



Affiliative behaviour of male bonobos (*Pan Paniscus*) and subsequent advantages in a large captive group



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Abstract

While selective pressure has been considered as pure set of competition in the animal kingdom, actual researches based on animal social cognition and behavioural ecology revealed how affiliation played an important role as well among social-living species. Among these species, bonobos *Pan paniscus* might be one of the best model to investigate the eventual benefits of affiliative behaviours and their recurrent use of sex for reconciliation and reduction of social tensions. While the debate around bonobos' peacefulness and egalitarian properties persists, female dominance over males is mainly accepted. This pilot study investigates how affiliative behaviours, which are familiar in this species, can provide benefits to males in terms of social acceptance or mating success. We collected data on a large captive group of bonobos at "La Vallée des singes", Romagne, France, using focal and scan sampling methods. We tested whether affiliative behaviours such as grooming or play with infants can be invest-like behaviours, providing different pay-offs to the group's four adult males. Do we observe high and low "ranked" males in this group? If so, does rank attribute different advantages from a rank to another? We noticed two "classes" including two males, one "high ranking" and one "low ranking, mainly explained by mother presence or not. Many solutions appeared to increase our males' mating success: playing with a female's son permitted to a "high ranked" male to increase his mating success with the mother, grooming females regardless to their rank provided more mating success to another high "ranked male". While low "ranked" males mainly benefited either from keeping stronger affiliation with subordinate females than did high "ranked" males, or from passive avoid of incest. Our results highlight the importance of mother presence on males' social and physiological benefits in a matriarchal social system, trying to depict the potential evolutionary roles of males in this unique case of matriarchy among the great apes.

Introduction

Since Huxley (1863), Wallace (1864) and Darwin (1870) suggested the common ancestry between humans and earlier primates, studies of animal behaviour, emotions and social organisation have challenged what we consider to be unique to humans. Over the last century, animal sociality has been one of the main topics in various disciplines such as comparative cognition, primatology or human evolution (Walters & Seyfarth, 1987; Paoli & Palagi, 2008; Kaplan & al, 2000). Cooperation and sociality provided several benefits in terms of food acquisition, cooperative hunting or antipredator strategies (Pullian & Caraco, 1984). Whereas cooperative hunting and alloparental care were the main factors favouring sociality in carnivores (MacDonald, 1983; Smith & al, 2012; Barberia, Shultz & Dunbar, 2007), it is mainly antipredator strategies which might have been one of the main factor in ungulates and primates (Nelson & Mech, 1991; Dunbar & Shultz, 2007). Primates for their part showed a coevolution between sociality and relative brain size. This taxon indeed, exhibited generally larger brain relative to their body size, associated with group size (Dunbar & Shultz, 2007; Kaas, 2008).

However, sociality also brings many costs due to competition for resources and the risks associate to conflict (Wittig & Boesch 2003; Setchell & Jean Wickings 2005). Both inter and intragroup conflicts require energy costs where individuals risk to be wounded or worse. But social animals such as wolves, *Canis lupus*, and chimpanzees, *Pan Troglodytes*, take benefits while joining forces with non-relatives during intergroup conflicts (Lehman & al, 1992; Goldberg & Wrangham, 1997). Such observations might suggest the importance of competition among social animals. Nevertheless, recent studies (Byrne & al, 2008; Burkett & al, 2013; Cordoni & Palagi, 2008; Fraser & Bugnyar, 2010) have shown how evolution cannot be reduced to a simple context of competitions. Social-living species appeared to be selected on aggression: chimpanzees *Pan troglodytes*, spotted hyenas *Crocutta crocutta*, white-nosed coatis *Nasua narica*, and wolves *Canis Lupus* gain fitness benefits by engaging in intergroup conflicts with potential risks of injury or death (Goldberg & Wrangham, 1997; Boydston, Morelli & Holekamp 2001; Gompper, Gittleman, & Wayne 1998; Lehman & al. 1992). However affiliative behaviours such as post-conflict reconciliation, consolation or other empathic attitudes appeared to have selective advantages in social species. Indeed, both African elephants *Loxodonta Africana* (Byrne & al, 2008), and rodents (Burkett & al, 2013) show empathic understanding of group-member's emotional states. Indeed, great apes, canids and corvids

frequently reconcile after conflicts (Mallavarapu & al, 2006; Cordoni & Palagi, 2008; Fraser & Bugnyar, 2010). Great apes, wolves *Canis Lupus*, and rooks *Corvus Frugeligus* even engage in unsolicited post-conflict third-party contacts, which permits to break-off aggressions and restore a victim's social cohesiveness (Seed & al, 2007; Palagi & Cordoni, 2009). Thus, empathic and affiliative behaviours are crucial for social cohesion among a wide range of species. These reported results suggest the importance of the topic for understanding the evolution of empathy and affiliative strategies across the animal kingdom.

Current literature on affiliative interactions in nonhuman primates permit us to find some similarities with humans' social behaviour. Human and non-human great apes both show aggressive such as war, rape and torture (Wrangham & Peterson, 1997) and affiliative dominance (de Waal, 1986) have been shown to occur in both children and adolescents of different stages, for instance by Rough-and-Tumble Play or reconciliations (Boulton & Smith, 1990; Pellegrini & al, 1999; Pellegrini & Bartini, 2001). *Homo* and *Pan* genus share a common ancestor that lived between 6 and 8 million years ago. Concerning the *Pan* genus, the two extant species are chimpanzees *Pan Troglodytes*, and bonobos *Pan Paniscus*, their lineages diverged around 3 million years ago (de Waal & Lanting, 1997. Sommer & al, 2011). These two species share similar social organizations: they both live in fission-fusion, multi-male and multi-female groups (Wrangham, 1987; Furuichi & Ihobe, 1994).

However, we observe certain distinctions between the two extant *Pan* species. While chimpanzees live in male-dominant societies, bonobo society is clearly dominated by females (de Waal & Lanting, 1997). Indeed, female bonobos are dominant over males (Franz, 1999). Female bonobos form strong coalitions, providing males' submission while other high-ranking females are present (White & Wood, 2007). These same coalitions seemed to be decisive in their access to dominance over males (Furuichi 1997; Paoli & Palagi 2008). Bonobos are reputed to be generally less aggressive than chimpanzees, even if evidence of cooperative attacks by females over males has been observed (Sommer & al, 2011). Current literature on bonobos' social life reveal contradictory results. While bonobos' female dominance is heavily supported (Surbeck, Mundry & Hohmann, 2011); it appears that this female dominance was not that exclusive compared to chimpanzees' male dominance (Wittig & Boesch, 2003 (b); Stevens & al, 2007). Other controversies recently appeared in literature about the reputation of bonobos' egalitarian societies. While hierarchical ranks of bonobos seem to be less linear and more egalitarian than in chimpanzees (Enomoto, 1990; de Waal, 2012), other studies showed opposite results (Paoli, Palagi & Tarli, 2006). If this is not our decision anyway to judge whether

bonobos live in more egalitarian societies than other primates or not, this controversy shows the complexity of this species' social life and organization.

As chimpanzees, bonobos show empathy and exhibit consolation towards conspecifics (de Waal, 1979; Clay & de Waal, 2013) and might be a good model to study affiliative behaviours and strategies in an evolutionary perspective (Parish & al, 2000). Bonobos tend to live in more egalitarian societies, providing more reciprocal interactions (Enomoto, 1990). Adults bonobos have more playful tendencies than adult chimpanzees, especially with infants (Palagi & Paoli, 2007). Male bonobos even show less female monopolization and lower sexual competition compared to chimpanzees (Kano, 1992; Vervaecke & Van Elsacker, 2000). Males' affiliative behaviours and relations with females might be helpful in terms of understanding the evolution of matriarchy in primates, and which selective advantages permit low-ranking males to increase their mating or reproductive success in a society governed by females. Due to their dominance over the society, adult female bonds and alliances are key factors to understand their social complexity (Furuichi, 1997). Thus, it might be interesting to see how males can get access to food or females in a matriarchal system if this is not by monopolization, male competition or strong alliance as is the case for females (Parish, 1994). As the philopatric sex, bonobo males are even more surprising in that they do not form strong alliances in a group they will never leave. For now, it seems that mother's social rank highly influence males' social status (Furuichi, 1997) and reproductive success (Surbeck, Mundry & Hohmann, 2011). However, there is less information on whether male bonobos actively use strategies to improve their access to food and females.

The "La Vallée des singes" primate park, in France, is an excellent setting for behavioural observations. The park houses one of the largest captive groups of bonobos including both kin and non-kin adult females, males plus many infants, giving a wide range of age-classes in the same group. Thus, studying this group gives an opportunity to observe a more complex captive social structure than we could find in smaller captive groups. Furthermore, mothers' social status and influence on sons' reproductive and mating success can be considered since half of the adult males have their mother in the group, and half of them do not. Thus, it is possible to see whether males behave differently according to their mother's presence or not. And how will they behave with both dominant or subordinate females and with their infants.

This pilot study aimed to see whether affiliative behaviours such as grooming females or play with infants provided more food tolerance or higher mating success with females to male bonobos in a large captive group. If male bonobos obtain selective advantages from reducing

aggressive behaviours, under the influence of females' mate choices (Wrangham and Peterson 1996; Hare & al, 2012), or hurt their fitness with such behaviours (Stanford, 1998), then we can ask ourselves whether playing with infants or other affiliative behaviours increase males' mating success or other privileges from females. We can find potential indices suggesting whether grooming or play with infants can have a role in males' food tolerance from females or on their mating success. Our group's multi-male multi-female composition might bring an interesting view of how male bonobos can behave in these very conditions.

Material & Methods

Field Site and population

Our data collection lasted 4 months from September to December 2016 and was carried out at “La Vallée des Singes” primate park in Romagne (France) which is home to one of the largest captive group of bonobos in the world. The group includes 17 bonobos: 10 females and 7 males. (Age range: 1-48 years old, see **Table 1**).

NAME (♀)	CODE	PARENT	AGE/CLASS	NAME (♂)	CODE	PARENT	AGE/CLASS
Daniela	DNL		48 / AD	Kirembo	KI		24 / AD
Ukela	UK		30 / AD	Diwani	DW	DNL	20 / AD
Ulindi	UL		23 / AD	David	DV	DNL x KI	15 / AD
Khaya	KH		15 / AD	Kelele	KEL		12 / AD
Lingala	LNG		13 / AD	Loto	LO	UL	7 / SA
Lucy	LY		13 / AD	Moko	MO	UK x DV	4 / JUV
Nakala *	NK	UK	8 / SA	Lokoro	LKR	UL x ?	1 / INF
Khalessi	KLS	KH x DV	4 / JUV				
Yuli	YU	LY x KEL	2 / INF				
Swahili	SWH	LNG x ?	2 / INF				

Table 1: Individual identity, code, in-group parents, age and age-class in the studied population. Age-class: AD = adult, SA = sub-adult, JUV = juvenile, INF = infant according to (Kano, 1982). The four adult male individuals followed are highlighted in the table. *: NK was separated from the group on November 11th to join a smaller sub-group.

The bonobos' enclosure (Fig. 1) consists of two large outdoor, wooded islands (total = 11 500m²) connected by a large indoor enclosure (400m²) providing shelter for the animals. The indoor enclosure is made up of two large cages and eight smaller cages. During September and

part of October, the bonobos had daily access to the islands and the outdoor feeding area on the large island (depending on weather conditions). During November and December, the group generally remained inside and was fed in cages 1 and 2.

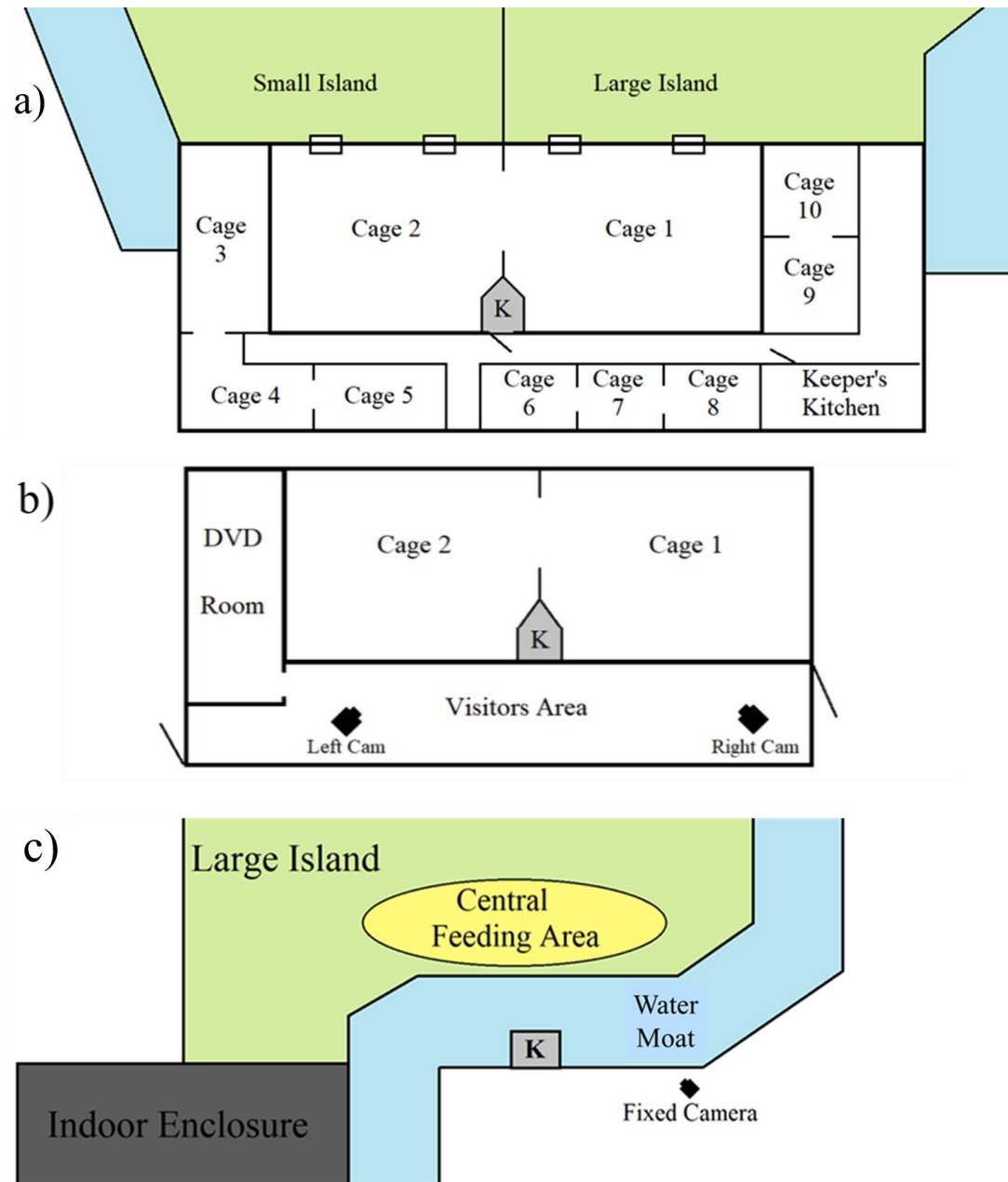


Figure 1: Indoor enclosure floor plan (a) ground floor: all surrounding cages are inter-connected and linked to cage 1 and 2 by tunnels. (b) upper floor: provides visual access to cages 1 and 2 from the visitor area. K = Keeper's position during feeding. Cameras were placed in the visitor area to capture the widest shot of the feeding area. (c) Central feeding area: where outdoor feeding take place. Situated on Large Island.

The group demography is composed of old and young, kin and non-kin individuals permitting us to investigate the influence of both age and kin on the affiliative relationships of four adult

males with the group's females and any subsequent advantages drawn from these bonds. Furthermore, the presence of infants and juveniles allowed us to observe play interactions with the males. This, and the females' dominance rank provide valuable information to help us understand whether males adopt certain behavioural strategies and what advantages these strategies can provide. This study follows four adult males: David (DV), Diwani, (DW), Kelele (KEL) and Kirembo (KI). Among them, DV and DW have their mother in the group. The two other ones do not benefit from mother's presence. KI has been moved from a previous park without his mother, whereas KEL lost his mother at early age. If our sample size is small for testing mother presences' influence, we can investigate anyway whether we find the same patterns as found in other populations.

The bonobos' living space is divided between two islands and an indoor enclosure. These spaces are vast for a captive environment. Even if outdoor observation was difficult in terms of visibility due to dense vegetation on bonobos' islands, indoor observation especially increased visibility due to every cages and tunnels disposition. However, major part of our observations took place indoor, because observation occurred between September and December and that bonobos are particularly weak to low temperatures.

Husbandry

Keepers fed bonobos throughout the day. Weather permitting, food distribution took place on the outdoor central feeding area. Otherwise, food was delivered from above cages 1 and 2 in the indoor enclosure (**Fig. 1.a**). Females and dominants generally occupy the closest positions to the keeper and the source of the food (higher positions on the extended nets and platform of the indoor and front post position in the outdoor enclosure) whereas subordinate individuals tend to stay on the ground or on peripheral nets (indoors) and further back (outdoors) (**Figures 3 and 4**).

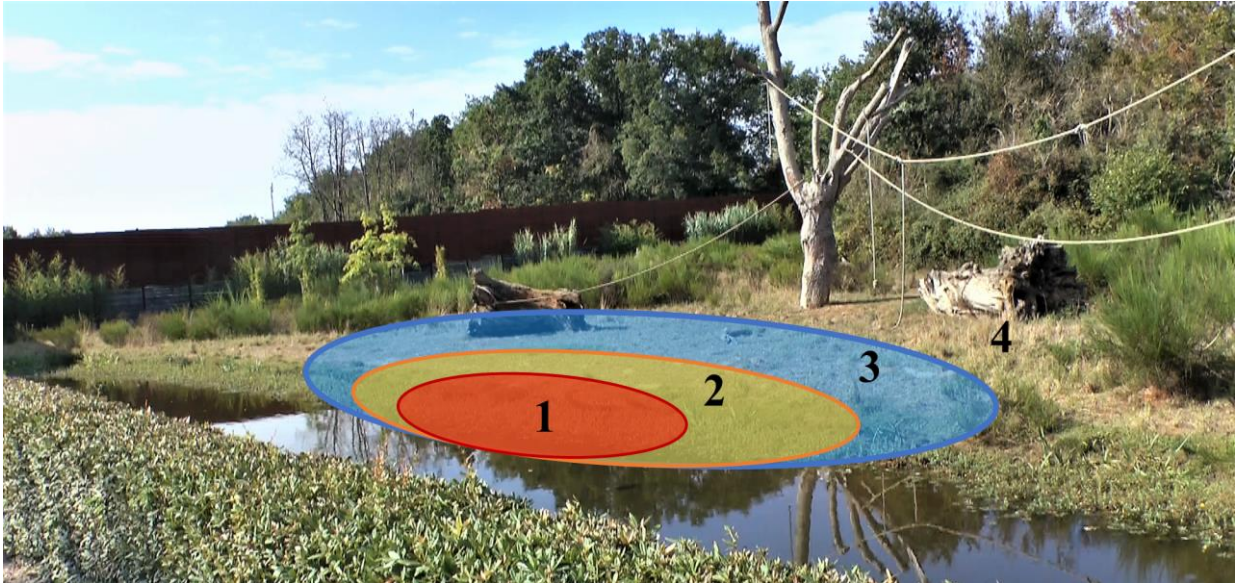


Fig 3: The central feeding area on the large island with the 4 zones used for determining female hierarchy. Zone 1 is the closest place to the keeper's reach.



Fig 4: The indoor enclosure which houses animals during winter. A wide space where the two fixed cameras were placed during feeding situations in cold weather conditions. (left side and right side). Keepers entered in the SAS situated between left and right sides (visible with the “cage” in the centre of zone 1).

Both focal and scan sampling were the two methods used in our data recording. Focal sampling was used to record each male's affiliative behaviour with adult females in focal feeding (FF) and non-focal feeding (FNF). From these same recordings, we used scan sampling to record males' proximity to females and female hierarchy scores in order to evaluate males' proximity with dominant and with subordinate females, thus, we used scan sampling method to evaluate female hierarchy scores.

Focal sampling

Behavioural observations took place from 8:00 am to 5:00 pm. Each day was divided into 3 time-periods: Morning (from 8:00 am to 11h00), Afternoon (from 12h00 to 3h45 pm) and Evening (from 3h45 pm to 17h00 pm). These time-periods are chronologically sequential

and are never spaced more than two days apart (between a Friday Evening and a Monday Morning). We carried out both FF and NFF which respectively lasted 10 and 20 minutes. The group was fed a total of 4-5 times a day (8h15 am; 10h30 am; 2h30 pm; 3h45 pm (while opening season) and 5h00 pm) allowing each subject to be observed for a FF at least once a day. NFF were carried out between feedings in three different timeslots (AM, early-PM, late-PM). The AM timeslot ran from 8am to noon, early-PM ran from noon to 3pm and late-PM ran from 3pm to 5 or 6pm when the last feeding took place. This division in time-periods permitted us to chronologically organized our data to see the influence of play interactions with juveniles or grooming interactions on sexual success with adult females along time periods of our observation.

Each male was observed for a total of 1130 minutes (18.83 hours), 410 minutes (6.8 hours) in Feeding condition and 720 minutes (12 hours) in the non-feeding condition. The order for subject observation was predetermined and pseudo-randomised to ensure that each subject was observed for the same amount of time during each timeslot and feeding. Videos were coded using Windows media player and Microsoft Excel. Following behaviours were recorded: frequency (for sexual contacts only), duration and partner of affiliative interactions (i.e. groom given, groom received and play) (**Table. 2**). We focussed only on interactions between the four subjects and the group's females and offspring. We did not record any male-male dyads because these interactions had no connection to our research. Besides, male-male interactions provide less benefits among bonobo groups in terms of mating success or food tolerance (Kano 1992, Parish 1994, White, 1996; Palagi et al. 2004). All male-female dyads were recorded for groom given (GG), groom received (GR) and sexual contacts (SX), as well as for male-juvenile dyad for play interactions (PY). We measured GG, GR and PY in duration. Sexual contacts with adult females, for their part, were measured in number of interactions. Our aim was to investigate which behaviours male bonobos display to get some advantages in a society governed by females. In fact, males might gain more benefits in dealing with females than with other males in terms of mating/reproductive success or social acceptance, especially in a matriarchal social system.

Focals were recorded using a hand-held Canon Legria HFS10 camera with vocal commentary. For the feeding condition, two (outdoor) or three cameras (indoor) were used. For feedings that took place outdoor, a first camera was placed on a tripod and directed to the central feeding area (illustrated in **Fig. 3**). Even if the animals can move in the dense part of the islands, it was

possible to film the main activities occurring on the central feeding area, where dominants usually stayed during food distribution. Whereas subordinate individuals stayed in periphery compared to their dominants. A second hand-held camera was used for focal sampling of the males. Observations carried out indoors required two fixed cameras (posted on tripods) in addition to the hand-held camera to have a global view of the whole upper part of the enclosure. Each adult male was observed for the same amount of time during both feeding and non-feeding situation.

Behaviours	Sex (n° of contacts)	Groom G (min)	Groom R (min)	Play with infants (min)
Total interactions	75	241	206	67

Table. 2: Total amount of affiliative behaviours towards females and infants during observation. Includes male-female sexual contacts frequency (n° of contacts). Duration of groom given by males and received from females (minutes). And duration of male-infant play interactions (minutes).

Scan sampling – Female hierarchy

To investigate the females' hierarchy during feeding, we defined four zones in each of the two feeding areas recorded with the help of fixed cameras (**Fig 3 & 4**). 1 = central zone (i.e., closest to the food source (K)); 2 = well-off position (i.e., surrounding zone 1, relative close to food source); 3 = medium position (i.e., surrounds zone 2, relatively far from food resource); 4 = lowest position (i.e., outdoor = peripheral areas of the feeding area; indoor = invisible on screen). Recording began one minute before the keeper arrived at their feeding position to record the whole feeding event. To evaluate female hierarchy, we seek which females spent more time into central feeding area. Females staying longer in this area were considered as more dominant due to their eventual priority in access for food. Females in more peripheral areas were then considered to less prior and more subordinate. Scan sampling was carried out on 5 minutes of observation. After 5 minutes of feeding, major part of food was already taken by bonobos, both in central and peripheral areas. Then, zone 1 was not highly-valued anymore in terms of food access. Scanning more than 5 minutes would begin to be meaningless, due to rarity of food. After 5 minutes on every 1 minute resulting in 6 scans for each feeding focal: from time 00:00 to time 05:00. To define female hierarchy, we considered that females who stayed more often in the resource zone (zone 1), closer to the keeper's reach, had priority on the access of food compared to females in further zones and must be higher-ranking on order to have access to these privileged zones.

Scan sampling - Proximity data

The videos obtained from subject feeding focal (FF) were also used to evaluate males' proximity to females during feedings, which permits to evaluate males' food tolerance given by females on these occasions. Every minute (at time 00:00, 01:00 until 10:00) we scanned each female's position relative to each male subject during recording. This permitted to evaluate each male's proximity with all females at every minute across our records. For each scan we recorded female proximity to the subject as follows: 1 = contact (i.e., physical contact); 2 = close (i.e., within arm's reach); 3 = distant (i.e., 2 - 4m); 4 = far (i.e., more than 4m). To record the whole feeding event, including a "pre-feeding" situation, we began recording at least one minute before the keeper arrived at the feeding site. Scan sampling was carried out with an observation every 1 minute resulting in 11 scans for each feeding focal, from scan 00:00 to scan 10:00.

Statistical analysis

Female hierarchy

Females hierarchical rank was calculated based on a matrix of positions during feeding time (score = 1 for being in zone 1, score = 2 for being in zone 2, score = 3 for being in zone 3 and score = 4 for being in zone 4 from scan sampling). Hierarchical scores were then determined by calculating the median of each female's position in each scan (from time 00:00 min to time 00:05 min). Females who stayed most of the scans in the central resource zone (zone 1 and 2) had the lowest medians, thus they were considered as higher-ranked compared to those who spend more time in zones 3 and 4, because they stayed more often in central feeding areas than those who stayed longer in zones 3 and 4. We then aimed to define two rank-classes of females between dominant and subordinate. All with the aim to see with which ranked females do males interact. Furthermore, we wanted to keep a minor dominant class of females compared to subordinates. We could create a middle-ranked class but we would have a lack of sample size for cross comparisons. Due to the rarity of interactions with these eventual "middle-ranked" females (UL, KH, NK), it was surer to include them in dominant or in subordinate class. The cut-off point was a matrix median score of 3 (Dominant female < 3 < Subordinate female).

Thus, we estimated that females in the “2” range were dominant; and those in the “3” range were subordinate.

Males' Proximity indices with females

As for females' hierarchical scores, males' proximity with females was calculated from a matrix collected with the help of a scan sampling. We evaluated males' proximity from zone 1, 2, 3 or 4 but relative to each female, not to feeding position. To evaluate each male's proximity indices with females during feeding time, we made a log transformed proximity to all females score with the help of a Kruskal Wallis test and post-hoc (pairwise) comparisons of individuals. All of our correlations have been adjusted with R function “p.adjust” via Holm method. We only calculated proximity indices during feeding due to the importance of being close to females during food distribution. As food tolerance from females can reveal the social relevance of a given male. We then assumed that closer males could be considered as higher-ranking than the more distant, less tolerated males during feedings.

Chronologically ordered data analysis

We also tested potential continuity or influences between two behaviours in a relation of investment and pay-off. See if an investment behaviour (such as groom given or play with infants) could bring some advantages to males (such as more proximity with females or more sexual contacts). We divided every day of observation in three types of day-periods (morning, afternoon, evening). Thus, we had similar number of observations for each male on the same very periods from September to December. This permitted us to test potential links between two behaviours in a chronological order. For instance, we aimed to see whether adult male-infant play interactions could predict more sexual activities in the group. Or if playing with infants permit a male to increase his mating success with females in the same or in later periods? Due to the distribution of our data, we chose to use non-parametrical tests. We used a Kendall Rank Correlation test with the cbind function on programming language R to present two variables among our data, as a time-series and their cross correlation. Each cross correlation has been adjusted with R function “p.adjust” via Holm method. The main problem of our observation was a lack of variability in our data. Most of the time, bonobos were inactive and some of our collected behaviours occurred rarely but intensely. We observed generally zero activities or intense interactions in a single focal, and almost no intermediate cases. Thus, as a proper time series analysis was not possible due to our data distribution, however non-

parametric tests such as Kruskal Wallis and Kendall Rank permitted us to find relevant results, despite the lack of variability in our data's distribution.

Affiliative behaviours and females' rank

We also wanted to test the relation of play, grooming and sex interactions according to the females' rank class to see which males tended to have more interactions with dominants or with subordinates. We observed that DV and DW had significantly better proximity indices with females during feeding time than the KEL and KI. Then we used Wilcoxon Ranked Sum test to compare each male's interactions with both dominant and subordinate females. With Wilcoxon Ranked Sum test, we could see whether if any males spent significantly more time interacting with dominants (or subordinates) than other males. As in the previous tests, all of our correlations were adjusted with R function "p.adjust" via Holm method. Because mother presence appears to influence reproductive and mating success in the wild (Surbeck, Mundry & Hohmann, 2011) a similar pattern might be observed in a large captive group. We also tested if any males spent significantly more or less time interacting with dominants than with subordinate. Wilcoxon Signed Rank test permitted to compare each male's behaviours (groom given, groom received, play (Mean of time) and sexual contacts (N° of contacts)) relative to females' rank classes. If we notice different "rank classes" among our four males, then it would be interesting to investigate the influence of males' "rank class" on their interactions with dominant and subordinate females. Following the female hierarchy scores, we tested whether:

- 1) Did "higher ranked" males entertain more affiliative interaction with dominant females than did "low ranked" males?
- 2) Did "low ranked" males entertain more affiliative behaviours with subordinate females than "high ranked" males did?
- 3) Did a male behave significantly more with particular females than another male, showing individual patterns or maybe different strategies between to males in the same "rank class"?

Results

Female hierarchy

To determine female hierarchy, we calculated the median of females' position during feeding (1, 2, 3 or 4), revealed the following order: UK: 2.73 > DNL: 2.77 > UL: 2.97 > KH: 3.23 >

NK: 3.3 > LY: 3.38 > LG: 3.6. Because Ukela (UK) had the lowest score, we assumed she was the alpha female. UL, KH and NK were more difficult to classify, due to their intermediate hierarchical scores (UL = 2.97; KH = 3.23; NK = 3.3) Corresponding to what has been observed concerning the “egalitarian” properties of bonobo societies (Paoli, Palagi & Tarli, 2006). As mentioned in our methods, only UL had a lower score than 3 and then joined the dominant females class. This choice was also logical due to her closer score to DNL than to KH. KH was not as often in zone 1 as UL. NK for her part was 8 years old: an age at which she was supposed to leave the group sooner, as females usually do in this species (Kano, 1982). Whereas KH and NK were included in the subordinate class. This separation is quite arbitrary, but as UK, DNL and UL are all in the ‘2’ range, while KH, LG, LY and NK are in the ‘3’ range. NK, for her part, was a subadult and meant to leave the group as it is usual in this species (Kano, 1982). In short, we considered dominant females UK, DNL and UL; while subordinate females were KH, LG, LY and NK.

Males’ proximity indices with females

We found a significant difference between DV-DW and KEL-KI in terms of female proximity during Feedings (Kruskal Wallis test: $\text{Chisq} = 35.06$; $\text{df} = 3$; $p\text{-value} < 10^{-6}$), adjusted p-values, Holm/other method). DV and DW did not have significantly different proximity scores with females ($\text{Chisq} = 23.75742$; $\text{df} = 2.8$; $p = 0.7851$). No significant differences either between KEL and KI ($\text{Chisq} = 23.75742$; $\text{df} = 2.8$; $p = 0.7175$). However, DV and DW had significantly higher proximity scores than KEL and KI (DV vs KEL: $p = 0.0003$; DW vs KEL: $p = 0.0008$; DV vs KI: $p = 0.0054$; DW vs KI: $p = 0.0096$) (adjusted p-values, Holm/other method). These results suggest the existence of two different male “classes” in terms of females’ proximity, one more accepted during feeding. One “high ranked” class, including DV and DW, who benefitted from more tolerance from females during feedings. A second “less ranked, including KEL and KI, who stayed longer away from females, suggesting less benefits in terms of food tolerance. This distinction curiously corresponds to mother presence in the group. Which is known as an important factor determining male bonobos’ social status as reproductive and mating success. In fact, we observed that the two in-group mother’s sons benefitted more food tolerance from females than the two “orphan” males. Because DV and DW stayed more time in contact or arm-length zones (zone 1 and 2), their proximity indices with females were higher than those

of KEL and KI, who stayed further from females. DV had significantly higher proximity indices than KEL ($p = 0.0003$) and KI ($p = 0.0054$). As for DW ($p = 0.0008$) ($p = 0.0096$). However, no significant differences were observed between DV and DW neither between KEL and KI in terms of proximity with females (**Fig. 5**). Proximity indices with females revealed DV and DW can be considered as more dominants than KEL and KI, as they obtained more food tolerance from females than KEL and KI. Only DV and DW seemed to significantly increase their sexual contacts by interacting with females and/or their infants.

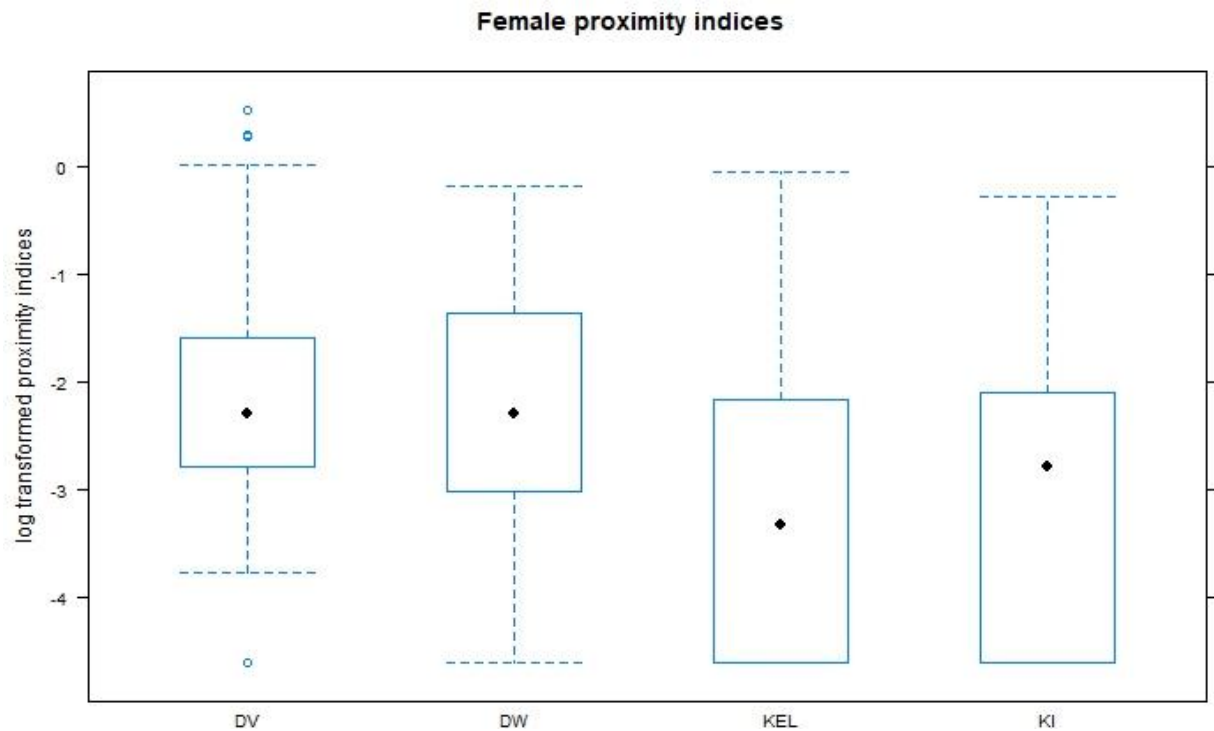


Fig. 5: Males' proximity indices with females during feedings. Points represent each score's median, boxes represent the 2nd and 3rd quartiles.

Total Behaviours

No food sharing took place during the observation. The total number of grooming interactions with adult females recorded was $N = 66$ ($T = 447$ minutes). Of these grooming interactions, $N = 45$ were males grooming females ($T = 241$ minutes), and $N = 21$ ($T = 206$ minutes) were grooming received from females. The total number of sexual interactions with females was $N = 75$. Finally, the total number of play interactions was $N = 28$ ($T = 67$ minutes). All play interactions occurred with juveniles, no play interactions with adult were observed.

Chronologically ordered data analysis

We tested potential influences between the sum of time of play interactions and sum of sexual contacts in the group per day-period (**Fig 6**). With this test, we noticed a continuity between play interactions and sexual contacts in the whole group, all individuals alike (Wilcoxon test: $z = 3.815$, $p\text{-value} = 0.0001$, $\tau = 0.23$). In other words, more play interactions with juveniles in each time-period generally predicted more sexual contacts in the same and following time-periods. However, once we reproduce the same test for one male, we noticed only DV showed individually the same continuity between plays and sex ($z = 3.155$, $p\text{-value} = 0.001$, $\tau = 0.383$). DW did not show this continuity ($z = 0.939$, $p\text{-value} = 0.347$, $\tau = 0.115$), and neither KEL nor KI played sufficiently to be analysed. Whereas play interactions seemed to predict more sex contacts in the following periods, DV is the only one who seem to apply this continuity.

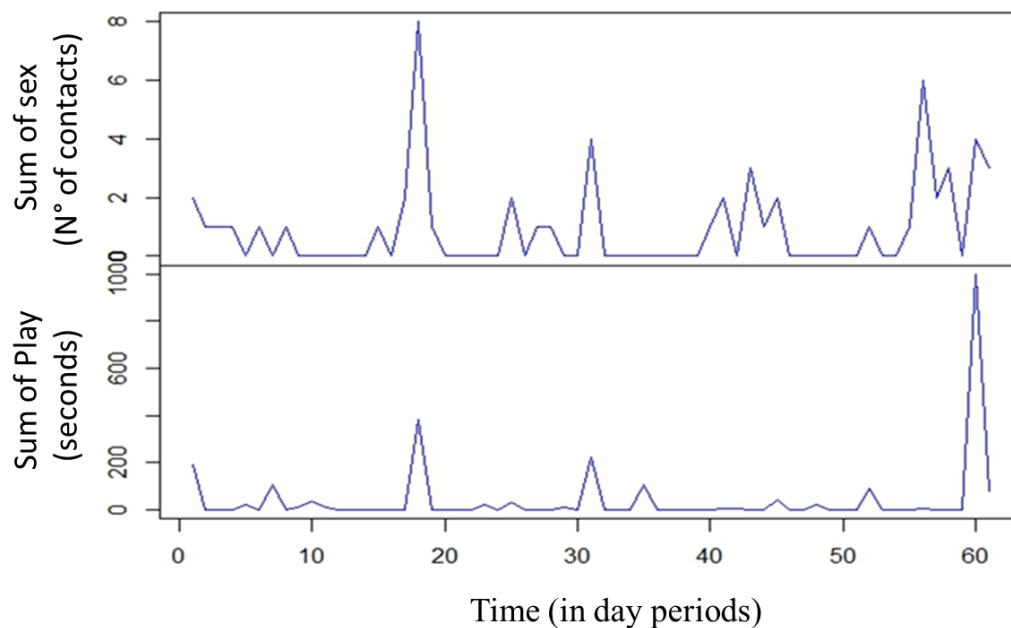


Figure 6: Total time of play interactions with infants (below) and total number of male-female sexual contacts (above) in the whole group (y) on each period of day observed from day period n°1 to day period N°60 (x). Play interactions with infants were positively correlated with sexual contacts with females (Wilcoxon test: $z = 3.8152$, $p\text{-value} = 0.0001$) suggesting that more play interactions could predict more sexual contacts in the following day periods (adjusted p-values, Holm/other method). However, this prediction failed once applied to one male individually, excepted DV ($z = 3.1554$, $p\text{-value} = 0.002$).

We also used time-series approach with groom given instead of play with juveniles. However, Males did not show continuity between groom given to females and sexual contacts. Conversely to play interactions, more grooming to females did not predict more sexual contacts in time (Kendall's correlation tau $z = 1.788$, $p\text{-value} = 0.073$, $\tau = 0.108$). Once we reproduce the test individually per male, we noticed groom given to females predicted more sexual contacts with them for DW ($z = 2.17$, $p\text{-value} = 0.029$, $\tau = 0.27$) but not for DV ($z = 1.835$, $p\text{-value} = 0.066$, $\tau = 0.228$), KEL ($z = -0.93$, $p\text{-value} = 0.352$) or KI ($z = -0.697$, $p\text{-value} = 0.485$).

We also tested the influence of groom given and sexual contacts (or mating success) for a male with a single female, instead of including all females. KEL and KI did not show any significant results with Kendall's Rank Correlation Tau, due to null standard deviation with many females. Nevertheless, we noticed a continuity between groom given by DV to UK and sexual contacts between them in the following periods (Kendall's Rank Correlation Tau $z = 2.899$, $p\text{-value} = 0.003$, $\tau = 0.363033$). Which was not the case for DW with UK ($z = -0.768$, $p\text{-value} = 0.442$, $\tau = -0.097$). DV increased his mating success with the alpha female by grooming her, while DW generally increased his mating success by grooming females with a wider range of females in the group.

Affiliative behaviours and females' rank

Groom given

DV and DW gave significantly more groom to dominant females than to subordinates (Wilcoxon Signed Rank test: $V = 77.5$; $p\text{ value} = 0.01383$). These two males did not show significant differences in the meantime of groom given to dominant females (Wilcoxon Rank Sum test: $W = 1902$, $p\text{-value} = 0.9108$). However, these two males showed different patterns. DV gave significantly more groom to dominant females than to subordinates (Wilcoxon Signed Rank test: $V = 15$; $p\text{ value} = 0.02953$). Whereas DW groomed females regardless to their rank ($V = 23.5$; $p\text{ value} = 0.2417$). Despite their similar social "rank", DV and DW showed different patterns. DV focuses his groom interactions towards dominant females, whereas DW casts a wider net across dominant and subordinate females.

Conversely to DV and DW, KEL and KI did not give significantly more groom to dominant females than to subordinate females ($V = 32$, $p\text{-value} = 0.836$). However, we noticed KEL gave

significantly more groom to subordinate females than DV (Wilcoxon Rank Sum test: $W = 1799.5$, $p\text{-value} = 0.027$). Among the two “low ranking” males, KI did not show distinctive participation on groom given to any female rank class, neither compared to other males. Nevertheless, KEL makes an exception, because he gave significantly more groom to subordinate females compared to a “high ranking” male. A gap appears between these two males. While DV focused on grooming dominant females, KEL, less tolerated during feedings, seemed to have more grooming interactions with subordinate females than one of the most “high ranking” males (adjusted $p\text{-values}$, Holm/other method).

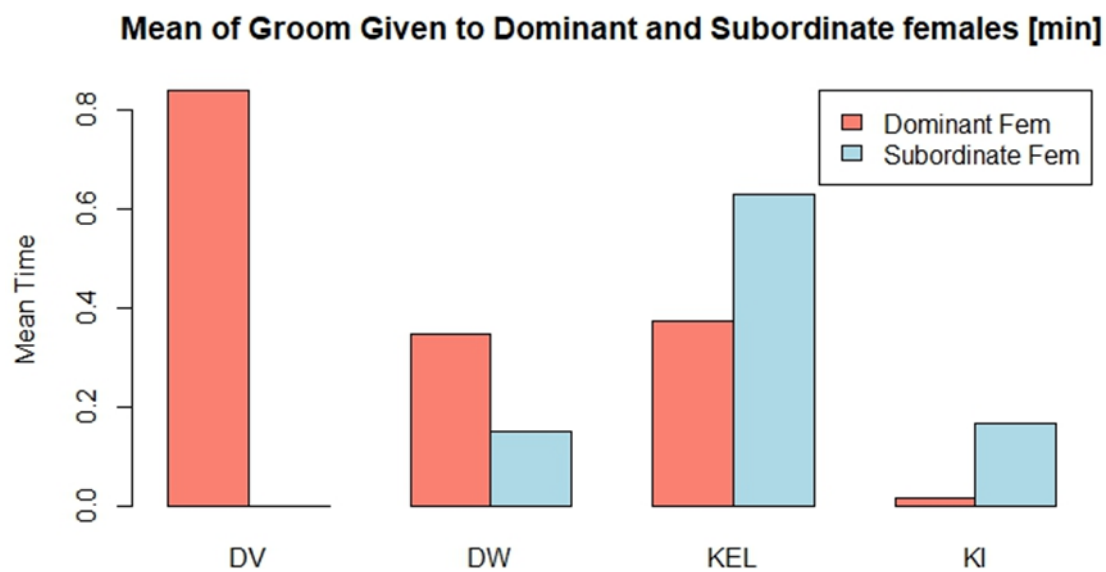


Fig 7: Time of groom spent on grooming females according to social rank. DV and DW spent significantly more time on grooming dominant females than subordinate females (Paired Wilcoxon test: $V = 77.5$; $p\text{ value} = 0.01383$); which was not the case for KEL and KI. However, KEL spent significantly more time on grooming subordinate females than DV (Wilcoxon Ranked Sum test: $W = 1799.5$, $p\text{-value} = 0.02702$.)

In sum, the two “high ranking” males spent significantly more time grooming high ranking females than subordinate females, which was not the case for the two “low ranking” males (**Fig 8**). DV spent significantly more time on grooming dominants than subordinate females. DV was however the only male who did so. Concerning subordinate females, only KEL distinguishes himself by spending significantly more time of grooming subordinate females than DV. Indeed, we did not notice any other significant difference between two males in terms of meantime of groom given to subordinate females.

Play with infants

Play interactions occurred less often than grooming. Among the four males, two showed too many 0 values for play with infants (KEL and KI). As for groom given to females, we aimed to see which male played more with dominant females' infants or with subordinates'. Conversely to grooming, DV and DW did not show a significant difference in terms of meantime of play between dominants' and subordinates' infants (Wilcoxon Signed Rank Test: $V = 105.5$, $p\text{-value} = 0.088$). Which was similar for KEL and KI ($V = 18$, $p\text{-value} = 0.5279$). In this case, no male showed significant differences in the meantime between plays with dominant's and subordinate's infants. Neither significant differences of meantime between two males. The only exception is DV once taken apart. Indeed, despite showing no significant difference of meantime with DW (Wilcoxon Ranked Sum test: $W = 2062$, $p\text{-value} = 0.106$) or KEL ($W = 1987$, $p\text{-value} = 0.7038$), DV played significantly more with dominant's infants than with subordinates' infants than with subordinates' (Wilcoxon Signed Rank test: $V = 46$, $p\text{-value} = 0.033$). As for groom given to females, DV's results in play interactions do not seem regardless to rank either (adjusted $p\text{-values}$, Holm/other method).

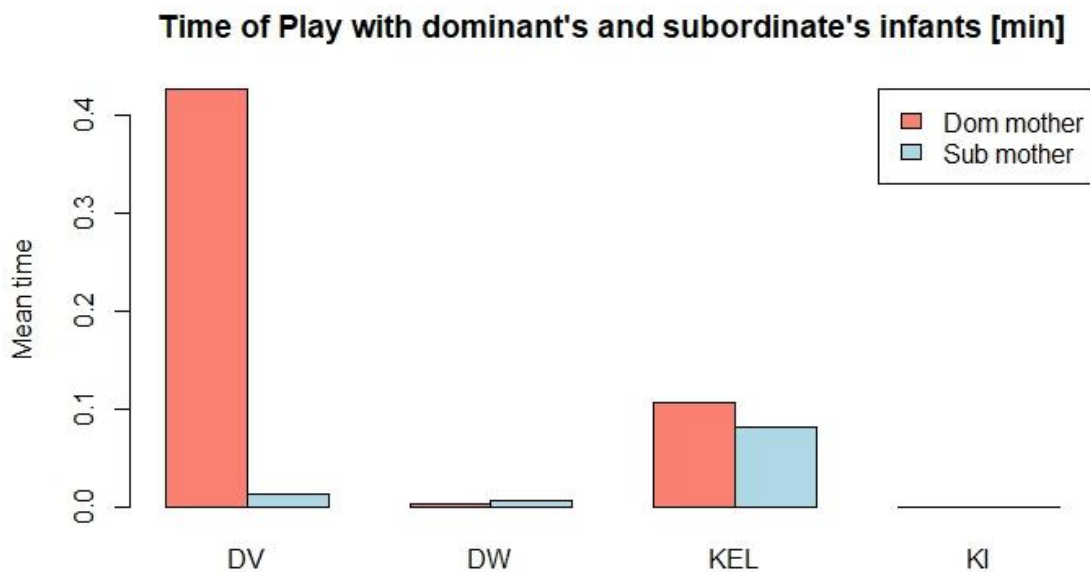


Fig. 8: Time spent on playing with infants, according to infants' mother's rank. While most of males rarely played with infants, DV seems to make an exception. DV indeed spent significantly more time on playing with dominants' infants than with subordinates' (Wilcoxon paired test: $V = 46$; $p\text{ value} = 0.03327$)

Sexual contacts

Finally, we tested males' sexual contacts regarding to females' rank. DV and DW together had significantly more sex contacts with dominant females than subordinates (Wilcoxon paired test: $V = 295$, p value = 0.0001752). Conversely, KEL and KI did not show significant differences between sexual contacts with dominants or subordinates. As for groom given, we observe "high ranking males" interacting significantly more often with dominant females, and "low ranking" males showing no significant difference with any female rank class.

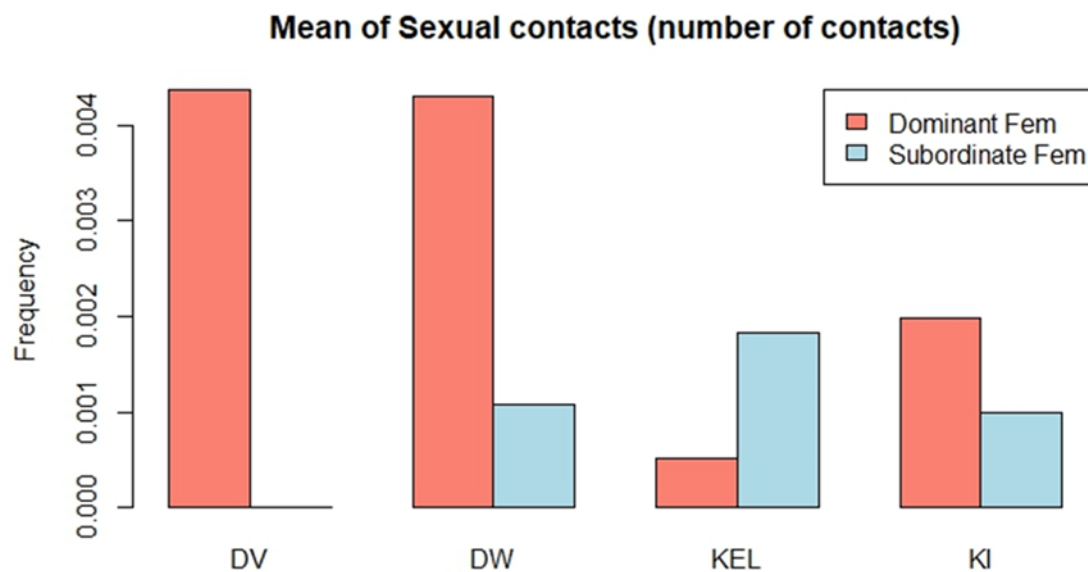


Fig 9: Number of sexual contacts with females according to rank class. Both DV and DW had more sex with dominants than with subordinate (Wilcoxon paired test: DV: $V = 36$; p value = 0.0006664; DW: $V = 36$; p value = 0.003942). KI had no significant differences of sexual contacts with dominants compared to DV (Wilcoxon Ranked Sum test: $W = 2165,5$; p value 0.2687). DW and KEL had significantly more sex with dominants compared to DV ($W = 1830$, p -value = 0.04903)

As for groom given to females and play interactions with juveniles, we notice DV had significantly more sexual contacts with dominant females than with subordinates ($V = 36$; p value = 0.0006664). We observe no significant difference between DV's and DW's sexual contacts with dominant females. DW had significantly more sexual contacts than DV (Wilcoxon Ranked Sum test: $W = 1769$, p -value = 0.04545). furthermore, DW had significantly more sexual contacts with dominants compared to KI and KEL (KEL: $W = 2403$, p value = 0.0005625; KI $W = 2165,5$; p value = 0.01033). Among "high ranking" males, DV had exclusively sexual contacts with dominant females, whereas DW casted a wider net, with many sexual contacts with both dominant and subordinate females.

Despite his “low ranking” status, KI showed ambiguous results concerning sexual contacts. In fact, KI had not significantly less sexual contacts with dominants compared to DV ($W = 2165,5$; p value 0.2687). However, KI did not have significant difference in sexual contacts compared to KEL, both with dominant and subordinate females. Although a “low” social rank, KI seemed to have some privileges in terms of mating success but not sufficiently to distinguish himself from “low” or “high” ranking males.

In this test, KEL can be seen at the opposite of DV. In fact, while DV had significantly more sexual contacts with dominant females than KEL ($W = 2152$, p -value = 0.03618), KEL had significantly more sex with subordinate females than DV ($W = 1830$, p -value = 0.04903). These results widen the gap between these two males’ status, which is coherent with groom given and females’ proximity results.

Respectively, DV and DW had significantly more sexual contacts with dominants than with subordinate females. Whereas DV had exclusively sexual contacts with dominants, DW had enough sex with dominant to be significantly different to KEL and KI. But also had enough sex contacts with subordinate to be significantly different to DV. KEL and KI for their part, had not significantly more sex contacts with dominant of subordinate females. Whereas KEL had especially sexual contacts with subordinate and few contacts with dominants. KI had ambiguous success in sexual contacts. KI showed no significant difference with neither DV for sexual contacts with dominants, neither significant differences with subordinates compared to DW and KEL (adjusted p -values, Holm/other method).

Discussion

We aim to investigate how male captive bonobos can obtain some advantages with the help of affiliative behaviours such as grooming or play with juveniles in a large group. Including a natural-like social structure (multi-male and multi female structure) we can find in the wild or in “semi-captivity”. For this, we used cross comparisons of grooming, play with infants and sexual contacts to identify the nature of males’ affiliative behaviours and relationships they entertain with females. Thanks to the composition of the group, our results show a real means of how male bonobos can behave in a large captive group including a multi-male multi-female structure with several differences of ages and hierarchy among this very group.

Females' proximity indices

Proximity scan results show a certain linearity between DV-DW and KEL-KI. But this linearity is clearly less visible between DV and DW, and so between KI and KEL. DV and DW, due to their higher proximity indices with females, gained more food tolerance from females than KEL and KI, who generally stayed far from the central resource zone (zone 1). This result is consistent with both wild and captive studies led on male bonobo hierarchies. In fact, whereas captive male bonobos tend to form strong and steep hierarchies (Stevens & al, 2007), we generally observe less linearity in male hierarchy among wild populations (Furuichi, 1997). Males in this group can be classified as “high-ranked” (DV and DW) or “low-ranked” (KEL and KI), which can be dichotomic due to the absence of intermediary categories, like “middle-ranked”. We noticed only males taking benefits from a dominant female’s high social status and males without any clear social status. However, both mother presence and proximity indices (linked with food tolerance) support our classification between these two male classes. As observed in other studies, age is not linked with hierarchical rank (Paoli & al, 2006). DV and DW are respectively 16 and 20, whereas KEL and KI are 12 and 24. While our sample size is low, proximity indices randomly correspond to the presence of the maternal presence, which is known to be a major factor in males’ tolerance in a group (Kano, 1996; Furuichi 1997; Surbeck, Mundry & Hohmann, 2011).

Our results must take consideration to the recent debate on the level of social tolerance in bonobos. Several studies (Stanford, 1998; Jaeggi, Stevens & Van Schaik, 2010; Cronin, De Groot & Stevens, 2015) question the traditional pacific, egalitarian and social tolerant Bonobos compared to other primates, especially chimpanzees. These nuances are real (de Waal, 1989) but must be experimentally controlled to prevent potential overinterpretations. For the case of food-tolerance, studies found evidence that captive bonobos exhibited less social tolerance compared to captive chimpanzees. Suggesting social tolerance of bonobos might not be that high compared to other great apes (Stanford, 1998; Cronin, de Groot & Stevens, 2015). Hence, we observed an avoidance in the resource zone for individuals that are not related with dominant females (UK, DNL and UL). Although DNL’s offspring (DV and DW) were regularly present in the resource zone. KI and KEL: an adult and subadult male were rarely observed in this same resource zone. This observation corresponds with both wild and captive results, where sons of high-ranked females benefit from both maternal social status and support, while other males

remained in peripheral areas (Cronin, de Groot & Stevens, 2015; Surbeck, Mundry & Hohmann, 2011; Furuichi and Ihobe, 1994). Such observation might be linked with food distribution and accessibility. In fact, food in captivity might be more monopolized than in the wild. While captive bonobos can obtain food from the branches, fruits or seeds that keepers left to their disposition in large enclosures, the main source of food comes from feeding times: where food arrives in a central resource zone, easily monopolized by high-ranked females (Parish, 1994). Besides, bonobos live in fusion-fusion societies (Aureli & al, 2008). Fission-fusion societies split in small foraging groups during the day, which permit to gain more energy-food with less monopolization or sharing necessity, as it is the case for primates, probably early *Homo* and some social carnivores, like spotted hyena *Crocutta crocutta* (Smith & al, 2012). Perhaps foraging in small groups among different and less concentrated resource zones (as in the wild) provides less tension or food-monopolization and maybe more food sharing in wild bonobos (Yamamoto, 2015). This might help us to see whether tensions or low social tolerance mainly appear in captive studies (Cronin, de Groot & Stevens, 2015; Jaeggi, Stevens & Van Schaik, 2010) as in this present study, especially for KEL and KI.

Chronologically ordered data analysis

Our results indicate a general continuity between play interactions with juveniles and sexual contacts in the group in general. However, we need to mention our small sample size (4 males). And furthermore, that only DV showed this pattern individually. Neither DW, KEL and KI applied this pattern. DV's play interactions are decisive to this global correlation. For the whole group, we do not know whether DV's play interactions alone are a significant event preventing tension or if this global continuity is just meaningless. Captive bonobos sometimes prevent tensions with the help of play during pre-feeding times and socio-sexual contacts for appeasement once tensions appear (Paoli, Palagi & Tarli, 2006). We do not see whether play with juveniles is an anticipation to more sexual contacts or just prevents potential tensions during non-feeding times, like a general appeasement. But we observe these two mechanisms having some peaks in very close periods. This result still supports the combination of play (during non-feeding time) and sexual contacts (during feeding) to prevent tensions and appeasements. Even if this pattern does not fit for most males, DV who is the only one following this pattern, has a high proximity with females, mainly interacted with dominant females and has privileged relationship with the alpha female.

Many observations in animal behaviour consider that individuals tend to play once they are free from both physiological and social stressors (Rensch, 1973; Martin and Caro, 1985). Due to his higher proximity indices with females during feeding, DV might be less plagued by physiological stresses like hunger. And his high-ranked maternal support might spare him from social stresses. Does DV play due to his relaxing position in the group, and if so, how could we explain why DW, who gained the same maternal support and high proximity indices, did not play as much as DV? Or does DV plays are an anticipation to increase his sexual contacts with females? This question can be developed with the second step of this play/sex timeseries tests. We used Kendall to see potential continuity between play with a juvenile and sex contacts with its mother. Once again, DV exhibited a continuity in his play interactions with MO and sex with UK (MO's mother), and only for this infant/mother combination. This result can suggest many possibilities. 1) Playing with MO permitted to DV to increase his sexual contacts with UK, suggesting playing with an infant as a strategy to increase sexual contacts with its mother. If so, this might be interesting to see how DV only used this strategy to have more sex with the alpha female (UK) and only her. 2) DV had significantly more sex with UK than with any other female, if so he might rather play with her offspring than any other female's. 3) As DNL's son, DV spent more time with other dominant females, and rather play with dominant females' infants than with subordinate females'. This last hypothesis might suggest the existence of cast-like social structure in this large captive group.

Short-Term Benefits of Play Behaviour

Recent studies recorded positive correlations between play, grooming and contact sitting interactions in captive adult bonobos (Paoli et Palagi 2007). However, our four males did not show the same pattern. DV and DW showed positive correlations between grooming and sexual contacts, and DV did with play. But KEL and KI for their part did not show such correlations with any variable in the use of timeseries analysis. Anyway, the difference is visible between DV-DW and KEL-KI regarding sexual contact success. Maybe DV and DW use efficient affiliative (playing and/or grooming) strategies to get access to females, that KEL and KI did not use. Or maybe DV and DW, as dominant's sons, undergo less stress or social pressures than KEL and KI, letting them to exhibit more grooming and playing interactions with females.

Concerning DV, this male might be freer from both physiological and social stressors due to his proximity with females and privileged relationship he entertains with the alpha female (UK).

This might be especially relevant for play interactions, corresponding with the idea that playful interactions generally appear once different sources of stress disappear (Rensch, 1973; Martin and Caro, 1985). If so, DV might be the less concerned by stress among the four males. In fact, only DV played sufficiently for making a positive correlation between play interactions and sex contacts for the whole group. If play behaviours are known for reducing tensions among bonobo societies, and might justify some “egalitarian” properties of these societies compared to chimpanzees, at least in terms of play interactions (Enomoto, 1990; Palagi, 2006). Then maybe DV alone had enough play interactions to reduce the whole group’s potential tensions. And if so, this might firstly suggest the importance of DV in the group, justifying his privileged relationships with dominant females. Secondly, if DV’s play interactions are sufficient for reducing tension in the group, maybe other males do not have the necessity to play as much as DV did. Especially DW, who despite being free from social stresses as his brother, did not have significantly less sexual contacts with females without playing as much as DV.

Short-Term Benefits of grooming

While exchanged sexuality provides several benefits (food acquisition, social interest from males), besides conception and benefits from paternity confusions (Wrangham, 1993). Males can get long-term benefits from exchanged sexuality. Males spending more time on grooming or sharing food with swollen females tend to be preferred as sexual partners. (Wrangham, 1993; Tutin & McGinnis, 1981). During our observation however, no female was at a state of swelling. Moreover, we did not observe any occurrence of food sharing by any individual. Testing males’ subsequent advantages from food sharing or influence of swelling period were impossible for this study. If males can obtain exchanged sexuality from grooming females (Tutin & McGinnis, 1981), this is not a general tendency for our group. Indeed, conversely to play and sex timeseries approach, we did not find any positive correlation between grooming and sex in the whole group. However, timeseries analysis revealed DV’s grooms towards UK predicted more sexual contacts for this dyad. Which was not the case for DW, who yet also regularly groomed this same female. No other similar correlation was observed between a male and a female. Conversely to DV, DW, who is the only other male who groomed UK, did not increase his mating success with her with the help of groom. This suggests, once again, the important relationship DV entertains with UK. In addition to be the most playful with infants, DV might be also chosen by UK for his groom interactions with her.

DW, for his part, displayed different results in terms of groom and sex behaviours in our timeseries approach. For this male, grooming females generally predicted more sex activities with females taken together. DW's result corresponds to what has been observed in other bonobo studies, suggesting the importance of grooming males in the sexual preference of females (Tutin & McGinnis, 1981). DW's grooming interactions in the group in general provided him several sexual benefits in the whole group. Which is not the case for DV, who focused on the alpha female. Among these two high-ranked males, we observed two different kinds of benefits: DV obtained most benefits from his interactions with the alpha female, whereas DW seemed to cast a wider net of females for getting sexual benefits.

Affiliative behaviours and females' rank

Grooming interactions, regarding to females' position rank.

Due to their high social status, high-ranked females generally gain more groom from males. Whereas female-female dyads are less linked to dominance hierarchy, male-female dyads seem to be clearly associated with dominance (Franz, 1999). Grooming competition is a matter of dominance rank: males generally prefer to groom high-ranked females (Stevens & al, 2005). As in previous studies, dominant females in our group received more groom from males than subordinates. Which can confirm how dominant females are generally the most interesting grooming partners in a matriarchal bonobo society (Franz, 1999 Stevens & al, 2005).

Our Wilcoxon tests revealed DV is the only male who gave significantly more groom to dominants than to subordinate females. Neither KEL or KI showed significant differences in time spent on grooming dominant and subordinate. Even DW, who is also a high-ranked male, did not groom significantly more dominant or subordinate. As for play and grooming timeseries approach, DV confirms once again his tendency to exclusively interact with dominant females, like acting exclusively in a dominant "cast". This result is consistent with timeseries approach due to DV's groom and sex contacts with UK or play interactions focused on dominant's infants (MO and LO). Once again, maybe DV groomed dominant females as an anticipation to get the subsequent advantages he obtained in terms of food tolerance or several sex contacts with the alpha female. DV due to his position as a high-ranked female's son, might not fall prey to stresses KEL or KI can be confronted to. Or DV's high social status might allow him to interact with the most attractive grooming and sexual partners that are dominant females.

KEL seems to be the one who spent more time on grooming subordinate females. As DW and KI, KEL did not show significant differences between grooming dominant or subordinate females, but is the only male that gave significantly more groom to subordinates than DV. This result emphasizes the strong divergence of treatments males can receive in such groups. While high-ranked males, especially DV, have a well access to dominant females, others “subordinate” males do not. And if so, they might need to fall back on lower-ranked females to groom and to have sex with. While DW and KI did not spend enough time to show a significant difference with DV, KEL may have entertained closer relationships to subordinate females. Anyway, compared to DV.

Play interactions with infants, regarding to mothers' position rank.

Play with infants was the most difficult behaviour to analyse, due to the very small sample size. KI even had too many 0 values they were not able to be submitted to any test including play interactions. Once again, DV distinguishes himself from the rest of the males. Timeseries approach indicates DV plays predicted more sex with females. Especially playing with MO and sex with UK. Moreover, DV also played more with dominant females' infants than with subordinates' in general. DV is the only one who shows a significant difference between time spent on playing with dominants' infants than with subordinates'. Our sample size remains too small to consider this result as representative for captive bonobos, however perhaps similar results will be found in further studies on the potential role of play on male bonobos' mating/reproductive success. Female bonobos are known to conceal their exact time of swelling, which permits to bias and confuse paternity, favouring females' choice of partners (Takahata, Ihobe & Idani, 1999; Vervaecke & van Elsacker, 2000; Reichert & al, 2002). Males, for their part, are also known for playing with infants in paternal care, anyway more often than male chimpanzees (Enomoto, 1990; Palagi, 2006; Palagi & Paoli, 2007). Playing with juveniles could be a sign of implication in paternal care, which can provide advantages to be chosen as a sexual partner, especially in a matriarchal society. Among our two high-ranked males, playing with infants provided to DV more exclusive relationships with the alpha female, compared to DW.

Sexual contacts, regarding to females' position rank.

Bonobos' sexuality has been well developed in recent literature. Bonobos are especially known for their use of sex to solve tensions or prevent potential conflicts in the group (Kano & Mulavwa 1984, Thompson-Handler & al, 1984; Blount, 1990; Paoli & al, 2007). In bonobo societies, males display low sexual coercion compared to other primate species, probably due to females' strong alliances (Smuts and Smuts, 1993). All sexual contacts can involve all sex and/or age class of individuals together, without almost no apparent discrimination (de Waal, 1990; Hohmann & Fruth, 2000).

However, our observation noticed that high ranked males had significantly more sex contacts with dominant females than with subordinates. Which was not the case for KEL and KI, who did not show significant differences between their ratio of sexual contacts with dominant and with subordinate females. While bonobos are known for sexual interactions regardless to sex or age class, we observed our two high-ranked males' tendency to mate with females of their mother's class rather than with subordinates, as in a "cast-like" society. This result might suggest three possibilities. 1) DV and DW are preferred as sexual partners by dominant females than KEL and KI. Observations revealed that most high-ranking males generally had higher mating success than low-ranked males, even if they did not always have the best reproductive success (Marvan & al, 2006). In captivity as well as in the wild, female bonobos are reputed to mate promiscuously while their menstrual cycle (Takahata, Ihobe & Idani, 1999) and can conceal their exact time of swelling to bias and confuse paternity (Reichert & al, 2002). 2) High ranked males (DV and DW) appeared to prefer dominant females as sexual partners (excepted for their mother, DNL). As for their apparent preference for grooming dominant females (Franz, 1999 Stevens & al, 2005), male bonobos might prefer having sex with dominant females, but only high ranked males can get priority on mating with these same females, as Kano (1996) observed in the wild. 3) As possibly suggested in timeseries approach, maybe DV and DW by their mother's rank (DNL) simply spend more time with dominant females in many terms (proximity, grooming) and providing more mating opportunities with them than with subordinate females. Higher males' mating success came alongside with mother's presence in the group. We assume our sample size is too small to officially conclude this too early. Nevertheless, our results correspond to other studies that showed how mother's presence in the group increased mating success of their sons compared to orphan males (Surbeck, Mundry & Hohmann, 2011). Mother's presence might influence both reproductive and mating success of sons compared to "orphan" males, without any maternal support or influence. While DV seems

to be especially preferred by the alpha female, DW apparently got sexual preference from a wider range of females in the group. DW even had sufficient sexual contacts with different dominants to have significantly more sexual contacts than both KEL and KI, while DV only had significantly more sexual contacts with dominants than KEL.

As for groom given, KEL seemed to exhibit more sexual contacts with subordinate females compared to DV. Confirming the strong difference between these two males' profiles. While DW and KI did not show significant differences of sexual contacts with dominant females compared to DW, we observe a steepness difference in terms of sexual contacts with dominants between DV and KEL, as we observed in groom given behaviours. In both cases, KEL seemed to exhibit more affiliative behaviours or relations with subordinate females, anyway compared to DV. Maybe if the two high-ranked males had prior access with dominant females, KEL might benefit from spending more time with subordinate females that are more accessible, free from high-ranked males' monopolization, as high-ranked male bonobos usually do with oestrous females (Kano, 1996).

While bonobo society is often described as more egalitarian than in other great apes (Parish, 1994; Sommer & al, 2011), our results correspond to recent studies showing linear dominance hierarchy on wild and captive male bonobos, as found in despotic societies (Stanford, 1998; Stevens & al, 2007; Surbeck, Mundry & Hohmann, 2011; Jaeggi, Stevens & Van Schaik, 2010; Cronin, De Groot & Stevens, 2015) according to the definitions given by Hand (1986) and Van Schaik (1989). KEL indeed, did not receive the same treatment and advantages DV and DW received in terms of high proximity or mating success with females, especially from dominants. KI, for his part, showed more ambiguous results. As KEL, he showed low proximity with females, did not play with any infant, gave less groom than the other males, but still had not significantly different sexual contacts with a dominant female than the two high-ranked males. However, DNL is the only one dominant female who had sex with him. An KI was her only male sexual partner during the whole period of observation. Because two of the four adult males (and all high-ranked males) are DNL's sons, KI might take benefit from incest avoidance (Leiber, 2006) and from the fact that KEL is a subadult. Thus, if KI has a prior sexual preference from a dominant female, he may not need to exhibit invest-like behaviours such as grooming or playing with infants to get sex or proximity with DNL. In fact, KI did not distinguish himself from any affiliative behaviour seen above, but entertained a certain mating success with a dominant female. Acting somehow like a free rider whilst having some privileges KEL did not get.

Conclusion

Our results are overall consistent to other observations made on both captive and wild populations of bonobos. While female hierarchy showed an evident dominance from two females and less linear ranking in following females, males exhibited a strong and linear hierarchy, especially from DV to KEL. Despite the small sample size of our population in this pilot study, we noticed the two most high-ranked males who gained more food tolerance and mating success with females were the two ones whom had their mother within the group. Which corresponds to the evident importance of mother's influence on males' social status and benefits in a group of bonobos, as frequently mentioned in literature (Furuichi & al, 1998; Surbeck, Mundry & Hohmann, 2011). Furthermore, we noticed that high-ranked males tended to interact more with dominant females, showing a similar rank-class of their mother, than with subordinate females. Whereas low-ranked males tended to either interact more with subordinate females than with dominants, or simply took account from incest avoidance for having sex with a dominant who could not mate with her two adult sons. If bonobos show steep and linear hierarchies, especially in captivity, maybe shall we observe kinds of "casts", meaning dominants and subordinate rarely interaction each other. Both grooming and sexual interactions implied two partners from similar rank "class". If dominant females generate more interest in grooming from males (Franz, 1999 Stevens & al, 2005), and that bonobos are known to have sex regardless so sex or age-class (Hohmann & Fruth, 2000), it might not be the case for rank-class for these affiliative behaviours among our captive group.

If play interactions with infants generally predicted more sex contacts in the group, only one male seemed to exhibit it individually. At least, playing with an infant predicted to this male more sexual contacts with the infant's mother, whilst was the alpha female. However, we cannot assume whether this pattern reflects an anticipation to increase mating success or just due to this male's high ranked position, providing less social stress and more playful activities. Neither if this pattern is representative for the whole group or captive groups of bonobos in general. That is why further studies will be necessary to investigate the potential influence of play with infants or other affiliative behaviours in males' mating/reproductive success with females. Such studies on males' affiliative behaviours and advantages in female dominance societies might help us to understand the variety of matriarchal species, as lemurs or hyenas. As a pilot study, we only suggest possibilities for new fields of research to understand female dominance societies, which remains a minority across the evolution of primates.

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