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60 YEARS OF ANIMAL BEHAVIOUR

Anniversary Essay

All's well that begins Wells: celebrating 60 years of *Animal Behaviour* and 36 years of research on anuran social behaviour

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The scientific study of frogs and toads as important systems in behavioural ecology traces its roots to an influential review published in this journal 36 years ago (Wells 1977a, 'The social behaviour of anuran amphibians', *Animal Behaviour*, **25,** 666–693). In just 28 pages, Wells summarized the state of knowledge on important behaviours associated with anuran breeding and introduced an evolutionary framework 'for understanding the relationship between social behaviour and ecology' (page 666) that was largely lacking in earlier treatments of this group. Not only is Wells's review one of the most cited papers ever published in *Animal Behaviour*, it is also responsible for setting broad research agendas and shaping much of our current thinking on social behaviour in an entire order of vertebrates. As such, it is entirely appropriate that we honour Wells's review and its contributions to the study of animal behaviour in this inaugural essay celebrating 12 papers selected by the community as the most influential papers published in the 60-year history of *Animal Behaviour*. In our essay, we place Wells's review in historical context at the dawn of behavioural ecology, highlight the field's progress in answering some major research questions outlined in the review, and provide our own prospectus for future research on the social behaviour of anuran amphibians.

When many folks think of the 1970s they may conjure up images of such cultural dross as leisure suits, hot pants, disco, pet rocks and waterbeds. Watergate, gas lines and *Star Wars* may also come to mind. For those of us who study amphibian behaviour one needs to add the seminal review by Kentwood D. Wells (1977a, *Animal Behaviour*, **25,** 666–693) on *The Social Behaviour of Anuran Amphibians.* Already formally recognized as a citation classic by 1991 (Wells 1991), this article is one of the most significant publications of its kind from this era, and it certainly ranks among the most influential papers ever published in the pages of this journal. In fact, Google Scholar indicates the paper has been cited more than 1000 times, and the paper's influence on the field shows little sign of waning (Fig. 1). By publishing in *Animal Behaviour*, Wells's cogent review was probably more widely read, and thus likely more influential, than it might have been had it appeared in a taxon-specific journal.

Wells's review has played a critical role in the inception of scores of research programmes over the past 36 years, including those of all three authors of this essay. One reason for this influence is straightforward. Anuran amphibians display an extraordinary number of reproductive modes (Duellman & Trueb 1994; Haddad & Prado 2005; Wells 2007; Gomez-Mestre et al., in press), posing significant challenges and opportunities for researchers searching for evolutionary explanations. Wells's review made sense of much of this diversity from an adaptationist perspective within the emerging paradigm of behavioural ecology. This was quite an impressive achievement considering he completed the manuscript while still a graduate student (Wells 1991).

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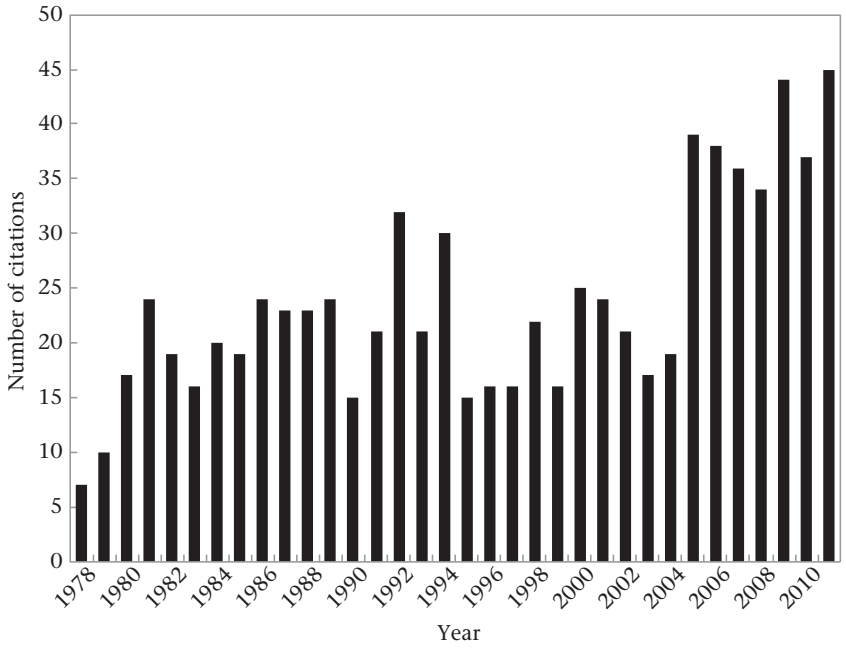

Figure 1. Number of citations to Wells's (1977a) paper, 'The social behaviour of anuran amphibians', each year between 1978 and 2011. Data are based on a total of 809 citations retrieved from a citation report generated using Thomson Reuters' Web of Knowledge v.5.7 on 28 August 2012.

Here we highlight and honour the landmark contributions of Wells's review to the ongoing study of anuran social behaviour in particular and the field of animal behaviour in general. As is obvious to anyone who has read Wells's review, or so much as glanced at his more recent (and far more massive) *The Ecology and Behavior of Amphibians* (Wells 2007), Wells has an extraordinary ability to synthesize vast amounts of information, provide a lucid summary, and articulate deficiencies and directions for future research. The broad areas addressed in his 1977 review include several aspects of sexual selection and mating systems, vocal behaviour, agonistic interactions and parental care. In this essay, we briefly describe the background and importance of the article in its historical context. Then we take up several of the research themes Wells covered, providing for each theme both a brief progress report on what we have learned since 1977 and a brief prospectus highlighting questions that require further study. For a comprehensive progress report and prospectus, we refer readers (of course!) to Wells' exhaustive review of these topics in his 2007 book (reviewed by Sullivan 2008). Many things have changed since 1977 when it comes to the study of anurans, including the scientific names of many species (Frost et al. 2006; Pyron & Wiens 2011). For consistency between Wells' review and this essay, we retain the species names used by Wells and, where appropriate, indicate recently modified nomenclature following Pyron & Wiens (2011).

HISTORICAL CONTEXT AND IMPORTANCE

The Beginning of Anuran Behavioural Ecology

The 1970s was an important decade for the field of animal behaviour. The work of Konrad Lorenz, Niko Tinbergen and Karl von Frisch, all early pioneers in ethology, was duly recognized with the 1973 Nobel Prize in Physiology or Medicine. The 1970s also witnessed the rise of behavioural ecology as a new paradigm for investigating the adaptive value and evolution of animal behaviours in their particular ecological and social contexts (Parker 2006). The linkage between ecological factors and the evolution of mating systems and other behaviours was receiving growing attention in the years prior to Wells's review (e.g. Orians 1969; Brown & Orians 1970; Fretwell & Lucas 1970). E.O. Wilson's (1975) tome *Sociobiology: the New Synthesis* highlighted much of this early work on mammals and birds, as did the contributions of Crook (1970), Brown (1975) and Alcock (1975). The brilliant insights of Trivers (1972) on parental investment had been recently published, and questions about the costs of signals used for mating were in the air (Zahavi 1975, 1977; Davis & Odonald 1976; Smith 1976). Of particular relevance in understanding mating systems was the framework articulated by Emlen & Oring (1977) illustrating how the spatial distribution of resources and temporal distribution of mates could influence the degree of polygamy. We would note that Stephen Emlen served on Wells's graduate committee at Cornell, and Emlen's review with Lewis Oring cited Wells's review as 'in press'. The near simultaneous publication of these two influential reviews highlights the fact that issues surrounding the ecology and evolution of mating systems was a 'hot topic' at the time (Wells 1991).

Although there was a wealth of information prior to 1977 on aspects of reproductive behaviour in amphibians (e.g. reviewed in: Bogert 1960; Rabb 1973; Salthe & Mecham 1974), most previous studies lacked the data necessary to test ideas rigorously within the context of the developing adaptationist paradigm of behavioural ecology. Fortunately, a shift to the behavioural ecology paradigm to investigate anuran social behaviour was to become the hallmark of many subsequent studies. To be certain, this shift was already underway in the late 1970s, as evidenced by the publication of Wells's own research on frogs (Wells 1976, 1977b, 1978a, b) as well as that of several contemporaries, including Stephen Emlen (Emlen 1976), Rick Howard (Howard 1978a, b, 1980), Nick Davies and Tim Halliday (Davies & Halliday 1977, 1978, 1979), among others (see Wells 1991). Wells's timely review facilitated and solidified the shift to studying anuran amphibians under the new behavioural ecology paradigm. In fact, we believe the single most important contribution of Wells's review was to place frogs and toads squarely at the leading edge of the behavioural ecology wave sweeping the field in the 1970s and early 1980s. As a result, anurans became and remain important model systems for testing theories and hypotheses in behavioural ecology.