PROGRESS

A century of getting to know the chimpanzee

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A century of research on chimpanzees, both in their natural habitat and in captivity, has brought these apes socially, emotionally and mentally much closer to us. Parallels and homologues between chimpanzee and human behaviour range from tool-technology and cultural learning to power politics and intercommunity warfare. Few behavioural domains have remained untouched by this increased knowledge, which has dramatically challenged the way we view ourselves. The sequencing of the chimpanzee genome will no doubt bring more surprises and insights. Humans do occupy a special place among the primates, but this place increasingly has to be defined against a backdrop of substantial similarity.

As long ago as Plato's failed attempt to define Man as the only creature at once featherless and walking on two legs (in response to which Diogenes arrived in the lecture hall with a plucked chicken), humanity has been hard-pressed to find ultimate proof of its uniqueness. The manufacture of tools, for example, was once regarded as so special that a book appeared under the title *Man the Tool-Maker*[1]. This definition held until wild chimpanzees (*Pan troglodytes*) were discovered modifying twigs to make them suitable for termite fishing. Another claim of human uniqueness concerned language, initially defined as symbolic communication. As soon as linguists heard about apes that had learned American Sign Language, however, they replaced the symbol requirement with their current emphasis on syntax. Humanity's special place in the cosmos is one of abandoned claims and moving goalposts.

The more we learn about apes, the more they seem as similar to us as their genetic material implies. Study of their behaviour began early last century with a handful of laboratory scientists. Wolfgang Köhler described how chimpanzees faced with an out-of-reach banana in the presence of boxes and sticks would sit around until the solution suddenly struck them: a flash of insight still referred to by insiders as a 'Köhler-moment'[2]. Robert Yerkes documented the temperament of apes, and conducted pioneering experiments on cognition and cooperation[3]. Nadezhda Ladygina-Kohts followed in Charles Darwin's footsteps by offering a point-by-point comparison of the emotional expressions of a young chimpanzee and a human child[4] (Fig. 1).

In those days, work in the natural habitat was frowned upon as unscientific: only laboratory approaches provided the controls required for conclusive science. Tension between these approaches persists today, even though the history of chimpanzee research is a showcase for the power of cross-fertilization between laboratory and field. The next series of insights came from attempts to study wild chimpanzees. At first, these attempts consisted of brief excursions, such as Henry Nissen's three-month stay in Guinea in the 1930s for the purpose of documenting chimpanzee feeding habits[5]. It was only in the 1960s that two pioneering long-term projects were initiated, and these were to inspire many more. On the Eastern shore of Lake Tanganyika in Tanzania, Jane Goodall set up camp in the Gombe Stream Reserve, and Toshisada Nishida did the same 170 km to the south, in the Mahale Mountains.

Studies in the field shattered the image of chimpanzees as peaceful vegetarians and began to reveal their astonishing social complexity. Meat consumption had been considered uniquely human among the primates, but chimpanzees were observed to catch colobus monkeys (*Colobus badius*), tear them apart and eat them alive[6]. Although the initial impression of chimpanzees had been that they lack social bonds (except for the tie between mothers and dependent offspring), it was discovered that all individuals in a particular stretch of forest meet regularly. However, interactions with individuals in neighbouring areas, if they occur at all, tend to be negative[7]. Field workers began to speak of 'communities' in order to avoid the term 'group', as

Figure 1 | One of the first cognitive primatologists: Nadia Kohts. From 1913–1916, Nadezhda Ladygina-Kohts (also known as Nadia Kohts) raised a young chimpanzee, Joni, in her Moscow home[4]. She conducted tool, mirror, art and discrimination tasks, in the process inventing the still-popular matching-to-sample paradigm. Kohts reported a wide range of emotional responses in Joni, from jealousy and guilt to empathy and fierce loyalty to loved ones. She described Joni's facial expressions in muscle-by-muscle detail. Even though her cognitive and socio-emotional approach was far ahead of its time, Kohts is less well-known than some of her contemporaries, perhaps because of her gender and publication in Russian. Photograph taken by A. F. Kohts in 1914, and reproduced with permission from the State Darwin Museum in Moscow, Russia.

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Figure 2 | Chimpanzees invite reconciliation by means of eye contact and hand gestures[19]. This scene occurred ten minutes after a protracted, noisy conflict between two adult males at a zoo. The challenged male (left) fled into the tree. He is now being approached by his opponent, who offers him an open hand. Within seconds, the two males had a physical reunion, kissed and embraced, then climbed to the ground to groom each other. Such peacemaking serves to maintain valuable relationships despite occasional conflict. Photograph by F. B. M. de Waal.

chimpanzees are rarely seen in large aggregations—they split up in ever-changing small 'parties' that travel through the forest, a system known as fission–fusion. Another claim of human uniqueness was abandoned when it was discovered that we are not the only primates to kill our own kind. Reports of lethal fighting between chimpanzee communities over territory[8] profoundly affected the post-war debate about the origins of human aggression.

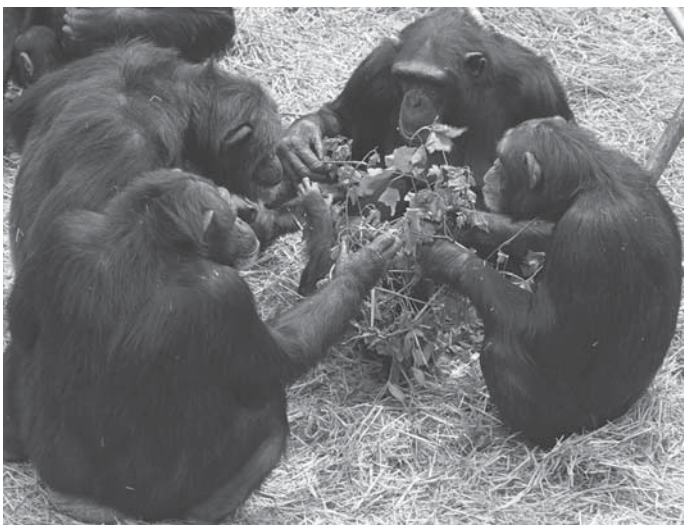
A second wave of influential chimpanzee studies in captivity in the 1970s placed them cognitively closer to humans than anyone had imagined. Gordon Gallup showed that apes recognize themselves in a mirror, indicating a level of self-awareness that sets humans and apes apart from all other primates[9]. Emil Menzel conducted experiments in which an ape that knew where an item was hidden was released together with fellow apes that lacked such knowledge, and recorded how they learned from or outwitted one another[10]. This work set the stage for the 'guesser' versus 'knower' paradigm of modern inter-subjectivity research on apes and children[11]. At about the same time, one of the world's largest colonies of outdoor-living chimpanzees was established at the Arnhem Zoo in the Netherlands, where I documented machiavellian power politics and conflict resolution capacities[12].

Since then, field studies have continued to work on elucidating chimpanzee social organization[13]. Instead of considering the behaviour of this species a unitary phenomenon, there is increasing focus on behavioural and 'cultural' diversity from site to site[14]. This focus must be complemented by attention to genetic diversity, which will no doubt be stimulated by publication of the chimpanzee genome. Below, I will highlight three further areas of interest in chimpanzee behaviour: (1) aggression and conflict resolution, (2) reproductive strategies and (3) cooperation.

War and peace

Chimpanzee aggressive behaviour is quite different within and between groups. As with humans, intergroup aggression knows few inhibitions. A small group of chimpanzee males may stealthily enter a neighbouring territory to overwhelm a single enemy male that they viciously beat, bite and leave to die[15,16]. Such attacks have actually been witnessed at a few field sites, whereas at other sites they have been strongly indicated. Initially, skeptics attributed chimpanzee 'warfare' to competition over the food that researchers provided in order to draw the apes out of the forest, but we now also have observations from unprovisioned sites.

Even though intragroup aggression occasionally turns deadly[17,18], it is far more constrained than intergroup aggression, owing to the adaptive value of group life. Intragroup tensions are actively coped with. After an open conflict, it is not uncommon for combatants to reunite with a kiss and embrace (Fig. 2). Known as reconciliation, this mechanism was discovered in captive chimpanzees[19], has since been confirmed in the wild[20], and is in fact widespread in the primate



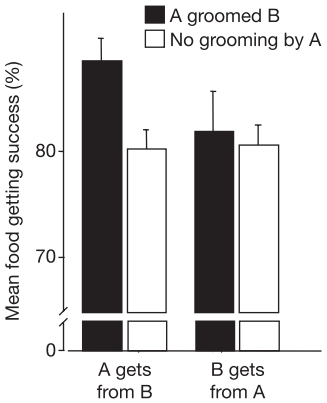


Figure 3 | Chimpanzees are known to reciprocally exchange favours. a, A cluster of chimpanzees gathers around branches with leaves provided in an experiment on reciprocity. The apes overcome their competitive tendencies and share the food. Photograph by F. B. M. de Waal. **b**, Mean (+s.e.m.) success at getting food per dyadic direction between adult chimpanzees during food trials. Two conditions are distinguished: either individual A groomed B in the hours before branches with leaves were provided, or no previous grooming of B by A occurred. The left-hand side of the graph shows the percentage of approaches by A to B that result in sharing by B (A gets from B); the right-hand side shows the same measure for B in obtaining food from A (B gets from A). A's success in obtaining food from B was significantly higher after A had groomed B, whereas B's success in obtaining food from A was unaffected by A's previous grooming, strongly suggesting exchange of food for grooming[32].

order and beyond[21]. The best-supported theory is that reconciliation serves to preserve valuable relationships despite the undermining effects of occasional conflict. Male chimpanzees are the more aggressive sex, but they are also the more conciliatory, which makes sense given that males stand more to lose if relationships deteriorate. They are together more often than females, and cooperate in hunting, intragroup politics and intergroup territoriality.

The deadliest form of intragroup aggression is aimed at young infants. Male infanticide is evolutionarily explained as the elimination of offspring sired by rivals, resulting in a shortened waiting time until a female's next ovulation[22]. This explanation proves problematic in relation to chimpanzees, however, as males sometimes kill infants they may well have fathered themselves[23,24]. Infanticide by females is much rarer, and is thought to relate to food competition between females and their dependent offspring[25].

Sexual competition

Although humans have nuclear families, bonobos (*Pan paniscus*) and chimpanzees have none—our closest relatives are thoroughly promiscuous. Chimpanzee females mate with many different males, and bonobos have an even wider-ranging sex life, with frequent same-sex partners[26]. Males are hardly involved in care for the young, and in fact often pose a threat (see above). It is thought that females mate with so many males partly to confuse the issue of paternity, thus countering male infanticide by making it hard for any male to exempt his own offspring[22].

This promiscuous mating system explains the intense sexual rivalry among males as well as the size of their testes. Corrected for body size, chimpanzee testes are about 10 times larger than those of our own species[27]. As females have multiple sex partners, sperm competition is likely: the higher the number of sperm cells per ejaculate, the better a male's chance of fertilization. No hominoid (that is, the primate family that includes humans and apes) apart from humans combines relatively small testes and minor sexual dimorphism. This suggests that human evolution has placed strong curbs on sexual competition, which may have been achieved by making mate choice less open-ended. Pair-bonding associated with male parental care probably traces as far back as *Australopithecus*[28].

The analysis of DNA from hair samples or fecal droppings is having a profound effect on our understanding of chimpanzee social structure. Genetic evidence can be used to determine whether male chimpanzees, which stay life-long in their natal community, are more closely related to each other than females, which tend to leave and join a neighbouring community around puberty. DNA data can also be used to determine paternity, so as to better understand what mating strategies actually lead to conception. Apart from confirming that the overwhelming majority of offspring are produced by intragroup fertilizations, thus explaining the observed male rivalry, it is too early to tell what these studies will reveal about chimpanzee social organization[29,30].

Quid pro quo

Chimpanzee society combines high levels of competition and cooperation. Cooperation is typical among kin (for example, mother and offspring) and among adult males, regardless of kinship. In pursuit of high status, young adult males operate mainly on the basis of fighting ability, but often cannot succeed without the support of older males. Like elder statesmen, post-prime males exert influence as alliance partners, without a chance of assuming top status themselves[12,31].

Political coalitions were recognized early on as part of an elaborate 'marketplace of services' in which chimpanzees trade grooming, sex, food and support[12]. The rules of reciprocity governing social exchange are only beginning to be understood, but evidence is accumulating that chimpanzees repay both positive acts (for example, sharing food preferentially with previous grooming partners[32]; see Fig. 3) and negative acts (for example, squaring accounts with those who previously opposed them)[33]. These tendencies are known in humans as 'gratitude' and 'retribution', respectively.

Perhaps the highest levels of cooperation and reciprocity have been observed during hunting. The chimpanzee diet includes substantial amounts of vertebrate meat[34]. The hunt of colobus monkeys in some locations is so difficult that hunting skills take years to develop, and pursuing males are said to adopt a role division (that is, adopting roles of driver, blocker and ambusher). As in humans, the oldest males tend to take on the most difficult hunting tasks[35]. The division of meat is a process of begging and sharing in which power, sex, and *quid pro quo* seem to meet in ways that are not yet fully understood. In one wild community, an alpha male with a tenure of more than a decade was described as having a 'bribery' system: he selectively shared prized meat with those that supported him or those from which support proved useful in the future[36]. To unravel these and other complexities is a daunting task for the relatively small number of devoted scientists who continue to work on chimpanzee behaviour in both captivity and the wild.

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