



Editorial

Cause and function in behavioural biology: A tribute to Jerry Hogan



Jerry Hogan lecturing in Sao Paulo, 2015.

This special issue of Behavioural Processes is dedicated to the contributions of Jerry A. Hogan to behavioural biology—or ‘ethology’ as this field used to be known. These contributions are manifold, and have inspired many researchers, not only in ethology, but also in experimental psychology and behavioural neuroscience, as can be seen from the different contributions to this issue. Hogan has conducted pioneering research into the causation and development of animal behaviour. In addition, he has written extensively on the theoretical foundations of the field. In particular, he has emphasised the logical distinction between cause and function in behavioural biology. This is a fundamental distinction, and its misinterpretations have often led the field astray. That this discussion is still ongoing is exemplified in several papers in the present issue (Lefebvre, 2015; Bolhuis, 2015; Laland, 2015).

Jerry Hogan started his scientific career at the University of Chicago, where he studied psychology. He then moved to the psychology department at Harvard University, where he conducted his PhD research. He initially had planned to work under the supervision of B.F. Skinner. But soon after arriving he realized that the Skinnerian ways were not for him and he quickly moved into the study of the behaviour of the Siamese fighting fish, *Betta splendens*, nominally under the supervision of E.B. Newman (Hogan, 1967). While at Harvard, Jerry became very much interested in developments in Europe, where ethology was a rapidly advancing new field, led by Konrad Lorenz and Niko Tinbergen. It was clear to Jerry that Europe was the place to be, and after getting his PhD at Harvard he was awarded a National Science Foundation Postdoctoral Fellowship that enabled him to work in the laboratory of Tinbergen's student Gerard Baerends at the University of Groningen in The Netherlands. Baerends suggested that Jerry should collaborate with Jaap Kruijt, who had started his PhD project on the development of behaviour in the red junglefowl (*Gallus gallus spadiceus*) (Kruijt, 1964). While at Groningen, Jerry conducted a number of

now classic studies on the motivation of behaviour in junglefowl chicks (Hogan, 1965, 1966). At this time, Jerry first developed his concept of behaviour systems (Hogan, 1971, 1988, 1994, 2015). During his postdoc in Groningen he met his future wife, Lidy Hogan-Warburg, whose PhD thesis with Baerends on the extravagant and unique lekking behaviour of the ruff, *Philomachus pugnax*, a shorebird, is one of the pioneering studies in what was to become the new field of behavioural ecology (Hogan-Warburg, 1966). Jerry himself also ventured into behavioural ecology when he studied lekking in black grouse with Jaap Kruijt (Kruijt and Hogan, 1967) and foraging in nutmeg mannikins and zebra finches with his postdoc Luc-Alain Giraldeau (Giraldeau et al., 1990). Jerry also collaborated with his long-time friend, the late Klaus Vestergaard, on a series of experiments on dustbathing and feather pecking in junglefowl (Vestergaard et al., 1990, 1993; Vestergaard and Hogan, 1992; Hogan et al., 1991).

In the course of his career, Hogan increasingly focussed on what he regarded to be a crucial issue in the field, namely the distinction between cause and function. In a famous paper, Niko Tinbergen had identified the four main problems in ethology: causation, function, development and evolution of behaviour (Tinbergen, 1963)—also known as Tinbergen's ‘four whys’. Hogan (1994) pointed out that these four questions are only one of several ways that questions about behaviour can be formulated. Importantly, he argued that cause and function are logically distinct, and should not be confounded. The issue of cause and function in behavioural biology takes centre stage in several papers in this issue (Insel and Frankland, 2015; Van Kampen, 2015; Daly, 2015; Bolhuis, 2015; Lefebvre, 2015).

Hogan's experimental work has mainly been concerned with Tinbergen's ‘causal’ whys, motivation and development. This work is still a source of inspiration for many, as several papers in this special issue demonstrate. At the same time, Hogan's ideas about causation and function (e.g., Hogan, 1994, 1997) have also inspired behavioural ecologists and evolutionary biologists, exemplified by a number of papers in the present issue (Bijleveld et al., 2015; Lefebvre, 2015; Laland, 2015). In addition, Hogan's influence is not limited to the behaviour of animals, but also extends to human research, particularly developmental psychology (Blass, 2015; Lovic and Fleming, 2015; Ashton, 2015).

The order of papers in this issue is roughly based on whether they are mainly concerned with causation, development, function or evolution. However, following Jerry's proposals on cause and function, many authors address both in their papers, and there

is thus considerable overlap. This demonstrates once again Jerry's continuing influence on the field. The opening paper is an analysis of the neural mechanisms of behaviour by Nathan Insel and Jerry's long-time Toronto colleague and friend Paul Frankland (Insel and Frankland, 2015). Hendrik van Kampen was a PhD student with Jaap Kruijt at Groningen, before he moved to Toronto to do a postdoc with Jerry. Here he puts his work on filial imprinting and courtship food-calling in the wider context of 'discrepancy theory' and 'prediction error', by concentrating on the involvement of exploration, fear, and aggression (Van Kampen, 2015). Carel ten Cate is another of Jaap Kruijt's PhD students, and a long-time colleague of Jerry's. Here he reports on some recent findings in the fascinating project of his group on the parallels between birdsong and human speech, with his former PhD student Jiani Chen (Chen and ten Cate, 2015). Elliott Blass spent a sabbatical year in Jerry's lab, and has been a friend of Jerry's ever since. Here he reviews how rat and human mothers minimise energy loss in their offspring (Blass, 2015). Alison Fleming is another of Jerry's long-standing Toronto colleagues. With Vedran Lovic, she reviews the work of her group on maternal behaviour in rats, and the parallels with human behaviour (Lovic and Fleming, 2015). Michael Ashton, a former undergraduate student, applies Hogan's framework to the study of human personality (Ashton, 2015). Magnus Enquist and Stefano Ghirlanda are long-time friends of Jerry's. Here, together with Johan Lind, they review delayed matching-to-sample data in the study of animal memory (Lind et al., 2015). David Sherry was another of Jerry's PhD students. Together with Caroline Strang, he compares cognition and behaviour of bumblebees and honeybees (Sherry and Strang, 2015). Martin Daly, another of Jerry's former students, and his late wife, Margo Wilson, did pioneering work in the new field of evolutionary psychology. Here he discusses the topic of cause and function in behaviour (Daly, 2015). Animal ecologist Theunis Piersma has been a friend of Jerry's ever since the latter spent a sabbatical at the University of Groningen in the mid 1980s. Although the work of Piersma is mostly ecological in character, they continued to develop their joint interests in animal 'design' and Jerry acted as one of two critical readers during the drafting of a book on the integration of physiological, behavioural and ecological approaches to organismal design as embodied in phenotypic flexibility (Piersma and van Gils, 2011). In this special issue, with a number of junior colleagues also inspired by Jerry, Piersma reports on their study of information use in red knots *Calidris canutus* (Bijleveld et al., 2015). Johan Bolhuis, whose PhD supervisors were Jaap Kruijt and Gabriel Horn, has known Jerry since they met at the International Ethological Congress in Toulouse in 1985. They have collaborated on a number of theoretical papers and two books (Hogan and Bolhuis, 1994; Bolhuis and Hogan, 1999). Inspired by Hogan, Bolhuis has published widely about the relationship between Tinbergen's four whys (Bolhuis and Macphail, 2001; Bolhuis, 2005; Bolhuis and Wynne, 2009; Bolhuis and Verhulst, 2009; Bolhuis et al., 2011). Here he reviews work that is pertinent to the question once raised by Bolhuis and Wynne (2009): 'Can evolution explain how minds work?', including recent analyses of the evolution of language (Bolhuis et al., 2014). The answer is a resounding 'no' (Bolhuis, 2015). One of the main figures in the debate about function and mechanism is Jerry's colleague Louis Lefebvre. Here he discusses the question whether 'neuroecologists' (Bolhuis and Macphail, 2001) should separate Tinbergen's four questions (Lefebvre, 2015). It was Louis Lefebvre who first introduced his finishing PhD student, Luc-Alain Giraldeau, to Jerry during an Animal Behavior Society meeting in Harrisburg USA. Giraldeau was later hired by Jerry as a postdoc and jumped into causal behavioural biology by having to maintain Jerry's red junglefowl colony and teach his behaviour course at the University of Toronto. This had two lasting effects on Giraldeau. One is a persisting respect for red junglefowl roosters, and the other, more profound, a keen sense of distinction between cause and

function, which led Giraldeau to argue that behavioural ecologists still commonly muddle the two in what he calls the behavioural gambit (Giraldeau and Dubois, 2008; Fawcett et al., 2013). Kevin Laland and colleagues have addressed the issue of evolution and causation in a high profile publication (Laland et al., 2011). Here he discusses his recent thinking on this issue (Laland, 2015). In the concluding paper of this special issue, the man himself reviews his ideas pertaining to the study of behaviour, for which he provides a framework (Hogan, 2015).

Apart from his theoretical and experimental papers, Jerry Hogan has also been co-editor of two books on behavioural development (Hogan and Bolhuis, 1994; Bolhuis and Hogan, 1999), and he contributed three chapters to a celebration of Niko Tinbergen's legacy (Hogan, 2009; Hogan and Bolhuis, 2009a,b; Bolhuis and Verhulst, 2009). He also was chief executive editor of *Behaviour*, an international journal of behavioural biology for 20 years, and an Associate Editor of *Behavioural Processes*. In addition, he served as president of the International Society for Comparative Psychology from 2002 to 2006.

Although officially retired as professor of psychology at the University of Toronto, Jerry continues with his theoretical scientific work as before, currently enjoying a visiting professorship at the Institute of Advanced Studies of the University of Sao Paulo, Brazil. Normally, a Festschrift such as this is put together for a colleague who has left the field through retirement or otherwise. Clearly, this does not apply to Jerry. In fact, he still has such a prominent position in the field of behavioural biology, that this special issue would have been incomplete without a contribution by him (Hogan, 2015). As the various papers in this issue demonstrate, Jerry Hogan continues to inspire scientists in different subfields of behavioural biology and psychology. Long may he continue!

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