John Alcock (1943–2023)

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An inspirational advocate for adaptation, animal behaviour and natural history.

n the 15 January 2023 the world of animal behaviour and evolutionary biology lost a measure of its shine with the passing of John Alcock. John's name and influence will be familiar to many in the field from his undergraduate textbook, Animal Behaviour: An Evolutionary Approach (1975). Many others have been inspired directly by John's teachings, public talks or scientific lectures, or have enjoyed any of his more than 200 scientific papers and 12 books. Still others - like ourselves - have enjoyed the gift of John's company or even been fortunate enough to join one of his field excursions in the south-west USA or Australia. Entire generations of animal behaviourists and behavioural ecologists have been touched in some way by his rich contribution to these fields. Following a battle with neurodegenerative illness, John sadly passed away near his home in Tempe, Arizona, and in the shadow of his beloved Sonoran Desert mountaintops.

John's undergraduate text is an educational masterpiece, which remained at the forefront of the field through ten editions over four decades. This text is exemplary of two outstanding qualities that John possessed. The first was his ability to articulate a clear and reasoned hypothetico-deductive approach to testing adaptive hypotheses for animal behaviour. Through his writings (including his numerous books for popular audiences), John outlined the basic procedure of hypothesis-driven science in a way that was inspiring and empowering for students, scientists and citizen-scientists alike. Second, John's text exemplified an approach based on natural history and whole-organism biology. Just as natural selection ultimately acts upon phenotypes in the wild, John emphasized that testable hypotheses need to be inspired by how animals behave in their natural environment. Testing these hypotheses often drew upon molecular, morphological or physiological analyses, yet the basis of such tests remained securely grounded in what the animal revealed about its behaviour and life in nature. This was



of course a reflection of John's personal source of inspiration – the natural world.

Following an undergraduate degree at Amherst College, John completed his PhD in 1969 at Harvard University under the tutelage of one of the most prominent evolutionary biologists of the 20th century, Ernst Mayr, He then briefly took a position at the University of Washington before joining the zoology faculty at Arizona State University (ASU) in 1973. This move was foreshadowed by an earlier visit to the Arizonan Chiricahua Mountains, where John was touched by the isolation and raw nature of the Sonoran Desert. ASU was his permanent base thereafter, where he taught until his retirement as a distinguished Regents Professor in 2008. Many of John's scientific papers are based upon his observations and experiments on hilltopping male insects in the Sonoran Desert, such as his extensive and indefatigable studies of tarantula hawk wasps defending their territories high in the Usery Mountains. In The Masked Bobwhite Rides Again (1993), John wrote of the region:

"As a born-again Arizonan transplanted from Massachusetts to the Sonoran Desert ... I can still barely believe my good fortune in being able to visit places where you can walk without bumping into other people. Where the earth is populated with so many strangely wonderful plants and animals, each one competing for the honor of the most beautifully adapted to a most rigorous environment or most unEastern in its aspect or most ascetically aesthetic."

John used his research on the reproductive behaviour of damselflies, solitary bees and wasps as the foundation for the highly influential text *The Evolution of Insect Mating Systems* (coauthored with Randy Thornhill in 1983), within which novel hypotheses such as cryptic female choice and the adaptive value of polyandry were first elucidated. This book motivated a generation of insect behavioural ecologists, and those studying other taxonomic groups were also quick to explore these conceptual ideas, which remain areas of substantial impact to this day.

Although John's name is considered by many to be synonymous with the study of animal behaviour, his interest in biology was wide-ranging. As a self-confessed 'card-carrying adaptationist', John's view of the biological world was firmly rooted in the theory of Darwinian evolution. This naturally extended to humans, whom — as he reasoned — were clearly generated by the very same adaptive processes as the entirety of other living

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organisms. As such, he wholly embraced the thesis of E. O. Wilson's *Sociobiology* in 1975 and stood as a staunch defender of the imprint of adaptive evolution upon human biology in his own book *The Triumph of Sociobiology* (2001).

John was also a creature of habit. One such habit was his almost biennial migration from Arizona to Australia, where he revelled in the remoteness of the Western Australian bush. John would arrive in July, in time to study the behaviour of Dawson's burrowing bees as they emerged from the clay pans of the Gascoyne deserts. John had a deep affection for Western Australia, advocating that an excellent cure for insomnia was to imagine oneself wandering among the individually unique clay pans of the Kennedy Ranges National Park. Bee research completed, John would travel in his camper the length and breadth of southwestern Western Australia, visiting its national parks or small patches of remnant vegetation in search of highly localized endemic orchids to photograph and identify. The discovery of a much sought-after species offered a 'frisson of excitement' beyond compare - especially when, as in the case of Alcock's flying duck orchid (Paracaleana alcockii), it turned out to be new to science. As with the Arizonan desert, John's appreciation of Darwinian evolution allowed a resonance with the land and

its natural inhabitants. John advocated in *After the Wildfire* (2017) for us all to connect with the natural world:

"So get out and take a hike somewhere, anywhere, and perhaps the discoveries that you make will provide you with pleasure and a sense that a natural world persists despite an overabundance of people. I hope so"

John was elected a fellow of the US-based Animal Behaviour Society, and then an exemplar of that society in 1996. His contributions were also recognized in the UK by the award of the Association for the Study of Animal Behaviour Medal in 2004. In addition to being one of the first Regents Professors at ASU, he received several prestigious teaching awards throughout his tenure and was the recipient of the John Burroughs Medal for the best natural history book of 1998. He was the mightiest of intellectual colleagues, a valued mentor and the dearest of friends.

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Additional information

D.I.K. is an associate professor of biology in the School of Natural Sciences, Macquarie University, in Sydney, Australia He first met John in 2002 while working as a postdoctoral associate with R.L.R. at ASU, Tempe, Arizona. USA, D.J.K. was at least partly adopted by John and his wife Sue, and spent many enjoyable mornings following in John's wake trekking up and down Usery mountain to study his beloved territorial hilltopping insects. The two subsequently enjoyed a strong friendship that spanned several decades and two continents, and published more than a few papers together. R.L.R. is an emeritus professor in the School of Life Sciences at ASU. He and John were close colleagues and friends for almost 50 years, starting when RLR interviewed for a position at ASU in 1975. Their relationship, both academic and personal, was built on a shared deep love of natural history and animal behaviour, and wonderful outings together in the USA, Europe, and Australia, L.W.S. is a professor of evolutionary biology at the University of Western Australia in Perth. He first met John in 1996 and began working with him on the mating system of Dawson's bees. L.W.S. spent many happy hours with John, standing among tens of thousands of bees as they went about their daily business, suitably marked and recorded, or searching for orchids in the national parks and reserves of the southwest of Western Australia.

Competing interests

The authors declare no competing interests.