


Warlike chimpanzees and peacemaking bonobos

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The evolution of our tendencies for warfare and peacemaking is of urgent interest. Between-group competition over resources is often invoked to explain out-group hostility and in-group cooperation and altruism (1). But humans also show strong propensities for between-group tolerance and large-scale cooperation. To explore the evolutionary basis for variation in violence and peacemaking, evolutionary anthropologists turn to consideration of the behavior of our closest living relatives, chimpanzees and bonobos (Fig. 1). They seek both to infer the behavior of the last common ancestor (LCA) with humans to identify homologous behaviors and to identify divergent or convergent behaviors that evolved in each lineage after the LCA (2). Chimpanzees live in permanent social groups (often called communities), in which individuals, mostly males, cooperatively defend a group territory. Between-group interactions are routinely hostile and sometimes lethal (3). In contrast, bonobos live in apparently similar groups, but, although between-group interactions are sometimes hostile (4), they can be tolerant, with adjacent groups associating peacefully for hours or even days (5). Because bonobos have been studied less thoroughly than chimpanzees, the question has arisen of whether these peaceful interactions are indeed between separate groups, or whether the groups are actually subsections of a larger group. In PNAS, Samuni et al. (6) address this question by comparing the associations of several adjacent groups of bonobos with those between subgroups within a single large chimpanzee community.

Chimpanzees live across the equatorial belt of Africa north of the Congo River, in habitats ranging from equatorial rain forest to seasonal savanna. Bonobos live only south of the Congo River in the Democratic Republic of Congo, in mostly forested habitats. Genetic evidence places their divergence from chimpanzees close to 2 million years ago when a population is thought to have crossed the Congo River during an unusually dry period (7, 8). Limited more recent admixture has been detected, but, in general, the Congo River appears to have acted as an effective barrier between the species. The LCA of humans and chimpanzees is dated around 8 million years ago (2). Although humans are equally related to chimpanzees and bonobos, a prevailing but not universal view is that the LCA was more like chimpanzees than bonobos and that many features of bonobos are derived. Under this scenario, features shared

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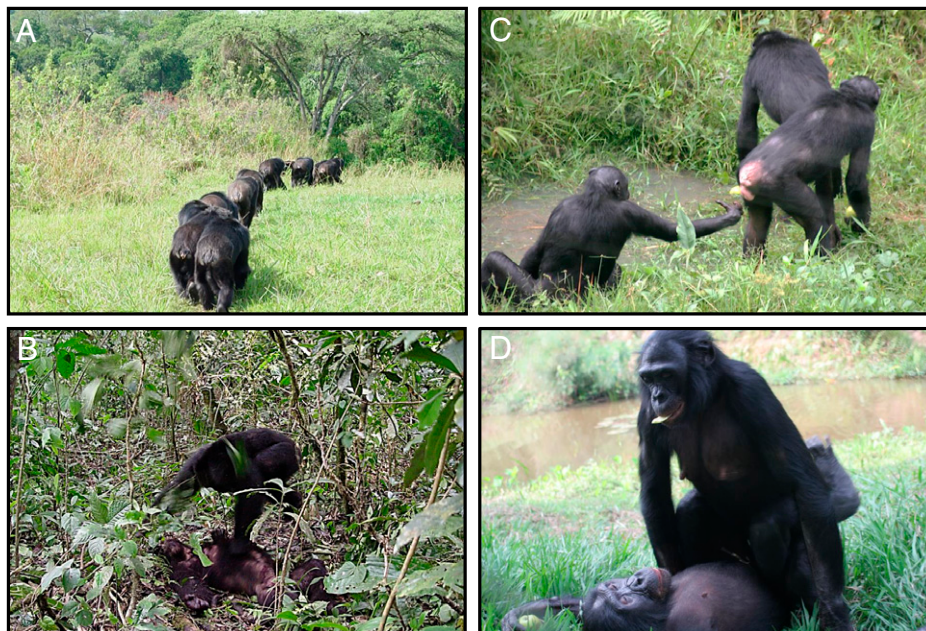


Fig. 1. Chimpanzees are territorial and aggressive to neighbors whereas bonobos sometimes interact peacefully and even have sex with neighbors. (A) Chimpanzees patrolling their territory at Ngogo. Image credit: John Mitani, University of Michigan, Ann Arbor, MI. (B) A male chimpanzee jumping on the body of a neighbor they have just killed. Image credit: John Mitani. (C) Bonobos interacting peacefully. Image credit: Vanessa Woods, Duke University, Durham, NC. (D) Bonobos mating. Image credit: Vanessa Woods.

by humans with bonobos but not chimpanzees would have evolved convergently after the split, rather than being present in the LCA (2).

The first long-term study of wild chimpanzees began in 1960 with Jane Goodall (9). Working in Gombe, Tanzania, Goodall identified and habituated a local population of about 60 chimpanzees, including multiple males, females, and their infants. For the first 10 y, she observed these individuals associate peacefully in various combinations, forming temporary groups of different sizes and compositions that fused and split over the day in a pattern called fission–fusion. In the early 1970s, this population split into two subgroups whose interactions became increasingly hostile until males from one group killed males and a female of the other group, leading to the group’s annihilation. Subsequently, the surviving group defended its territory from neighboring unhabituated groups, during which males conducted border patrols. Starting work south of Gombe soon after Goodall, Japanese scientists realized more quickly that chimpanzees were living in large but separate groups with hostile relations (10). In the 1970s to 1990s and beyond, other long-term sites have been established (10). From all sites large enough to contain more than one group, chimpanzees have been found to live in similar permanent groups, with fission–fusion grouping patterns, in which males are more social than females and remain in their natal groups, aggressively defending the group range, while most females transfer to other groups. Territorial behavior and lethal aggression can lead to expansion of the territory at the expense of neighbors (11), and increased territory size provides more food and hastens female reproduction (12, 13). Hence, groups of chimpanzees appear to compete aggressively for feeding grounds.

Field studies of bonobos began in the 1970s. They are harder to maintain, owing to the remoteness of the sites and political instability. The most continuous study was established at Wamba by Japanese scientists in 1973 but was halted for several years by civil war, during which several of the groups disappeared (5). A second study at LuiKotale was initiated in 2002, with two groups habituated and a third underway (4). At a third site, Lomako, one and sometimes two groups were studied in the 1970s to 1990s, and studies resumed in 2005 (14). The population reported on by Samuni et al. (6) resides close to the Wamba site at Kokolopori, where habituation of the bonobos started in 2007 and scientific study began in 2016. The site currently contains four habituated groups.

At all these sites, bonobos resemble chimpanzees in living in multimale, multifemale groups that exhibit fission–fusion grouping, and in which males are philopatric while females disperse. They differ from chimpanzees in having weaker male–male and stronger female–female and male–female associations. Unlike chimpanzees, where all adult males dominate all females, female bonobos can dominate males, especially in alliances, and exclude them from feeding sites (7). Most salient for this discussion is the apparent lack of male patrolling and territorial behavior. While groups sometimes avoid each other or interact aggressively (4), groups may also remain together for hours

or days after the initial meeting, amounting to 30% of observation time in some cases, during which members from different groups may groom, interact sexually, and even share food. Such tolerant interactions have been described at all sites but appear to be more common in Wamba and Kokolopori, and also vary considerably in frequency between different groups at the same site (5–7).

Given the shorter study lengths and less complete knowledge of the history of bonobo groups, one possibility is that the peacefully interacting groups are, in fact, all members of a larger permanent group. In eastern chimpanzees, neighborhoods of individuals that share a subsection of the group range and interact more within than between neighborhoods have been described (15). Neighborhoods were particularly evident for many years in the exceptionally large Ngogo community of Kibale National Park, Uganda, observed since 1995, where females and most males resided in distinct neighborhoods but the males of the whole group still cooperated to defend the community range. In 2015, after increasing separation, one neighborhood split permanently from the others, and, from then on, the resulting two groups occupied distinct territories and had hostile and sometimes lethal interactions (16).

Samuni et al. and others draw parallels between the tolerant relations between bonobos groups and those between human groups and propose that bonobos represent a valuable model for the evolution of human tolerance.

To test whether bonobo groups are homologous to chimpanzee neighborhoods or whether they are, in fact, discrete groups, equivalent to chimpanzee communities but more tolerant, Samuni et al. (6) compare the associations among the individuals of four bonobo groups at Kokolopori with the neighborhoods of the Ngogo chimpanzee community, 2 y to 4 y before it fissioned. They calculate dyadic association indices between all members of each population and use a variety of clustering techniques to identify clusters and examine their robustness. They find that all methods consistently find that the bonobos exhibited the same four distinct clusters, equivalent to the four groups, while the number of clusters and their robustness among the Ngogo chimpanzees are less consistent, and varied depending on the method. Delving deeper into the association patterns of the bonobos, they find that dyadic associations are consistently much higher within than between clusters, that the home ranges of individuals within clusters are more similar, and that, following fission of the mixed groups into smaller subgroups, individuals always remain in association with members of their own rather than the other cluster. Finally, they find that individuals of the same cluster stay closer together when they are in association with another cluster. From their results, they conclude that bonobo groups, despite prolonged associations between some of them, are distinct groups homologous to chimpanzee communities.

Samuni et al. (6) and others (17) draw parallels between the tolerant relations between bonobo groups and those between human groups and propose that bonobos represent

a valuable model for the evolution of human tolerance. Among human groups, between-group tolerance can lead to clear benefits such as exchange of information and ecological buffering whereby adjacent groups reciprocally tolerate each other's use of resources currently unobtainable in their own range. Whether bonobos derive these or any other positive benefits from between-group association is an active topic of study but yet to be determined.

If we accept the view that the LCA was chimpanzee-like, we must first explain the selective pressures that led to the evolution of more peaceful relations among bonobo groups and then assess the influence of similar pressures during human evolution. Attention has long focused on the possibility that differences in chimpanzee and bonobo sociality have been driven by ecological differences. One hypothesis holds that differences in food availability and distribution in bonobo habitats enabled more-stable female associations, such that they could effectively ally against males, thus reducing the benefits to males of aggressive dispositions (8). Proposed ecological differences include a generally greater abundance of food in bonobo habitats, greater abundance of and reliance on terrestrial herbaceous vegetation for bonobos owing to the absence of gorillas in their habitat, less seasonal change in fruit availability, and differences in fruit patch size allowing more individuals to feed together (14). In support of the importance of food

type and distribution, a recent study of human avatars behaving in virtual ape worlds with different features resulted in the predicted chimpanzee-like or bonobo-like behavior (18). However, real measurements of the ecology of complex tropical forests necessary to identify ecological differences are inherently difficult. So far, the evidence in support of any of these habitat differences is mixed (5). A related angle that merits greater investigation is an increasingly apparent species difference in group range size and density. Bonobos seem to live at considerably lower densities than chimpanzees (3), in possibly smaller groups, in relatively larger home ranges with higher overlap (5, 6). Such conditions reduce the economic defensibility of the home range (19) such that defusing aggression with affiliative behavior rather than fighting when groups meet may be the more economic option.

The multiple ongoing studies of chimpanzees and bonobos living in different habitats are engendering more-thorough comparative studies to test socioecological hypotheses. Despite the challenges they face in procuring continuous funding and the discomforts and dangers of working in remote areas, long-term research studies maintained by dedicated teams of researchers not only continue to provide insights into our own evolution but play a major role in conserving our fascinating but grievously endangered relatives.

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