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DOI
10.1163/1568539X-bja10351
Publication date
2026
Document Version
Final published version
Published in
Behaviour

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Link to publication

Citation for published version (APA):
Kret, M. E., Ploeger, A., & de Backer, C. (2026). Frans de Waal's legacy: looking back and forward. *Behaviour*, *163*(3-4), 203-209. https://doi.org/10.1163/1568539X-bja10351

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Download date:17 Nov 2026

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Behaviour 163 (2026) 203–209

Behaviour
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Editorial

Frans de Waal's legacy: looking back and forward

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Published online 2 April 2026

On 14 March 2024, we lost a giant of primatology: Frans de Waal. This special issue dedicated to him, appears two years after his passing, in the journal *Behaviour*, where he served for several years as Editor-in-Chief. It brings together a rich and diverse collection of empirical articles, book reviews, reflections, and opinion pieces by scholars, collaborators, and inner circle — individuals either directly influenced by him or deeply inspired by his ideas. The issue originated at the annual meeting of the Cognition Behaviour and Evolution Network (CBEN), held at the University of Antwerp on 18–19 September 2025. The conference, organized by Charlotte de Backer, professor of communication studies, and Carolyn Declerck, professor of neuroeconomics, both at Antwerp University, built on the foundation laid a decade earlier when CBEN was established by Annemie Ploeger, senior lecturer in evolutionary developmental psychology at the University of Amsterdam and Mariska Kret, professor of comparative psychology and

Published with license by Koninklijke Brill BV | DOI: 10.1163/1568539X-bja10351
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affective neuroscience at Leiden University; both still active board members, together with Charlotte and others. The aim of CBEN is to facilitate research and education in relation to the evolution of cognition and behaviour. Its basis is in the Netherlands and Belgium, but we invite scholars from other countries to join us.

The 2025 conference theme, "Looking Back and Forward", provided a natural opportunity to honour de Waal's legacy in a way that was not only retrospective but also aspirational. For the first time, CBEN established a Frans de Waal Honorary Lecture, delivered by his former postdoctoral researcher, Zanna Clay, now a professor of comparative and developmental psychology at Durham University. Also for the first time, CBEN initiated the Frans de Waal PhD Dissertation Prize, awarded this year to Tom Roth, behavioural biologist and assistant professor at Utrecht University. Both the lecture and the prize were generously sponsored by De Gruyter Brill, the publishers of *Behaviour*. The intellectual vibrancy and emotional resonance of the conference inspired us to propose this special issue — both to capture the moment and to establish a hopeful new tradition: an annual recognition of de Waal's scientific and societal impact through a lecture, prize, and themed issue in this well-respected journal once founded by another giant: Niko Tinbergen, a Dutch behavioural biologist who earned in 1973 the Nobel Prize in Physiology or Medicine with Karl von Frisch and Konrad Lorenz for their groundbreaking studies on animal behaviour.

The special issue opens with a contribution by Prof. Catherine Marin, de Waal's wife and a retired professor of French at the Georgia Institute of Technology (Marin, 2026). Her scholarship focused on feminine power and subversion in late 17th-century French fairy tales. A delightful connection to her husband's work is that, in one of her publications on power and sexuality in women's fairy tales — stories written for adults rather than children — she drew on de Waal's research on dominance. In addition to being a scientist herself and a supportive partner, Marin served as de Waal's literary consultant and critic, offering guidance, refinement, and sharp intellectual companionship throughout his writing career. Her contribution provides a deeply personal and uniquely informed perspective. She offers us a preview of de Waal's final book, currently in its concluding stages — a manuscript that, perhaps fittingly, shares its central theme with both the CBEN conference and this special issue: looking back and forward (de Waal, in press). Through her blend of intimacy, scientific insight, and literary sensitivity,

Marin brings us closer to de Waal and gestures toward the intellectual path he hoped future generations would continue to take.

The second contribution comes from Zanna Clay, who transformed her honorary lecture into a thoughtful and integrative essay (Clay, 2026). She explores the evolutionary and developmental roots of empathy across great apes and human infants, arguing for profound continuity rather than categorical separation. Early-emerging mechanisms — such as mimicry and emotional contagion — appear across both human and non-human primates and form the foundation for empathy, prosociality, and moral sensitivity. Insights from comparative research and developmental psychology converge to suggest that empathy is not a uniquely human construct but an inherited primate trait shaped by evolutionary history and early social context. Her essay captures the essence of de Waal's intellectual legacy: the conviction that understanding morality and sociality requires looking both across species and across development.

The third contribution, by Edwin van Leeuwen (2026), behavioural biologist and assistant professor at Utrecht University, deepens this discussion by placing culture at the centre. Drawing on an impressive body of recent empirical work, van Leeuwen examines variation in social behaviour within primate species. His findings indicate that differences in social structure, grooming styles, affiliative behaviour, and social tolerance are not fully explained by genetic or ecological factors. Instead, these patterns often reflect group-specific traditions — socially learned, culturally transmitted ways of interacting. In a twelve-year dataset, for example, chimpanzees maintained stable group-specific grooming traditions despite demographic changes, demonstrating cultural resilience. Other work shows that both chimpanzees and bonobos structure their social relationships into concentric "circles" of closeness, much like humans do. These findings challenge broad, species-wide generalizations and underscore the importance of culture, context, and group history when interpreting primate behaviour.

In the fourth article, Tom Roth (2026) expands on the research that earned him the inaugural Frans de Waal PhD Prize. His paper discusses the critical role of partner choice in reproductive success, highlighting its implications for captive breeding and conservation. Traditional partner-preference tests often require physical co-presence, which can be logistically difficult or stressful for the animals. Roth proposes long-distance partner-preference testing as a more humane and efficient alternative. He reviews existing

attempts, identifies methodological limitations, and offers suggestions for improving validation and implementation. His work represents a thoughtful synthesis of cognitive research, animal welfare, and applied conservation science.

The special issue then turns to two book reviews. Annemie Ploeger (2026) reviews the Dutch book *Een uniek dier* (which in English translates as "A unique animal") written by Rens Bod, professor of digital humanities at the University of Amsterdam. The book raises questions central to de Waal's life's work: What distinguishes humans from other animals? Which capacities are shared, and which are newly evolved? Bod challenges long-standing claims about unique human faculties — reason, morality, self-awareness, language, religion — and re-examines them in light of decades of comparative evidence, much of which de Waal helped introduce into mainstream discourse. Bod suggests that there's one aspect of human cognition that makes us special: the ability of unlimited recursion. Many species are capable of recursion in their way of thinking and doing, but only humans are able to apply an activity to the results of that same activity in an unlimited way. But in general, Bod argues, in line with Frans de Waal, that the true distinction between humans and other animals may lie less in possessing entirely unique traits and more in the degree to which certain capacities can be developed. Ploeger believes that de Waal would have appreciated this book's willingness to dismantle human exceptionalism, because he strongly endorsed Darwin's view that evolution happens gradually and that all species are interrelated in the tree of life.

A second review by Ivan Norscia, associate professor of biology at the University of Turin, covers *The Arrogant Ape* by Christine Webb, a former PhD student of de Waal, and now assistant professor in animal behaviour at New York University (Norscia, 2026). Webb's book challenges deeply ingrained human-centric assumptions by highlighting remarkable cognitive, communicative, and cultural abilities across a wide range of non-human species — including songbirds, prairie dogs, reef fishes, plants, and fungi. Norscia emphasizes how Webb's work resonates with de Waal's lifelong efforts to reveal continuity between humans and other species and to question inflated narratives of human superiority.

The issue also includes two eye tracking studies. De Waal mostly used observational methods himself but was always interested in technologies

or methodological advances and later in his career he also embraced computer experiments, appreciating its capacity to disentangle perceptual and cognitive processes under controlled conditions. The first study, conducted at Leiden University by postdoc Yena Kim and former PhD student Evy van Berlo, now postdoctoral researcher at Utrecht University, and Mariska Kret, compares how bonobos and humans visually scan faces and bodies of conspecifics, shedding light on attentional and emotional mechanisms in social perception (Kim et al., 2026). The second, led by Lucrezia Lonardo, postdoc at the University of Vienna, applies eye tracking to dogs — our closest human-associated species — exploring how visual attention in dogs maps onto social and communicative abilities that have co-evolved with humans (Lonardo et al., 2026).

Finally, and intentionally placed last, is a paper by Liesbeth Sterck, professor of animal behaviour at Utrecht University, and her team, reporting 17 cases of surprising social behaviour in long-tailed macaques: covert hair-pulling (Sterck et al., 2026). What we like so much about this contribution, is that it began as a single, serendipitous observation. De Waal made many remarkable observations, some of which that also evolved into more than one. Sterck et al.'s observation turned into a systematic collection of cases consistent with tactical deception, a behaviour in which an individual acts to mislead another, either by concealing aggressive intent or by presenting an affiliative front. The authors examine several functional hypotheses (dominance reinforcement, teasing, social manipulation) and consider how group context influenced expression of the behaviour. We chose to end the issue with this contribution because it exemplifies how close observation can suddenly reveal unexpected behavioural complexity. Is such behaviour meaningful? Is it random? De Waal strongly believed that anecdotal observations could inspire to raise new scientific questions. For this reason, Sterck and colleagues' study adheres very much to the spirit of de Waal's approach to science.

Taken together, the contributions in this special issue embody Frans de Waal's legacy by combining curiosity and rigorous science. As we herewith open this special issue of *Behaviour*, we invite all readers to join us in honouring Frans de Waal's legacy by continuing in his footsteps: to probe continuity rather than sharp divides, to value both observations and experiments, and to remain open to the unexpected. We hope that this special issue serves as a springboard for new research and a dialogue between researchers

from different disciplines and backgrounds who study the origin of the mind and we hope to see you at the yearly CBEN conference or at any of the other wonderful meetings to come.

Funding

The conference of the Cognition Behavior & Evolution Network was sponsored by The Research Foundation — Flanders (FWO). Mariska E. Kret was supported by a Starting Grant from the European Research Council (#804582).

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