C, then A>C) (*Shizuka & McDonald, 2012*). Considering that hierarchies which share comparable linearity indices can highly differs in the asymmetry of the distributed power among individuals, linearity coefficient is not enough to describe despotism level in a society (*Flack & de Waal, 2004*). For this reason we used another property of dominance hierarchies: the *steepness* (*de Vries et al., 2006*). In operational terms, the steepness derive from the width of the absolute differences in the general success level of individuals who occupy adjacent steps of hierarchic scale. When differences in the scale are high we speak about *despotic hierarchy* but when differences are low we are in presence of a *tolerant hierarchy.* Contrary to the linearity, that is grounded on binary dyadic relationship, *steepness* asks a rank cardinal measure (*Flack & de Waal 2004*; *de Vries et al. 2006*) and is grounded on useful of *David's scores* (DS) to collocate each subject in its hierarchic step. Calculation of DS is grounded on the weighted and no-weighted sum of the victory proportion, combined with the weighted and no-weighted sum of the defeat proportion of each individual inside a dyad (*Gammel et al., 2003*).

David scores allow to weigh dyadic success of each individual on total success of the same subject: in this way hierarchical position of individual A is valued in function of the other's subjects strength and a defeat of a high ranking individual will give an higher weight of a low ranking one (*de Vries et al., 2006*).

2.3.2 – Randomization test

Randomization test, designed by Ronald Fisher, can be used for non-indipendent sample with pseudo-repeated data (the same individual appear in different dyads). This test make bivariate analysis establishing correlation probability between an independent variable and a dependent one. We used randomization tests for two paired samples to check for influences of female menstrual cycle upon sexual contacts (mounts, copulations and GGR) and to investigate gender differences in sexual contacts. For the analysis it's been used *Resampling Procedures 1.3 by David C. Howell* (*freeware*), employed with 10,000 permutations.

Limit level of probability (*p-value*) are fixed by convention as follow:

- if $p<0.05$ then test is significant (*);
- if $p<0.01$ then test is very significant (**);
- if $p<0.001$ then test is extremely significant (***);
- if $0.05<p<0.1$ results are considered as a statistical trend

Finally, it is important make some clarifications about the term "menstrual cycle". In the analysis of frequency variation of mounts, copulations and genito-genital rubbing, menstrual cycle was divided in two different phases. The first one included all the days in which the *sexual tumescence/swelling* was on its maximum peak, whereas the second one was composed by all remaining days.

2.3.3 – General Linear Mixed Model (GLMM)

GLMM is a statistic instrument designed by Nelder e Wedderburn (*Stroup*, 2012), which permits of valuing interactions of many fixed variables upon the dependent variable using repeated measure and non independent data. Contrary to randomization test, GLMM give the best model and not the highest significant, indeed are the evaluated variables that are significant or not.

We used GLMM to evaluate the influence of many parameters on sexual contacts (in regards of their total number) and on sexual invitations (in regards of their total number and their rate of failure).

We used the variables as follow:

1) Random variables: actor and receiver identity;
2) Dependent variables: sexual contacts, sexual invitations, frequency of unsuccessful sexual invitation and frequency of genito-genital rubbing between females;
3) Fixed variables: actor and receiver sex, *Normalized David's score* of actor and receiver, bonding. We used sexual invitations variables also in the sexual contacts model.

Every distribution used as dependent variable was tested before to control any violation of normality conditions thanks to software *Easyfit 5.5* (see **Results**) and since *sexual contacts per hours* distribution was identified as a *Log-Normal distribution* we decided to use the *logarithm of sexual contacts per hours* for the GLMM.

We tested models for each combination involving the variables of interest, spanning from a single-variable model to a model including all the fixed factors (full model). We used the *Akaike's Corrected information Criterion* (AICc) to select the best model, that is a measure to compare mixed models based on -2 probability (*Restricted*) log. The model with the lowest value of AICc was considered as the best.

For the analysis we used the software *SPSS 20.0.*

Only adults and the immature subjects who were independent from their mothers were included in the analyses. Data from the three colonies where cumulated in the same model.

2.3.4 – Nonparametric test

Nonparametric statistics was used, because of the small sample size and deviation from normality (Siegel and Castellan 1988) verified through Kolgomorov-Smirnov test (K-S tests distribution of sample). The Wilcoxon test was used to assess differences between the frequency of gestures *versus* facial expressions during different contexts (*sexual* and *nonsexual*). The Friedman test was used to evaluate the best *unimodal communicative signal* in sexual context (*tactile gestures, visual gestures, facial expressions*) from the trigger and from the receiver point of view. Wilcoxon test is the corresponding nonparametric of Student's t test for two related sample data while Friedman test is for k-related sample.

We used software *SPSS 12.0* (IBM SPSS Inc., *Statistical Package for Social Science*) for the analysis.

CHAPTER 3

RESULTS

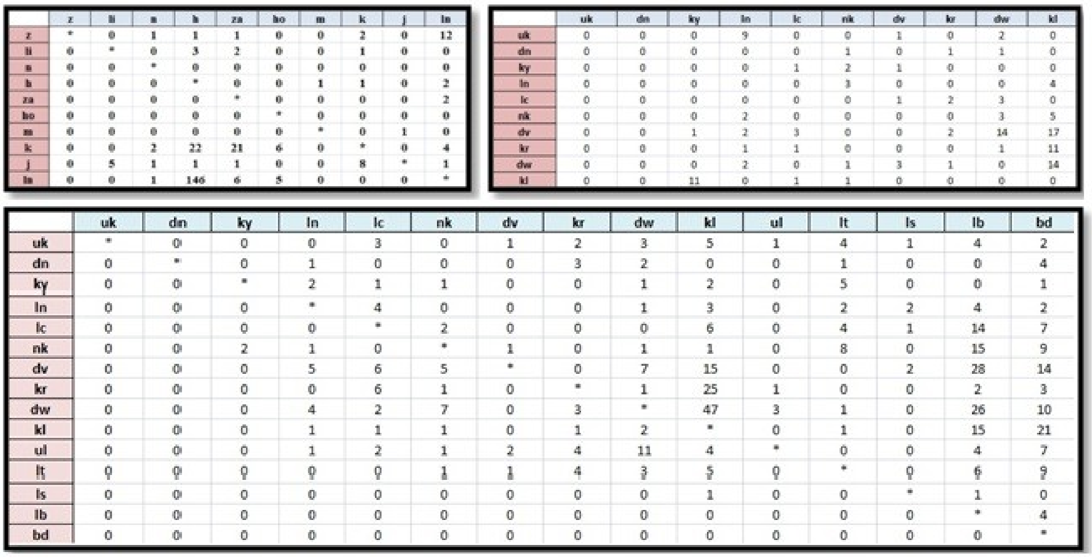
3.1 – Dominance relationships

In order to establish *dominance* relationships within the different colonies we collected the *agonistic encounters* (see **Ethogram**) between individuals to produce the sociomatrices.

Thanks to the free software *Steepness 1.0 by Leiva and de Vries*, we calculated the David's Score value, that weighs each single victory on total victory distribution obtained by each individual of the group. Our results are in agreement with existing literature and hierarchy analysis shows a non-linear hierarchy in each colony:

- Apenheul Primate Park 2009 – non-linear hierarchy; *steepness* = 0.346 (**Plot 3.1**)
- La Vallée de Singes 2012 – non-linear hierarchy; *steepness* = 0.305 (**Plot 3.2**)
- La Vallée de Singes 2014 – non-linear hierarchy; *steepness* = 0.369 (**Plot 3.3**)

Each colony shows sexual co-dominance with the highest place occupied by a female.

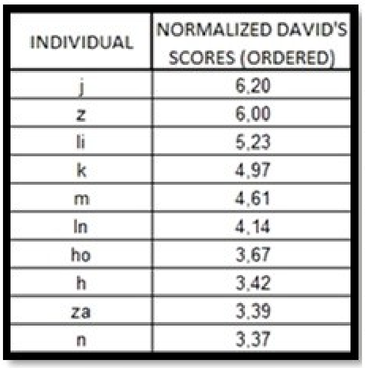


	z	li	n	h	za	ho	m	k	j	ln
z	*	0	1	1	1	0	0	2	0	12
li	0	*	0	3	2	0	0	1	0	0
n	0	0	*	0	0	0	0	0	0	0
h	0	0	0	*	0	0	1	1	0	2
za	0	0	0	0	*	0	0	0	0	2
bo	0	0	0	0	0	*	0	0	0	0
m	0	0	0	0	0	0	*	0	1	0
k	0	0	2	22	21	6	0	*	0	4
j	0	5	1	1	1	0	0	8	*	1
ln	0	0	1	146	6	5	0	0	0	*

	uk	dn	ky	ln	lc	nk	dv	kr	dw	kl
uk	0	0	0	9	0	0	1	0	2	0
dn	0	0	0	0	0	1	0	1	1	0
ky	0	0	0	0	1	2	1	0	0	0
ln	0	0	0	0	0	3	0	0	0	4
lc	0	0	0	0	0	0	1	2	3	0
nk	0	0	0	2	0	0	0	0	3	5
dv	0	0	1	2	3	0	0	2	14	17
kr	0	0	0	1	1	0	0	0	1	11
dw	0	0	0	2	0	1	3	1	0	14
kl	0	0	11	0	1	1	0	0	0	0

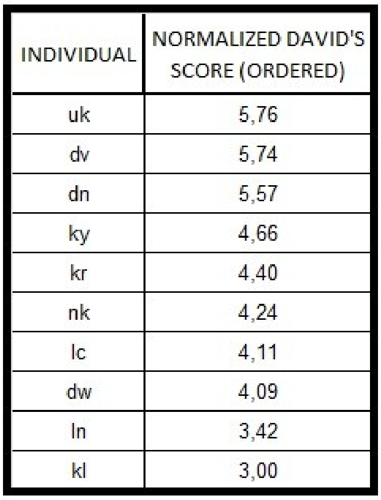
	uk	dn	ky	ln	lc	nk	dv	kr	dw	kl	ul	lt	ls	lb	bd
uk	*	0	0	0	3	0	1	2	3	5	1	4	1	4	2
dn	0	*	0	1	0	0	0	3	2	0	0	1	0	0	4
ky	0	0	*	2	1	1	0	0	1	2	0	5	0	0	1
ln	0	0	0	*	4	0	0	0	1	3	0	2	2	4	2
lc	0	0	0	0	*	2	0	0	0	6	0	4	1	14	7
nk	0	0	2	1	0	*	1	0	1	1	0	8	0	15	9
dv	0	0	0	5	6	5	*	0	7	15	0	0	2	28	14
kr	0	0	0	0	6	1	0	*	1	25	1	0	0	2	3
dw	0	0	0	4	2	7	0	3	*	47	3	1	0	26	10
kl	0	0	0	1	1	1	0	1	2	*	0	1	0	15	21
ul	0	0	0	1	2	1	2	4	11	4	*	0	0	4	7
lt	0	0	0	0	0	1	1	4	3	5	0	*	0	6	9
ls	0	0	0	0	0	0	0	0	0	1	0	0	*	1	0
lb	0	0	0	0	0	0	0	0	0	0	0	0	0	*	4
bd	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*

Table 3.1 – Agonistic encounters' sociomatrices of the colonies: on the left Apenheul 2009; on the right La Vallée2012; on the centre La Vallée2014



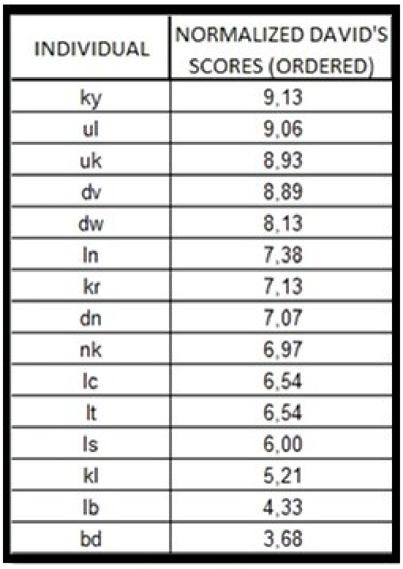
INDIVIDUAL	NORMALIZED DAVID'S SCORES (ORDERED)
j	6,20
z	6,00
li	5,23
k	4,97
m	4,61
ln	4,14
ho	3,67
h	3,42
za	3,39
n	3,37

Apenheul 2009



INDIVIDUAL	NORMALIZED DAVID'S SCORE (ORDERED)
uk	5,76
dv	5,74
dn	5,57
ky	4,66
kr	4,40
nk	4,24
lc	4,11
dw	4,09
ln	3,42
kl	3,00

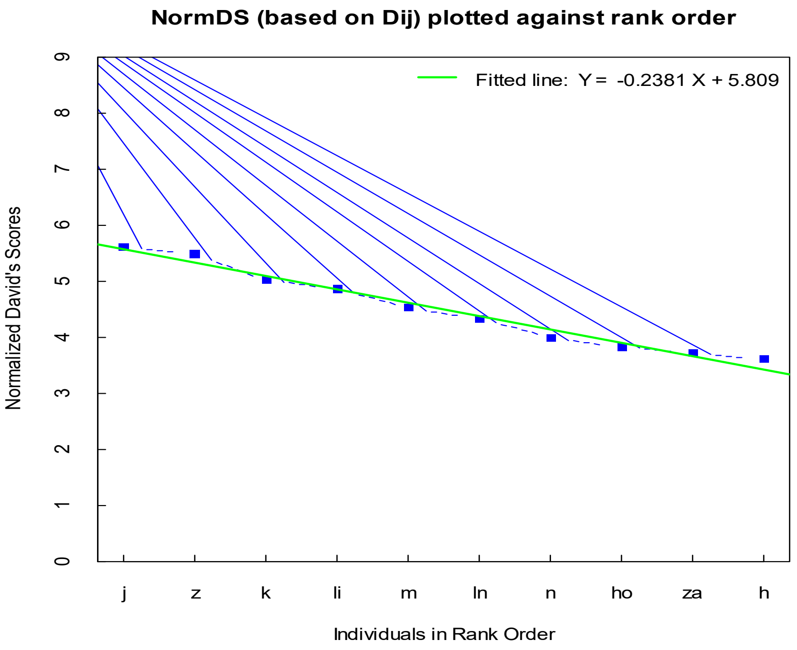
La Vallée des Singes 2012



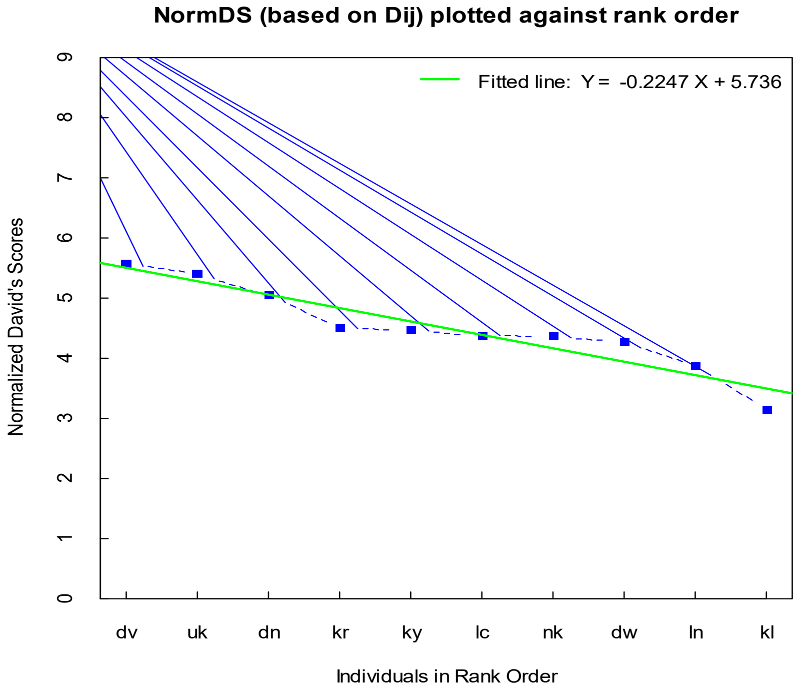
INDIVIDUAL	NORMALIZED DAVID'S SCORES (ORDERED)
ky	9,13
ul	9,06
uk	8,93
dv	8,89
dw	8,13
ln	7,38
kr	7,13
dn	7,07
nk	6,97
lc	6,54
lt	6,54
ls	6,00
kl	5,21
lb	4,33
bd	3,68

La Vallée des Singes 2014

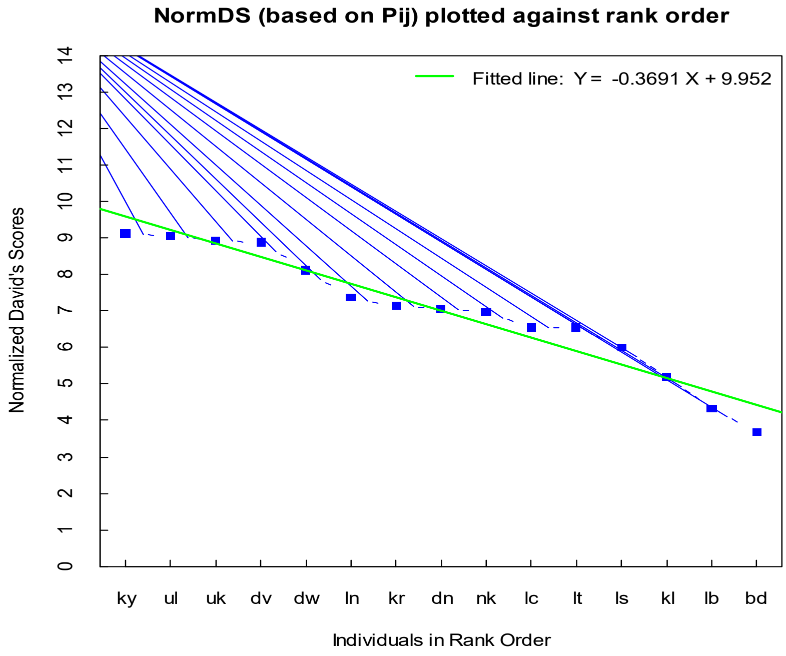
Table 3.2 – Normalized David's Score of the individuals of each colony. For initials of individuals see Materials and Methods



Plot 3.1 – Steepness of Apenheul primate park colony in 2009. For initials of individuals see Materials and Methods



Plot 3.2 – Steepness of La Vallée des Singes colony in 2012. For initials of individuals see Materials and Methods



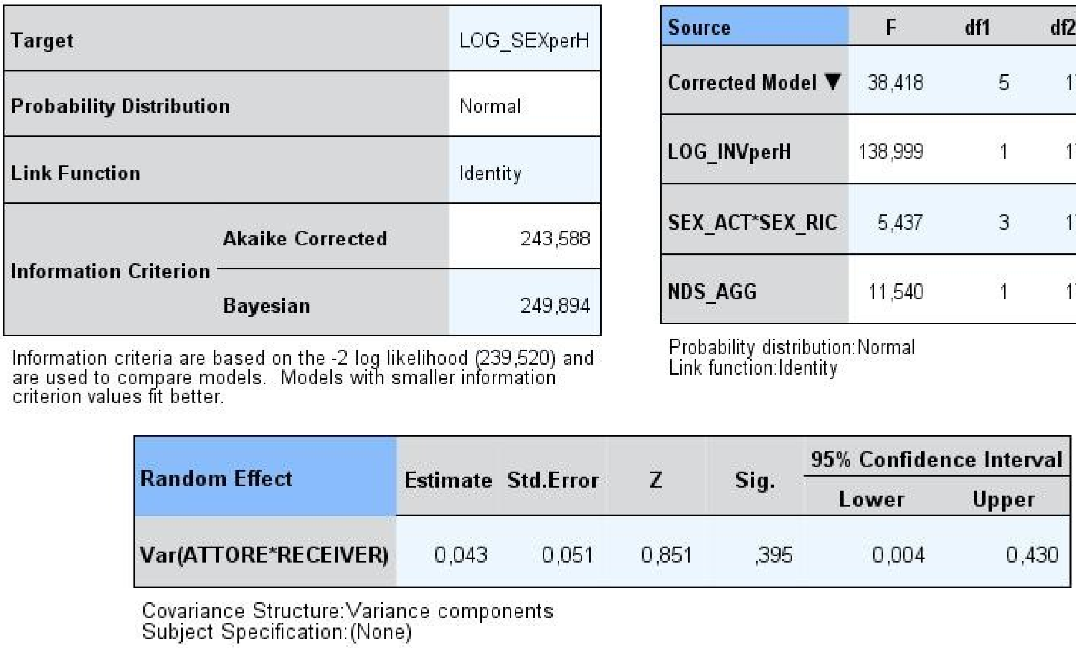
Plot 3.3 – Steepness of La Vallée des Singes colony in 2014. For initials of individuals see Materials and Methods

3.2 – General Linear Mixed Models

Using GLMM we evaluated which parameters influence distribution of: sexual contacts and sexual invitations (relatively to their total amount and their failure) and genito-genital contacts (relatively to its total amount).

3.2.1 – Sexual contacts

In order to analyze sexual contacts within the three colonies we used as dependent variable the number of sexual contacts per hours of observation of each possible dyad. The best model (see **Table 3.3**) to explain the distribution of *sexual contacts per hours* (LOG_SexH) includes the following variables: sexual invitations, *Normalized David's Scores* (*NDS*) of the *actor* and the combination of *actor and receiver sex* . This model reports a AICc = 243.588 (AICc intercept = 357.308); whereas, the second best model (AICc = 244.695) includes the same variables plus *bonding.*



Target		LOG_SEXperH
Probability Distribution		Normal
Link Function		Identity
Information Criterion	**Akaike Corrected**	243,588
	Bayesian	249,894

Information criteria are based on the -2 log likelihood (239,520) and are used to compare models. Models with smaller information criterion values fit better.

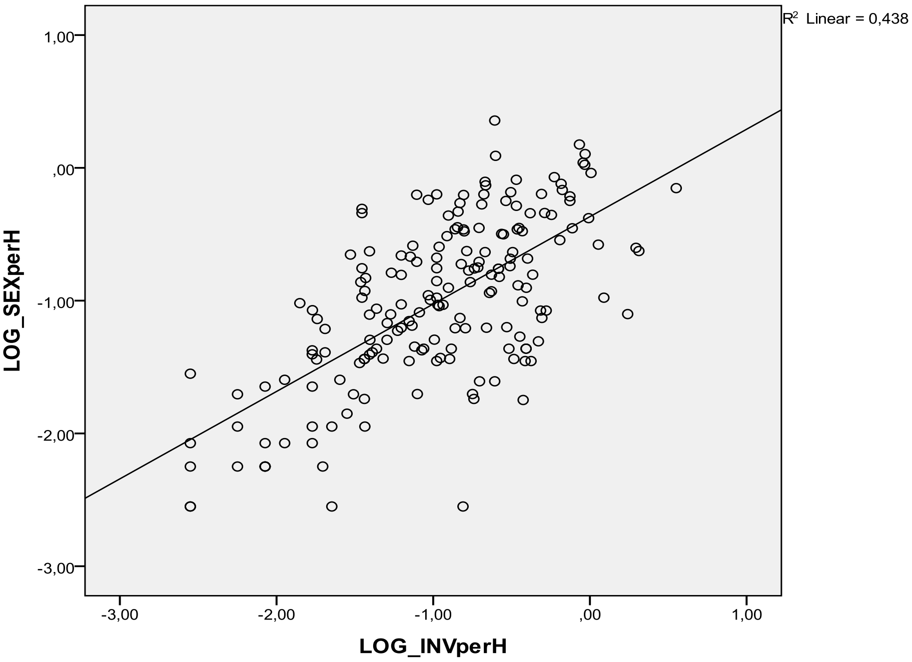
Source	F	df1	df2	Sig.
Corrected Model ▼	38,418	5	179	,000
LOG_INVperH	138,999	1	179	,000
SEX_ACT*SEX_RIC	5,437	3	179	,001
NDS_AGG	11,540	1	179	,001

Probability distribution:Normal
Link function:Identity

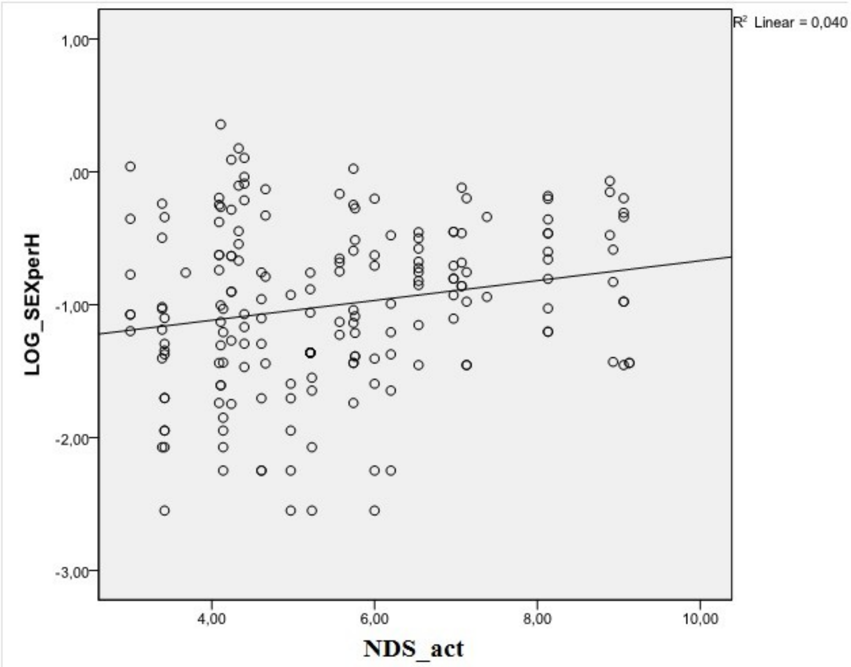
Random Effect	Estimate	Std.Error	Z	Sig.	95% Confidence Interval	
					Lower	Upper
Var(ATTORE*RECEIVER)	0,043	0,051	0,851	,395	0,004	0,430

Covariance Structure:Variance components
Subject Specification:(None)

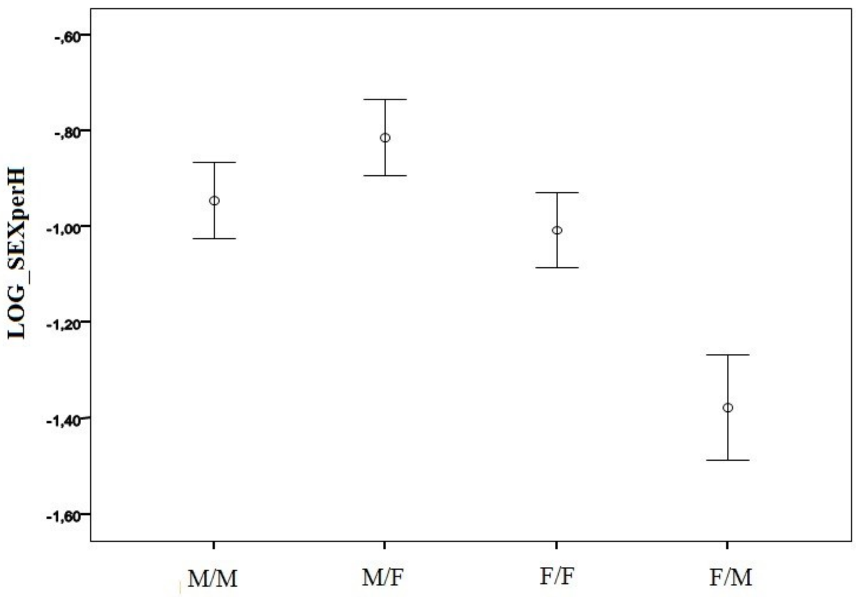
Table 3.3 – Best model obtained by using of SPSS for the GLMM analysis of logarithm of sexual contacts for hours.



Plot 3.4 – Scatter plot showing relationship between *logarithm of sexual contacts per hours* and *logarithm of sexual invitation per hour*. This is not a direct correlation but just a relation of a single fixed variable of the model and the dependent variable. The combination of the three variables express the authentic relationship.



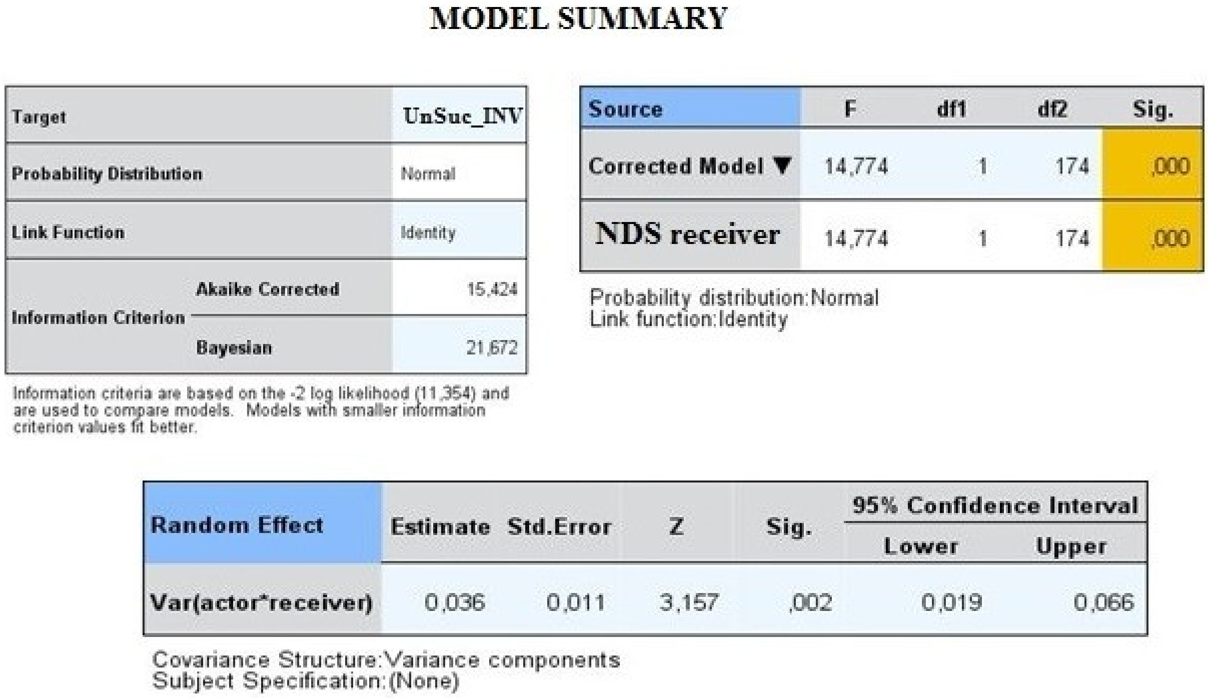
Plot 3.5 – Scatter plot showing relationship between *Normalized David's Score (NDS) of the actor* and *logarithm of sexual contacts per hours*. This is not a direct correlation but just a relation of a single fixed variable of the model with the dependent variable. The combination of the three variables express the authentic relationship.



Plot 3.6 –Relationship between *sex actor and sex receiver paired* and *logarithm of sexual contacts per hourss*. M=male; F=female;
This is not a direct correlation but just a relation of a single fixed variable of the model with the dependent variable. The combination of the three variables express the authentic relationship.

3.2.2 – Unsuccessful sexual invitations

In order to analyze unsuccessful sexual invitations within the three colonies we used as dependent variable the frequency of unsuccessful sexual invitations (number of negative response received on the total invitations performed) of relative to each possible actor within dyad. We tested the distribution of this variable with software *Easyfit 5.5* that identify our distributions as a *Normal distribution*. The best model (see **Table 3.4**) to explain the distribution of *unsuccessful sexual invitations* includes only the *NDS of receivers* (AICc = 15.424; AICc intercept = 22.352); whereas the second best model includes the *NDS of receiver* and the *sex of the actor* (AICc = 16.811).



MODEL SUMMARY

Target		UnSuc_INV
Probability Distribution		Normal
Link Function		Identity
Information Criterion	**Akaike Corrected**	15,424
	Bayesian	21,672

Information criteria are based on the -2 log likelihood (11,354) and are used to compare models. Models with smaller information criterion values fit better.

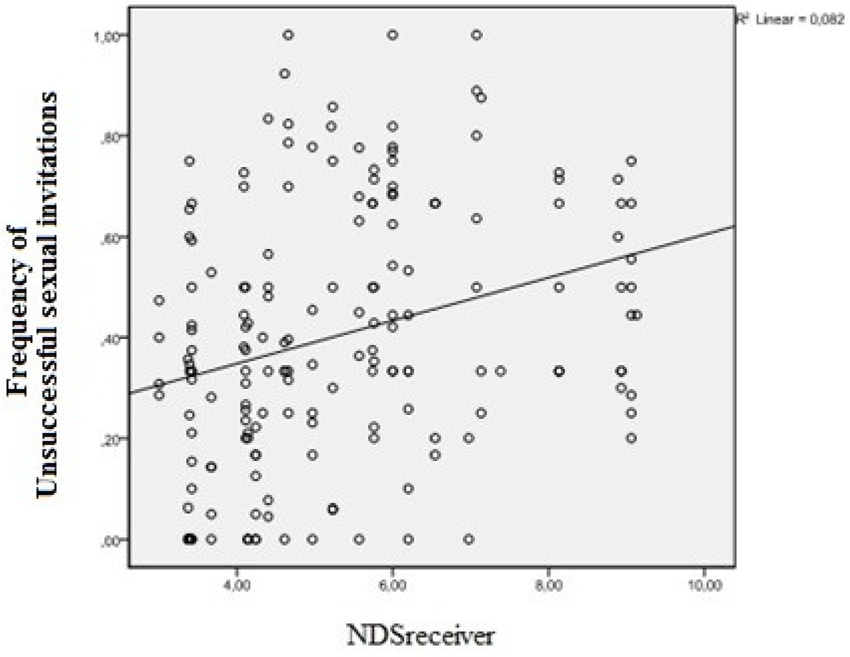
Source	F	df1	df2	Sig.
Corrected Model ▼	14,774	1	174	,000
NDS receiver	14,774	1	174	,000

Probability distribution:Normal
Link function:Identity

Random Effect	Estimate	Std.Error	Z	Sig.	95% Confidence Interval	
					Lower	Upper
Var(actor*receiver)	0,036	0,011	3,157	,002	0,019	0,066

Covariance Structure:Variance components
Subject Specification:(None)

Table 3.4 – Best model obtained by using of SPSS for the GLMM analysis of unsuccessful sexual invitations.

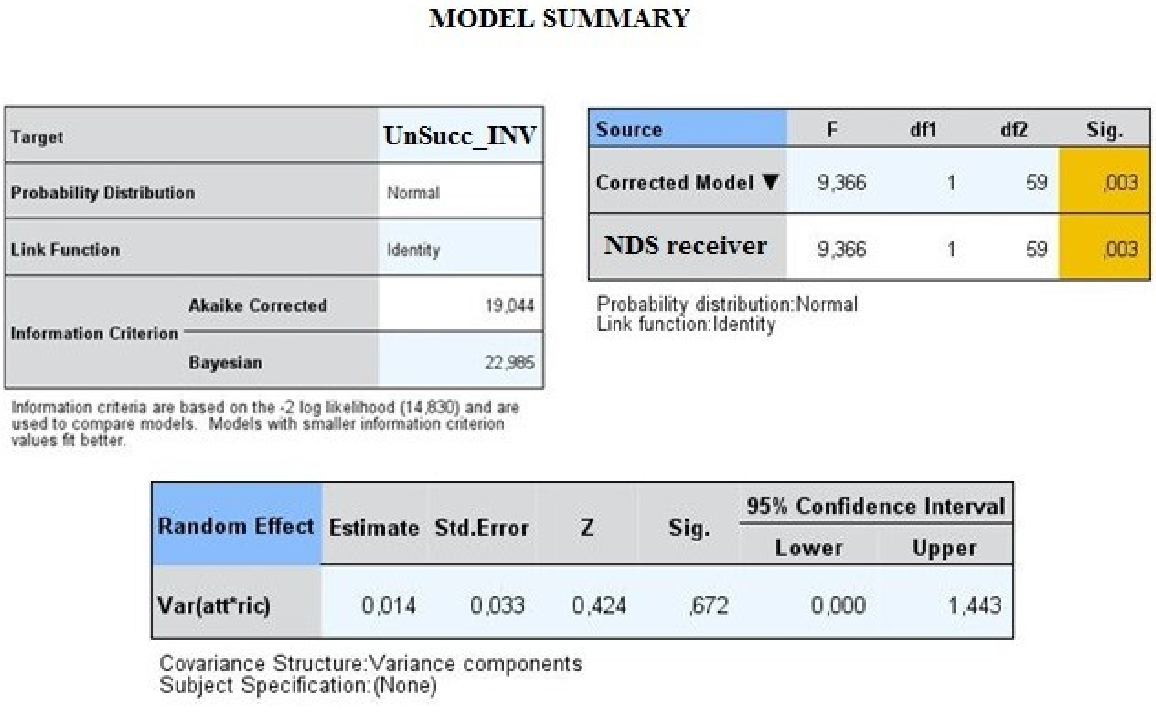


Plot 3.7 – The correlation between *NDSreceiver* and *unsuccessful sexual invitations.*

3.2.3 – Unsuccessful sexual invitations: the case of females

In order to analyze female sexual invitations within the three colonies we used unsuccessful sexual invitations failure (number of negative response received on the total invitations performed).

We tested the distribution of this variable with software *Easyfit 5.5* that identify our distributions as a *Normal distribution*. The best model (see **Table 3.5**) to explain the distribution of *unsuccessful sexual invitations* includes only the *NDS of female receivers (NDSric)* (AICc = 19.044; AICc intercept = 21.986); whereas the second best model includes the *NDS of females receiver* with the *NDS of females actor* as fixed variables (AICc = 21.298).



MODEL SUMMARY

Target		UnSucc_INV
Probability Distribution		Normal
Link Function		Identity
Information Criterion	Akaike Corrected	19,044
	Bayesian	22,985

Information criteria are based on the -2 log likelihood (14,830) and are used to compare models. Models with smaller information criterion values fit better.

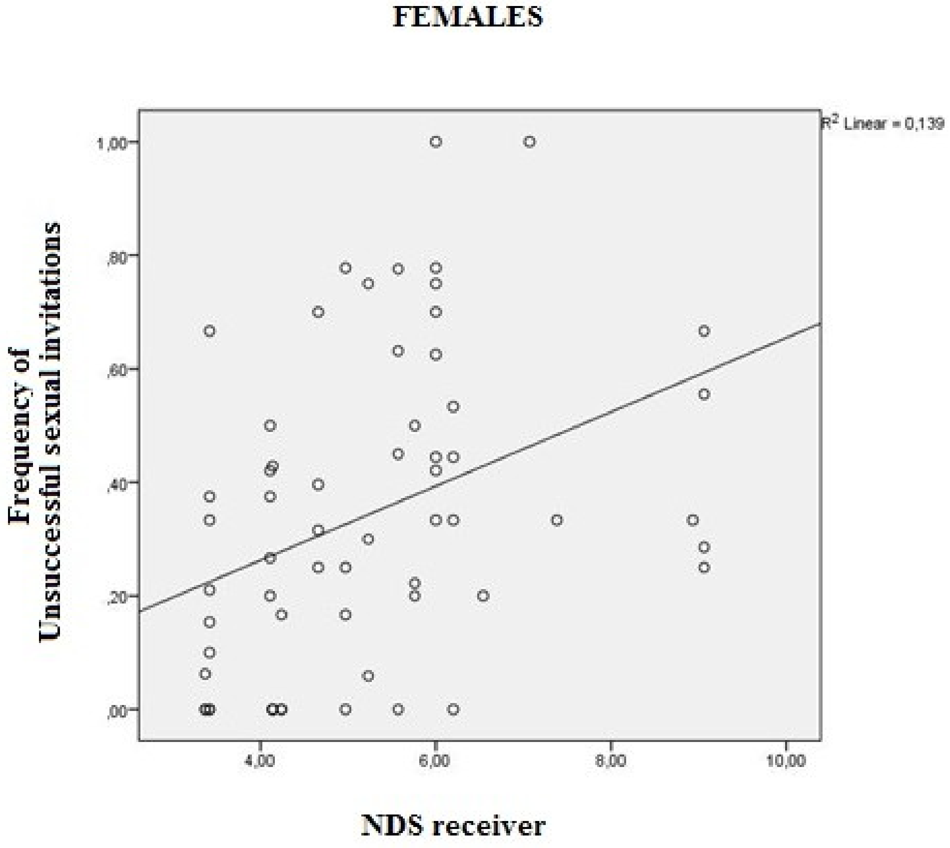
Source	F	df1	df2	Sig.
Corrected Model ▼	9,366	1	59	,003
NDS receiver	9,366	1	59	,003

Probability distribution:Normal
Link function:Identity

Random Effect	Estimate	Std.Error	Z	Sig.	95% Confidence Interval	
					Lower	Upper
Var(att*ric)	0,014	0,033	0,424	,672	0,000	1,443

Covariance Structure:Variance components
Subject Specification:(None)

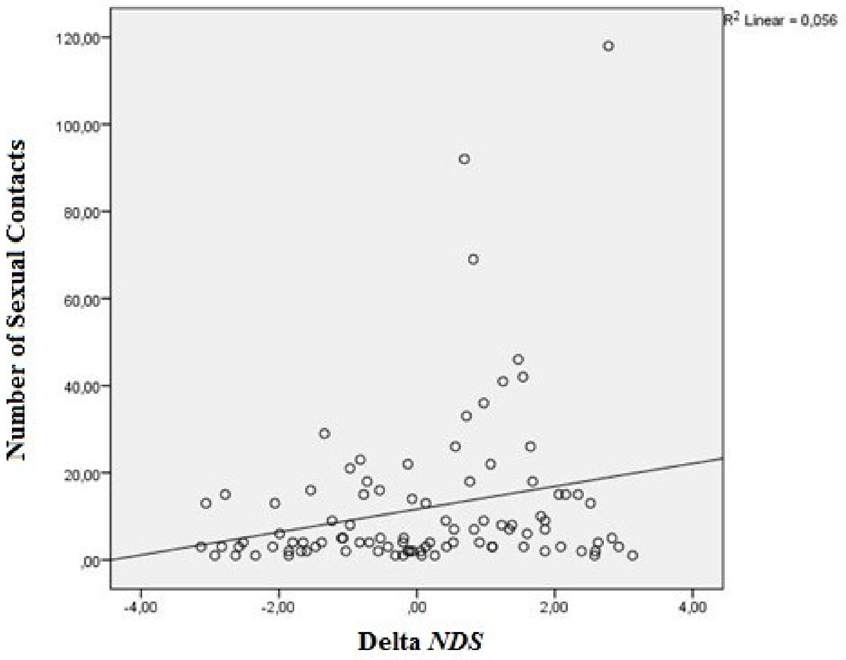
Table 3.5 – Best model obtained by frequency of unsuccessful sexual invitations analysis in the females.



Plot 3.8 – The correlation between *NDS of receiver* and *unsuccessful sex invitation* in females

3.3 – Rank and position

The Pearson's correlation coefficient showed a positive linear correlation between sexual contacts and the *NDS* difference between actor and receiver ($n_{dyad} = 95$, $r = 0.237$, $p = 0.021$).



Plot 3.9 – Correlation between sexual contacts and NDS differences between actor and receiver.

3.4 – Randomization test analysis

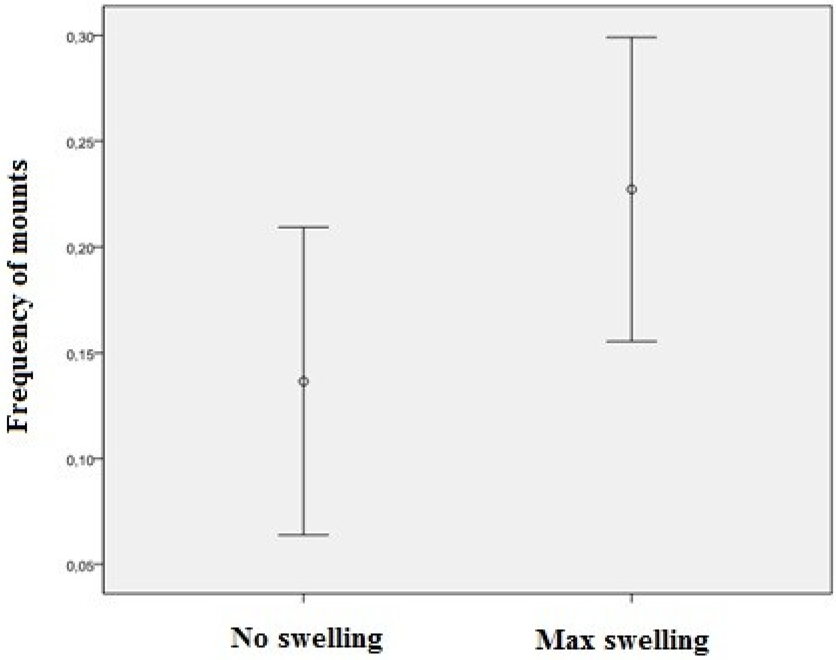
Two-paired sample randomization test was used to check:

- influence of menstrual cycles on genital contacts
- intentionality and emotionality communication in sexual and no-sexual contexts
- efficiency of communication in sexual and no-sexual contexts
- influence of body postures on sexual communication
- influence of signal complexity on obtained responses

3.4.1 – Sexual activity variation depending on menstrual cycle

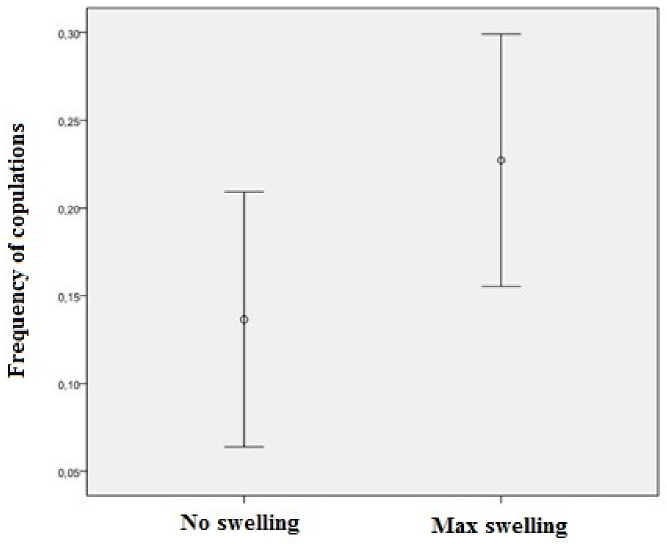
- **Heterosexual genito-genital contacts**

Regarding to non reproductive heterosexual genito-genital contacts we observed that even if mount frequency occurring in days with absence of *sexual swelling* is higher than mount frequency occurring when the female experiences *maximum sexual swelling,* this result is not statistically significant ($t = 1.031$; $n_{dyads} = 42$; $p = 0.343$; see **Plot 3.10**).



Plot 3.10 – Daily frequency of mounts during *no-swelling* and *maximum swelling* days.

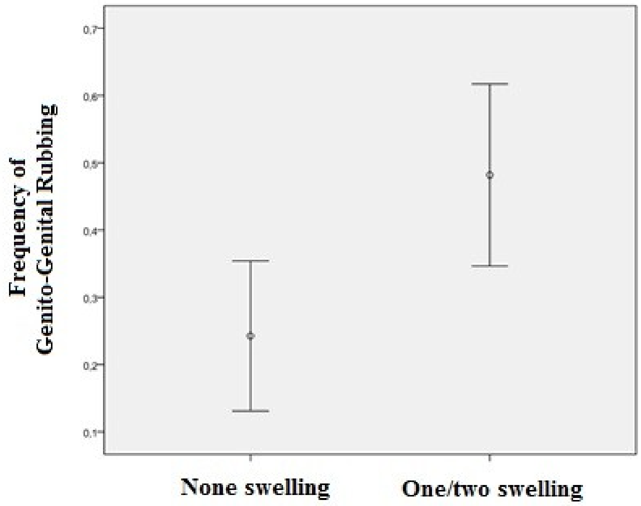
Reproductive eterosexual genito-genital contact analysis showed a higher frequency of copulations in days characterized by *maximum sexual swelling* than in days with absence of *sexual swelling* ($t = 1.956$; $n_{dyads} = 42$; $p=0.042$; see **Plot 3.11**).



Plot 3.11 – Daily frequency of copulations during *no-swelling* and *maximum swelling* days.

➢ Homosexual genito-genital contacts (GGR, Genito-Genital Rubbing)

In order to analyze homosexual contacts we divided the female sample in two categories: one composed by every dyads with both females presenting *no swelling* and another one with at least one female presenting genital *swelling*. We observed an interesting increase in the frequency of GGR when one of the two females experience *maximum swelling,* even though the differences failed to reach a complete statistical significance. The plot shows our results represented by statistical trend ($t = 1.962$; $n_{dyad} = 28$; $p=0.054$; see **Plot 3.12**)

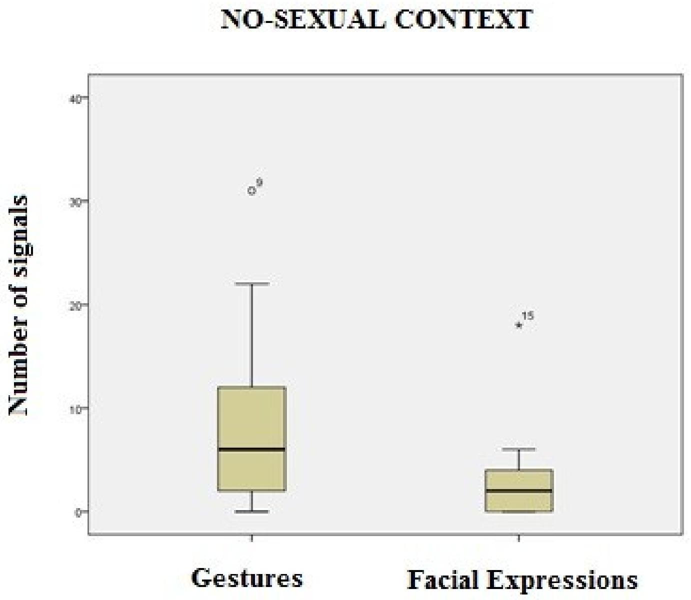


Plot 3.12 – Daily frequency of GGR in two categories of dyads. Both females presenting no swelling versus at least one female presenting maximum swelling.

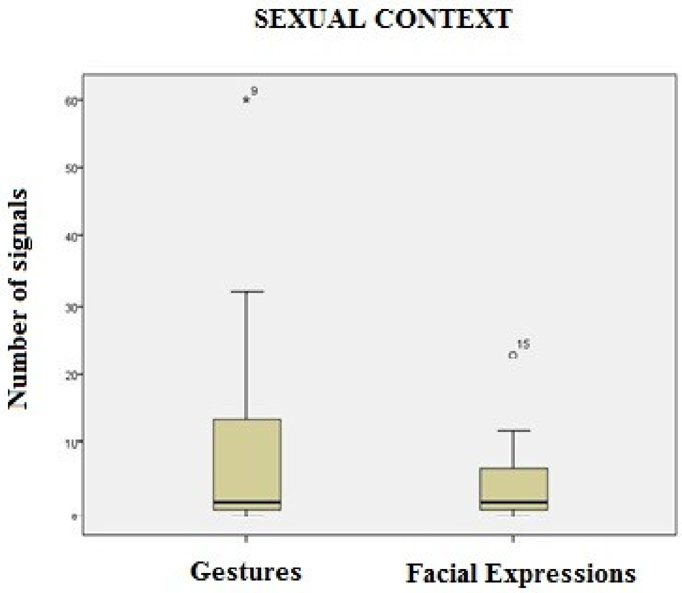
3.4.2 – Communicative signals

- **From the actor’s perspective**

The analysis of gestural communication compared with facial expressions shows a statistical trend with a little preference in the use of gestures in *no-sexual* context (see **Plot 3.13**; Exact Wilcoxon’s: T=4, N=15 , ties=1, p=0.060) contrary to a no significant difference in the use of these communicative patterns in *sexual* context (see **Plot 3.14**; Exact Wilcoxon’s: T=4, N=15, ties=2, p=0.236)



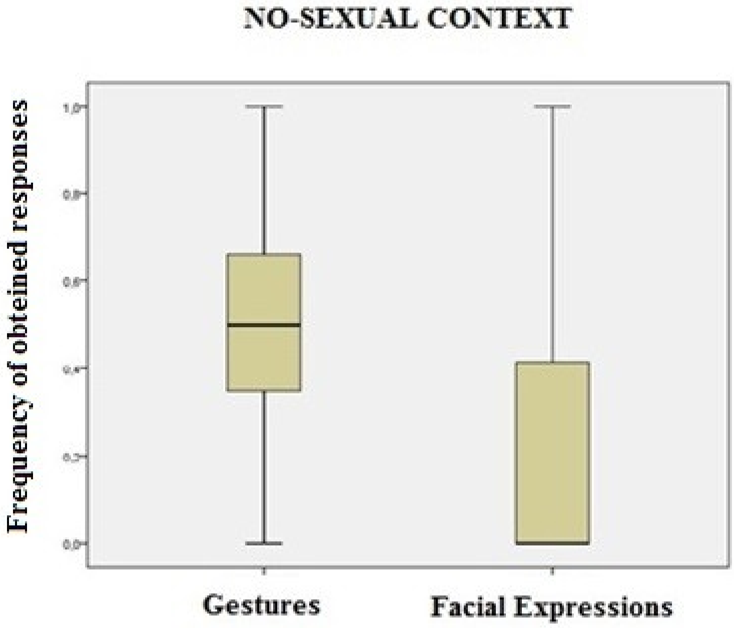
Plot 3.13 –Frequency of Gestures and Facial Expressions used as communicative signals in *no-sexual* context.



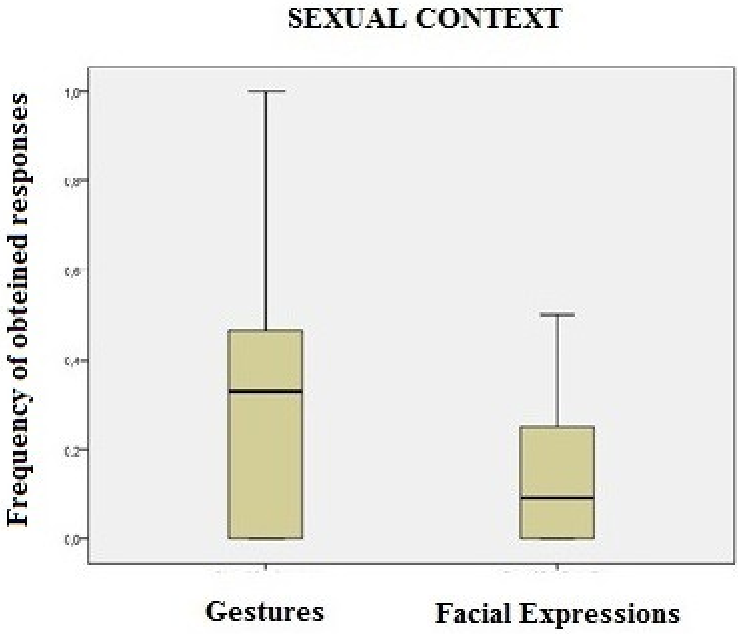
Plot 3.14 –Frequency of Gestures and Facial Expression used as communicative signal in *sexual* context.

- **From the receiver’s perspective (signal efficiency)**

The analysis of receiver responses showed a preference to respond to gestures in *no-sexual* context (see **Plot 15;** Exact Wilcoxon’s: T=3, N=15, ties=2, p=0.042) and this preference is confirmed in *sexual* context (see **Plot 16**; Exact Wilcoxon’s: T=3, N=15, ties=3, p=0.052)



Plot 3.15 – Frequency of obtained responds to Gestures and Facial Expressions used as communicative signal in *no-sexual* context.

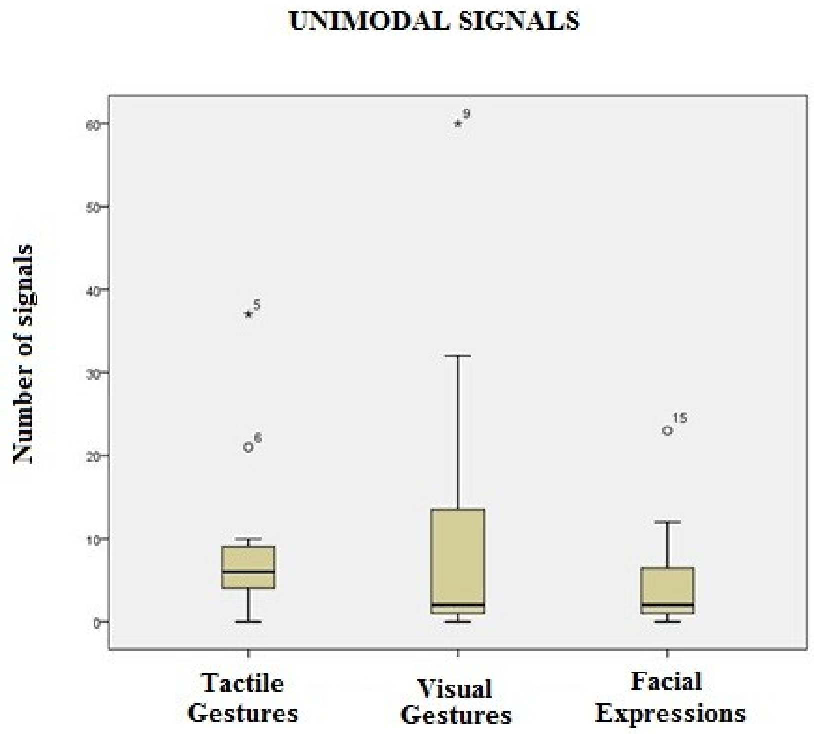


Plot 3.16 – Frequency of obtained responses to Gestures and Facial Expressions used as communicative signal in *sexual* context.

3.4.3 – Communication in sexual context

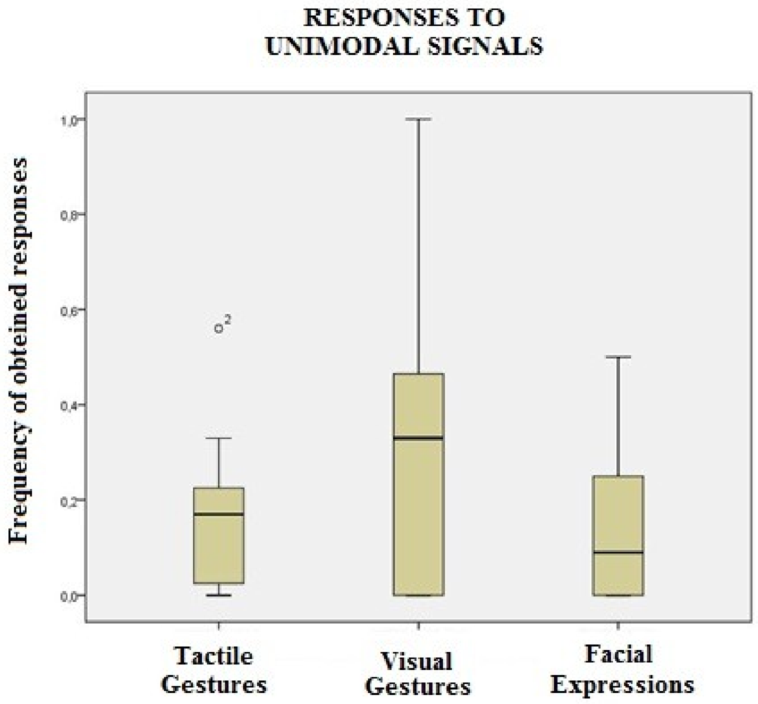
➢ Unimodal signals

The Exact Friedman's test showed no significant difference in the use of different signals in sexual context: tactile gestures, visual gestures and facial expressions (χ^2=1.655, *N*=15, *df*=2, *p*=0.472; see **Plot 3.17**).



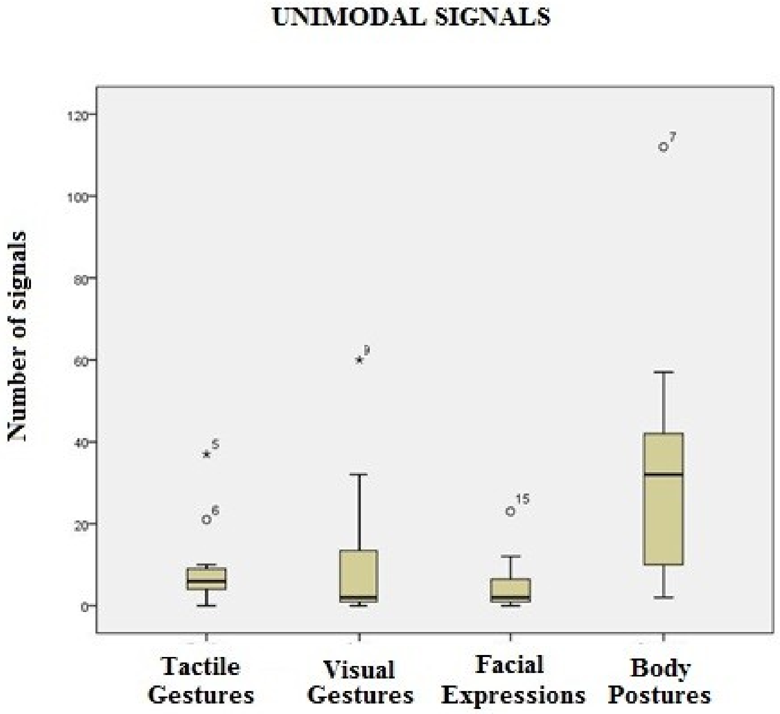
Plot 3.17 – Frequency of different communicative pattern used: tactile gesture, visual gesture, facial expression in *sexual* context.

As for the responses to such signals, we did not find any significant difference according to the nature of the stimulus perceived (χ^2=3.660, *N*=15, *df*=2, *p*=0.163; see **Plot 3.18**).

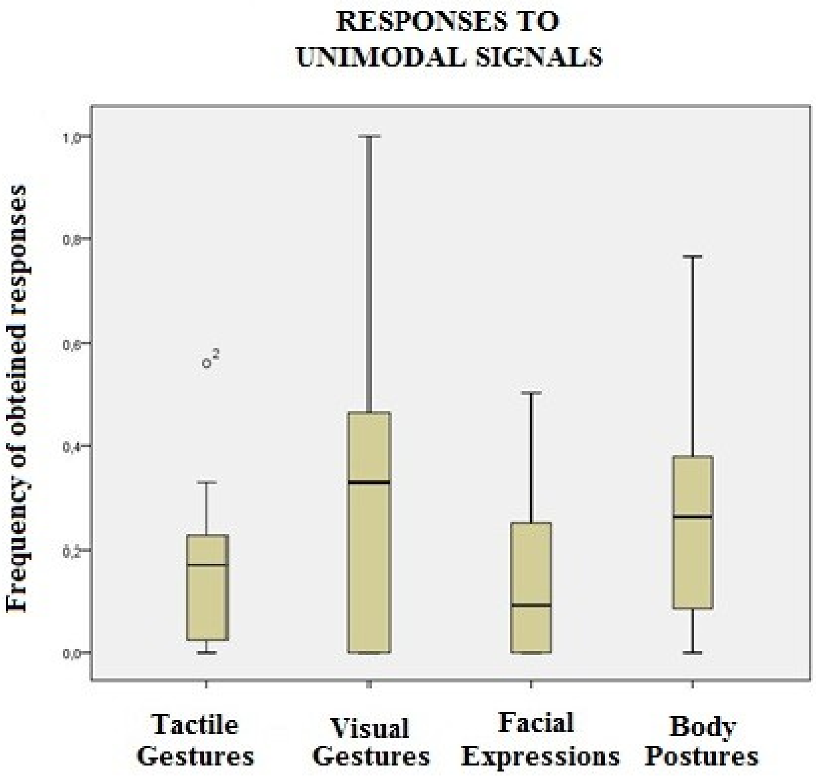


Plot 3.18 – Frequency of obtained responses with signal: tactile, gestural and Facial Expression used in *sexual* context.

The Exact Friedman's test showed an extreme significant difference in the use of different signals when we add the body postures as variable (χ^2=15.000, N=15, df=3, p=0.001; see **Plot 3.19**) but this difference disappear when we analyzed the responses to these categories (χ^2=4.035, N=15, df=3, p=0.262; see **Plot 3.20**)

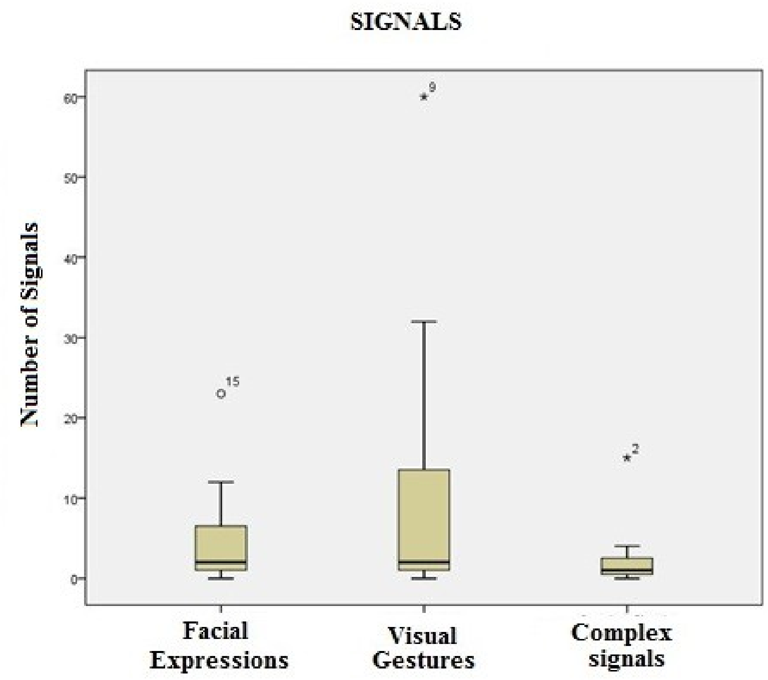


Plot 3.19 – Frequency of signals used in sexual context with *body postures* includes.

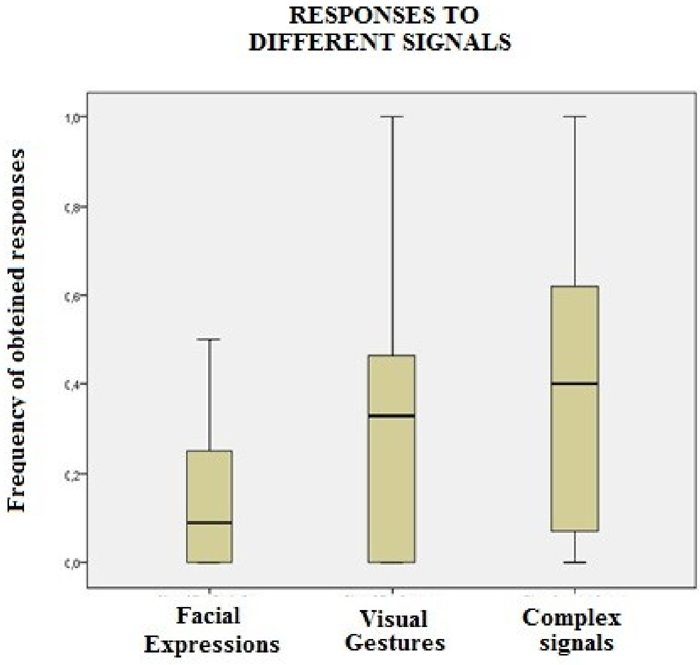


Plot 3.20 – Frequency of responses to signals used in sexual context with body postures includes.

The Exact Friedman's test showed a trend in the use of different signals (χ^2=5.607, *N*=15, *df*=2, *p*=0.058; see **Plot 3.21**) and a trend in the difference of obtained responses to different communicative pattern with an increase in the responses to complex and elaborated signals (χ^2=5.080, *N*=15, *df*=2, *p*=0.082; see **Plot 3.22**).



Plot 3.21 –Different typology of signals used in sexual context. In the *Complex signals* category are included: unimodal complex, multimodal, and signal sequences.



Plot 3.22 – Frequency of responses to different typology of signals used in sexual context. In the *Complex signals* category are included: unimodal complex, multimodal, and signal sequences.

CHAPTER 4

DISCUSSION

4.1 – Hierarchy and dominance relationships

Dominance relationships between males and females are usually a characteristic trait of a species' social system and have implications for differentiated access to resources, mating strategies of both sexes, and life history patterns (*Yanca & Low,* 2004; *Parker* 2006). Female-biased asymmetries in intersexual dominance relationships are rare among social mammals and there are ongoing debates about the proximate and ultimate mechanisms involved in shifting dominance relationships between the sexes (*Goymann* et al. 2001; *Kappeler & Schäffler,* 2008; *Watts et al.* 2009).

Dominance in bonobos is not an exception being a topic already under study. Many reports have claimed that bonobos are characterized by female dominance (*Parish 1994, 1996*; *Parish & de Waal, 2000*) others, on the contrary, suggest that the species is characterized by a high level of flexibility in dominance hierarchy (*Furuichi 1989*; *Hohmann & Fruth 2002*; *Kano 1992*; *White 1996*).

The focal point of the debate is how to consider food priority access of females. Is food priority an essential part of dominance expression or a distinct phenomenon (*White & Wood, 2007*)? Whereas female dominance can only be achieved through an agonistic power, female feeding priority is generally based on *"male deference"* (*Hrdy,* 1981). Moreover, the term *dominance* should be referred to the ability of evoking submissive signals (*Bernstein*, 1981). Following Kappeler's definition of dominance (1990, 1992) based on observations of lemurs, females of bonobos cannot be defined the predominant gender. Many authors converge on the idea that bonobo males overcome females in dyadic agonistic encounters (*Kano 1992;*

Hohmann & Fruth 2002; *White & Wood, 2007*) and this is usually used as a criterion to define hierarchies (*Drews, 1993*).

Furthermore, we have to stress that bonobo males mainly engage in *display* behaviours in which they charge the females by emitting excited vocalizations and dragging branches. Such behaviours rarely involve actual physical attacks (*Furuichi*, 2011). In feeding context the situation switches. When females approach males who are feeding in a preferred feeding spot, males yield their positions to late-arriving females (*Furuichi*, 2011). When overt conflict occurred at feeding sites, allied females sometimes chase males, but males never form aggressive alliances against females. It is interesting to note that even the strongest male retreats when approached by middle or low-ranking females (*Furuichi*, 2011).

The “concept of power” describes asymmetries within dyads and accounts for this variability as it predicts that the outcome of conflicts depends on multiple parameters (*Lewis,* 2002). First, dominance is regarded as the combined effect of *intrinsic* and *derived* factors (*Surbeck & Hohmann,* 2013). Intrinsic factors are based on an individual's own ability to use or threaten to use force; while, derived dominance, a component lacking in many species, comes from agonistic support obtained by group members (*Chapais*, 1995; *Surbeck & Hohmann,* 2013).

In bonobos, it is not possible to explore the dominance relationships without taking into account their alliances and coalitions (derived factors *sensu Surbeck & Hohmann,* 2013). Actually, many studies conducted in captive and semi-captive conditions underline the importance of the formation of female coalitions to gain dominance over males and control the available resources (*Parish 1994*; *Vervaecke et al. 1992*). In a comparative study of various captive populations, Stevens and colleagues (2007) showed that dominance linearity and steepness strongly vary. The authors found that female dominance is not exclusive (not all females are dominant over all males), even though the highest ranking individuals were always females and the lowest-ranking individuals were always males.

Our results indicate an absence of a hierarchical linearity in all the colonies considered, making impossible to adjust subjects in an ordinal ranking scale. Thus, we cannot establish if the bonobos of our colonies are characterized by a clear female dominance or by co-dominance, even though some speculations can be made. In agreement with Stevens et al. (2007), most females of our colonies occupy the top of the hierarchical ranking scale. On the other hand, the last positions are occupied by both males and females in heterogeneous way.

An intrinsic problem in defining hierarchy is resides in the methodological procedures. For example, the use of different behaviours to quantify the hierarchical relationships can lead to different results (*Norscia & Palagi, 2015*). Considering the high individual variability in engaging in intimidating displays, these behaviours *per se* are not reliable enough to accurately predict dominance relationships. Due to the different aggressive attitudes typical of males and females, by integrating our sociomatrices with behaviours as *dismiss* and *avoid* we could obtain a more reliable framework on dominance relationships. Different individuals, with different ranking positions, express aggressiveness in different ways. Moreover, low-ranking individuals usually prevent aggressive *displays* by high-ranking subjects (especially females) just *avoiding* them. Therefore, in a complex social system based on strategic politics, it is reductive to limit the analysis of ranking networks to the "*exhibited aggressiveness*" of the most demonstrative individuals. The integrative approach has to be applied by considering not only the "*reverence*" to the most authoritarians but also the important role of agonistic alliances, which cannot be quantified by using a simple sociomatrix.

4.2 - Possible factors influencing sexual contacts

In bonobos, sex is a multifunctional behaviour. In this species, sexual contacts regulate stress by acting as a social glue, alleviate tension and facilitate peaceful co-existence between members, who generally lack close genetic ties (*de Waal*, 1987; *Hohmann & Fruth*, 2000; *Fruth & Hohmann*, 2006; *Clay & de Waal*, 2014). Therefore, sex represents one of most important resources, not only in term of reproduction but also in terms of social regulation.

Investigating who controls the resources, in *direct* or *indirect way,* may provide a more realistic panorama of dominance relationships. We analyzed anatomical (e.g. sexual swelling phases) and social factors (e.g. bonding and rank) which potentially can affect the distribution of sexual contacts.

In bonobos, females mitigate any potential for excessive sexual competition among males and thereby avoid male harassment with a prolonged estrus. In addition, the long periods of pseudo-estrus may prevent infanticide through paternity confusion (*Furuichi*, 2011). Moreover, female alliances are a strong deterrent against sexual coercion by males (*Smuts & Smuts, 1991*). Males are not able to monopolize estrus females and, at the same time, they do not attempt to interrupt others' copulations (*Furuichi 1997; Hohmann & Fruth 2003*). Therefore, female choice is not based on male aggressive propensity (*Hohmann & Fruth 2003; Muller et al. 2011; Surbeck et al. 2011*; *Furuichi, 2011*). Nevertheless with the appearance of *sexual swelling*, females are characterized by an increase in proceptivity, receptivity and attractiveness to males (*Beach, 1976; Furuichi,* 1987) and to females (*Kano*, 1994; *Ryu et al.,* 2014). Sexual swelling is, therefore, a motor engine not only for reproductive sexual contacts but also for socio-sexual ones.

The large sexual repertoire typical of the species involves many different behaviours copulations, mounts and GG-rubbing. Copulations are defined as reproductive sexual contacts characterized by penetration, thrusting and ejaculation, contrary to the mounts during which ejaculation and usually penetration do not occur. Mounts (together with GG-rubbing) has therefore a social value, they are not linked to physiology of reproduction and can be observed regularly over time.

Our data show that copulations occurred more frequently when the females experienced *maximum swelling*. This shift was not valid for *mounts* thus claiming the different functional meaning of these two hetero-sexual contacts. The presence of a higher rate of copulations during maximum tumescence is in line with reports by Kano (1980, 1989, 1992), Furuichi (1987), Paoli et al. (2006) and contrasts with the results by Savage-Rumbaugh and Wilkerson (1978) and Thompson-Handler et al. (1984). Specifically, a higher rate of copulations during maximum tumescence is often reported for wild populations, whereas a less variable level of copulations throughout swelling cycles is often reported for captive groups (*Paoli et al.*, 2006). In any case, copulation rates should be affected by the peculiar history of a given group and by individual temperament, a factor that cannot be ignored in great apes.

We observed a statistical trend in the analysis of GG-rubbing frequency during the two different conditions. GG-rubbing occurred more frequently when at least one female of the dyad was in the *maximum swelling* phase. Even though the low level of dyads ($n_{dyad} = 28$) does not permit to make clear assumptions, our results are in agreement with those of Hohmann and Fruth (2000) and Paoli et al. (2006). This finding is consistent with the natural scenario in which females that reach sexual maturity migrate to neighboring groups when they experience a maximum swelling (*Furuichi*, 1989; *Idani*, 1991). In bonobos, the *maximum tumescence* may also be used as a means to access to high-ranking females (i.e., "social passport" tool) in order to enhance social integration. Dahl (1986) observed that the occurrence of swelling shifts the location of the clitoris to a more ventral position, and this finding is consistent with the hypothesis of Takahata et al. (1996) that female bonobos may show maximal swelling in order to exchange GG-rubbing with other females, rather than to copulate with males. Female homosexual interactions and copulatory rates, recorded in our colonies, were higher during *maximum tumescence*, suggesting that *sexual swelling* may be attractive not only for males but especially for females.

Following the assumption that mounting behaviour is the expression of dominance in several monkey species (*Wickler 1967; Maestripieri* 1996) and that high-ranking bonobo females usually engage in GG-rubbing by placing themselves in the upper position (*Hohmann & Fruth*, 2000), we explored the relationships between sexual contacts and the delta of *NDS* values (see **Materials and Methods**) within each dyad. We observed that sexual contacts increase concurrently with the *NDS difference* between actor (upper position) and receiver (lower position). Broadly speaking we can say that the individuals with highest *NDS* ranking values usually occupy the upper position during sexual contacts. Asymmetries in the performance of genital contacts were described by Clay and Zuberbühler (2012), Hohmann and Fruth (2000), Parish (1994; 1996) and de Waal (1987), with high-ranking females observed more often as the mounter than the mountee and our results are in agreement with them for hetero-sexual contacts (**Plot 3.9**). However, it is difficult to establish the cause-effect relationship and at this time we cannot express if *sex* is a way to restate dominance or a tool to create leadership, but we can suggest that position during sexual contacts can be interpreted as a hierarchy indicator.

To have a wider scenario of variables affecting sexual contacts we used GLMM (see **Materials and Methods**) starting by a full model including the following parameters: *NDS values*, *bonding*, *invitations* and *the sex of the two interactants*. In agreement with Paoli et al. (2006) our results show that bonding is not a good predictor of sexual contact distribution. The *invitations*, *NDS values of actor and the sex of the two interactants* remained in the best model. Particularly, *NDS of actor*, as previously mentioned, and especially *invitations* represent the most interesting variables to explain the distribution of sexual contacts (**Plot 3.4**). If a higher amount of invitations induces a higher response by the receiver to engage in sexual contacts, the investment of inviting others becomes a winning strategy to employ especially when the receiver is a high-ranking subject. The sexual invitation per se becomes a communicative tool to gain important *social resources*.

To further explore the effectiveness of the inviting behaviour, we considered the incidence of invitations which did not elicited any sexual response (*unsuccessful sexual invitation*s). The *NDS value of the receiver* was one of the best predictor of *unsuccessful sexual invitation*s: the more the NDS value of the receiver, the more the failure of the invitations. The high-ranking individuals tended to refuse invitations more than low-ranking ones, and this holds true also when analyzing female-female interactions. A good communicative strategy in persuading high-ranking individuals to engage in sexual contacts could be essential for subjects that want (and need!) to preserve the continuity of social relationships with high-ranking subjects.

4.3 – Communicative strategies

Living in social groups strongly reinforces the development and expansion of cognitive and emotional abilities underlying social competence (Social Brain Hypothesis - *Dunbar & Shultz* 2007; *Schyns et al.*, 2009). Communication is essential for survival, cohesion, and coordination of a group. Signal complexity, in both execution and recognition (*Schyns* et al. 2009), parallels the evolution of social systems (*Schmidt & Cohn* 2001; *Parr et al.,* 2005; *Demuru et al.*, 2015).

The modification in the use of a given communicative signal according to environmental and social factors, entails some degree of *intentionality* and is of particular importance for establishing the proximate factors leading to its emission. Therefore, *intentional* communicative signals are produced under voluntary control and they are the product of complex cognitive capacities, differently from *emotional* signals, produced by internal emotional states. It must be noted that the boundary between intentional and emotional communication is less clear-cut than previously thought. Sherwood et al. (2004, 2005) demonstrated the presence of two different neuro-anatomical routes determining the emission of facial expressions: an involuntary "emotional" path (through the facial nucleus in the pons of the brainstem) and a voluntary "intentional" path (through activity in the facial representation area of the motor cortex). Moreover, recent neuro-anatomical and neurological studies in human and non-human primates indicated the presence of a tight connection between the intentional and emotional communication systems (*Cattaneo & Pavesi* 2014), even though the degree to which they intermingle for the emission of a given signal is still not known.

Two main criteria define intentional signals, they must be: used in social contexts (*Leavens et al.* 2005) and influenced by the attentional state of the observer (*Bakeman & Adamson,* 1986; O'Neill 1996). Eye contact, body orientation, response waiting, and persistence are all critical features that must be considered to support the intentional nature of a communicative signal (*Cartmill & Byrne 2011*). All primates regularly communicate by means of vocalizations, facial expressions, body postures, and locomotion patterns but free brachiomanual gestures (i.e., manual communication without touching another individual or a substrate) are typical of humans and apes (de Waal, 2003).

Gestures are conventionally classified as *intentional* signals, because they are used in social contexts and are adjusted according to the attentional status of the observer (*Leavens* et al. 2005; *Call & Tomasello*, 1994; *Hare et al.*, 2000; *Hostetter et al.,* 2001; *Pika et al.* 2003; *Liebal et al.,* 2004; *Poss et al.*, 2006; *Pollick & de Waal*, 2007; *Leavens et al.*, 1996, 2004a, b). One reason to set gestures apart from other bodily communication is that the two are neurologically distinct in both their production and perception by others (*Perrett et al.*, 1996; *Rizzolatti et al.*, 1996).

In bonobos, *sexual behaviour* has become largely decoupled from its original reproductive function

with a diversification into the social domain and, it was been demonstrated a corresponding diversification in their communicative behavior. The functional meaning variety of sexual contacts is the reflection of different *emotional status* experienced by individuals thus a very complex system for communicating emotions and intentions is used by bonobos as other apes. Whereas gestures are intentional signals, facial expressions can disclose both emotions and intentions. The Emotional experience has long been viewed as an important phenomenon underlying animal behavior and helping to organize physiological, motivational and cognitive systems. Moreover, it facilitates adaptive responses to aid the survival of the organism (*Parr et al.*, 2005). Facial expressions and vocalizations are the primary means for communicating about emotion among primates and some authors argue that intentionality and emotionality are not mutually exclusive in the signal-production process but, rather, may represent two mechanisms that interact during signal production (*Demuru et al.*, 2014; *Liebal et al.*, 2014). Different from other forms of communication more strictly linked to emotional components (facial expressions), gestures are mainly based on cognitive capacities and experience (*Palagi et al.,* 2015), representing a more flexible communicative signals (*gestural flexibility hypothesis* - Pollick & de Waal, 2007).

We investigated communicative signals in *sexual* and *no-sexual context* in order to evaluate the role of the different communicative components: *intentional* and *emotional*. Our data support the *gestural flexibility hypothesis* of Pollick and de Waal (2007) according to which our relative closest primate uses brachiomanual gestures more flexibly across contexts than they do through facial expressions. Gestures are used similarly in both *no-sexual* and *sexual* contexts and seem less closely tied to particular emotions (*sexual context*), hence they possess a more adaptable function (**Plot 3.13, 3.14**). At the same time, during *sexual contacts,* we observed an increase in *facial expression*s as the expression of a higher emotional involvement. Considering the high emotional component involved in *play* (*Palagi et al.*, 2015), this behavior was excluded by our *no-sexual context* to better distinguish *emotional* and *intentional* component. In order to test the efficiency of *intentional* (gestures) and *emotional* (facial expressions) signals in both sexual and no-sexual contexts, we analyze the receiver's responses. In agreement with Genty and colleagues (2015), we observed a significant preference in the responses to *gestures* in both contexts (**Plot 3.15, 3.16**) even if responses to facial expressions tended to increase only in *sexual context.*

As previously mentioned a good communicative strategy in persuading high-ranking individuals to engage in sexual contacts could be essential for subjects that want, and need, to preserve the continuity of social relationships with high-ranking subjects. Thus, we focused our attention to communication in *sexual contacts*. In particular we investigated unimodal signals used as invitations to sexual contacts. We observed no significant difference in the use of *Tactile Gestures, Visual Gestures* and *Facial Expressions* as invitation signals and in the response to these unimodal signals (**Plot 3.17, 3.18**). These results claim not only any preference in the use of signals to invite other group members, but also that these signals are efficient in the same way. The results changed when we included *Body postures* in our analysis. The Exact Friedman's test showed an extreme significant preference ($p = 0.001$, **Plot 3.19**) in the use of *Body postures* to sexually invite a fellow, even though the efficiency of signal was not higher (**Plot 3.20**).

In general, invitations via sexual *Body postures* were more successful than those via *Tactile Gestures* and *Facial Expressions* but less than *Visual Gestures*. Therefore, we can broadly say that even though *Body postures* are a strong sexual context-specific signal conveying specific information, they are not the best in terms of efficiency to optimize sexual responses. Clearly, unimodal signals do not differ in term of optimization of signal efficiency (positive responses).

Earlier work on ape gestures suggested that the production of signal sequences is a sign of persistence in reaching a goal in response to the recipient lack of responsiveness (*Genty et al.*, 2011; *Hobaiter et al.*, 2011) and an attempt to increase success. We compared *Gestures* and *Facial Expressions* (unimodal simple signals) with *Complex Signals* (unimodal complex signals, signal sequences and multi-modal signals) in order to evaluate these hypotheses. Unimodal complex signals are defined as a combination of many signals belonging to the same sensory modality (e.g. visual gesture of hand combined with head movement as a reinforcement). Sequences were defined as strings of two or more unimodal signals made by the same individual within less than 5s of each other, whereas multi-modal combinations were defined as a combination of two or more signals of different sensory modalities produced simultaneously (e.g. visual gesture and vocalization). We found a tendency to increase the likelihood of success in sexual invitations (statistical trend, p=0.082; **Plot 3.23**), in agreement with previous studies showing that multi-modal signals are more efficient than single signals (*Liebal et al.*, 2013; *Ghazanfar et al.*, 2005; *Pollick & de Waal*, 2007). The analysis of the signal used in terms of *number,* instead revealed an interesting difference in the use of this signals (statistical trend, p=0.058; **Plot 3.22**) showing that complex signals are used very parsimoniously.

Complex signals represent therefore the best efficient way in terms of positive responses to engage in sexual contacts even though their costs probably limit the application. Thus, complex signals can be interpreted as indicators of a *communicative effort* to gain particular resources (in this case, *sexual resources*) and it is significant that we have excluded in our data collection most of complex signals that not accidentally were used by group members to gain another fundamental resource, *food*.

In conclusion, our results, in agreement with Pollick and de Waal (2007) and Genty et al. (2015), suggest that *complex signals* are not only the product of communicative effort but they could be interpreted by receivers as *honest signals* of intention and for this reason they are more efficient in eliciting a response. It is not surprising that complex signals in bonobos are used not only to obtain the most important energetic resource (food), but also the most important social resource: sex.

CHAPTER 5

CONCLUSIONS

Bonobos has a society with clear female-biased asymmetries in intersexual dominance relationships. Even if Furuichi (1989), Kano (1992), Hohmann and Fruth (2002) suggested a high level of flexibility in dominance hierarchy we can glimpse that could it be just the product of a methodological imprecision. We think that in bonobos, it is not possible to explore the dominance relationships without taking into account their alliances and coalitions and broadly speaking, we have to start to think in terms of resource control. Actually, many studies conducted in captive and semi-captive conditions underline the importance of the formation of female coalitions to gain dominance over males and control the available resources. But what are the most important resources for a bonobo? Obviously *food* is the first, but there is another kind of resources that seems to be not significantly emphasized at all: *sex*.

That females control food is in complete agreement, no discussions about that, so the first of the most important resources is controlled by females. But what about sex? We find many proofs that females control sex also in different way. Sex as *reproductive resource* is strongly conditioned by females thanks to *sexual swelling*. Thanks to prolonged pseudo-oestrous periods, and therefore prolonged sexual swelling, females of bonobo had reduced both competition of males and male sexual coercion (*Furuichi, 2011*). This is the most important difference with chimpanzee: females choice of reproductive partners is significant and the best way to obtain reproductive contacts for a bonobo male is not domination of other males or coercion through brute strenght but is become the first choice of females (*Hohmann & Fruth 2003a, b; Muller et al. 2011; Surbeck et al. 2011*; Furuichi, 2011). Thus, sex as reproductive resource is also controlled by females and our data are in agreement with this. Moreover, considering that females usually occupy prominent and ruling positions in society and that, following our results, distribution of sexual contacts is conditioned by rank of individuals, it is obvious that females conditioned distribution of sexual contacts (reproductive and socio-sexual) more than males. Therefore, in a complex social system based on strategic politics, it is reductive to limit the analysis of ranking networks to the "*exhibited aggressiveness*" of the most demonstrative individuals. We suggest that an integrative approach has to be applied by considering not only the "*reverence*" to the most authoritarians but also the important role of agonistic alliances, which cannot be quantified by using a simple sociomatrix.

Our purpose, for future investigation, is to apply the *social network analysis* method to inspect how social behaviors as *grooming*, *sex* but also *aggressive behavior* create rank differences and how they are maintained within a colony. First of all, we need a characterization more profound of hierarchy because current criterions highlight just only the most demonstrative individuals. Then we need to improve the study of communication. In this species indeed, complex signals represent the best efficient way to engage in sexual contacts. Complex signals are indicators of a *communicative effort,* hence are indicators of intentionality. Both sequences and multi-modal signals represent the modulation of the signals in order to optimize its efficiency and achieve any social goals and exactly this kind of signal modulation is a clue of high motivation. If good communication can make the difference in the achievement of resources, *ipso facto* enhance the comprehension of the communicative strategies is essential to really understand the most closet relative primate.

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ATTACHED I

GESTURE ETHOGRAM *Pan paniscus*

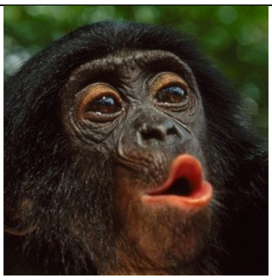
GESTO	SIGLA	DESCRIZIONE
ARM PUSH	**ARMPS**	Rapida estensione laterale del braccio dall'interno verso l'esterno.
ARM RAISE	**AR**	Una o entrambe le braccia alzate in genere con un movimento veloce e a scatto; le dita sono leggermente piegate e il palmo può essere rivolto verso l'altro individuo e verso l'alto, o lontano dall'altro individuo e verso il basso. Non c'è contatto. (da Pollick & De Waal, 2007)
ARM WAVE	**AW**	L'animale si alza in posizione bipede mentre si trova di fronte ad un altro individuo e o oscilla le braccia davanti al torso o alza una o entrambe le braccia rapidamente nell'aria. Non come parte di un display bluff. (da Pollick & De Waal, 2007)
BECKON	**BK**	Una o entrambe le braccia alzate in avanti e verso l'alto in modo ampio e rigido con i gomiti meno piegati rispetto all'arm raise; le mani sono lasciate penzolare verso il basso e le dita sono generalmente flesse; il movimento viene bloccato alla fine dell'oscillazione verso l'alto mentre l'individuo fissa il ricevente. (da Pollick & De Waal, 2007)
BEG WITH HAND	**BWH**	Mettere una o entrambe le mani intorno o sotto le labbra o il mento di un altro individuo o toccare con la mano con la bocca dell'individuo che mastica. (da Pollick & De Waal, 2007)
BENT WRIST	**BWR**	Piegare il polso mentre si tende il dorso e lato della mano verso un altro individuo; il contatto è possibile. (da Pollick & De Waal, 2007)
CLAP HANDS/FEET	**CLAPH/ CLAPF**	I palmi appiattiti delle mani sono portati in contatto tra loro in posizione orizzontale o verticale; può essere ripetitivo. (da Pollick & De Waal, 2007)
CLASP SELF	**CLPS**	Le braccia sono incrociate in fronte al torso, le mani sono piegate e colpiscono le braccia con un movimento a schiaffo. Ripetuto due o tre volte in successione. Riportato solo per gli scimpanzé. (da Pollick & De Waal, 2007)
DAB	**DAB**	Toccare un individuo mentre questo si avvicina o è fermo con il dorso delle dita piegate, subito dopo il contatto la mano è retratta immediatamente; la sequenza è ripetuta un numero di volte in una veloce successione. (da Pollick & De Waal, 2007)
EXTENDED ARM	**EXTA**	Allungare il braccio verso un altro individuo.
FINGER FLEX	**FF**	Le dita si muovono velocemente avanti ed indietro; il palmo può essere verso l'alto o verso il basso e il polso non è piegato. Riportato solo per gli scimpanzé. (da Pollick & De Waal, 2007)
FINGER/HAND IN MOUTH	**FM/HM**	Mettere le dita o la mano nella bocca di un altro individuo. Riportato solo per i bonobo. (da Pollick & De Waal, 2007)

FLAIL	**FLAIL**	Le braccia e le mani sono completamente alzate sopra la testa e sono scosse in rapida successione (generalmente in tantrum o approccio). Ripetitivo. (da Pollick & De Waal, 2007)
FLAP	**FLAP**	Un braccio è alzato e fa un movimento a schiaffo verso il basso con la mano in direzione di un altro individuo - non c'è contatto violento col substrato (terreno, muro, ecc…). (da Pollick & De Waal, 2007)
FOOT/LEG GESTURE	**FOOT/LEG**	Ogni allungamento di una gamba o piede verso un altro individuo. (da Pollick & De Waal, 2007)
GENTLE TOUCH	**GTOU**	Ogni tipo di contatto fatto con la mano (palmo o dorso) o con la punta delle dita su un altro individuo, senza forza apprezzabile. (da Pollick & De Waal, 2007)
HAND LEAD	**HL**	Prendere la mano di un altro individuo e portarla in contatto col proprio corpo, ma senza forza sufficiente a muovere l'intero corpo del ricevente. Riportato solo per i bonobo. (da Pollick & De Waal, 2007)
HARD TOUCH	**HTOU**	Ogni sorta di contatto fatto con la mano (dorso o palmo) o con la punta delle dita, senza forza apprezzabile, ma il contatto è più vigoroso del semplice appoggiare la mano sul corpo di un altro individuo. (da Pollick & De Waal, 2007)
HEAD RIGHT & LEFT	**HEADRL**	Movimento orizzontale della testa da destra a sinistra (come per dire no).
HEAD SIDE	**HS**	La testa viene fatta oscillare dal lato destro a quello sinistro avvicinando l'orecchio alla spalla e mantenendo la faccia fissa in avanti.
HEAD UP AND DOWN	**HEADSUD**	Movimento verticale della testa (come per dire sì).
HUNCHOVER	**HOVER**	Un braccio è fatto scivolare sulla schiena di un altro individuo, ma non c'è abbraccio o un lungo contatto (meno di 2 secondi). (da Pollick & De Waal, 2007)
MOVE	**MOVE**	Un animale muove un oggetto di fronte ad un altro animale, per esempio un ramo, paglia, ecc… (da Pika *et al.*, 2005)
OPEN ARMS	**OPARM**	Movimento dell'avambraccio dal basso verso l'alto e dall'interno verso l'esterno in una specie di diagonale. Palmo rivolto verso il basso o di lato e polso rilassato.
PAT	**PAT**	Toccare rapidamente e ripetutamente un altro individuo con il palmo appiattito delle mani; non nel gioco. Ripetitivo. (da Pollick & De Waal, 2007)
POINT	**POI**	Indicare con l'intera mano o con uno o più dita il ricevente, un altro individuo o un oggetto (da Pollick & De Waal, 2007).
POKE	**POKE**	Spingere la punta di uno o più dita con un movimento improvviso sul corpo di un altro individuo. Ripetitivo. (da Pollick & De Waal, 2007)
RAP KNUCKLES	**RAPK**	Bussare con le nocche di una o entrambe le mani sul terreno, sul muro o su un oggetto mentro si guarda il ricevente. Ripetitivo. (da Pollick & De Waal, 2007)
REACH OUT DOWN	**ROUTD**	Tendere una mano verso un altro individuo, stendendo il braccio, il polso, la mano e le dita in una posizione più o meno orizzontale con il palmo rivolto verso il basso. Non c'è contatto. (da Pollick & De Waal, 2007)
REACH OUT SIDE	**ROUTS**	Stesso come il reach out down ma il palmo della mano è rivolto di lato. (da Pollick & De Waal, 2007)
REACH OUT UP	**ROUTU**	Stesso come il reach out down ma il palmo della mano è rivolto verso l'alto. (da Pollick & De Waal, 2007)
SELF PAT	**SPAT**	Pat rivolto su se stessi (idiosincratico).

SELF POKE	**SPOKE**	Poke rivolto su se stessi (idiosincratico).
SHAKE	**SHAKE**	L'animale dondola appeso a un ramo o una corda e fa oscillare le braccia o le gambe da un lato all'altro di fronte ad un altro individuo. (da Pika et al., 2005)
SHAKE WRIST	**SWR**	Scrollare vigorosamente la mano tenendo il polso flessibile. Ripetitivo. (da Pollick & De Waal, 2007)
SLAP GROUND	**SLAPG**	Il palmo appiattito della mano è portato con forza a contatto col terreno di fronte o su un oggetto fisso come una rete o una muro. (da Pollick & De Waal, 2007)
SLAP GROUND AND STOMP	**SLST**	Simultaneo slap ground e stomp. (da Pollick & De Waal, 2007)
STOMP	**STOMP**	Colpire un oggetto o il terreno con la pianta di uno o entrambi i piedi; può essere fatto con entrambi i piedi in veloce alternanza. (da Pollick & De Waal, 2007)
THROW AIMED	**THA**	Lancio in avanti dall'alto o dal basso di un oggetto, incluso escrementi, mentre si guarda al target; non nel gioco. (da Pollick & De Waal, 2007)
THROW HOLD	**THH**	Il braccio è alzato sopra la testa, come in un lancio, ma il movimento non dura per più di 2 secondi. Riportato solo per gli scimpanzé. (da Pollick & De Waal, 2007)
OPEN ARMS	**OPARM**	Movimento dell'avambraccio dal basso verso l'alto e dall'interno verso l'esterno in una specie di diagonale con il palmo rivolto verso il basso o laterale e il polso morbido.
HANDSHAKE	**HSK**	Prendere una parte del corpo di un altro individuo (solitamente mano, piede o mento) e scuoterla.

ATTACHED II

FACIAL EXPRESSION ETHOGRAM *Pan paniscus*

Espressione facciale	Sigla	Descrizione (FOTO)
BARED TEETH	**BT** SILENT OR VOCALIZED (SCREAM)	
TENSE MOUTH	**TM**	La bocca è tenuta chiusa, le labbra sono leggermente protruse e le estremità sono portate verso l'esterno come in un sorriso.
POUT FACE	**POF** SILENT OR VOCALIZED (POUT MOAN)	
PLAY FACE	**PF**	
FULL PLAY FACE	**FPF**	

ATTACHED III

GENERAL ETHOGRAM *Pan paniscus*

Comportamenti di gioco

ACP, Acrobatic Play (event): gioco acrobatico fatto da un solo animale (quindi non sociale) o da due o più animali (sociale) che consiste nel dondolarsi appesi ad un sostegno e nel saltare da un albero all'altro.

AIR, Airplane (event): madre o altro adulto che sostiene il piccolo con le mani o con i piedi sopra la propria testa mentre è sdraiata a terra.

FPF, Full Play Face (event): faccia da gioco nella quale vengono scoperti anche i denti superiori, effettuato quando il gioco si fa molto intenso.

GRG, Grab Gentle (event): massaggi dolci, fatti spesso dalla madre (o da un adulto) ad un piccolo.

PBIT, Play Bite (event): morso per gioco, quindi con intensità non troppo forte.

PBR, Play Brusque Rush (event): balzo che un animale compie su un altro generalmente compiuto da un piccolo su un adulto o tra due coetanei.

PF, Play Face (event): faccia da gioco con la bocca, i denti inferiori scoperti ma i superiori coperti dalle labbra.

PINV, Play Invitation (event): è l'invito al gioco nel quale un animale si avvicina ad un compagno e dopo averlo colpito fugge via. Per parlare di invito è però necessario che subito dopo si abbia una sequenza di gioco. Se l'invito è comunque evidente, si considera un PINV* anche se non segue una sequenza di gioco. <u>(in questa voce possono essere inclusi anche tanti pattern gestuali – vedi sotto in inglese)</u>

PIRO, Pirouetting (event): l'animale esegue capriole e piroette su se stesso oppure appeso ad una fune.

PL, Play (stato): gioco in senso generale (sociale e non sociale), voce utilizzata quando il gioco ha durata superiore a 10 secondi (stato). Tutta la sequenza di gioco è poi classificata come ***ROUGH PLAY*** se il gioco è "duro", con molte play run e play bite intensi o comunque quando è evidente che è un gioco "pesante" e potenzialmente rischioso;

GENTLE PLAY quando il gioco è "gentile", ovvero delicato come spesso avviene tra adulti e piccoli; ***VIOLENT PLAY*** quando tutta una sessione di gioco termina con uno dei partecipanti che mostra segni di paura come bared teeth o screaming, oppure fugge.

PMAN, Play Manipulation (event): viene tenuto in mano ed esaminato un oggetto (anche il cibo purché non venga ingerito) per gioco.

PPS, Play Push (event): spinta data con le mani o con i piedi.

PPU, Play Pull (event): tirare un compagno con le mani o con i piedi

PRCO, Play Recovering a Thing (event): è il gioco del rubabandiera, nel quale un animale ruba un oggetto ad un compagno e poi fugge via per essere a sua volta inseguito.

PRE, Play Retrieve (event): trattenere qualcuno impedendogli di allontanarsi.

PRUN, Play Run (event): corsa che un animale compie da solo (non sociale) o insieme ad altri compagni (sociale). A run B vuol dire che A rincorre B.

PSL, Play Slap (event): pacca data su qualsiasi parte del corpo.

PST, Play Stamping (event): balzo che un bonobo effettua a piedi uniti su un altro. Utilizzato nel gioco solo dai piccoli e mai dagli adulti.

RISS, Rub Infant With Sexual Skin (event): la madre strofina i propri genitali sul piccolo (anche un non parente.

RT, Rough And Tumble (event): lotta e scappa, generalmente fatto da piccoli e giovani, ma comune anche tra gli adulti. Include colpetti, morsotti e rotolamenti.

TK, Tickle (event): solleticare con le mani o con i piedi.

SLIDE, SLI (event) - Scivolare sugli arti anteriori spingendosi con quelli posteriori

DON (event) – dondolare aggrappati a qualcuno. A don B (A dondola appeso a B)

DONS (event) - dondolare sopra qualcuno, usato anche come invito al gioco (c'è qualcuno che tenta di afferrare chi si dondola)

TIRF (event) – tiro alla fune

Comportamenti affiliativi

CL, Clinging (stato): due animali camminano fianco a fianco abbracciandosi.

DC, Dorsal Carrying (stato): trasporto dorsale di un piccolo.

EM, Embrace (event): abbraccio a scopo di saluto tra due animali.

FO, Follow (stato): un animale segue un compagno camminando proprio nella sua scia o lungo un percorso parallelo.

GR, Grooming (stato): pulizia del pelo di un altro animale effettuata sia con le mani che con la bocca.

BS, Body Shake: partendo da una posizione di standing, scuotere ritmicamente le anche piegando le ginocchia.

RGR, Grooming reciproco (stato): idem come sopra ma scambiato contemporaneamente.

HIH, Hand In Hand (event): mano nella mano.

HU, Huddle (stato): abbraccio effettuato da due animali stando seduti, comportamento frequente tra i piccoli.

KS, Kiss (event): bacio che può essere dato su tutte le parti del corpo tenendo la bocca aperta.

MW, Mount Walking (stato): un animale cammina dietro ad un altro appoggiando tutte e due le mani sulla schiena di quello che lo precede o per terra nel caso che l'animale che lo precede sia un piccolo.

PR, Peering (stato): un animale fissa negli occhi un compagno per alcuni secondi per poi iniziare un'interazione sociale con esso (esclusivo di *Pan paniscus*).

PX, Proximity (stato): due animali si trovano seduti ad una distanza che non supera quella di un braccio disteso.

RC, Recovering (event): comportamento della madre (o di un adulto) che va a recuperare il proprio figlio che si è allontanato.

RE, Retrieve (event): trattenere o trascinare a sé qualcuno impedendogli di allontanarsi. Spesso questo comportamento viene svolto dalle madri sui piccoli quando non vogliono che si allontanino.

ROG, Request of Grooming (event): un animale si avvicina ad un altro e mostra una parte del corpo che subito dopo viene sottoposta al grooming.

ROG*, Request of Grooming (event): un animale si avvicina ad un altro e mostra una parte del corpo che non viene sottoposta al grooming.

SITC, Sit in Contact (stato): due o più animali stanno seduti in contatto.

VC, Ventral Carrying (stato): trasporto ventrale di un piccolo.

Comportamenti rivolti verso se stessi

BWA, Bipedal Walk (event): spostamento sugli arti posteriori.

BSTA, Bipedal Standing: stare fermi sulle gambe.

LD, Lying Down (stato): l'animale sta sdraiato.

GSCR, Gentle Scratching (event): grattarsi dolcemente.

RSCR, Rough Scratiching (event): grattarsi pesantemente

NGSCR, nose gentle scratching: grattarsi il naso con il dorso della mano o del polso.

CR, Crouch: "appallottolarsi"

SGR, Selfgrooming (stato): grooming effettuato su se stessi.

SIT, Sit (stato): quando un animale sta seduto da solo.

STA, Stand (stato): stare fermi in piedi su quattro arti o su quelli posteriori.

WA, Walk (stato): qualsiasi spostamento escluso il run.

Y, Yawning (event): sbadigliare

Comportamenti sessuali

DVCO, Dorso-Ventral Copulation (event): accoppiamento completo di monta, penetrazione e thrusting (spinte pelviche) nel quale la femmina assume posizione accovacciata e riceve il maschio da tergo. Termina con l'estromissione.

DVMO, Dorso-Ventral Mounting (event): il maschio si pone dietro la femmina senza penetrarla. Il mounting può essere fatto anche da un maschio su un altro maschio.

ER, Erection (event): erezione.

SBITE, Sexual Bite: morso dato durante il sessuale.

GGR, Genito-Genital Rubbing (event): svolto tra due femmine in posizione ventro-ventrale, dorso-dorsale o ventro-dorsale con movimenti laterali del corpo per strofinare insieme i genitali (esclusivo di *Pan paniscus*). - VVGGR, DVGGR, DDGGR, GGRRR (maschio in sexc, femmina si struscia da dietro).

IN, Inspecting (event): un animale si avvicina ad un altro e gli ispeziona l'area genitale, toccandola ed annusandola. L'azione viene effettuata sia dai maschi sia dalle femmine. Questo comportamento può essere effettuato anche su sé stessi.

INV, Invitation (event): è un comportamento che differisce a seconda che sia effettuato da un maschio o da una femmina. Il maschio si siede, batte i piedi per terra, allarga le gambe, si dondola lateralmente, avanti ed indietro, mostrando il pene eretto. L'invito sessuale nei maschi è uguale nelle due specie *Pan paniscus* e *Pan troglodytes*.

La femmina cammina davanti al maschio, lo guarda, si ferma, lo aspetta e ricomincia la sequenza. Nei *Pan paniscus* la femmina può sdraiarsi e assumere la posizione della copula guardando l'animale (maschio o femmina) con il quale intende avere un'interazione sessuale.

MA, Masturbation (event): manipolazione dei propri genitali o di quelli di un altro individuo.

MMA, Mouth Masturbation (event): manipolazione dei genitali di un altro individuo effettuata con la bocca.

RRR, Rump-Rump Rubbing (event): comportamento comune tra i maschi di bonobo, nel quale due animali strusciano insieme i genitali disponendosi con i propri posteriori in contatto e strofinandoli insieme.

RRGGR, Rump-Rump Genito-Genital Rubbing (event): femmina sdraiata a gambe aperte altro individuo si avvicina e struscia sedere o genitali su quello sdraiato.

SBT, Sexual Bared Teeth (event): espressione in cui entrambe le arcate dentarie sono scoperte che indica profonda emozione (esclusivo di *Pan paniscus*).

SEXC, Sexual Crouching (event): posizione accovacciata che può assumere la femmina nell'accoppiamento da tergo.

SPR, Sexual Presenting (event): un individuo si avvicina ad un altro e gli mostra i genitali, spesso da dietro.

VVCO, Ventro-Ventral Copulation (event): accoppiamento completo di monta, penetrazione e thrusting (spinte pelviche) nel quale femmina e maschio sono in contatto ventro-ventrale.

VVMO, Ventro-Ventral Mounting (event): il maschio si pone sopra la femmina con contatto ventro-ventrale dei genitali, ma senza penetrarla.

Comportamenti di sottomissione

AV, Avoid (event): si ha quando un animale evita di interagire con un altro compagno, o cambiando direzione di spostamento o allontanandosi dall'altro animale. E' un "girare alla larga".

BT, Bared Teeth (event) raro nei bonobo**:** espressione facciale di paura dove tutti i denti sono scoperti; in genere vi è associato lo screaming.

FL, Fleeing (event): fuga che viene effettuata in un contesto aggressivo.

PRES, Presenting (event): un animale subordinato si avvicina ad un dominante mostrandogli i genitali.

SCM, Screaming (event): si tratta di un urlo di paura in genere associato al bared teeth.

UR, Urinate (event): un animale urina per la paura in un contesto aggressivo.

Comportamenti aggressivi

ABIT, Aggressive Bite (event): morso.

ABR, Aggressive Brusque Rush (event): si tratta di un balzo che un animale compie su di un altro.

ACR, Aggressive Crouching (event): posizione accovacciata che viene assunta da chi viene aggredito, serve per difendersi dai colpi dell'aggressore.

PS, Aggressive Push (event): spinta data con le mani.

APU, Aggressive Pull (event): tirare un individuo con atteggiamento aggressivo.

ASL, Aggressive Slap (event): schiaffo.

AST, Aggressive Stamping (event): è un salto che un animale effettua su un altro animale o su un oggetto a piedi uniti.

CDS, Charging Display (event): si tratta di una serie di comportamenti (piloerezione, corsa, faccia da display, branch dragging, dondolamento delle braccia, bipedismo, etc.) che generalmente vengono eseguiti dai maschi per minacciare e ribadire la loro dominanza. Nei bonobo è comune anche tra le femmine.

CH, Chase (event): inseguimento. A chase B vuol dire che A insegue B.

Comportamenti neutri

AP, Approach (event): avvicinamento di un animale ad un altro. Dopo un approach deve seguire una interazione (event o stato).

BG, Begging (event): un animale chiede qualcosa (che non sia cibo) con il braccio teso e la mano aperta con il palmo rivolto verso l'alto (VEDI GESTI)

COP, Coprofagia (event): mangiare le feci.

DI, Dismiss (event): un adulto fa un mezzo inseguimento od un movimento qualsiasi per allontanarne un altro.

LEA, Leave (event): un animale lascia un compagno con cui ha interagito (stato o event).

MAN, Manipulation (event): un animale manipola un oggetto per un certo scopo o per esaminarlo.
POF, Pout Face (event): espressione facciale effettuata generalmente dai piccoli, nella quale le labbra vengono protratte e la bocca viene tenuta socchiusa (simile ad un piagnucolio) (faccia becco d'anatra).

RCO, Recovering a Thing (event): recuperare un oggetto che non sia cibo.

RUN, (event): correre per spostarsi

WB, Watching back (event): guardare indietro in direzione di un altro individuo.

GRASP, grasp: afferrare un oggetto con forza (FGRASP) o con precisione (PGRASP) controllare se è associato un movimento bocca.

Comportamenti cibo

FBG, Food Begging (event): un animale chiede del cibo ad un compagno avvicinando la propria mano o la propria bocca alla bocca di un altro individuo. (VEDI GESTI)

FEED, Feeding (event): l'animale mangia. - FEEDALTO e FEEDBASSO, a seconda della posizione del posteriore.

FFC, Food Forced Claim (event): due individui si avvicinano a del cibo e uno dei due ha la meglio sull'altro nell'impossessarsene (ad esempio tira via il cibo dalle mani dell'altro ignorandone i segnali agonistici e la resistenza fisica). Attore è chi prende il cibo.

FS, Food Steal (event): un individuo si avvicina di soppiatto al possessore del cibo e glielo ruba correndo via prima che esso possa reagire. Attore è chi ruba.

FSHCO, Food Sharing Co-feeding (event): un individuo si unisce al possessore del cibo condividendolo pacificamente con esso.

FSHR, Food Sharing Relaxed Claim (event): un individuo, in piena vista del possessore, toglie parte o tutto il cibo dalle sue mani in modo rilassato e senza contatti agonistici. Chi fa food sharing è chi ha il cibo in mano.

RG, Regurgitating (event): rigurgitare il cibo.

SK, Suckling (event): succhiare dal capezzolo di una femmina.

SR, Suckling Rejection (event): la madre impedisce al piccolo di succhiare il latte staccandolo con le mani dai capezzoli.