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Latest news from the bonobos: *Pan paniscus* myths and realities

Historique

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1 Introduction

- 1 Bonobos are one of the large mammal species most recently discovered by science. First informally described in 1929, they were named *Pan paniscus* in 1933 (Coolidge, 1933). Since Robert Yerkes in the thirties, bonobos were studied in captivity and more recently in the wild beginning in 1973 with Takayoshi Kano at Wamba field site, DR Congo (Kano, 1980). With Congolese wars and political instability, studies in the field were slowed down but research teams persevered and new exciting discoveries about this great ape allow us to better know our cousins' biology and also allow insights into our own origin. This paper reviews the latest news from the bonobos. Some old views of bonobos are obsolete; some previous questions have been answered while others remain unsolved. This review based on recent literature is also punctuated by my own observations with an habituated free-ranging bonobo community at the LuiKotale field site (Hohmann and Fruth, 2003c). My main research focused on the bonobo ecology. I recorded 1879 hours of behavioral data within this community of 25-35 identifiable bonobos, through 22 months of field work (2008-2011). Other discoveries, I hope, will astonish you with new insights about one of the planet's most fascinating animals and one of our closest living relatives.

2 Our closest living relative

- 2 Within our own family of the Hominidae, great apes of the genus *Pan*, including bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), are our closest living relatives. Chimpanzees live in four major populations, including those located in western Africa (*P. t. verus*), equatorial Africa (*P. t. troglodytes* and *P. t. schweinfurthii*), and the Gulf of Guinea region (*P. t. ellioti*); with distinct and full species proposed and still debated today (Gonder *et al.*, 2011). Described as pygmy chimpanzees in literature before the 1980s, bonobos have more gracile limbs than chimpanzees but are similar in many other morphological traits and in body size (Females = approx. 33-36kg, Male = approx. 43-46kg; (Coolidge and Shea, 1982; Parish, 1996)) to the other *Pan* species. However, their frequently bipedal posture (D'Août *et al.*, 2004), their morphology, and neotenic characteristics (Shea, 1983) which they share with us (*Homo sapiens sapiens*), caused many anthropologists to propose the bonobo as the best model for our closest living relative.
- 3 However, contrary to popular belief, bonobos are not more closely related to us than are chimpanzees. We share a common ancestor with both *Pan* which dates to 5-6 million years ago, and approximately 98% of our DNA (Wildman *et al.*, 2003; Patterson *et al.*, 2006; Prufer *et al.*, 2012) with both species. Bonobos and chimpanzees diverged from 0.93 (Won and Hey, 2005) to 2 million years ago (Raum *et al.*, 2005) and are separated by the Congo River, which acts as a biogeographic barrier by splitting the Congo basin. Therefore, both are genetically equidistant to us.
- 4 *Pan troglodytes* and *P. paniscus* are so close to us that an increasing number of scientists propose a fusion of the genus of our cousins *Pan*, with our own genus *Homo*; with the proposed classification: *Homo sapiens* (humankind), *Homo troglodytes* (chimpanzee), and *Homo paniscus* (bonobo) (Wildman *et al.*, 2003). This little taxonomic revolution could be difficult for the general public to accept, but an extraterrestrial taxonomist would not hesitate. One day we might accept ourselves as the third chimpanzee (Diamond, 1991). Another more philosophical rapprochement is the Great Ape Project (GAP) launched in the 1990s (Cavaliere

and Singer, 1993). It is an appeal of 36 scientists from different disciplines aiming at the legal equalization of the non-human great apes with humans. The central point of the initiative is the "Declaration on Great Apes", claiming the inclusion of great apes in the "community of equals" and thus securing three basic rights for all great apes: 1. The Right to Life; 2. Protection of Individual Freedom; 3. The Prohibition of Torture. Furthermore, the project pleads for the idea of conferring the "moral status of person" on great apes. But beyond religion and ethics, rejection of this idea is mainly due to pressure for maintaining the use of living apes as "biological material" for experimentation in industry (Carlsson *et al.*, 2004). We can note that the United States and Gabon are the only remaining countries allowing such research.

3 A tool maker

- 5 Chimpanzees are well recognized as tool makers in the wild, with cultural variation in usage among populations across Africa (Whiten *et al.*, 1999). For bonobos, tool-related behaviors are observed in wild populations but are rare and less sophisticated than those observed in chimpanzees (Kano, 1982; Ingmanson, 1996; Hohmann and Fruth, 2003a). This bonobo difference could be explained by the fact that they inhabit a less challenging environment than chimpanzees with no need for weapons, or may simply the general lack of studies of this species compared to chimpanzees. However, in captivity, tool making and usage by bonobos have both been well described (Jordan, 1982; Toth *et al.*, 1993; Gold, 2002; Mulcahy and Call, 2006; Gruber *et al.*, 2010). Kanzi and Pan-Banisha, a famous male and female who have gained widespread attention for their skills in language and have lived in the stimulating environment of the Great Ape Trust of Iowa since 2005 (Savage-Rumbaugh and Lewin, 1994). They can light a fire with a lighter, cook a meal, roast marshmallows and perform other impressive tasks. They have the basic stone-tool making skills required to produce usable flakes and fragments by hard-hammer percussion (Toth *et al.*, 1993) and their techniques are improving (Schick *et al.*, 1999). Their reported tool production and utilization for food retrieval (digging or breaking wooden logs) exhibits *Homo-like* technological competencies (Roffman *et al.*, 2012).
- 6 The most recent results appear to describe bonobos as having a similar repertoire in captivity, and equal tool-using capabilities equal as to those of chimpanzees (Herrmann *et al.*, 2008; Gruber *et al.*, 2010). Bonobos as chimpanzees use less dramatic tools for social purposes, games or comfort (cleaning with specific leaves, use of leaves as an umbrella against rain), while chimpanzees use also impressive reported tool techniques in the context of difficult food-acquisition tasks. Another remarkable point is that just like chimpanzees, female bonobos are more willing to use tools than males (Gruber *et al.*, 2010). Because wild and captive bonobos share the same cognitive abilities required for tool use, such behavior is expected to occur in wild bonobos as well.

4 Communication

- 7 Bonobos, like gorillas and chimpanzees, show a human-like asymmetry in language-related brain areas, which has been correlated with language dominance (Cantalupo and Hopkins, 2001). But articulation of speech is physically impossible and language is restricted to vocalizations and gestures (Pika *et al.*, 2005; Pollick and de Waal, 2007). We share several communicative roots like the gestural NO by head shaking (Schneider *et al.*, 2010) and almost all of these are understood by humans. Gestural communications include sexual invitation with body posture and hand raising, begging, embracing, mouth/tongue kissing, kicking, slapping, etc. with facial nuance and context dependence (Pika *et al.*, 2005).
- 8 Apes cannot 'speak'. They can however communicate a wide range of information and are even able to talk with us with the help of technology. Kanzi understands spoken English and communicates with a lexigram keyboard. He also modulates his vocalization with evident structural differences produced within a specific semantic context (Taglialatela *et al.*, 2003). A similar structural difference was observed in other captive bonobos which use a specific acoustic structure in long and complex call sequences related to a precise type of food. This suggests that bonobo food-calling sequences convey meaningful information to other group members (Clay and Zuberbuhler, 2009).

9 In the wild, bonobos exchange long distance calls (high hoot) between groups (Hohmann and Fruth, 1994). What kind of information do they exchange? The study of communication in wild bonobos is promising and may lead to fascinating discoveries.

5 A female dominant society

10 Bonobos live in a male-philopatric structure. This means that males are born and die in the same group while females of 6-13 years emigrate to neighboring groups (Furuichi *et al.*, 2012). Males will stay all their lives with their mothers. Females are accepted into new groups weaving future alliance bonds. Female chimpanzees do not have frequent social interactions with other females, whereas female bonobos maintain close social associations with one another (Furuichi, 2011).

11 The result is a singular primate society: a matriarchal bonobo society in clear contrast with the patriarchal societies of chimpanzees, other primates and most human societies (Parish, 1996; Sommer *et al.*, 2011). This unique trait attracted feminists, public attention and debate about male-female dominance. In early studies (mainly male) scientists described this behavior as "strategic male deference" or males being chivalrous to females as a strategy to obtain sex. This made it easier to admit female dominance in bonobo groups (Parish *et al.*, 2000). Females most often initiate sexual interactions and ranging behavior (Furuichi, 2011), have priority of access to preferred food (Hohmann and Fruth, 1993; White and Wood, 2007) and will sometimes chase or be aggressive towards males (i.e. the definition of 'dominance'; NB: not within chimpanzees). Females are so influential in the groups that mothers improve the mating success of their sons when present (Surbeck *et al.*, 2011). In male-male aggression, mothers and females can intervene and decide the outcome of the situation, and eventually influence their son's rank in the hierarchy (Furuichi, 2011). Despite modest physical dimorphism (female body size is 82.5% that of males) females gain power by cooperation and coalition formation (Parish, 1996; White and Wood, 2007). However, female dominance over males is not a rule. Males are consistently dominant in dyadic interactions (White and Wood, 2007). To conclude, it is clear that adult females occupy high dominance status in bonobo societies and that females are rather co-dominant to males (Surbeck *et al.*, 2012). Differences in dominance among individuals are slight but measurable (see below) but we should keep in mind that bonobos show nothing that is comparable to the strong dominance with submission enforced by violence that is characteristic of chimpanzee societies. Are we close to an egalitarian society? Not really, but non-violence gives us this impression.

6 A peaceful vegetarian society

12 Because they use sexual behavior in several contexts where other species use aggression, bonobos may be viewed as peaceful. However several injuries have been observed in captivity and in the wild, resulting from beatings, or biting on fingers, faces, or genitals (Parish *et al.*, 2000, personal observation). Recently, the public was shocked by a case of cannibalism among wild bonobos where a baby was consumed by a group, including the mother (Fowler and Hohmann, 2010). We should note that the cause of death remains unknown and violence was not observed. Before the carcass was eaten (it was, after all, meat), the mother, with great affection, carried her offspring's body around with her for a whole day. Indeed, bonobos are not the pure vegetarians that we first thought them to be (Fig. 1). Bonobos kill and eat duikers, birds, rodents and monkeys (Hohmann and Fruth, 1993; 2008; Surbeck and Hohmann, 2008; Surbeck *et al.*, 2009). However, although bonobos appreciate and are excited by meat, they are not organized hunters and carnivory thus remains opportunistic and accounts for only a marginal part of their diet (Oelze *et al.*, 2011), i.e., $0.9\% \pm SE 0.2$ of feeding sessions; N = 1879 hrs of observation (Beaune, 2012).

13 Although linear dominance can be determined by agonistic interactions, bonobos are non-violent and mainly engage in chasing acts, submissive behaviours and deference (Hohmann and Fruth, 2003b; Surbeck *et al.*, 2011). Bonobos are highly tolerant and cooperative (Hare *et al.*, 2007). While most primate groups have territorial conflicts, bonobos behave peacefully with neighbouring community, with a large inter-group home range overlap (at Wamba 66% of

the group's home range overlaps with those of neighbour groups (Kano and Mulavwa, 1984)). When two groups meet, they often engage in inter-group sexual relations (often female-female), grooming, feeding and foraging together, and sometimes sleeping at the same nesting place (Hohmann and Fruth, 2002; Furuichi, 2011). So far, infanticide and lethal aggression have never been observed in *Pan paniscus*. We can definitively say that the bonobo has a peaceful nature.

Figure 1



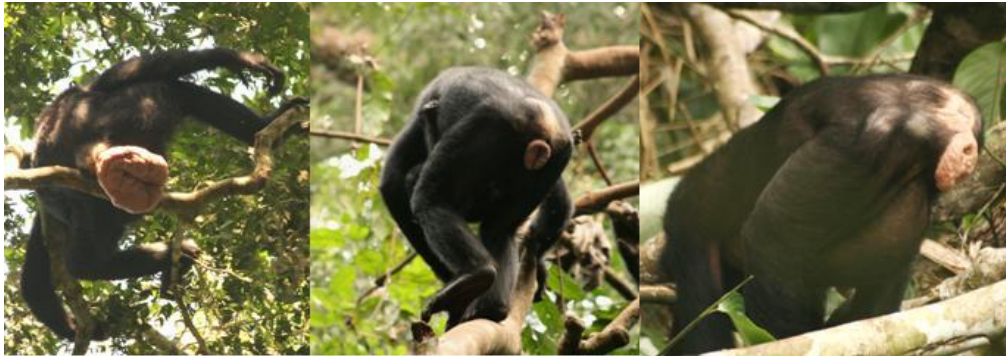
Female Olga and her daughter Opale eating a red colobus (*Procolobus tholloni*), opportunistically killed by the group, LuiKotale, DRC. David Beaune/MPI.
Femelle Olga et sa fille Opale mangeant un colobe rouge (*Procolobus tholloni*), tué de façon opportuniste par le groupe, LuiKotale, RDC. David Beaune/MPI.

7 The most lascivious hominid

- 14 For the public, the bonobo is our lubricous cousin, performing Kama Sutra positions all day long (de Waal, 1997). Actually, the frequency with which bonobos engage in sex is less than an average of 0.3 copulation/hour (Furuichi and Hashimoto, 2002), with intercourse lasting less than a minute (usually a few seconds). Compared to us, bonobos' frequency of intercourse is definitely higher, with humans averaging 1 to 3 marital coitus per week, the frequency declining with age (Kinsey Institute, 2012). The length of coitus for humans is generally longer than a minute with an average of 5 min for humans (Kinsey Institute, 2012). Bonobos do not have more sex than chimpanzees, nevertheless females of this species do have more sex and start earlier in life than male bonobos (Takahata *et al.*, 1999; Hashimoto and Furuichi, 2006). Most importantly females have sex during non-fertile periods or in non-swelling episodes (Furuichi and Hashimoto, 2004). And when fully tumescent, sexual swelling signals occur even during non-conceptive periods. This is called "pseudo-estrus" (Furuichi, 2011). Thus females with true and confusing estrus signals are proportionally more numerous than females displaying no estrus signals so they are less monopolizable by an alpha male (preventing sexual harassment and infanticide) (Furuichi, 2011). See Fig. 2 for sexual swellings. Male bonobos do not sexually coerce females (Hohmann and Fruth, 2003b) and therefore, their sexual solicitation has to be accepted by the female for intercourse to occur. This strategy, contrasting with chimpanzees, is evolutionarily stable and quite similar to behaviour in most human societies (except that our species lost the receptive signals potentially as a result of similar selective pressures).
- 15 Sex is routinely used for non-reproductive goals (tension-reduction, reconciliation, bartering for social favors, and sex for food exchanges). Behavioral observations support the hypothesis

that sex reduces tension and is the basis of this largely peaceful society (Hohmann and Fruth, 2000; Palagi *et al.*, 2004; Hare *et al.*, 2007) and now scientists are trying to test this hypothesis through hormonal experimentation (Hohmann *et al.*, 2009; Wobber *et al.*, 2010).

Figure 2



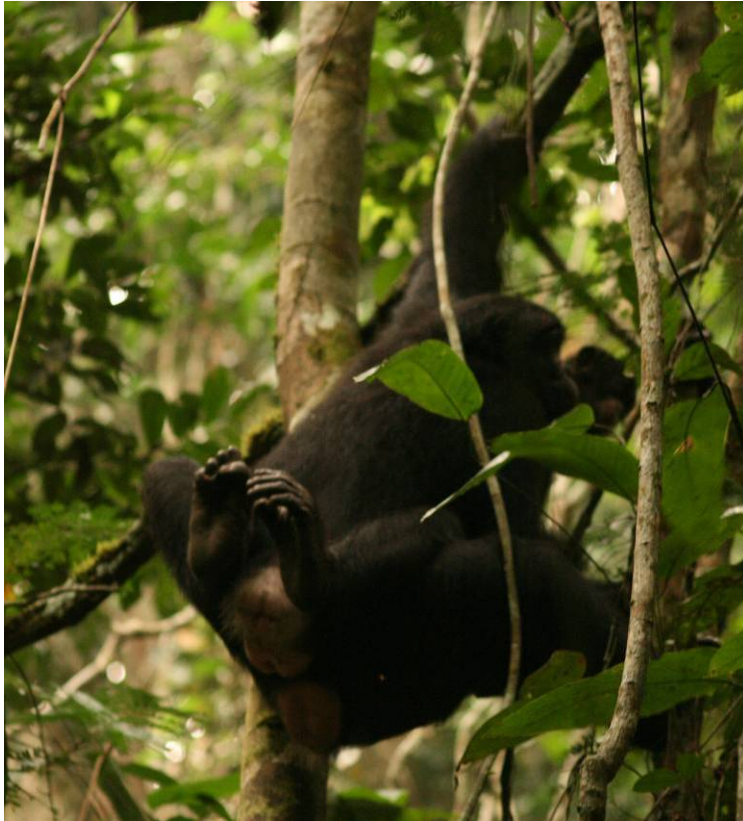
Female bonobos' sexual swellings David Beaune/MPI.
Gonflements sexuels chez les femelles bonobos. David Beaune/MPI.

8 Sexual taboos? Homosexuality does not matter

- 16 Bonobos practice public sex (Clay and Zuberbühler, 2012) rather than the more secretive sexuality of humans and chimpanzees. Bonobos are bisexual apes and homosexual encounters are common, especially among females (Fruth and Hohmann, 2006). Female bonobos engage in a unique sexual behavior also found in humans (tribadism) termed genito-genital (GG) rubbing in which they embrace ventro-ventrally and rub their genital swellings together with rapid sideways movements (Hohmann and Fruth, 2000) (Fig. 3). Sex seems to be the cement for social bonds. This is why females use it predominantly for their alliance. Sex with high-ranking females could be strategic for subordinates, who can call loudly an audience to acknowledge the scene (Clay and Zuberbühler, 2012). Bonobos can have oral, manual and foot sex. They perform multiple positions not found in other non-human primates (such as ventro-ventral or missionary position in humans). Males can be observed mounting other males without intromission, dorso-dorsally rubbing their scrota with sideways movements, or performing face to face ersatz fencing with erect penises. Juveniles can also be involved (de Waal, 1997; personal observation). Bonobos seem to have no limits to the choice of sexual partners with the exception of incest.

9 Gardener of the forest

- 17 The ecological role of the bonobos has been recently studied at LuiKotale (Beaune *et al.*, in press; Beaune, 2012). Bonobos are efficient seed dispersers; they spend approx. 3.5 hrs/day swallowing the seeds of trees, lianas and herbs of more than 91 species and disperse them at very long distances (0-4.5km). In its entire lifespan, a bonobo should disperse almost 12 million seeds (or 9 tons; excluding seeds <2 mm such as *Ficus* spp). The great majority of the seeds passed through the gut is viable (34/35 tested species). Compared with seeds not passed through the gut, bonobos' seeds germinate faster and at a higher rate. Furthermore, seeds disseminated by endozoochory with bonobos are better able to escape seed predators, thank to dung beetles attracted by bonobos' faeces (Beaune *et al.*, 2012). For certain species such as the velvet tamarind, bonobos are germination activator (Beaune, 2012). In a Congo forest we estimate that 65% of the individual trees in the forest community are disseminated by bonobos. The great majority of the tree species does not recruit and self-replace without seed dispersal (18/19 plant species). Bonobos seem to be tree planters of the Congo forest.

Figure 3

Female-female genito-genital (GG) rubbing. David Beaune/MPI.
Frottements génito-génital (GG) entre femelles. David Beaune/MPI.

10 Threatened by extinction

18 Bonobos are limited to areas south of the Congo River. Their survival depends on the
 conservation policies and decisions of the one country where they live: the Democratic Republic
 of Congo. The species' range covers 500,000 km² of the Cuvette Centrale (Thompson *et al.*,
 2003). Deforestation in DRC occurs at an average rate of 311,000 ha/year (FAO, 2010) and in
 the past two decades, bonobos have suffered a 29% loss in their habitat (Junker *et al.*, 2012).
 However, human hunting and bush meat trafficking is the main cause of bonobo extinction
 (Hart *et al.*, 2008). Bonobo numbers are hard to estimate. They could number between 10,000
 and 50,000 but it is also possible that there are fewer than 10,000 (Thompson *et al.*, 2003).
 Bonobo populations are decreasing and the species is in danger of extinction (IUCN, 2012).

11 Conclusion. Myths... and realities

- 19 - Bonobos are our closest living relatives...No more than chimpanzees.
 20 - Bonobos do not use tools...They do. Sophisticated tools (such as chimpanzees') were not
 observed in wild populations but bonobos do use and built tools.
 21 - Girls' power is within bonobos...Not really. Females' alliance in this matriarchal society
 allows dominance towards males. But bonobos are rather co-dominant.
 22 - Bonobos are peaceful...Yes. Lethal aggression was never reported, although aggressions
 exist.
 23 - Bonobos are the primate sex-champion....No. Bonobos use sex for social issues in various
 ways and without taboos but no more often than chimpanzees in frequency.
 24 - Homosexuality is common in bonobos...Yes. Especially female-female.
 25 - Bonobos can disappear...Yes.

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Notes

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Résumés

Bonobos are our closest living relatives along with chimpanzees. They attract much attention from anthropologists who want to better understand our primate origins and more recently from the public because of their remarkable behavior and matriarchal social system. New published insights from recent years allow us to better know *Pan paniscus*. This review describes the most recent findings: bonobos, chimpanzees, and humans ought to be part of the same genus (*Homo* or *Pan*) according to our genetics. bonobos have impressive cognitive ability to communicate with lexigram and sign-language, solve problems and use tools. Females have high social status in the group due to female association and coalition. The society is not really characterized by female dominant but rather by co-dominance of associated females. They are not purely egalitarian but non-violent and tolerant. Neither lethal aggression nor infanticide were observed and are not expected. Sex has a pivotal role in this pacifist society, which lacks sexual restrictions with the one exception of incest. Bonobos are probably a key species in forest ecology through their seed dispersal mutualism with plants whose fruits they eat. We continue to discover fascinating biological facts about our cousins who are in danger of extinction. A few of these are described here.

Dernières nouvelles des bonobos: Les mythes et réalités de *Pan paniscus*

Les bonobos sont nos plus proches parents vivants avec les chimpanzés. Ils attirent beaucoup d'attention de la part des anthropologues qui cherchent à comprendre nos origines simiesques. Plus récemment, ils attirent l'attention du grand public en raison de leur comportement remarquable et de leur système social matriarcal singulier. Les médias et certaines aspirations philosophiques ont rapidement érigé les bonobos comme nos plus proches parents, vivant en société pacifique de végétariens féministes, et gouvernée par le sexe. Mais la barrière entre l'homme et l'animal était sauve pour beaucoup tant que ce lubrique primate ne manifestait aucune capacité à exécuter ce qui fait le propre de l'homme. Or les nouvelles découvertes publiées ces dernières années nous permettent d'en savoir plus sur *Pan paniscus*. Cette revue décrit les résultats les plus récents : Selon les généticiens, bonobos, chimpanzés et humains appartiennent au même genre (*Homo* ou *Pan*) avec plus de 98% de gènes communs et un ancêtre partagé il y a 5 à 6 millions d'années. Il est récemment prouvé que les bonobos possèdent les capacités cognitives pour communiquer mais sans pharynx (langage des signes, lexigramme). Les bonobos peuvent résoudre des problèmes complexes et utiliser des outils. En captivité certains bonobos taillent des pierres, allument du feu avec un briquet ou utilisent une pelle pour creuser. Les femelles ont le statut social le plus élevé du groupe grâce à l'association et à la coalition entre femelles. La société n'est pas vraiment femelles-dominantes, mais plutôt co-dominante. La société n'est pas purement égalitaire, mais non violente et tolérante. Ni les agressions mortelles ni l'infanticide n'ont été observés à ce jour en milieu naturel ou en captivité. Le sexe a un rôle primordial dans cette société pacifique. Il n'y a pas de restriction sexuelle excepté l'inceste. Les bonobos sont une espèce clef dans leur écosystème, grâce au service écologique fournit de dispersion de graines. De plus en plus de découvertes fascinantes naissent au sujet de nos cousins qui sont en danger d'extinction et pourraient disparaître d'ici quelques décennies.

Entrées d'index

Mots-clés : comportement sexuels, grands singes, Hominidé, homosexualité, matriarchale, Pan

Keywords : great apes, hominid, homosexuality, matriarchal, Pan, sexual behavior.

Thématique : Ethology