The Other Sister, Bonobos

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Kevin D Hunt
Indiana University Bloomington
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Chimpanzee

The chimpanzee is one of our planet's best-loved and most instantly recognizable animals. Splitting from the human lineage between four and six million years ago, it is (along with its cousin, the bonobo) our closest living relative, sharing around 99 percent of our genes. First encountered by Westerners in the seventeenth century, virtually nothing was known about chimpanzees in their natural environment until 1960, when Jane Goodall traveled to Gombe to live and work with them.

Accessibly written, yet fully referenced and uncompromising in its accuracy and comprehensiveness, this book encapsulates everything we currently know about chimpanzees: from their discovery and why we study them to their anatomy, physiology, genetics, and culture. The text is beautifully illustrated and infused with examples and anecdotes drawn from the author's 30 years of primate observation, making this a perfect resource for students of biological anthropology and primatology as well as non-specialists interested in chimpanzees.

Kevin D. Hunt is Professor of Anthropology and an affiliate of the Stone Age Institute at Indiana University, Bloomington. He is also Founder and Director of the Semliki Chimpanzee Project, which was established in 1996 to study and preserve the chimpanzees within the Toro-Semliki Wildlife Reserve. Broadly trained in various anthropological disciplines, much of Professor Hunt's published work has centered on functional morphology and what chimpanzee locomotion, posture, and ecology can tell us about what led humans to diverge from apes and what advantage bipedalism gave our chimpanzee-like ancestors roughly five million years ago. ago.

Chimpanzee

Lessons from our Sister Species

KEVIN D. HUNT
Indiana University, Bloomington

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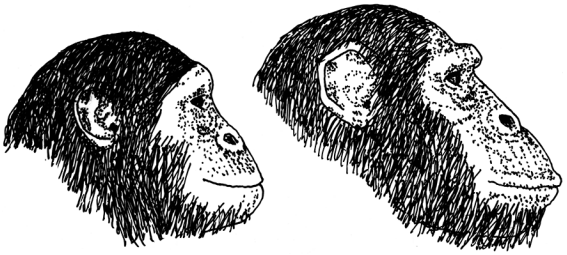
The Monkey Convergence Hypothesis



Drawn by author

The startling contrast between bonobo and chimpanzee societies comes into sharp focus in a story Nahoko Tokuyama tells of the intemperate eagerness of a quartet of young males and the rigid social control several females exercised to restrain them (Angier, 2016). It was in the evening, past the time bonobos normally have settled into their sleeping nests for the night. A female was in estrus, her flamboyantly swollen estrous swelling stimulating an unrestrained sexual excitement among four males, including the community's alpha male. Perhaps these males suspected they were skirting the edges of societal norms as they noisily leapt from branch to branch around the female, displaying erections and disturbing what should have been a time of quiet repose for the group. The males, however, were not interested in repose; the presence of this attractive female was simply too much for them to bear. Their overheated commotion went on and on, seemingly with no end in sight. At last, three high-ranking females had had enough. Exploding from beneath them, they attacked the four males, scattering them and then ignominiously banishing three of the four into the night, each yelping in retreat. The females surrounded the fourth, the alpha male, seized him, and, ignoring his screams of panic, bit him repeatedly – part of a toe was bitten off completely. As the attack wore on he was at last able to break free from the females and flee into the darkness. He failed to reappear the next day, and the day after that; then his absence extended for an entire week. In fact, he limped back into the group only three weeks later, short both a bit of dignity and a bit of a toe.

29.1 The Anti-Chimpanzee

Three females routing four males, males screaming for mercy in the face of female aggression, female social arbiters putting a tight lid on male social lives – this is behavior unimaginable for chimpanzees. And the females who exercised this dominance did so despite inferior numbers and body weights that measure only three-quarters those of males (Table 29.1), a significantly[1] lower proportion than found among chimpanzees; the combined weight of the three females would have been only about 100 kg, versus 180 kg for the four males.

While there is strength in numbers, it is not the number of the bonobos in the fight that counts, but strength of the bonds among the fighters, and the females have the stronger bonds in this ape sisterhood. Females share food (Yamamoto, 2015), travel together often (Surbeck et al., 2017), and even attend to one another during birth (Douglas, 2014). There are many other primates where female bonds impart political power, despite their lesser body weights, but in these societies the sisterhood is a more literal one; females are kin. Not so among bonobos (Furuichi, 2011; Surbeck & Hohmann, 2013). To one familiar only with chimpanzees, female dominance is a shock, but equally shocking is the complete absence of male cooperation; males seem to make no effort to band together to counter female alliances.

[1] For my fellow scientists, I mean this literally: at the $p = 0.008$ level, ($F\ [445, 525] = 10.18$, $p = 0.008$). Data and statistical analysis courtesy of William L Jungers.

Table 29.1 **Chimpanzee and bonobo body weights (kg)**

Species	Female (*n*)	Male (*n*)	Midsex mean	F/M percentage
Bonobo (*Pan paniscus*)[a]	33.7 (7)	45.0 (7)	39.4	74.9
Eastern chimpanzees (*Pan troglodytes schweinfurthii*)[b]	31.3 (26)	39.0 (31)	35.2	80.3
Chimpanzee (*Pan troglodytes*)[c]	40.4 (27)	49.6(33)	45.0	81.4

[a] Weights from Smith & Jungers, 1997; [b] Weights from Pusey et al., 2005; [c] Average of three subspecies, weights from Smith & Jungers, 1997.

The dominance of the sisterhood is readily apparent in the easy, relaxed moment-to-moment interactions of females who take the food they want (Parish, 1994), move through the group confidently, and socialize with all variety of age–sex classes; males cower on the sidelines, attentively watching females, hoping to avoid an upbraiding.

29.2 The Discovery of Bonobos

Bonobos (most often pronounced bah-NO-boe, though one sometimes hears BONN-uh-boe) are often seen as the underappreciated stepsister to chimpanzees. Frans de Waal and his coauthor Frans Lanting (1997) titled their bonobo book *The Forgotten Ape*. But bonobos are not forgotten so much as never completely discovered, despite heroic efforts on the part of ape researchers. Bonobos are confined to Congo, a war-ravaged country beset by political instability and violence, difficulties that have hampered research efforts – and such efforts are difficult enough even in stable countries. Consequently, there are many fewer bonobo than chimpanzee study sites, many fewer researchers, and a shallower time depth to what research projects there are. As this gap is filled, surely we will encounter any number of surprising discoveries.

Perhaps bonobo research was stunted from the start by the fact that for years we thought bonobos were merely a variety of chimpanzee. Henry Nissen (1931) had already published the first study of wild chimpanzee behavior, limited though it was, before we even knew there was such a thing as a bonobo (Coolidge, 1933). Even those intimately familiar with the two species, zookeepers, thought they were the same species until the 1930s. Too bad. The prospect of describing a completely new species – which we now know they are, of course – might have motivated explorers to confront the risk of working in this heart of Africa, a motivation that may have been weaker when bonobos were considered merely a variety of chimpanzee. They are even diminished by their name, "**pygmy chimpanzee**": little chimpanzees.

We now recognize their distinctiveness and their importance, though some specialists worry that we have not yet completely adjusted to the idea that chimpanzees and bonobos are very different animals (Figure 29.1). Their distinctiveness starts with their appearance. It would be difficult to improve on Frans de Waal and Frans Lanting's description:

> In physique, a bonobo is as different from a chimpanzee as a Concorde is from a Boeing 747. I do not wish to offend any chimpanzees, but bonobos have more style. The bonobo, with its long legs and small head atop narrow shoulders, has a more gracile build than does a chimpanzee. Bonobo lips are reddish in a black face, the ears small and the nostrils almost as wide as a gorilla's. These primates also have a flatter, more open face with a higher forehead than the chimpanzee's and – to top it all off – an attractive coiffure with long, fine, black hair neatly parted in the middle.

It is that delicacy of build that caused bonobos to be mislabeled "pygmy chimpanzees"; in fact, their body weight is only slightly less than that of chimpanzees, certainly not enough to merit the label "pygmy"; they actually weigh more than Gombe chimpanzees (Table

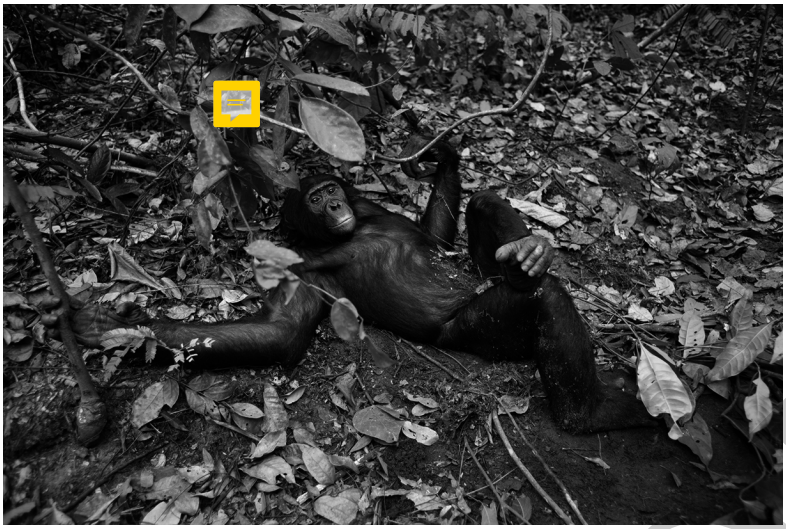


Figure 29.1 Bonobos have neatly parted hair, a more delicate face than chimpanzees, and red lips. Credit: Anup Shah / Stone / Getty Images.

29.1; Morbeck & Zihlman, 1989), which are smaller than other common chimpanzees.

29.3 Bonobo versus Chimpanzee

Despite the differences de Waal and Lanting point out, there are important similarities. Like chimpanzees, bonobos knucklewalk. They have long fingers, short thumbs, mobile shoulders, and powerful upper bodies. Both apes have sexual swellings and both have prodigious copulation rates when females are in estrus. Both bear pale complexions at birth that darken with age. They can interbreed (Vervaecke & Van Elsacker, 1992). Facial expressions, attentiveness, social focus, reactions to social events, body postures, and manual gestures are very similar in the two. In my experience watching Kanzi, only his high-pitched vocalizations (de Waal, 1988) were distinctly un-chimpanzee-like.

Both species hunt monkeys, bushbabies, birds, and small antelopes (Hohmann & Fruth, 2008; Surbeck et al., 2009), though bonobos hunt much less often. Both are intelligent, highly social primates that have strong mother–offspring bonds, a long period of infant dependency, and fission–fusion social systems. Their diets are similar, though not identical.

29.4 Sexual Dimorphism

Bonobos are thought to have low levels of sexual dimorphism, and this does appear to be the case for measurements of the skull (Furuichi, 1992; Schaefer et al., 2004), brain (Cramer, 1977), and teeth (Almquist, 1974; Fenart & Deblock, 1974; Johanson, 1974). Canines in particular differ little between the sexes, in striking contrast to chimpanzees, suggesting females engage in aggressive struggles as often as males. This is important.

But the head is only part of the body. The most authoritative data on bonobo body weights (Table 29.1) show that females are only three-quarters of the size of males, versus 80 percent for chimpanzees. An explanation for this difference is offered in the following.

29.5 Other Anatomical Differences

Bonobos have longer, more muscular hindlimbs, both legs and feet; their thorax is narrower and they are generally more delicately built. Their proximal phalanges (from the knuckle to the first joint of the finger) have faint or absent flexor sheath ridges and the rest of the finger bones are smaller (Susman,

Table 29.2 **Chimpanzee and bonobo arboreal locomotion (%)**

Locomotor mode	Chimpanzee[a]	Bonobo[b]	Bonobo[c]
Quadrupedal walking on level supports	26.1	35.3	32.0
Quadrupedal walking, climbing on sloped supports	63.5	50.4	69.0
Brachiation or other suspension	6.7	8.9	3.0
Bipedalism	3.0	1.5	3.0
Leaping	0.7	4.0	0.5

[a] Hunt, 1989, 1992; [b] Doran & Hunt, 1994; [c] Ramos, 2014.

1979). Their face is more delicate than that of chimpanzees, and their foramen magnum is placed farther forward, in a slightly more human-like position (Shea, 1984). Bonobos have slightly smaller brains (Rilling et al., 2012). The vagina is oriented in a more ventral position and following this anatomy copulation tends to be more often face to face.

29.6 Locomotion and posture

Much has been made of the fact that bonobos appear more at ease when standing and walking bipedally, but in fact studies of both zoo and wild populations have found no difference between the species (Table 29.2); if anything, chimpanzees are *more* bipedal (Doran & Hunt, 1994; Videan & McGrew, 2001).

Studies across the primates tell us that long hindlimbs, long feet, narrower bodies and lower body weights are found among leapers or runners, compared to climbers, so we might expect more leaping among bonobos. The particularly narrow scapula suggests high frequencies of armhanging. One of the two bonobo locomotor studies is perfectly consistent with expectations based on this anatomy (Table 29.2); Diane Doran found that bonobos at Lomako leapt and brachiated more than chimpanzees (Doran & Hunt, 1994). She had 1456 observations, fewer than we would like. The Lomako bonobos, though, were poorly habituated, and their shyness around humans meant she could only observe them in the trees, where they felt safe from the potentially dangerous observers; still, leaping and brachiation are arboreal behaviors, so this limitation would not bias her data. On the other hand, when primates are fearful, they are more likely to engage in risky behaviors while fleeing – behaviors like leaping and perhaps brachiation.

We were all looking forward to a study on fully habituated subjects that would include observations both on the ground and in the trees. My student Gil Ramos (Ramos, 2014) provided just such a study at Lui Kotale, Congo. His massive study included over 65,000 observations, nearly 50 times as many as Doran, which should have answered all our questions. Instead, his conclusions conflicted so much with expectations they could not help but be controversial. He found that bonobos engaged in less brachiation and less leaping than Doran had found – and even less than observed among chimpanzees (Table 29.2), quite in conflict with expectations based on their anatomy. Bonobos do have smaller flexor sheath ridges than chimpanzees, suggesting *less* suspensory behavior (Chapter 9). We are left wondering if our expectations about the anatomy related to leaping is wrong, whether the Lui Kotale chimpanzees were observed during a period when they were behaving atypically, whether Lui Kotale is an unusual habitat that requires less leaping and brachiation than "normal" bonobo environments, or whether some other unexpected variable has thrown a monkey wrench in our interpretations.

29.7 Greater Terrestriality?

In another surprise, Ramos found that bonobos also spent more time on the ground than do chimpanzees.

Given bonobo anatomy, it is tempting to suspect that Doran's observations, even though they were few and were on somewhat fearful primates, were better – except that we find support for Ramos' data from a completely unexpected quarter. Human semicircular canals resemble those of bonobos more than those of chimpanzees (El Khoury et al., 2014). These canals house an organ that helps to keep the head steady during locomotion. Demands for balance and stabilization are different when moving in trees than on the ground, suggesting that bonobos are more terrestrial than we thought. A narrow body plan is more efficient during terrestrial locomotion because it reduces moments around the joints of the stance phase limbs (if this seems baffling, see Chapter 9). There is a further confirming bit of data. A critical food for bonobos is **terrestrial herbaceous vegetation** (THV), pithy foods that are found only on the ground, and the lure of this terrestrial food may keep bonobos on the ground more than chimpanzees.

29.8 Female Bonds

We started out the chapter with a look at the confident authority females exert in bonobo society. Bonobo males fail to form close bonds, and groom one another less often than they groom females. Among bonobos, a male's closest social partner and most dependable ally is not another male, but his mother (Parish & de Waal, 2000; Hohmann & Fruth, 2002; Surbeck et al., 2011, 2017). The closest bonds among bonobos are among females, not males, yet females transfer groups at adulthood (Gerloff et al., 1999; Eriksson et al., 2006; Hashimoto & Furuichi, 2001; Hohmann & Fruth, 2002); among other primates, only females who are philopatric – who do not disperse – form close bonds. Evolution favors kin bonds. When two individuals join forces to secure a resource against competitors, kin are preferred as allies because the alliance benefits both actors, increasing the inclusive fitness of each (Wrangham, 1980). When food is defensible, females form alliances that yield a kin-based female-bonded society. Female bonobos flout this rule; they have close alliances but are not kin.

When a female enters a new group, rather than traveling with males for protection as do chimpanzee females, the new female seeks out an older, more established female to serve as an ally (Badrian & Badrian, 1984; Parish, 1996; Parish & de Waal, 2000; Hohmann & Fruth, 2002; Clay & Zuberbühler, 2012). These female–female bonds are forged in fire: The older female comes to the aid of the younger during conflicts (Tokuyama & Furuichi, 2016).

Even more unexpected than the female bonds is the mechanism through which females fortify their friendships – with sexual contact, or **genito-genital rubbing** – "**g-g rubbing**." They embrace face-to-face and rub their sexual swellings together in a sexual encounter that is little different from that of heterosexual copulation. While bonobo same-sex activity is often described as merely tension-relieving behavior, many observers maintain they see evidence of real sexual pleasure and some female–female bonds are said to resemble human love. The genitalia of bonobos differs from that of chimpanzees, perhaps having evolved to accommodate this copulatory preference; the clitoris and vaginal opening are more ventrally placed (more toward the front of the body), reflecting their tendency to engage in more face-to-face sex, whether homosexual or heterosexual (Dahl, 1985). Interestingly, face-to-face sex is more common among female–female partners than among male–female couples. The unusual genitalia of bonobos may have evolved to foster bonds among females! The female–female bond formed during the new female's early days in her new group seems to continue at least until the immigrating female has her first infant and is established in the community (Parish, 1996; Paoli et al., 2006).

Pair bonds can be powerful, perhaps even more so when they are sexual. Humans have discovered this type of homosexual bonding as a tool for social cohesiveness in war as well. Homosexuality among Greek warriors was thought to bond warriors together and encourage greater bravery in battle (Dover, 1978; Crompton, 2003; Hanson, 2009)

Sexual activity not only extends to all possible combinations of males and females, but to all age and sex combinations, whatever the rank, whatever the age, even down to infants (Kano, 1989).

It may be that not all females disperse; at Lui Kotale an approximately equal number of males and females disappeared from the study community, indirect evidence that some males transfer; two males transferred into the Lui Kotale community (Hohmann & Fruth, 2002). Reinforcing these observations is some genetic evidence for at least occasional male dispersal (Schubert et al., 2011). Independent of this observation, the importance of mother–son alliances suggests that when males disperse it will be more often orphans that transfer than males with living mothers. Given the advantages of kin-based bonding, I expect that we will find that some females who stay home refrain from dispersing in part due to the advantage of a powerful sister. We might expect to find some extremely close alliances among females that are not sexual. Of course, as sexually liberal as bonobos are, for all we know incest may not be taboo.

When a female is challenged, she need not rely only on a female friend for help – if she has a son who is old enough, he will help as well (Parish, 1996; Furuichi, 1997; Hohmann & Fruth, 2002). Grooming patterns reflect these relationships; while a female's most common grooming partner is her son, the next most common partner is another female, and male–male grooming is the least common combination (Idani, 1991; Kano, 1992; White, 1996, 1998; Hohmann & Fruth, 2002).

The reason for the greater female political power within bonobo society is now apparent: Males have as a consistent ally only their mother (Surbeck et al., 2011), whereas the mother has the help of her closest girlfriend, her son, and often other females as well. Surprisingly, a mother may even support her girlfriend over her son (Legrain et al., 2011).

Sons help mothers, but *vice versa* is true as well. Males who achieve high rank typically do so only if they have strong support from their mother; they need it, since there are no male coalitions among bonobos. Mother's help is so important that it can increase a son's mating opportunities, mostly by intervening during one-on-one male contests surrounding estrous females (Surbeck et al., 2011, 2019). Males with living mothers are three times more likely to sire offspring than are orphans (Surbeck et al., 2011, 2019).

As with chimpanzees, dominant males sire most infants (Gerloff et al., 1999), but keep in mind that mothers are active participants in a male's quest for dominance. It may even be that one motivation for older females in forming alliances with younger females is to increase the likelihood that the young females will mate with their sons – mothers as matchmakers. Mothers are so involved in their son's success that it may have even extended maternal lifespans. Among chimpanzees, only 41 percent of males have a living mother; it is 56 percent in bonobos (Surbeck et al., 2011).

29.9 Cohesive, Mixed-Sex Travel Parties

Perhaps the most significant difference in party composition between chimpanzees and bonobos is that bonobos form larger, more cohesive, mixed-sex parties that are less likely to dissolve into smaller groups (White, 1998). Bonobos are less fission–fusion than chimpanzees. This social cohesiveness is seen in captive studies that show that bonobos are more tolerant of one another, allowing them to engage in more cooperation (Hare et al., 2007).

29.10 Vocalizations

The sex role-reversal extends to party formation. Among chimpanzees, males loud-call, or pant-hoot, to tell fellow males of rich food sources so that they can gather to larger groups for protection or to allow patrolling. Among bonobos long-distance calls are much less frequent (de Waal, 1988; Mitani & Nishida, 1993; Hohmann & Fruth, 2002) and have a completely different function. Bonobo females loud-call mostly as a signal to female allies (White et al., 2015). Males loud-call in hopes of attracting mates (White et al., 2015). The relative insignificance of long-distance vocalizations is apparent in the smaller, less effective sound-gathering part of the ear among bonobos, the pinna or external ear.

Male chimpanzees know who is alpha, who is beta, and so on, and each individual must respect his betters – with a specialized vocalization

acknowledging subordinance, the pant-grunt. The pant-grunt is one of the most common vocalizations among chimpanzees, heard virtually every time there is a reunion among individuals. Bonobos have no pant-grunt nor any vocalization to perform the same function (Kano, 1992; Parish, 1996; Furuichi, 1997; Hohmann & Fruth 2002, 2003; Paoli et al., 2006).

29.11 Reproduction

While chimpanzee females have hit on a reproductive strategy that lessens the danger to their infants from males, some infants are still killed. Bonobo mothers have a better way: Their sisterhood gives them protection, and males are more thoroughly confused about paternity, compared to chimpanzees.

Among chimpanzees, ovulation is fairly predictable – as the swelling reaches maximal size and slows its expansion, ovulation is near. Females provoke competition among males by advertising ovulation, even as they confuse paternity by mating with all the males. Bonobo females disguise ovulation rather than advertise it (Reichert et al., 2002). Their estrous period is extended across nearly the entire month, with no cue to males that they are about to ovulate (Furuichi, 1992; Parish, 1996). While an aggressive male chimpanzee can prevent other males from copulating with a female near ovulation, this is less often accomplished among bonobos (Furuichi, 1997; Hohmann & Fruth, 2003). In one study even though the top male did manage to isolate the female during the entire period of maximal tumescence, he did not father her offspring (Marvan et al., 2006). Female bonobos have both thoroughly confused paternity and formed alliances that can prevent infanticide.

29.12 Territoriality: Group Defense

Male political ineffectiveness redounds to all corners of bonobo society. Because they fail to form alliances, males not only fail to form coalitions within their community, their lack of bonding means they cannot engage in intercommunity coalitionary violence, either. Absent this male–male cooperative violence (Wrangham, 1999), bonobos lack the signal characteristic of chimpanzee society, the rigid community territorial defense (Kano, 1992; Parish, 1996; Parish & de Waal, 2000; Surbeck & Hohmann, 2013; Table 29.3). As we learned earlier, chimpanzee males defend their community range – it is a territory – and they make war on neighboring communities as a tightly allied paramilitary unit. Bonobos are so much less territorial that males from different communities mingle and may nest near one another without conflict. Communities are peaceful to the extent that males and females of different communities can interact peacefully (Kano, 1992; Hohmann & Fruth, 2002; Furuichi, 2011), and females even copulate with males from other communities in full view of resident males (Idani, 1990, 1991; Furuichi, 2011; Hohmann & Fruth, 2002). If a male chimpanzee contemplated such a thing his head would explode.

Less-aggressive males and lack of territoriality means that murder is extremely uncommon among bonobos. After 40 years of study at four different bonobo communities, there is but one suspected within-species killing – *one* (Wilson et al., 2014) – whereas 50 years of study of 18 chimpanzee provides us with 152 killings (58 observed, 41 inferred, and 53 suspected).

Chimpanzee violence leaves its mark on their skeletons. Healed fractures and puncture wounds are common on chimpanzee crania, found at 5.5 percent in museum collections and a spine-chilling 28.6 percent for Gombe males. For bonobos it was only 1.4 percent of individuals (Jurmain, 1997).

Let us not go too far down this road of nonviolence, however. We began the chapter with a male losing part of a toe to violence. Both male and female bonobos engage in aggressive behavior, it is just less common and less dangerous compared to the (literally) bone crushing, genital-removing violence of chimpanzees.

29.13 Tool Use

In the wild, bonobos, compared to chimpanzees, utilize fewer tool types and use them less often

Table 29.3 Comparison of chimpanzees, bonobos and savanna baboons

General information	Chimpanzee	Bonobo	Olive Baboon
Distribution	Equatorial Africa	Congo	Panafrican
Cranial capacity	389 cm^3	350 cm^3	177 cm^3
Gestation length	230 days	240 days	182 days
		Societal structure	
Dispersal pattern	Female dispersal	Female dispersal	Male dispersal
Community society?	Yes	Yes	No
Fission–fusion	Yes	Less than *P.t.*	No/minimal
Territoriality	Yes	No/overlap	No
Intercommunity relations	Aggressive	Tense to peaceful	Tense to avoidance
Dominance	Males dominant	Females dominant in coalitions	Females sometimes dominant in coalitions
Single-sex male groups	Frequent	Rare	Rare
Male bonding	Primary	Very limited	Very limited
Male–male alliance	Frequent	Rare	Rare
Female–female association	Infrequent	Frequent	Constant
Female–female bonds/ alliances	Limited	Great	Greatest
Female kin bonds	Very limited	Very limited	Pervasive
Females bond to control food	No	Yes	Yes
Mixed-sex groupings	Common only w/ estrus	Unrelated to estrus	Unrelated to estrus
Heterosexual pair bonds	Occasional but weak	No	Present but weak
Mother–son association	Through adolescence	Throughout life	Lacking in adulthood
Party size	Small	Medium	Large
		Social behavior	
Short-range contact calls	No	Yes	Yes
Long distance calls	Yes	Less common	No
Submissive greeting	Pant-grunt	None	None
♂ on ♀ physical aggression	Yes	No	Occasional

Table 29.3 (*cont.*)

♀ on ♂ physical aggression	No	Yes	No
Infanticide	Yes	No	Yes
Intercommunity relations	**Murderous**	**Tense to peaceful**	**Tense to avoidance**
Male coalitionary murder	**Yes**	**No**	**No**
Reconciliation	**Common**	**More common**	**More common**
Grooming	**Mostly male–male**	**Mostly female–female**	**Mostly female–female**
Other behavior			
Vocalization pitch	Low	High	Low
Hunting	Mostly males	Mostly females	Rare, mostly male
Food sharing	Among males	Among females	None
Food control	Mostly males	Mostly females	Mixed or female
Physical features			
Cranial capacity	**Larger**	**Smaller**	**Smaller**
External ear size	**Large**	**Medium**	**Small**
Tool use	**Common**	**Less common**	**Less common**
	Sexual characteristics		
Promiscuous copulation	Within community	Within or between	Within
Extra-group copulation	Secret	Public	Probably secret
Sexual coercion	**Yes**	**No**	**No**
Testes size	Large	Large	Large
Concealed ovulation	No	Yes	No
Continuous receptivity	Some	Extensive	None
Genital swelling	At ovulation	Extended	At ovulation
Elaborate sexual repertoire	No	Yes	No
Sexual partners	Mostly heterosexual	All combinations	Heterosexual
Genital contact among females	No	Yes	No
Rump contact among males	No	Yes	No

Bold = bonobos being more monkey-like.
After Parish & de Waal (2000), with some updating

Table 29.4 **Bonobo diets (percentage of time feeding)**

Site	Fruit	Piths, stems, roots	Leaf	Invertebrates	Meat	Flowers	Bark, seeds other
Bonobo[a]	55	25	14	2	0	2	2
Chimpanzee[b]	65.8	9.9	12.1	5.5	0.8	2.9	3.1

[a] Conklin-Brittain et al., 2001; [b] Chapter 5.

(Ingmanson, 1996; McGrew et al., 2007; Furuichi et al., 2015); only one is used for feeding, the leaf sponge (Furuichi et al., 2015). This is puzzling because in captivity bonobos seem just as adept at tool use as chimpanzees, if not more so; they can make stone tools and use them to gain access to a food reward (Toth et al., 1993).

29.14 Ranging

We talked about the extraordinary spatial memory of chimpanzees; you might expect it would be the same in bonobos. Nope. Chimpanzees are superior (Rosati & Hare, 2012). This suggests that bonobos are more like monkeys, sweeping across their habitat, encountering foods as they hit upon them, whereas chimpanzees, particularly females, must memorize the location of important food resources to forage efficiently.

29.15 Diet

Like chimpanzees, bonobos prefer ripe to unripe fruit (Table 29.4; Badrian et al., 1981; Badrian & Malenky, 1984; White & Wrangham, 1988; White, 1989, 1998; Malenky & Stiles, 1991; Malenky & Wrangham, 1994; Malenky et al., 1994; Furuichi, 2009). Still, even though ripe fruit is important to bonobos, **they eat less fruit than chimpanzees**, substituting an abundant food item they rely on: **terrestrial herbaceous vegetation** (Table 29.4). Chimpanzee spend up to 19 percent of their time eating piths and herbs, but as a species the average is only 10 percent; it is 25 percent for bonobos. Bonobos eat duikers, rodents, birds, bushbabies, and in one case a mangabey (Hohmann & Fruth, 2003), but they eat meat rarely enough that it rounds to zero in Table 29.4. Among bonobos, females, more aggressive than males overall, are observed to lead hunting more often (Hohmann & Fruth, 2003), though trace element reports find no difference in meat consumption (Oelze et al., 2011).

29.16 Evolutionary History

The fact that females disperse among bonobos (Hohmann & Fruth, 2002; Eriksson et al., 2006) suggests that the common ancestor of bonobos and chimpanzees was chimpanzee-like. Perhaps when bonobo ancestors found themselves in an environment where alliances to secure food (more on this below) and protect infants was advantageous, evolution acted to coopt sexual bonding machinery to forge close female bonds.

29.17 Are Bonobos Infantilized?

In the 1980s Brian Shea noticed that many bonobo traits are "neotenized" versions of those of chimpanzees – they resemble infant or juvenile versions of chimpanzees. The more delicate face, more slender build, longer limbs, blacker fur, longer cheek hair, reduced frequency of balding, and even their squeaky vocalizations make them resemble immature chimpanzees (Shea, 1984; Jungers & Susman, 1984). Adult bonobos more often engage in play (Palagi, 2006; Hare et al., 2007, 2012) and are less aggressive, more like juvenile chimpanzees. The alternative, that each of these traits has been selected for and the

pattern is coincidentally infantilized-looking, seems quite unlikely, given the long list. While bonobo anatomy and behavior are suggested to be the result of retaining immature traits, this hypothesis does not consider why. I will suggest a new hypothesis for why below.

29.18 Are Bonobos Self-Domesticated?

Others have noted that bonobos differ from chimpanzees in the same way that domesticated animals differ from their wild counterparts. They have smaller faces (similar to the smaller snout of domesticated dogs versus wolves), smaller brains, and reduced tooth size (Wrangham & Pilbeam, 2001; Hare et al., 2012; see also McHenry & Corruccini, 1981). Domesticated animals are less fearful of humans – if they were not they would suffer from a plethora of stress-related diseases – they are also less aggressive (people prefer to mix with animals unlikely to maul them). As is the case with domesticated animals, bonobos seem to cope with crowded conditions well, and they more actively embrace social opportunities (McHenry & Corruccini, 1981; Aureli & de Waal, 1997; Trut et al., 2009; Hare et al., 2012; Wilkins et al., 2014). Dogs will run right up and greet you; wolves will stay back unless they want to eat you. Extended reproductive periods are common in domesticated animals – we usually want them to reproduce quickly – another feature of bonobos (Hare et al., 2012). Bonobos more often retain the white tail tuft into adulthood that chimpanzees lose on maturing (Kano, 1992).

The self-domestication hypothesis (SDH) subsumes the neoteny hypothesis. Many of the SDH traits, including tolerance of social crowding and reduced levels of aggression, are more prominent both among juveniles and also in domesticated animals, suggesting that infantilization is merely the path natural selection travels to reach self-domestication. Keep in mind, though, that not all agree that bonobos have greater social tolerance (Cronin et al., 2015).

Perhaps, SDH holds, larger and more stable parties reduced the benefit of male territoriality, reducing selection for male aggression, and selecting for infantilized behavior, which in turn drove some of the anatomical differences. To sum up, SDH (Wrangham & Pilbeam, 2001; Hare et al., 2012) is reconciled with the neoteny hypothesis in the assumption that selection for reduced aggression and other bonobo traits followed the path of least resistance to achieve greater social cohesiveness, a juvenilization.

29.19 A New Wrinkle: The Monkey Convergence Hypothesis

Thus, bonobos have traits of domesticated animals, which are in part infantilized traits said to be selected to reduce male–male aggression. Perhaps both of these hypotheses can be subsumed under a new hypothesis I propose here: The monkey convergence hypothesis (MCH). The SDH focuses more on withered bonds among males than the flip side, the strengthening of female bonds. The MCH is built on the consequences of females traveling together, rather than remaining in core areas. Female mobility and female bonding in turn eliminate the advantage of territoriality and male bonds.

The key to all this, as it is so often, is food.

Chimpanzees are ripe-fruit specialists, but ripe fruit is a notoriously variable food supply and often chimpanzees must fall back on grasses and terrestrial herbaceous vegetation (THV) when fruit fails. Among bonobos, there is a much greater focus on THV, in part because bonobos have much more edible THV in their habitat than do chimpanzees (Badrian & Malenky, 1984; White & Wrangham, 1988; Malenky & Stiles, 1991; Malenky & Wrangham, 1994; Malenky et al., 1994; Furuichi, 2009). THV is a consistent food supply (White, 1998) compared to fruit. Not only does the bonobo habitat offer more piths and herbs, there are no gorillas in the bonobo habitat taking a gorilla-sized share of THV, as they do elsewhere (Wrangham, 1993; Malenky & Wrangham, 1994).

The greater availability of THV in the bonobo habitat and a greater year-round food availability in general, due to less seasonality, allows bonobos to gather in larger parties (Furuichi, 2009); the parties are both larger and more consistent in number (Furuichi, 2011) – chimpanzees sometimes gather in

huge parties, but are mostly found in small ones. Bonobo parties are more often mixed-sex, with females remaining in the traveling group even when not in estrus (White, 1988, 1989, 1996, 1998; Chapman et al., 1994; Furuichi, 2009). Bonobos are, in other words, less fission–fusion than chimpanzees, and it is the fission–fusion nature of chimpanzee society that promotes violence by allowing imbalances of power. Less fission–fusion promotes female bonds.

Evolutionary pressures related to food acquisition are intense among females because females gestate, care for infants, and provide nutrition for that infant by nursing – all of which are nutrient-intense activities. As a consequence, when food is defensible and females can gather in groups, they tend to form bonds (Wrangham, 1980) to defend that food. Bonobo feeding sites typically can accommodate more than one female, so females ally themselves with other females (White & Wood, 2007). Larger party sizes and more frequent mixed-sex parties also place females in direct competition with males. Females are more attuned to food, so they are selected to fight harder for it; bonds allow food defense.

Typical monkeys are found in large, stable groups. Their tolerance of antifeedants, including both fiber and secondary compounds, allows them to experience their food supply as more evenly distributed compared to apes. They include not only ripe fruit in their diet, but flowers, leaves, or unripe fruit. The bonobo habitat contains abundant THV, which fills in the gaps between the more dispersed ripe fruit supply (Wrangham, 1986). Bonobos so effectively utilize THV that unlike chimpanzees, fruit availability has no influence on party size (Serckx et al., 2014).

Let me be clearer about why chimpanzee females have not gone down the same path. Chimpanzee food is too dispersed for females to travel together; two females must double the feeding sites they visit, doubling the distance they must travel. The cost of group travel is heavy, while the advantages of group life are minimal. Female feeding efficiency is highest when they are alone (Wrangham, 1979, 2000; Wrangham & Smuts, 1980). The consistent food supply in the bonobo habitat allows females to travel together, allowing them to bond to control access to food (Parish, 1994), much as do female monkeys (Wrangham, 1980).

Bonobos have many other monkey-like characteristics. They keep tabs on their compatriots' locations with contact calls (Bermejo & Omedes, 1999; Furuichi, 2009), a type of vocalization that is common among monkeys (e.g., baboons [Andrew, 1976; Owren et al., 1997; Rendall et al., 1999, 2000, 2004]). When walking among baboons one hears a chorus of grunts on all sides as group members monitor the location of their kith and kin. Such monitoring is found when maintaining group cohesion is important in the social system, as it is among many monkey species. Gorillas also rely on contact calls to maintain group cohesion (Fossey, 1972). Bonobos maintain group cohesion with a "travel" call that notifies party members that travel is imminent (Schamberg et al., 2016).

The difference in foraging strategies is reflected in cognition. Chimpanzees have evolved to know exactly where their resources are and to scour their habitat vacuuming up sugar. Chimpanzees seem to know where the resources are at all times (Wrangham, 1977), and their incredible skill at spatial tasks and spatial memorization (Chapter 18) reflects the strong selective pressure that has acted on their cognition to allow them to harvest dispersed foods efficiently. Bonobos lack the spatial competence of chimpanzees (Rosati & Hare, 2012).

The stationary distribution of chimpanzee females allows males to guarantee mating access to them by guarding a territory. Orangutan females are also stationary and orangutan males are territorial; there is greater similarity in the two systems than many appreciate. Because bonobo females are mobile; guarding a territory does not guarantee mating access. Instead, bonobo males follow females and mate opportunistically – like monkeys.

Not only is there less motivation to guard a territory among bonobos, larger, more stable party sizes eliminate imbalances of power that allow successful coalitionary violence (Wrangham, 1999). With little advantage to territoriality and little prospect of successful coalitionary violence, male bonds have little advantage.

Greater sexual dimorphism in bonobos than in chimpanzees reflects the one-on-one male contest competition in bonobos. One-on-one combat selects for larger body size (Table 29.3), much like we see among baboons or gorillas. A greater reproductive

skew among bonobos (Ishizuka et al., 2018) may well be due to a lesser need for bonobo males to defer to one another to maintain bonds; an alpha chimpanzee may have to tolerate a lower-ranking male hovering around an estrous female because chasing him off may disrupt a bond needed for territorial defense. Bonobos have no such need.

The self-domestication hypothesis sees smaller brains and less sexual dimorphism in weaponry and skull size (Figure 29.2) as somewhat unintended consequences of domestication. The monkey convergence hypothesis sees reduced brain size as a consequence of a lesser need for mind-reading and information exchange. Because there are fewer "off-stage" events among bonobos, due to a less fission–fusion society, less brain power is required (Hunt, 2016). While there is currently no evidence that domesticated animals are less intelligent than their wild counterparts, I am predicting we will find this to be the case, despite evidence that some skills are improved, e.g., interpretation of pointing (Hare et al., 2002). As we discussed in Chapters 18 and 19, monkeys have a socially cohesive system in which any two individuals have almost exactly the same social knowledge, because the group always travels together.

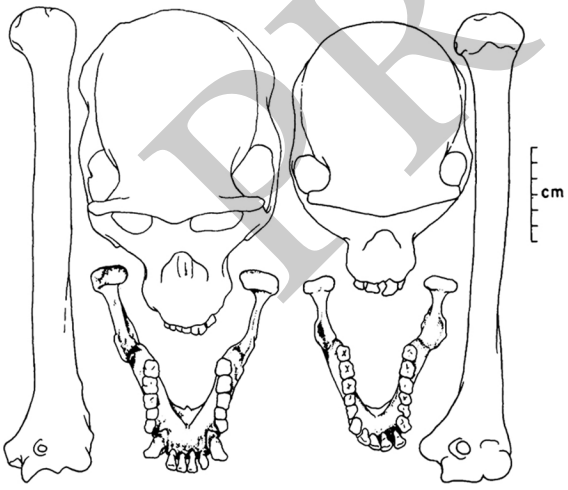


Figure 29.2 Chimpanzees (left) have more prognathic faces, larger brow ridges, larger brains, larger muscle attachment areas (notice the larger temporal fossa though which the temporalis muscle, a chewing muscle, passes), more robust jaws, and larger canines compared to bonobos (right). Image courtesy of Henry McHenry.

If not an eye witness to interactions that resulted in rank changes or alliance changes, they were almost certainly auditors – fighting baboons are noisy. Chimpanzees, on the other hand, each have different social knowledge due to the constant shuffling among parties – and "mind-reading" is therefore advantageous.

Because male bonobos need not go easy on one another, as chimpanzee males must (Chapter 26), we should expect a bigger disparity in wounding aggression between male–male and female–female interactions. I know of no report that suggests that male–male contest competition is more intense among bonobos, but let us hope someone examines it. The SDH predicts less wounding among males, while the MCH expects more because there is less need for deference and bonding. While I am willing to accept a few unexpected observations in melding the SDH and MCH, it would be very interesting to have data that directly compares male–male aggression levels in bonobos, chimpanzees, and a representative Old World monkey; this is an important area for future research.

29.20 Conclusions and Future Research

Perhaps bonobo specialists already have data to test some aspects of the MCH. In review, among bonobos we might expect to find a lower rate of female transfer than in chimpanzees, accompanied by alliances among sisters; there is some evidence of this, because males more often have both their mother *and* their grandmother in the group of residence (Schubert et al., 2013). The MCH expects that male bonobos will have more one-on-one aggressive interactions with higher rates of wounding compared to chimpanzees, whereas the SDH predicts the opposite. More detailed study of sex differences in vocalizations would be valuable; the MCH expects that females more often, rather than males, should engage in ally-drawing long-distance vocalizations, but a lower level of long-distance communication because groups separate less. We expect higher rates of male transfer among bonobos; there is indirect evidence this is so (Hohmann & Fruth, 2002). Many monkeys display allomothering – with tighter female bonds, this aunting behavior should be more common among bonobos than chimpanzees.

Monkeys have cheek pouches that, in part, allow them to keep up with the rest of the group by doing their chewing later, when everyone has stopped. We might expect more wadging among bonobos than is seen among chimpanzees. I am certain my monkey-studying colleagues will come up with many more testable predictions.

29.21 Lessons

It is tempting to generalize a behavior we see in any one primate species to all primates, but bonobos and chimpanzees show us that there can be dramatic differences even in closely related species. In particular, some might look to chimpanzees to find some justification for male patriarchy and male social dominance. You have already noticed, I am sure, that our equally closely related relative the bonobo shows that nature can go in exactly the opposite direction, even when females are smaller than males.

Let us remember, however, that female power is not equal to peace. In chimpanzee-land, males bully other males and all females; if only the females could bond together, it is tempting to think, all would be peace. Not so. While bonobos teach us that banding together can stymie male bullies, strong female alliances are not necessarily all sweetness and light. It is cold comfort to a bonobo male who lives in fear of an oppressive gang to know that it is a female group rather than a single bully that is oppressing him. If we are searching for a utopia, it would be a society the reverse of chimpanzee society, but one where neither male nor female gangs oppress a minority.

Humans may have found the solution. Or at least, they do a better job of ameliorating gang violence than apes. Among hunter-gatherers, when one individual becomes too violent and too oppressive – a condition that prevails in many such societies, since there is no organized policing body – subordinates band together to put him in his place, and sometimes that place is a grave (Boehm, 2009). While legal bureaucracies and policing have failed to completely stamp out physical violence in industrialized societies, there has been some progress. Preliminary data suggest murder is hundreds of times less common in industrialized versus hunter-gatherer societies (Wrangham et al., 2006).

Sadly, as we have advanced on one front to institutionally prohibit and punish murder, we have lost ground on another; in our large, fluid, impersonal, hierarchical society we have not found a foolproof way to reign in oppressors. Too often crime syndicates find a way to compromise institutional checks. Perhaps here is a case where we can take a lesson from ourselves, rather than apes. At various times in human history an enlightened band of right-thinkers has realized that when oppressors threaten them with absolute despotism, it is their right and indeed it is their duty to throw off such oppression and band together to provide new guarantees of freedom from tyranny. Chimpanzees have never done that. Yet.

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