



BIOGRAPHICAL MEMOIRS

FRANS B. M. DE WAAL

October 29, 1948–March 14, 2024

Elected to the NAS, 2004

A Biographical Memoir by Sarah F. Brosnan

THE LAST DECADES have seen a fundamental shift in how we view animals and our relationship with them. Much of this is thanks to Frans B. M. de Waal, a Dutch ethologist who spent a career highlighting behavioral, cognitive, and emotional continuity across all animals, including humans. De Waal began his work in a world in which nature was still largely seen as “red in tooth and claw,” yet his early work demonstrating that animals actively avoid, ameliorate, and resolve conflict to maintain their beneficial social relationships reshaped that narrative. Averse to the then-common tendency to ascribe only negative human traits to animals while calling attempts to do the same with positive traits anthropomorphic, he went on to show reconciliation, consolation, cooperation, fairness, empathy, culture, emotion, and morality in primates, singlehandedly changing how we view humans’ place in the animal kingdom. As he saw it, “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.” Equally important, de Waal was a well-known public academic, sharing his and other scientists’ findings through packed public lectures and fifteen bestselling books that became a part of the popular discourse, quoted in everything from talk shows to novels. He was tireless in his enthusiasm for the natural world and did more than perhaps anyone else to change the way a generation thinks about our place within it.

DUTCH BEGINNINGS

Franciscus Bernardus Maria de Waal was born on October 29, 1948, in ‘s-Hertogenbosch, the Netherlands, to C. de Waal van Dongen and J. A. de Waal, the fourth of six



Figure 1 Frans de Waal. Photo by Catherine Marin.

boys. The roots of his success were evident early, although it might not have been obvious exactly how they would manifest. A thoughtful, curious, driven teenager, he grew up in post-war Netherlands, an ethos that permeated his studies on peacemaking and cooperation. He was a gifted artist, at one point seriously considering going to art school; he later used this skill to illustrate his books and articles himself. He was a prolific writer, filling journal after journal with thoughts on himself, the world, and his place in it. As a teenager, he wrote a book on outer space that he submitted to a publishing house. He was persistent—the book was rejected, but that did not deter him from writing. And of course, he was



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Figure 2 Drawing by de Waal of a chimpanzee experiment. Courtesy of Catherine Marin.



Figure 3 De Waal observing chimpanzees at Burger's Zoo in Arnhem, the Netherlands. Photo by Catherine Marin.

fascinated by animals, including humans. His childhood was full of explorations through the Dutch polders; his mother let him keep a tank of sticklebacks he gathered in the back kitchen. At university, he expanded to a tame jackdaw, a cat, and pet rats, as well as his ubiquitous fish tanks. His experience with so many brothers taught him not only the reasons for conflict, but the importance of repairing relationships afterwards. In retrospect, his career can seem almost pre-ordained, although his path was not direct.

De Waal studied biology, receiving a kandidaats (equivalent to a bachelor's degree) in 1970 from the Catholic University of Nijmegen (now Radboud University), a doctoraal (equivalent to a master's degree) in 1973 from the University of Groningen, and finally a Ph.D. in 1977 from the University of Utrecht. In graduate school, de Waal first studied neuroscience in mice but did not enjoy it. Fortunately, he had a supportive advisor who encouraged him to set his own path (a lesson in good mentoring that stayed with him, to the benefit of his own students), and so for his dissertation, he studied how Java monkeys dealt with agonistic interactions.¹ In 1975, he had finished data collection on the Java monkeys and, while still a graduate student, began working with Jan van Hooft, studying the chimpanzees at the Royal Burger's Zoo in Arnhem, the Netherlands, which he continued as a research associate after receiving his Ph.D. It was here, against the dominant view that animals' lives were full of aggression and that collaboration was both incidental and selfish, that de Waal saw another way.

CHIMPANZEE POLITICS

Perhaps de Waal's greatest strength was his ability to observe, looking past scientific preconceptions to what the animals were actually doing. He was also lucky enough to be in the right place at the right time. The Arnhem colony was unusual for the era; whereas most zoos had very small, tightly managed groups of apes with a single male,

Burger's chimpanzees lived in an enclosure that emulated the chimpanzees' natural environment, with a multi-male, multi-female group of chimpanzees on a large island. This forward-thinking living arrangement allowed for normal social interactions, including fighting and, importantly, what happened *after* a fight. Counter to the bleak view, de Waal saw predominantly peaceful, relaxed interactions. Of course, he also saw some aggression. Riding home one evening on his bicycle, he had an epiphany, realizing that an unusually intense bout of grooming he'd seen involved the same chimpanzees who, earlier in the day, had fought. This was the beginning of a lifelong study of reconciliation.

Another strength was his ability to intuit what the animals were doing, then design a rigorous and careful experiment to study it. To test his hypothesis that these friendly interactions after a fight were functioning as reconciliation, de Waal compared post-conflict periods with the same timeframe on a different day on which no fight had occurred. Chimpanzees showed more affiliative behavior, such as grooming, after fights than at other times, which he argued was the result of the former combatants actively seeking each other out to repair the relationship.² Since that time, myriad species have been shown to reconcile. With Filippo Aureli, Peter Verbeek, and Peter Judge, he continued his work on post-conflict behavior and peacemaking, ultimately showing that while reconciliation is widespread across the animal kingdom, consolation, in which uninvolved individuals affiliate with the recipient of aggression to offer support, is more rare, suggesting that it requires more advanced cognition.

It was also at this time that de Waal began his second career as an author. *Chimpanzee Politics*, published in 1982, followed the social alliances among three adult male chimpanzees at Burger's over a four year period as they jockeyed for power and dominance.⁴ These, he demonstrated, could be decoupled; one male, Jeroen, was politically savvy and preferred by the females, a situation he used to consolidate the

most power, in a senior statesman-like role, despite not being the alpha male. The book is striking for combining accessibility with rigorous science. It also highlights de Waal's gift for seamlessly integrating disciplines, long before "multidisciplinary" was a buzzword. In *Chimpanzee Politics*, he likens the chimpanzees' political behavior to that which Machiavelli described in *The Prince*, opening a new field of eponymous research. It is a testament to its success that later editions of *Chimpanzee Politics* are still in press, more than forty years after it was initially published.

TO ATLANTA VIA WISCONSIN

In 1981, de Waal accepted a position as a research scientist at the Wisconsin National Primate Research Center. There he returned to macaques, continuing his research on conflict resolution and dominance styles. Two types of macaques lived at Wisconsin, the aggressive rhesus macaque and the relatively more pacifistic stump-tail macaque. In a key demonstration of behavioral flexibility, de Waal housed a cohort of juvenile rhesus with an existing group of slightly older stump-tails. The rhesus' behavior changed to mimic their stump-tail tutors, becoming far less aggressive and more conciliatory than typical rhesus interactions.⁵ This transfer of peaceful behavior was his first work to so clearly demonstrate social learning without explicit reward.

In Wisconsin he also got the opportunity to begin working with two new-to-him species who became lifelong foci. He had long wanted to study bonobos, who are closely related to chimpanzees and yet quite different in social organization and behavior, and began observing them at San Diego Zoo in 1983. He found female-dominant behavior, as compared to chimpanzees, and documented the use of sex to ameliorate conflict.⁶ He also started his colony of capuchins, a species he helped make famous for their advanced cognition. The



Figure 5 De Waal recording observations of bonobos at San Diego Zoo. Photo by Catherine Marin.

capuchins were also the result of being in the right place at the right time; the University of Wisconsin Medical School had a colony of capuchin monkeys who needed a home, and de Waal, intrigued by their behavior, offered to take them. When he moved to Atlanta in the summer of 1991, he brought the capuchins south and set them up in large, indoor-outdoor enclosures like those at Royal Burger's Zoo.

In Atlanta, he became the C. H. Candler Professor of Primate Behavior in the Department of Psychology of Emory University and the founder and director of the Living Links Center for the Advanced Study of Ape and Human Evolution at what was then the Yerkes National Primate Research Center (now the Emory National Primate Research Center). He continued to work with capuchins and rhesus, but also returned to chimpanzees, working with two large social groups of chimpanzees housed at the Field Station. His research turned more experimental, but he never stopped watching the primates' behavior. He used his knowledge of their natural behaviors to design better studies and his knowledge of the individuals and their social relationships to supplement the interpretation of his studies with historiography, both lessons he impressed upon us as graduate students. It was this combination of experiment, observation, and careful interpretation that allowed him to uncover animals' complex thoughts, goals, and emotions.

Shortly after de Waal arrived at Emory, a study came out arguing that capuchins did not understand cooperation. This did not match what he saw in their interactions, so he did what he did best, designing a task to better elucidate the monkeys' true abilities. The original task had required monkeys to push levers simultaneously to obtain a juice reward. Although pushing levers is easy for capuchins, the monkeys, he argued, do not perceive any intuitive physical link



Figure 4 Frans de Waal. Photo by Catherine Marin.



Figure 6 Female chimpanzee at the Yerkes Primate Center Field Station (now the Emory National Primate Research Center). Photo by Frans de Waal, courtesy of Catherine Marin.

between each individual's actions in that task, making it very difficult for them to learn the contingencies of cooperation. In his extensive reading, de Waal had come across a "barpull" cooperation task, originally used by Meredith Crawford with juvenile chimpanzees nearly 100 years prior,⁷ that he adapted for the capuchins. The monkeys had to work together to pull in a heavily counterweighted tray to bring themselves food rewards. Critically, if one monkey let go, the tray became heavier, providing immediate kinesthetic feedback and, therefore, that intuitive physical link. The capuchins succeeded on the barpull task, but not on a replication of the lever task,⁸ emphasizing the importance of careful study design. Moreover, their behavior suggested that they understood the task, as they pulled preferentially when their partner was present rather than absent, showing that they knew that they needed their partner. They also did so when they could see one another, suggesting visual coordination,⁹ and preferred to help those who shared with them, suggesting strategic decisions about cooperation.¹⁰

I joined the lab around this time. I initially intended to study cooperation in chimpanzees, but like de Waal, I was captivated by the curious capuchin monkeys. In keeping with de Waal's exhortations to get to know our animals, my first year I spent a lot of time observing them. One afternoon I was feeding the capuchins peanuts in their outdoor yard, which required distracting the alpha male, Ozzie, with a just-out-of-reach peanut while surreptitiously feeding the others. Eventually Ozzie, apparently frustrated, began trying to trade other foods from their enclosure for a peanut. He progressed from boring monkey chow to a quarter of an orange, which he really liked. Was it possible, I wondered to de Waal, that he only wanted the peanut because everyone else had one? Perhaps they were even judging their outcomes relative to

those of others. Humans do this; we call it a sense of fairness. De Waal, in a typical display of his trust for his students' instincts, told me to test it. We designed a simple task to see how primates responded when they got a less-preferred reward than a partner for the same effort. Our results, published in *Nature*,¹¹ were first to show that animals care about equity. We then showed responses to inequity in chimpanzees,¹² and that inequity impeded cooperation,¹³ supporting the hypothesis that responses to inequity evolved to support effective partner choice.¹⁴ As notable as the science was the support I received from de Waal, who helped me develop my interest and ensured that I got credit, both as a student and when I began my independent research career.

De Waal's research always explored the importance of relationships. At a time when research on social learning focused on the cognitive mechanisms (i.e., imitation, emulation, etc.), de Waal studied who primates learned from. With Andy Whiten, Kristin Bonnie, Victoria Horner, and Marietta Danforth, he showed that they conform to their group¹⁵ and copy those with prestige and skill.¹⁶ In his book *The Ape and the Sushi Master*,¹⁷ he proposed that much social learning occurs through younger or less experienced members of the group absorbing the behavior of older ones, much like the sushi apprentice learns from the master. In other words, the social context mattered as much or more than the reward.

Similarly, research on cooperation at that time largely focused on the benefits and costs of working together and even questioned whether animals had the cognitive capacity necessary for many types of cooperation. De Waal showed that primates preferred to cooperate with their friends or with others who had recently benefitted them (so-called attitudinal reciprocity),^{18,19,20} suggesting again that relationships were at least as important as outcomes. They were also savvy, only cooperating when it was to their benefit. He and Malini Suchak, Darby Proctor, and Matthew Campbell found that chimpanzees understood when their partners' help was needed²¹ and used behavioral mechanisms to mitigate competition.²²

Effectively negotiating social relationships requires understanding your partners' needs. De Waal was one of the first primatologists to consider whether social behavior in primates was underpinned by empathy and, with Stephanie Preston, developed a model to explain the origins and evolution of empathy that continues to dominate decades later.²³ Closing the circle begun at Burger's Zoo many years before, later work with Teresa Romero, Zanna Clay, and Christine Webb linked empathy with consolation, showing that individuals disproportionately consoled friends and relatives²⁴ and that some individuals consistently consoled more often than others, suggesting empathetic personalities among primates.²⁵

These complex social negotiations require an ability to recognize individuals quickly and accurately. He and Lisa

Parr showed that chimpanzees could identify kin relationships amongst even individuals that they did not know.²⁶ Moreover, he and Jennifer Pokorny found, chimpanzees could match familiar individuals' faces with their posteriors, suggesting that they had mental representations of their group mates that incorporated whole body schemas.²⁷ He won an Ig Nobel Prize for this work, an honor that thrilled him "because scientists tend to take themselves too seriously."

De Waal was a strong advocate for species who had received too little attention. He continued to work with bonobos, first at San Diego Zoo, where he and Amy Parish studied their much more affiliative, female-dominant behavior as compared to chimpanzees,²⁸ and later with Zanna Clay at Lola ya Bonobo Sanctuary in the Democratic Republic of Congo, where they showed the extent of the bonobos' reconciliation, consolation,²⁹ and empathy.³⁰ Primates were not the only focus of his attention. He and Josh Plotnik found that Asian elephants also cooperate³¹ and console.³² His 2016 book—one of my personal favorites—*Are We Smart Enough to Know How Smart Animals Are?*³³ makes a compelling case that other species are much smarter than we give them credit for, but we fail to design studies that accurately measure their abilities and thus, to their detriment, underestimate them.

With its vibrant intellectual environment, his lab was an exciting place to be. De Waal encouraged each of us to pursue our own research, so at any given time there would be research on all or most of the above topics. With the capuchins and chimpanzees housed at facilities thirty miles apart, the lab was both phylogenetically and geographically split; de Waal knew the importance of group cohesion, so he held regular field trips for lab meetings from one facility to the other and "Simian Soirees" at his house, at which he and his wife, Catherine Marin, cooked us spectacular meals and served us good French wine while discussion went late into the evening on the back porch of their home nested in the Georgia woods. Others in the lab became our friends and collaborators, and his lab became our home.

De Waal's advising was comprehensive and committed. He gave us credit for our ideas, taught us to navigate publication and publicity, and reminded us that criticisms of our work were suggestions for our next study. He encouraged us to pursue the topics we found interesting and later supported us in pursuing the path that was right for us; in a recent obituary co-authored by his students,³⁴ a common theme is de Waal's unwavering support for us both personally and professionally. His support did not end when we graduated. We continued to collaborate with him, and he continued to send us interesting papers and invitations to his home, along with excellent students to join our labs and even the capuchin monkeys to start our own colonies. Most importantly, his

example constantly reminded us that the individuals we studied were thinking, feeling beings that deserved to be treated with respect and dignity.

A MULTI-FACETED LEGACY

De Waal was accomplished in all the typical ways; he was the editor-in-chief of *Behaviour*, a journal founded by one of his academic grandparents, fellow Dutchman Niko Tinbergen, was on the editorial boards of fifteen other journals, and published more than 400 peer-reviewed papers, chapters, and commentaries in multiple languages (he spoke four fluently). He was a member of the U.S. National Academy of Sciences and the Royal Dutch Academy of Sciences, and a fellow of the American Academy of Arts and Sciences, the Japan Society for the Promotion of the Sciences, and the Association for Psychological Science. He was the recipient of seven Doctor Honoris Causa degrees (one conferred posthumously) and the American Society of Primatologist's Distinguished Primatologist Award, along with numerous other awards. In 2013, he was appointed as Distinguished Professor at the University of Utrecht, where he had received his Ph.D. thirty-six years prior, becoming the first Utrecht Ph.D. graduate to also receive an honorary degree.

He was also accomplished in less typical ways; he published fifteen editions of his books between 1982 and 2022 (one more will be published posthumously), through which he taught the public how impressive animals are while also showing them a little something about themselves. His books topped best-seller lists and won awards, including the Pen/E.O. Wilson Literary Science Writing Award (*Mama's Last Hug*), the Liberales Book of the Year (*The Age of Empathy*), and the *Los Angeles Times* Book Award (*Peacemaking Among Primates*). He used his books to highlight a wide variety of scientists, including those obscured by geographic



Figure 7 De Waal giving a lecture to a packed auditorium after a recent book release. Photo courtesy of Catherine Marin.



Figure 8 De Waal with his students and collaborators at his Festschrift. Photo courtesy of Catherine Marin.

and linguistic barriers, bringing them mainstream attention that they might not have otherwise received. Aside from his books, he gave hundreds of talks, including two TED talks that have accrued nearly 10 million combined views. He became known outside of the academy, named one of *Time Magazine's* 100 Most Influential People in 2007 and one of *Discover magazine's* "47 Great Minds in Science" in 2011. I recently picked up a novel and found that the quote opening the book was one of de Waal's.

It is always hard to know what someone's enduring impact will be, but I suspect that if de Waal could choose his, he would hope that his work had helped to make the world a better place for *all* organisms, not just humans and the megafauna we tend to be most enthusiastic about. Later in his career, de Waal considered what it means that so many organisms feel pain, experience emotions, develop relationships with friends and relatives, and have the capacity to understand their world. Not every species shows each of these, but all show at least some. Moreover, he argued, in many cases the absence of an ability is an absence of our ability to demonstrate it, not an absence in the animal. We do not experience the world the way other species do, thus our tests may be illogical or out of context to the organisms we are testing, or the animals may be in conditions that are not conducive to developing or expressing the behavior. When we design proper tests, we often find that an ability has rippled down to another species. It is imperative for us to consider, as he did, what this means for our relationship with them.

De Waal was a beloved mentor, colleague, and friend. He died of cancer at home with his partner of fifty-three years, Catherine Marin, on March 14, 2024. Although his legacy will live on through his publications and students, the natural world lost an important advocate, and we all lost a remarkable scientist and writer who changed how we view animals and what that means for our place in the world.

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