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Frans de Waal – A pioneer who shone a light on the primate mind

Zanna Clay

Department of Psychology, Durham University, South Road, Durham DH1 3LE, UK

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Biology has just lost one of its greatest thinkers. An intellectual pioneer and exceptional observer of animals, de Waal inspired us all to think differently about animals as well as ourselves - his far-reaching impact within and beyond biology and psychology cannot be overstated. He was especially known for his ground-breaking work investigating the social minds of our two closest great ape cousins, the chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*), well as other primates. He leaves behind him a rich and varied legacy of research that continues to inspire and push the field forward.

Following the footsteps of the Dutch founding fathers of ethology, de Waal's work emphasised the principle of evolutionary continuity, whereby closely related species are expected to show similar evolved traits. Given their close phylogenetic relationship, de Waal sought to identify potential commonalities between humans and other primates, and breaking taboos of the time, was prepared to use the same terminologies for traits observed in both. Through his many scientific articles and popular books, de Waal showed us that primates - and other animals - have sophisticated social intelligence and a rich emotional life: they show empathy, cooperate, have sex for fun, reconcile after conflicts, have rich forms of communication, learn socially, engage in reciprocal social interactions, and may even have a sense of fairness. Decades of behaviourism had left most other scientists at the time reticent to attribute human-like traits to other animals. It is thanks to de Waal's careful observations and intellectual bravery that the continuity between humans and other primates has since come to be accepted into mainstream thinking. De Waal championed the breadth and sophistication of the animal mind and through doing so, effectively downgraded human exceptionalism. It is for this reason he is so loved and respected. In his own words in 2014 "*We always end up overestimating the complexity of what we do. That's how you can sum up my career: I've brought apes a little closer to humans but I've also brought humans down a bit.*" De Waal was never afraid to ask new questions, including those that had been considered off-limits –this courage paved the way for generations of scientists to have the privilege to expand them into new areas within growing field of primatological research.

1. Illuminating the minds of our great ape cousins: the chimpanzees and bonobos

De Waal's scientific journey famously began with his doctoral studies in the 70s studying a captive colony of chimpanzees at Burgers Zoo in Arnhem, which formed the basis for his seminal book '*Chimpanzee Politics*' (1982). A now classic work, that represents an important gateway to delve into the world of great ape behaviour, Chimpanzee Politics offers a fascinating and deeply insightful window into the political strategizing of chimpanzees, their rich social relationships and complex personalities. The escapades of Luit, Yeroen and other colony members have captivated readers for decades and have cast a net of impact far into mainstream public awareness. They may have even influenced politics as well. In his recent talks, de Waal often quipped that the political ascent of US politician Newt Gingrich, himself a confessed fan of de Waal's book, closely resembles the manoeuvring of Yeroen and other chimpanzees in the book.

As well as chimpanzees, de Waal played a crucial role in raising scientific and public understanding of bonobos- our other closest cousin. Along with chimpanzees, bonobos diverged from our own line around 7 million years ago and the two ape species subsequently speciated themselves around one to million years ago. Despite being closely related and largely overlapping in life histories, bonobos and chimpanzees show some striking differences in behaviour and social

E-mail address: zanna.e.clay@durham.ac.uk.

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Fig. 1. Expressions of empathy in great apes: in both chimpanzees (a) and bonobos (b), bystanders will offer consolation to distressed victims following a conflict. Photo credit (a) Frans BM de Waal and (b) Zanna Clay/Lola ya Bonobo Sanctuary.

structure, particularly with regards to outgroup tendencies, dominance relationships, role of females and aggressivity (Gruber and Clay, 2016) Fig. 1. Noting these differences, de Waal rightly stressed that both apes must be investigated in order to gain an accurate picture of what our last common ancestor might have been like.

Having first observed bonobos in San Diego Zoo in the 1980's, de Waal was struck by their distinct nature as compared to chimpanzees, and spent the following decades bringing this knowledge into scientific and public awareness, this included the influential book *Bonobo* co-authored with photographer Frans Lanting (1997). De Waal played a pivotal role in highlighting the significance of their female-led society for models of human evolution, their prolific use of sex and play to solve social issues, reduced levels of aggression and high levels of tolerance and empathy. All such observations challenged current rhetoric of the time and catapulted this little-known ape right into the spotlight, almost overnight. Crucially, de Waal's observations forced anthropologists to reconsider their behavioural models of early Hominins, which had until that point, been largely biased towards a male-centric view. De Waal is also famously credited for giving bonobos their reputation as the 'make-love-not-war hippie ape' and his research explored the role that sex played in smoothing social tensions (e.g. de Waal, 1987). This work has had far reaching impact which continues today. More recently however, some research has challenged the view of the sex-loving pacifist ape, or at least shown a more nuanced and variable picture - for instance, while some bonobo groups do show reduced aggression and high social tolerance others, in both captivity and the wild, overlap more with chimpanzees than previously appreciated (e.g. Mouginot et al., 2024; van Leeuwen et al., 2023). Population level differences was not something de Waal himself shied away from, and in his last book *Different (2022),* he revisited some of the stereotypes surrounding bonobos that he himself was largely responsible for.

2. Ape empathy

As our closest living relatives, chimpanzees and bonobos also provided de Waal an opportunity to explore the origins of another distinctly human trait: *empathy*. Broadly defined, empathy refers to the sharing and understanding of others' emotional states (de Waal & Preston, 2002). An ongoing topic of intense empirical and theoretical research across his career, de Waal's interest in ape empathy emerged, like many of his discoveries, from anecdotal observations, such as witnessing a captive bonobo carefully rescuing a bird from a moat in San Diego Zoo (de Waal, 1997) or how chimpanzees would comfort one another after fights, a form of other-oriented concern known as consolation. Through a systematic research programme, which included comparing post-conflict prosocial behaviour to matched control periods (known as the PCMC method, de Waal and van Roosmalen, 1979), de Waal and colleagues showed us that great apes and other animals care about others, such as by comforting them in distress and providing help targeted towards their needs. Along with collaborator Stephanie Preston, de Waal is credited for developing arguably the most influential model of empathy – known as the Perception-Action Model (de Waal and Preston 2002). According to this model, empathic processes arise from the perceptions of another's external state or action, which trigger inner representations of such states, which leads to a corresponding response. Relatedly, de Waal's Russian Doll Model of empathy describes how this perception–action pairing sits as the core central mechanism of empathy, that facilitates more other-oriented behaviours, including consolation, targeted helping and emotional perspective-taking (de Waal & Preston, 2002). The Perception Action Model and the Russian Doll concept has had an extremely influential impact on the field, providing a clear evolutionary framework for complex traits like empathy to emerge and the tools to identify where they should be evidenced across the animal kingdom.

Overall, through his courageous thinking and brilliant capacity to fuse scientific evidence with illuminating descriptions, Frans de Waal has left a tremendous legacy in his quest to understand the social minds of primates and other animals. Not only a prolific and highly accomplished scientist, de Waal also stood out as an exceptional mentor, educator and communicator of science: he filled lecture halls and auditoriums around the world, and authored 16 popular science books. Ask anyone with a keen interest in animal behaviour, particularly primates, and they will most likely have been inspired by at least one of his books. Through his engaged, curious yet playful communication style, de Waal brought the world of animal behaviour to the masses and showed us all our inner ape. It is auspiciously fitting then, that de Waal's was himself named by his parents Franciscus, after the Patron Saint of Animals, *Francis of Assisi*.Fig. 2

As a former lab member and collaborator for over a decade, I remain enormously grateful for his mentorship, friendship and the opportunity to know and learn from him. Frans de Waal will be ever remembered and greatly missed –

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Fig. 2. Zanna Clay and Frans de Waal at Lola ya Bonobo Sanctuary, DR Congo in 2018. This was de Waal's first visit to the bonobo sanctuary, a place he always wanted to go to observe the bonobos.

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