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.

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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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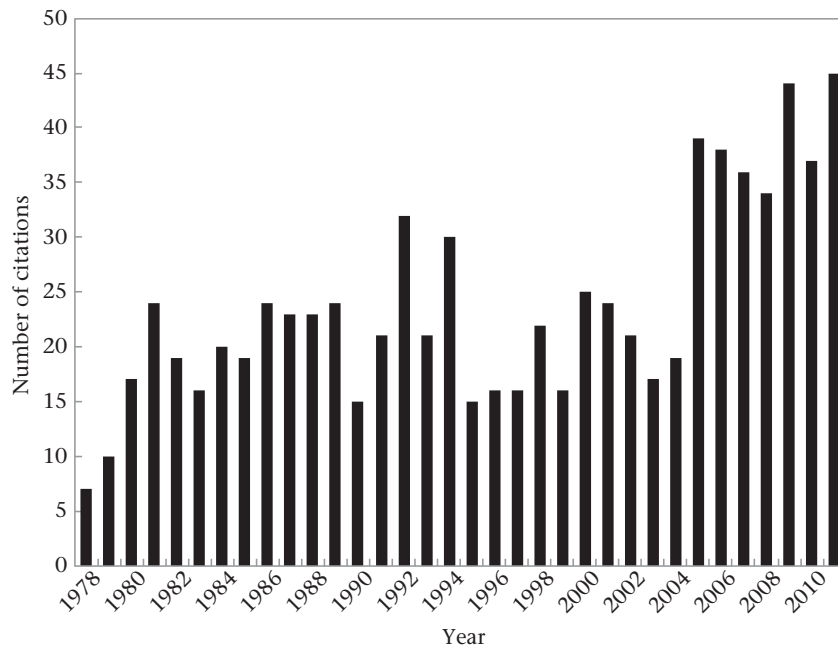 E-mail address: mbee@umn.edu (M. A. Bee).

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.

The Explosive–Prolonged Framework

The second most important contribution of Wells's review is that it established a simple and lasting framework for empirically investigating anuran social behaviour in a way that explicitly ties variation in the spatiotemporal distribution of reproductive females to the intensity and form of competition for mates. A major thesis of the review was that various biotic factors (e.g. predators) and abiotic factors (e.g. rainfall, pond hydroperiod) influence the temporal and spatial patterns of breeding activity in anurans; breeding activity patterns, in turn, are critical factors shaping the evolution of mating systems and the intensity of sexual selection (Wells 1977a, 2007). Wells's essay outlined a framework based on two fundamental temporal patterns of anuran reproductive behaviour, 'explosive' and 'prolonged' breeding. He was careful to emphasize that these patterns represent opposite ends of a temporal continuum. Although Wells typically discussed explosive and prolonged breeding as species-specific patterns, we now know that different populations of a species can differ with respect to explosive versus prolonged breeding (e.g. Sullivan 1989).

The most important characteristic of anurans conforming to the explosive breeding pattern was a short breeding period, for example, one lasting just a few days each year. Because such short breeding assemblages have high densities, females are consequently constrained in their ability to compare and then select a mate. Males often employ scramble competition for mates under such circumstances, although female choice can also operate (e.g. Howard & Palmer 1995; Howard & Young 1998). Behavioural plasticity in males occurs within and among aggregations of explosive breeders, with the likelihood of adopting a searching or satellite strategy over a calling strategy increasing with density (e.g. Sullivan 1982, 1989).

In contrast, prolonged breeders typically have breeding periods of one or more months. Gravid females may arrive at the breeding area over an extended time period and operational sex ratios can be highly male biased. Females have the *potential* then to evaluate and compare attributes of different males and this sets the stage for what can be intense male–male competition of a different kind. Males of prolonged breeders attempt to attract females using 'advertisement calls' (a term advocated in Wells's essay as a replacement for 'mating calls'), and females can choose a male based on characteristics of his calling behaviour, his defended territory, or both. The mating systems of prolonged breeders are most commonly described as lek polygyny or resource defence polygyny, although elements of both may be present within a single species at different times or in different places (e.g. Emlen 1976; Howard 1978b). Males of prolonged breeders typically engage in vocal competition that requires considerable expenditure of energy and modification of individual calls.

Wells's explosive–prolonged framework has become the lens through which we view anuran social and reproductive behaviour. Since 1977, there has been an explosion of knowledge about the behaviours considered by Wells, and his *Animal Behaviour* review is arguably the most important paper stimulating much of this progress. In 2013, we now have an extensive body of information not only describing but also explaining much of the rich diversity of anuran social behaviours associated with reproduction (reviewed in Wells 2007). In the following sections, we focus on a select subset of topics covered in Wells's (1977a) paper on which progress has been substantial and that we have pursued in our own research programmes.

A Brief Disclaimer

It is clearly not possible for us to address in this essay all aspects of the historical context surrounding Wells's review and its importance to the field. Nor can we cover all of the progress made since 1977 toward understanding anuran social behaviour. We freely acknowledge that other colleagues, were they writing this essay, might focus on different themes from Wells's review than those we have chosen. One such theme would no doubt be mating system evolution. Wells (1977a) generally described anuran mating systems in terms of scramble competition (typical of explosive breeders) and lek polygyny and resource defence polygyny (typical of prolonged breeders). Since 1977, we have learned a great deal more about anuran mating systems (Sullivan et al. 1995), which now include examples of sequential and simultaneous polyandry (reviewed in: Roberts & Byrne 2011; Byrne & Roberts 2012), as well as social and genetic monogamy (Caldwell 1997; Brown et al. 2010a). Other colleagues might focus more on what we have learned about how and why the intensity of sexual selection varies within and between populations and species, particularly as a function of temporal aspects of breeding (Sullivan 1985, 1986, 1987, 1989). Still others might choose to focus more on the evolution of alternative mating strategies, such as satellite male behaviour (e.g. Perrill et al. 1978; Sullivan 1982; Arak 1988; Leary et al. 2006; Humfeld 2008). While such themes are clearly interesting and important, we must refer readers to Wells's more recent treatment of anuran social behaviour for a review of these and other topics not covered here (Wells 2007).

CRITERIA FOR FEMALE MATE CHOICE

At present, very little is known about the criteria that females use to choose among potential mates in most animals (Trivers 1972), and virtually nothing is known about it in frogs. (**Wells 1977a, page 671**)

Progress

A major theme in Wells's review concerned the behavioural strategies male frogs use to gain access to mates. He speculated that female choice might be an important determinant of male mating success, particularly in prolonged breeders, and that males should try to make themselves more attractive to females. We return in a subsequent section to behavioural modifications males make to increase their attractiveness to females. Here, we discuss the criteria that females use to choose among potential mates. A number of excellent field studies, particularly on North American toads (e.g. Sullivan 1983a, b), have since confirmed Wells's speculation by showing that female preferences can exert consistent selection on male calling behaviour (reviewed in: Sullivan & Kwiatkowski 2007; Wells 2007). Perhaps more than for any other anuran social behaviour, tremendous advances have been made towards understanding the acoustic criteria female frogs use to select among advertising males. Wells's review no doubt stimulated a vast number of *empirical* studies on this topic, and we refer readers to a number of excellent reviews that already treat these empirical studies in detail (reviewed in: Gerhardt 1988, 1994; Ryan & Keddy-Hector 1992; Andersson 1994; Sullivan et al. 1995; Ryan 2001; Gerhardt & Huber 2002; Sullivan & Kwiatkowski 2007; Wells 2007). For brevity's sake, we choose to highlight two important *conceptual* advances in the general study of mate choice for which research on frogs was particularly instrumental.

The first involves a conceptual framework proposed by Gerhardt (1991; reviewed in Gerhardt & Huber 2002) that explicitly considers the criteria that female frogs use to choose among potential mates. Based on his extensive work with North American treefrogs, Gerhardt (1991) suggested call properties could be placed along a continuum of within-male variability between 'static'

properties (low variation within males) and 'dynamic' properties (high variation within males). Static properties tend to be physically or physiologically constrained; they often represent useful cues to species identity; and they tend to be subject to female preferences resulting in stabilizing or weakly directional selection. Two common static properties of frog calls include spectral properties (e.g. dominant frequency) and pulse rate. Dynamic properties, in contrast, tend to be more variable within individuals over time because they are condition dependent, vary according to social context, or both. Gross temporal properties, such as call rate and also call duration in species with pulsatile calls, tend to be categorized as dynamic properties. When females have directional preferences, these most often favour extreme values of dynamic properties (e.g. longer calls, faster call rates; Ryan & Keddy-Hector 1992). As Gerhardt (1991) pointed out, comparisons between female preference functions and statistical descriptions of signal variation not only within individuals, but also among individuals within populations and among populations, provides a robust method for predicting evolutionary changes in signals in response to female mate choice. Although it has been criticized (Reinhold 2009), the paper by Gerhardt (1991) outlining criteria for female mate choice in North American treefrogs has been cited over 300 times (according to Google Scholar), testifying to the widespread adoption of this conceptual framework by the broader animal behaviour community.

A second conceptual advance in the study of mate choice furthered by investigating female frogs is the sensory exploitation model of sexual selection (Ryan et al. 1990; Shaw 1995; Ryan 1998). The sensory exploitation hypothesis holds that signals can be evolutionarily favoured because they tap into pre-existing preferences or sensory biases of receivers that evolved in some other context. Particularly important in the development of the hypothesis was work by Mike Ryan, Stan Rand and their colleagues integrating sensory physiology and phylogenetic analyses to investigate female mate choice in the túngara frog, *Physalaemus pustulosus* (*Engystomops pustulosus*), and its close relatives (Ryan et al. 1990; Ryan & Rand 1990, 1993, 1995, 1999; Wilczynski et al. 2001). Male túngara frogs produce a call consisting of an obligate 'whine' that can be followed by one or more facultative 'chucks'. Females prefer calls with chucks. Behavioural and neurophysiological experiments combined with phylogenetic reconstructions suggested the chuck evolved to exploit a pre-existing preference. While the general sensory exploitation hypothesis remains viable, increased taxon sampling and a more recent phylogeny have cast some doubt on the ability of this hypothesis to explain the evolution of chucks in túngara frogs (Ron 2008). Regardless of whether chucks evolved via sensory exploitation, research on female mate choice in túngara frogs continues to have profound impacts on our understanding of fundamental issues in animal behaviour (e.g. Baugh et al. 2008; Akre & Ryan 2010; Akre et al. 2011).

Prospectus

Despite extraordinary progress, many fascinating and important questions about mate choice in frogs remain to be answered. Here, we highlight two questions (among many possibilities) that should be addressed in future research. First, given that male mating signals are perhaps often multimodal, how do the criteria females use for mate choice in one modality compare with other modalities, and how do preferences for different signal components interact in choosing a mate? Second, how do male signals and female preferences for specific signal properties respond to realistic natural and sexual selection pressures encountered in the natural environment?

Historically, acoustic signalling has been the focus of mate choice studies in frogs. This trend is likely to continue as we learn

more about the vocal repertoires of newly described species (e.g. Bee et al., in press) and with the exciting recent discovery of ultrasonic signalling and hearing in frogs (Feng et al. 2006; Arch et al. 2008, 2009; Feng & Narins 2008). Other sensory modalities, however, must not be neglected. Many frogs have abandoned or significantly reduced their efforts at acoustic signalling in favour of visual signalling (reviewed in Hödl & Amézquita 2001), yet we still know very little about female mate choice in these systems. Recent work in acoustically signalling species is also highlighting the potential importance of visual cues in anuran mate choice, not only in terms of overall colour patterns in diurnal species (Summers et al. 1999; Richards-Zawacki et al. 2012), but also those present in the pulsating vocal sacs of primarily nocturnal ones (Taylor et al. 2007, 2008, 2011; Cummings et al. 2008). Chemical signalling also could be more important in anuran mate choice than previously believed (Wabnitz et al. 1999; Pearl et al. 2000; Brizzi et al. 2002; Byrne & Keogh 2007). Some frogs even have conspicuous chemical glands on their vocal sacs (Drewes 1984), suggesting the tantalizing possibility of *tri*modal signalling in some species. Do preference functions for static and dynamic visual, chemical and multimodal signals conform to Gerhardt's (1991) ideas about acoustic signals? Might visual signals or signal components commonly evolve to exploit pre-existing sensory biases that evolved in other contexts, such as prey detection? New technology, such as robotics, provides the means of answering such questions in future field and laboratory tests (Narins et al. 2003, 2005; Taylor et al. 2008).

While male mating success often depends on chorus attendance, many field studies have now demonstrated selection on male signals as a result of female choice (e.g. Sullivan 1983a, b, 1987; Cherry 1993; Wagner & Sullivan 1995; Grafe 1997; Smith & Roberts 2003; Friedl & Klump 2005; Friedl 2006). Selection on male calling behaviour resulting from female choice most commonly favours greater calling activity (e.g. higher rates of calling) and rarely size-related call properties, such as dominant frequency. Selection on other call properties (e.g. pulse rate) is seldom measured (but see Friedl 2006). Furthermore, we know that female preferences can lead to direct benefits (e.g. increased fertilization success, Robertson 1990; decreased search costs, Grafe 1997) and indirect benefits (Welch et al. 1998). However, demonstrating that selection on signals exists and that preferences lead to benefits tells only an incomplete story about the potential for evolutionary change in signals and preferences for the following reason. We know next to nothing about the magnitude of additive genetic variance and the potential for gene × environment interactions underlying the expression of signals and preferences. As an upper-bound estimate of heritability, several studies have measured the 'repeatability' (sensu Boake 1989) of male calling performance (reviewed in Gerhardt & Huber 2002), but we generally still lack equivalent data on female preferences (e.g. Jennions et al. 1995). To our knowledge there are no published data from quantitative genetic studies estimating the actual heritabilities of male calling behaviours and female mating preferences. Future studies should aim to fill this critical gap in our knowledge of anuran social behaviour.

ACOUSTIC INTERACTIONS AND CHORUS ORGANIZATION

…there have been few attempts to examine the evolutionary implications of acoustic interactions between individuals in a chorus. (Wells 1977a, page 673)

Progress

A significant portion of Wells' review dealt with acoustic interactions among male frogs in choruses, particularly in prolonged

breeders. He discussed a range of issues related to call timing, such as synchronous chorusing, overlap avoidance and chorus leadership. Wells's treatment built not only on the limited body of anuran research available at the time but also on the more substantial work on insects that had recently been reviewed by Otte (1974) and Alexander (1975). How males time their calls relative to those of other males in the chorus may serve ultimately to enhance a male's ability to attract a mate, although the proximate basis for increased mate attraction can vary (Höbel & Gerhardt 2007). Since 1977, considerable progress has been made towards understanding the dynamics of vocal interactions in choruses, as well as both ultimate and proximate explanations for call-timing behaviours. This work has involved recording and monitoring interacting males, playback experiments with males and phonotaxis tests with females. What we have discovered is that call-timing behaviour can be significantly more complex than was appreciated when Wells wrote his review.

Chorus environments are replete with sources of acoustic interference, such as the background din created by the aggregate calling of chorus members as well as the individual vocalizations of neighbours. How anurans successfully communicate in such acoustically cluttered conditions has been the focus of extensive research on both signallers and receivers (reviewed in Bee 2012; Schwartz & Bee, in press; Vélez et al., in press). Reductions in signal overlap through call-timing adjustments by males can improve the ability of females to detect, discriminate among and localize call sources. Adjustments can occur on both coarse timescales (e.g. tens of seconds to minutes) and fine timescales (e.g. milliseconds).

In a classic study of coarse-scale call timing, Littlejohn & Martin (1969) demonstrated how two Australian myobatrachids alternate bouts of chorusing, and subsequent reports have described additional cases of coarse-scale call timing involving interspecific inhibition (e.g. Mac Nally 1982; Littlejohn et al. 1985; Sun & Narins 2005). For example, Schwartz & Wells (1983a, b) observed a comparable pattern of bout alternation between two Panamanian hylids and demonstrated how this behaviour can improve the probability of attracting a female. Most recently, Susan Herrick (unpublished data), a doctoral student of Wells, has found that male green frogs, *Rana clamitans*, avoid calling during bouts of vocal activity by male bullfrogs, *Rana catesbeiana*. In some species, the timing of calling by heterospecifics in mixed-species choruses might provide information about relative safety following recent exposure to predators (Phelps et al. 2007).

A tremendous body of data is now available on fine-scale adjustments in call timing (Klump & Gerhardt 1992; Gerhardt & Huber 2002; Höbel & Gerhardt 2007; Wells & Schwartz 2007; Schwartz & Bee, in press). In some cases, the precision of response timing can only be described as remarkable (Schwartz & Wells 1985; Zelick & Narins 1985; Ryan 1986; Schwartz 1993; Grafe 2003). For example, males of *Hyla microcephala* (Schwartz & Wells 1985; Schwartz 1993) and *Kassina kuvangensis* (Grafe 2003) can rapidly adjust note timing such that notes of overlapping multinote calls interleave rather that interfere. Males of *Eleutherodactylus coqui* can exploit very brief drops in background sound level to reduce their susceptibility to acoustic interference (Zelick & Narins 1985).

One of the most interesting and important findings from anuran signal-timing research in the last couple of decades is that males show so-called 'selective attention' to subsets of other callers, as revealed by associations between the spatial distribution of males and the relative timing of their calls. Males of some species modify call timing such that it reduces overlap with just their nearest or loudest neighbours while allowing their signals to overlap those of other, more distant males that they still certainly can hear (Brush & Narins 1989; Schwartz 1993). In other species there is greater overlap among the less widely separated males (Schwartz et al. 2002; Simmons et al. 2008; Bates et al. 2010). Males may also show a dynamic pattern of selective attention when it comes to call timing (Greenfield & Rand 2000). At an ultimate level, female preferences may impose selection on fine-scale call-timing behaviours. In some species, for example, females discriminate in favour of leading calls and thus a male that calls shortly after another may be at a disadvantage (Dyson & Passmore 1988a, b; Howard & Palmer 1995; Grafe 1996; Greenfield 1997; Greenfield & Rand 2000; Bosch & Márquez 2002; Tárano & Herrera 2003). That such a leader preference can be a manifestation of a true psychoacoustic 'precedence effect', whereby females perceptually *localize* the source of the following signal at the position of the leader, has only recently been demonstrated (Marshall & Gerhardt 2010).

Prospectus

Frog choruses truly are dynamic environments for social communication, and we suggest the following directions for future research on these wonders of nature. First and foremost, we advocate the continued development and deployment of new technology to study frog choruses. Until recently, efforts at understanding chorus interactions have been limited to recordings of interactions occurring over relatively small spatial scales involving just a few individuals (e.g. dyadic or triadic interactions among neighbours). Recording interactions over large spatial (and also temporal) scales was too technologically challenging, labour intensive, or both. New technological advances promise to change all this by enabling researchers to explore the complexity of chorus organization in ways only imagined in the late 1970s (Schwartz 2001; Jones & Ratnam 2009; Bates et al. 2010; Mizumoto et al. 2011). Particularly important in this regard are new microphone arrays that not only localize calling males in a chorus, but also recover their original signals for subsequent acoustical analyses (Jones & Ratnam 2009). This is no small technical feat! Future studies should exploit this remarkable new technology to understand better how frog choruses function in the contexts of communication networks (Grafe 2005; Phelps et al. 2007) or social networks (Krause et al. 2009) of signalling males and how females navigate these complex networks when selecting mates. Studies using multichannel recordings and monitoring would enable us for the first time to assess the spatial extent of fine-scale call-timing interactions and their dynamics (i.e. if and how they change) during prolonged periods of chorusing.

Second, many questions also remain for future research into the mechanisms, function and evolution of call-timing interactions in the context of networks of signallers. For example, how widespread is selective attention among species? In the lingo of Greenfield & Rand (2000), what ecological, social and historical factors determine the 'rules' used by species that have selective attention, and how and why might these rules differ across species? Interactive playback studies will be needed to answer these sorts of questions, but they will need to be expanded to involve broadcasts from multiple speakers that better simulate the acoustics near calling males. The utility of interactive playbacks (Schwartz 2001; Goutte et al. 2010), in which a call synthesizer or computer can be instructed to respond selectively to certain call elements with specified latencies (Narins 1982; Schwartz 1993), has already been demonstrated. The true test of whether or not we understand the rules of selective attention and call-timing interactions will be in showing that we can inject artificial callers (e.g. speakers or perhaps even robotic frogs) into a chorus that can effectively play by the rules to attract mates.

Finally, characterization of vocal interactions in choruses must be followed up with tests of hypotheses about female preferences

and auditory discrimination abilities. Such studies have been conducted on a relatively small number of species (Gerhardt & Huber 2002; Wells 2007; Vélez et al., in press), and taxonomic coverage must be broadened and acoustic realism increased. The alternative is to be satisfied with facile, and perhaps, erroneous ultimate explanations for male behaviour. Take, for instance, the hypothesis that females prefer males that produce 'leading' calls. If we find that call-timing relationships between neighbouring males are not particularly stable (e.g. Grafe 2003; Höbel 2011), how sensitive are females to these changes? It could be that discrimination in favour of leading males by females in the laboratory only rarely contributes to mating success in the field. More work is also needed on the perceptual consequences of call overlap (e.g. masking and interference) in species of frogs with different types of calls (e.g. amplitude modulated, frequency modulated, constant frequency, simple, complex). Other areas ripe for additional research include the influence of call timing on both aggressive and nonaggressive interactions among males, as well as the adaptive significance of punctuated bouts of chorusing (Schwartz 1991; Schwartz et al. 1995; Phelps et al. 2007; Dapper et al. 2011).

AGGRESSION AND SOCIAL SPACING

In many anurans, there is some degree of spatial separation between calling males, and the role of vocalizations in maintaining this separation has received considerable attention. (Wells 1977a, page 675)

Progress

A third major theme in Wells's review covered aggressive behaviour and its role in social spacing in choruses. He described the considerable previous work on aggressive calls and other display and fighting behaviours used to defend locations in space. Wells made clear the important distinctions between males that defend calling sites in resource-based leks (e.g. by excluding other nearby males to reduce acoustic interference) and males that defend territories containing resources needed for survival, oviposition or courtship. He also raised questions about how and why males choose particular calling sites or territories, and the consequences of those choices in terms of future mating success. We still lack general answers to these questions. Although Wells provided few specific directions for future research on aggression and social spacing, his lucid treatment of these topics provided a firm foundation for the significant progress made since the 1970s. The emerging theme of this research is that frogs show remarkable behavioural plasticity in aggression that depends on social context.

Wilczynski & Brenowitz (1988) first showed that call amplitude (which decreases with distance from the source) functions as an acoustic cue for maintaining nonrandom spacing in frog choruses (see also Brenowitz 1989; Gerhardt et al. 1989). In many frogs, males switch from producing advertisement calls to producing distinctly different aggressive calls when the amplitude of another male's calls exceeds an 'aggressive threshold' (i.e. the minimum call amplitude eliciting aggressive responses; Rose & Brenowitz 1991). However, in other species, males can dynamically vary their aggressive responses towards intruders by producing graded vocalizations that become progressively more like aggressive calls and less like advertisement calls as intruders get closer (Schwartz 1989, 1993; Wagner 1989b; Wells 1989; Grafe 1995; Owen & Gordon 2005; see also Stewart & Rand 1991).

In Pacific treefrogs, *Pseudacris regilla* (Brenowitz 1989; Rose & Brenowitz 1991, 1997; Brenowitz & Rose 1994, 1999), and spring peepers, *Pseudacris crucifer* (Marshall et al. 2003; Humfeld et al.

2009), males have aggressive thresholds that depend on local density in a chorus, and hence the proximity of nearby neighbours. Early on nights of chorusing, when only a few males have begun to call, males will interact aggressively over much larger intercaller distances than they do just a few hours later when many more males have joined the chorus and intercaller distances have contracted considerably. In both species, repeated playbacks of a new neighbour's calls elevated aggressive thresholds and subsequent cessation of calling by that neighbour allowed thresholds to return to baseline levels. Hence, a form of short-term behavioural plasticity enables males to adjust their aggressiveness to accommodate the arrival and departure of other nearby males in the chorus, thereby tracking dynamic changes in the local density of signallers on short timescales.

While some aspects of anuran signalling dynamically depend on social context, others generally appear more constrained. Spectral call properties, for example, are negatively correlated with male body size because their larger vocal apparatus constrains larger males to produce lower-frequency sounds (Martin 1972; Gerhardt & Huber 2002). Playback studies have revealed that receivers can exploit this size constraint to make adaptive decisions about escalating aggressive conflicts. Male frogs often tend to retreat or become noncalling satellites in response to low-frequency calls simulating large opponents, whereas they are more likely to produce encounter calls or to attack sources of higher-frequency calls simulating small rivals (Davies & Halliday 1978; Arak 1983; Robertson 1986; Given 1987; Wagner 1989a). Interestingly, however, some frogs appear to ignore the size–frequency correlation when it comes to responding to intruders (Bee 2002; Burmeister et al. 2002). In some species, males actually have limited abilities to modify the spectral properties of their calls (see Lardner & bin Lakim 2002 for an exceptional case). In most such species, males usually lower fundamental frequency or shift energy to lower harmonics (Wagner 1989a, 1992; Bee & Perrill 1996; Bee et al. 1999, 2000; Given 1999; Bee & Bowling 2002). Such findings have led to the consideration that the 'pitch' of frog calls may not always function as an honest signal of size and fighting ability (reviewed in Searcy & Nowicki 2005).

Whatever their function in size assessment by male frogs, spectral call properties impart individual distinctiveness to anuran vocalizations (Bee & Gerhardt 2001a; Bee et al. 2001, 2010; Pröhl 2003; Bee 2004; Gasser et al. 2009). At least one species exploits this information to identify territorial neighbours. Davis (1987) showed that territorial male bullfrogs, *R. catesbeiana*, a prolonged breeder that defends oviposition sites (Howard 1978b), responded more aggressively to the calls of strangers compared with those of neighbours. Moreover, as shown in many songbirds (reviewed in Stoddard 1996), Davis (1987) found that male bullfrogs associated a neighbour's calls with the correct location of its territory. This form of social recognition, which can only come about through learning, is commonly referred to as the 'dear enemy' effect (reviewed in Temeles 1994). In subsequent studies of this species, Bee & Gerhardt (2001a, b, c, 2002; Bee 2003a) showed both that males learned about size-related variation in spectral properties to identify new neighbours and that reduced aggression towards neighbours depended on a form of long-term, stimulus-specific behavioural plasticity. Work in three other species suggests that neighbour–stranger discrimination might be more common among frogs than previously appreciated (Bourne et al. 2001; Lesbarrères & Lodé 2002; Feng et al. 2009), although one study failed to find evidence for this form of social recognition in a territorial poison frog (Bee 2003b).

Prospectus

The discovery that learning mediates social recognition in territorial frogs is perhaps one of the most significant (and least

anticipated) advances in our understanding of anuran social behaviour since the publication of Wells's review. Such discoveries are important because they open up completely new lines of inquiry. This is certainly the case for social recognition in frogs. Many fundamental questions remain to be addressed in future research, and we offer the following directions to guide these efforts.

First, we have little notion of how taxonomically widespread this form of social recognition is among anurans and what sorts of social and ecological factors favour its evolution. So far, the behaviour has been reported to occur in only four species in two families (Ranidae and Dendrobatidae). Additional field playback tests with more species reporting both positive and negative (see Bee 2003b) results are needed to evaluate patterns of presence and absence across species. Temeles (1994) has made cogent arguments outlining social and ecological conditions (e.g. defence of breeding/ multipurpose territories versus feeding territories) that select for territorial neighbours that behave as dear enemies. His hypothesis, however, has never been tested in a broad phylogenetic framework. The variety of things aggressively defended by frogs (e.g. home ranges, burrows, calling sites, courtship areas, oviposition sites; Wells 2007), the diversity in mating systems across species, and the plasticity of mating systems within some species, make frogs one of the best taxonomic groups for testing hypotheses about factors that favour the evolution of social recognition. Along these lines, it will be important to investigate the costs and benefits of both learning to recognize neighbours and being a recognizable neighbour. Considered within the framework of a phylogenetic hypothesis, we predict that social recognition in frogs has almost certainly had multiple independent origins.

Second, it will be important to test the hypothesis that social recognition selects for greater information content of calls in terms of individual distinctiveness. Such signal evolution has occurred, for instance, in colonial swallows in the context of parent−offspring recognition (Beecher 1989a, 1991). Addressing this issue will require comparative studies of the information content of signals (e.g. in 'bits'); one recommended approach was outlined by Beecher (1989b). Ideally, one should compare closely related species that do and do not show social recognition. Given the current paucity of relevant studies, however, an alternative first approach might be to examine a broad range of taxa to estimate variation in the information content of anuran signals.

Third, it will be important to test hypotheses about the mechanisms underlying the long-term, stimulus-specific plasticity associated with dear enemy behaviour. Could habituation, as a form of learning, account for social recognition in frogs, or are more complex mechanisms required (Bee & Gerhardt 2001b; Bee 2003a)? Studies using immediate early gene expression (Mello et al. 1995) and neural recordings (Gentner & Margoliash 2003) have successfully probed questions about the neural mechanisms of social recognition in songbirds, but we still lack such studies of frogs. In addition, it will be important to uncover the relationship between the long-term, stimulus-specific plasticity demonstrated in bullfrogs and the short-term plasticity in aggressive thresholds demonstrated in Pacific treefrogs and spring peepers. Are these distinctly different processes, or do they represent different places along a more generalized continuum of behavioural plasticity based on similar underlying physiological mechanisms?

Questions broadly similar to those already mentioned in this section also should be addressed in future studies of graded aggressive vocalizations and assessments of size and fighting ability. What are the proximate and ultimate reasons that some frogs have these social behaviours while others do not? Frequency-based size assessment in frogs has found its way into textbooks as a canonical example of honest signalling in animal contests (Krebs & Davies 1993; Bradbury & Vehrencamp 1998; Alcock 2005; Davies et al. 2012). But the real story will certainly be far more interesting than any of these textbook accounts. It is imperative that we understand why some frogs appear to ignore size-related cues, while still others actively lower the pitch of their calls during agonistic encounters, as one might predict if they were acoustically bluffing. Evaluating the status of the bluffing hypothesis in more frog species will shed important light on the evolution of assessment and signal honesty (Searcy & Nowicki 2005).

The advantage of studying aggressive social behaviours in frogs is that no matter what the behaviour, some frogs seem to do it and others do not. This remarkable diversity is precisely the state of affairs that should excite comparative biologists, because it lends itself to using a particular taxonomic group to uncover the mechanisms, functions and evolution of behaviour.

CALLING ENERGETICS

…very little is known about the energetic costs of various types of behaviour in frogs. (**Wells 1977a,** page 670)

Progress

Considerations of the costs of mate attraction signals have featured prominently in behavioural ecology since the early work of Zahavi (1975, 1977). Competition among males to attract mates, especially when manifest in vocal behaviour, can make profound demands on energy use. Although this may seem obvious now, in 1977, there were virtually no empirical data on this topic. Wells's review made explicit this gap in knowledge about anuran signalling. Since 1977, Wells and his collaborators and students, along with many others, have made enormous progress remedying this situation. For example, studies related to the energetics of vocal behaviour in frogs have now explored the relationship between calling behaviour and both muscle morphology (at a range of scales) and biochemistry (Marsh & Taigen 1987; Bevier 1995a, b; Ressel 1996, 2001) and investigated the role of energetic constraints and nutritional status (Murphy 1994; Schwartz et al. 1995; Marler & Ryan 1996), seasonal effects (Kiss et al. 2009) and hormonal influences (Marler & Ryan 1996; Emerson 2001; Moore et al. 2005; Leary 2009). Studies have also compared tropical and temperate anurans (e.g. Ressel 2001), and similar relationships between calling rate and calling muscle attributes such as lipid reserves, standardized mitochondrial volume and relevant enzyme activity levels are evident (Bevier 1995a, b; Ressel 1996, 2001; Wells 2007).

We also have learned how differences in energetic costs associated with the broad temporal patterns of breeding activity discussed by Wells (1977a) can be shaped by abiotic as well as biotic factors. For example, the threat of predation and the availability of food can interact with the energetic cost of male advertisement to influence whether individuals adopt explosive, prolonged episodic or continuous chorusing (McCauley et al. 2000). Patterns of calling behaviour and fuel use (carbohydrate and fat), the relative importance of energy sources (reserves and food), and constraints on vocal activity imposed by the associated morphological, physiological and biochemical machinery can differ based on the time course of breeding activities (Wells 2007). In both tropical and temperate zone anurans, different strategies may be exploited by different species even under similar environmental conditions (Bevier 1997; Wells & Bevier 1997).

Rates of oxygen consumption during intense vocal activity can exceed that during rest by a factor of 20 in some species (Wells 2007), and calling can represent the most energetically demanding behaviour of male frogs, well exceeding demands of

forced locomotory exercise. As indicators of the competitive environment, the social and acoustic milieu can impact metabolic rates dramatically through their effect on male calling behaviour. For example, males of *P. pustulosus* (Ryan 1985) and *Hyla microcephala* (*Dendropsophus microcephalus*) (Schwartz & Wells 1985) may increase call rates if the number of calls heard from nearby males increases. To enhance their attractiveness to females, they also add more secondary notes to their calls under such circumstances. Metabolic rate rises in a linear fashion with call rate (or note rate in *H. microcephala*) and can reach very impressive levels. For example, in *H. microcephala*, VO_2 max levels (a measure of maximum aerobic power) can exceed 40 ml of O_2/kg/min for males giving over 100 notes/min (Wells & Taigen 1989); these levels of VO_2 max match or exceed those achievable by healthy men and women.

Some nifty abilities have evolved with implications for such high energetic demands of calling. For example, the energetic cost of adding chuck notes to their whines for males of *P. pustulosus* is essentially nil, evidently because chuck production is the result of passive vibration of a structure in the vocal apparatus rather than muscular effort, per se (Gridi-Papp et al. 2006). Male *Hyla versicolor* also modify their calling behaviour in response to their acoustic environment in a way that doesn't noticeably alter metabolic rate. They accomplish this by lowering call rate as they elevate the number of pulses per call and thus maintain a relatively stable 'pulse effort' (Wells & Taigen 1986) while simultaneously broadcasting signals that females may find more appealing (Klump & Gerhardt 1987). Male *H. microcephala* also show a neat behaviour. To reduce the chance that very high rates of note production deplete trunk muscle glycogen reserves during hours of chorusing in an evening, males structure their calling into alternating bouts of activity and quiet (Schwartz et al. 1995).

Prospectus

As Wells made clear in his review, there is considerable interspecific variation in patterns of male vocal behaviour. Nevertheless, given there are more than 6000 species of anurans, the number of species for which both calling behaviour and energy use have been examined is still quite small, phylogenetically limited, and involves mostly those species in which males call vigorously (Wells 2007; Wells & Schwartz 2007). We here suggest two avenues for future research on calling energetics directed towards understanding the causes and consequences of variability in energy use within and among species.

First, although we see a number of interesting correlations between various social and reproductive behaviours and aspects of calling energetics across species, we do not yet know the direction of causation. For example, do the attributes of a particular species tied to relevant muscle function determine the levels to which males of that species are vocally active? Or is it the other way around? A comparative approach within a phylogenetic framework will be needed to assess patterns of energy use, adaptations and constraints on behaviour among anurans with different vocal and reproductive strategies.

Second, to understand the evolution of male signals and female preferences, we need to understand factors related to how individual variation in energy use influences individual variation in calling performance and ultimately mating success. Energy use is clearly tied to condition, and the use of condition-dependent, dynamic call properties (e.g. call rate) in mate choice is widespread in anurans (Gerhardt 1991; Ryan & Keddy-Hector 1992; Sullivan & Kwiatkowski 2007). To what extent might heritable differences in structural and biochemical attributes associated with energy use represent an important linkage, in terms of genic capture (Rowe & Houle 1996), between overall condition and heritable differences in condition-dependent calling behaviours? Efforts directed towards answering such questions should be coupled to those advocated above for estimating heritability of calling behaviour.

PARENTAL CARE

Unfortunately, most accounts of parental care in anurans are anecdotal, and the details of the behaviour are unknown for most species… The selective factors that favour parental investment by one sex or the other have not been explored. **(Wells 1977a, page 681)**

Progress

The evolution of parental care has been a focal point of interest in behavioural and evolutionary ecology for decades, and the subject had attracted substantial theoretical attention before Wells's review (e.g. Williams 1966; Trivers 1972). Yet when Wells wrote his review, there had been few attempts to put the parental behaviour of frogs into a hypothesis-testing framework. Wells's genius was to firmly place anuran parental care in the theoretical framework of behavioural ecology, and to make explicit arguments concerning the ecology and evolution of parental care in this group that could be used to develop testable hypotheses. Furthermore, Wells did not just talk the talk: he also walked the walk in developing specific hypotheses himself and going to the tropics (where most parental anurans live) to test them (e.g. Wells 1978b, 1980, 1981).

Consider, for example, work on the green poison frog, *Dendrobates auratus*. Based on anecdotal reports, Trivers (1972), in his classic paper on parental investment and sexual selection, suggested that sex-role reversal might occur in this species. Wells (1977a) predicted that high levels of paternal care in frogs might drive the evolution of female competition for mates, and carried out fieldwork on *D. auratus* that confirmed this prediction (Wells 1978b). Although later research revealed this species has not evolved true sex-role reversal (Summers 1989; Wells 2007), the species turned out to provide an early example of the effect of sexual conflict on mating systems, a subject that has become a focal point of interest in behavioural ecology (Davies 1989; Summers 1992b; Fricke et al. 2010). This combination of grounding in current theory, development of testable hypotheses and hard-core fieldwork inspired many other researchers (including one of us) to pursue this approach to the study of parental care in anurans.

The ecology and evolution of parental care (and the relationship of parental care to mating systems and sexual selection) have attracted increasing attention since Wells wrote his review (and a later review focused specifically on parental care: Wells 1981). For example, while little was known about the costs or benefits of parental care prior to 1977, substantial progress has been made since. In terms of benefits of parental care, numerous studies have demonstrated increases in egg and larval survivorship in a variety of contexts, including avoidance of desiccation (e.g. Hayes 1991; Bickford 2004; Vockenhuber et al. 2009), protection against attacks from conspecifics (e.g. Kluge 1981; Stewart & Rand 1991; Burrowes 2000; Rogowitz et al. 2001) and predators and pathogens (e.g. Simon 1983; Townsend et al. 1984; Cook et al. 2001; Prado et al. 2002; Bickford 2004). Costs of parental care to adults have been demonstrated in a variety of species, in terms of reduced food intake (e.g. Simon 1983; Townsend 1986), energetic costs (e.g. Simon 1983; Townsend 1986), reduced mating opportunities (e.g. Wells 1980; Kluge 1981; Townsend 1986; Cheng & Kam 2010) and

increased risk of predation (e.g. Cook et al. 2001). Furthermore, researchers have begun to quantify levels of genetic relatedness between adults and their putative offspring, which is obviously important when evaluating the costs and benefits of parental care (Brown et al. 2010a; Chen et al. 2011). The attention focused on costs and benefits of parental care in frogs after Wells's review is no doubt related to the emphasis he placed on evaluating the ecology and evolution of anuran parental care in a cost−benefit framework. Complementing research on ultimate mechanisms, there also has been increased attention to the proximate mechanisms whereby frogs carry out complex patterns of parental care, such as tadpole transport, deposition and feeding (e.g. Stynoski 2009; Schulte et al. 2011).

Further interest in many other aspects of anuran reproductive strategies associated with parental care was stimulated by Wells's review. For example, parental effort and parental care are valuable resources, and this opens up the possibility of various forms of reproductive parasitism and related alternative strategies (e.g. Kok & Ernst 2007; Brown et al. 2009). Increased attention also has been paid to investigating factors predicted to correlate with parental care on the basis of ecological and evolutionary considerations, such as large egg size (e.g. Shine 1978; Nussbaum & Schultz 1989; Summers et al. 2006, 2007).

The evolution of parental care has been (and remains) a highly contentious subject in the field of animal behaviour, yet since Wells's review, most researchers that have focused on the general evolution of parental care have been careful to consider data from frogs and other amphibians in developing their arguments (e.g. Clutton-Brock 1991; Reynolds et al. 2002; Perry & Roitberg 2006). Furthermore, the natural history of parental care in some groups of frogs has provided the inspiration and opportunity to develop new general insights into parental care evolution. For example, observations on the interaction of parental care and sexual conflict in Neotropical poison frogs led to the development of game-theoretic models that demonstrate how sexual conflict associated with a cost of polygyny can drive evolutionary changes in the form of parental care (Summers & Earn 1999). These models may be relevant to similar phenomena in other taxa.

With respect to the relationship between parental care and mating systems, much progress has been made since Wells's review. In the Neotropical poison frogs, careful studies of multiple species differing in patterns of parental care have revealed differences in mating systems that correspond to differences in sexual selection consistent with general arguments presented by Trivers (1972) concerning the influence of relative parental investment, and by Davies (1989) concerning sexual conflict over parental care. Species in which female parental investment predominates (e.g. *Dendrobates (Oophaga) pumilio*) show high levels of male−male competition and female selectivity about mating (e.g. Summers 1992a; Pröhl & Hödl 1999). Species with predominantly male parental care show both male and female competition for mates in some cases, especially when the quality of male parental care is variable and related to number of mates (e.g. Summers 1989, 1990). This makes sense in the context of sexual conflict over parental care (Summers 1992b). While the evolution of male parental care has apparently not led to sex-role reversal in poison frogs (as predicted by Trivers 1972), there is evidence that high levels of parental care may have driven classic sex-role reversal in the midwife toad, *Alytes muletensis* (Bush & Bell 1997). In some species of poison frogs, both males and females invest substantially in parental care and maintain pair bonds (Caldwell 1997). Recent research indicates that a key ecological factor, the size of breeding pools, was crucial in driving the evolution of both biparental care and social and genetic monogamy in at least one species of poison frog (Brown et al. 2008, 2009, 2010a).

Prospectus

While progress so far towards understanding parental care in frogs has been considerable, we suggest four directions for future research on this topic. First, although not necessarily 'sexy' or 'hypothesis driven', we still need more basic natural history observations and descriptions of parental care behaviours in frogs. On a purely descriptive level, we know far more now about parental care in frogs than we did when Wells wrote his original essay. Yet each of the subjects discussed above remains understudied, and there is a pressing need for further studies on all these topics in frogs. Basic descriptions of parental care are lacking for many taxa (e.g. frogs in the family Aromobatidae), and there may be many new and fascinating forms of parental care waiting to be described in detail. For example, while several forms of reproductive parasitism have been described recently (Kok & Ernst 2007; Brown et al. 2009), the myriad forms of parental care in frogs likely provide a wealth of opportunities for exploitation in ways not yet detected or even imagined. Recent research has revealed remarkable cases of convergence, such as the evolution of trophic egg feeding in poison frogs in Madagascar with numerous parallels to the complex parental care of some Neotropical poison frogs (Heying 2001). Other examples of convergence in reproductive strategies are no doubt waiting to be discovered, as suggested by a recent large-scale comparative analysis of reproductive strategies across the order Anura (Gomez-Mestre et al., in press). With respect to costs and benefits, while progress has been made, the number of species for which we have detailed and thorough assessments remains woefully small, and more detailed studies are needed before valid comparisons can be made with more intensively studied taxa such as birds and mammals.

Second, as Crump (1996) pointed out, we have begun to accumulate data on the costs and benefits of parental care in a variety of species, but there is relatively little data on variation in care relative to the benefits and (especially) costs of care. Some research has addressed the hypothesis (Clutton-Brock 1991) that effort placed into parental care should be higher when environmental conditions are poor (e.g. Kluge 1981) and when clutch size is large (e.g. Thompson 1992), but there is little research addressing how variation in costs relate to variation in parental care effort. An intriguing subject related to this issue concerns the relationship between parental care and cannibalism. Both parental cannibalism of offspring and sibling cannibalism are common in frogs (Crump 1992). Parents may need to adjust to environmentally imposed changes in the cost/benefit ratio of parental care by consuming offspring in an attempt to recoup nutrients from a reproductive attempt that is bound to fail (Clutton-Brock 1991). In other situations, parents may deposit small tadpoles in the same pool as larger sibling tadpoles in the expectation that their siblings will consume them if environmental conditions deteriorate and other food becomes scarce. This 'Icebox Hypothesis' (Mock & Parker 1997) may have broad applicability across taxa, yet has rarely been tested rigorously in frogs or other taxa.

Third, future research should take more integrative, synthetic approaches to understand relationships between parental care and other social and reproductive behaviours in anurans. For example, there is a large body of research addressing parental care ecology and evolution, and a relatively new but rapidly growing body of research on hatching plasticity (Warkentin 2011a, b). Until recently, however, no research had addressed the possibility that parental care and hatching plasticity interact. Recent studies of Neotropical glass frogs provides a valuable opportunity to investigate this interaction, as these frogs display both hatching plasticity in response to environmental variation (e.g. desiccation) and intensive parental care (Delia 2011). Likewise, we still know relatively

little about the extent to which female frogs might receive direct benefits in the form of paternal care by selecting good fathers based on aspects of male behaviour. Kluge (1981) provided circumstantial evidence to suggest female gladiator frogs, *Hyla rosenbergi* (*Hypsiboas rosenbergi*) might assess a male's commitment to guard eggs laid in his nest. Recent work on the golden rocket frog, *Colostethus beebei* (*Anomaloglossus beebei*), suggests females might choose good fathers based on aspects of male calling behaviour (Pettitt 2012).

Finally, the hypothesis that patterns of parental care and sexual selection interact to influence large-scale processes such as speciation in anurans is just beginning to be evaluated and more work remains. For example, research on the strawberry poison frog, *D. pumilio*, in the Bocas del Toro Archipelago of Panama suggests that female preferences for male colour patterns may (in part) drive the evolution of distinct colour patterns in allopatric populations on different islands (Summers et al. 1997). This process may be exacerbated by the presence of predominately female care in this species, which 'frees' females to choose males on the basis of traits that are likely independent of parental care ability, such as colour pattern (e.g. Summers et al. 1997, 1999; Reynolds & Fitzpatrick 2007; Maan & Cummings 2008, 2009; Brown et al. 2010b; Tazzyman & Iwasa 2010; Richards-Zawacki & Cummings 2011; Richards-Zawacki et al. 2012). The general argument is that rapidly evolving female choice in the context of strong sexual selection will facilitate evolutionary divergence among populations, as each population rapidly evolves along an independent trajectory driven by the interaction between female preferences and male traits specific to that population (West-Eberhard 1983). The environment may also play a role, as different traits (e.g. colours) may be preferred by females in different populations due to location-specific environmental differences (Maan & Cummings 2008). In poison frogs, this process can drive change in colour in both males and females, as aposematism is most effective when all members of the population share the same signal (Summers et al. 1997). Recent theory confirms the plausibility of this hypothesis, although genetic drift probably plays a more important role than originally thought (Tazzyman & Iwasa 2010).

CONCLUSION

Wells's essay went a long way towards ensuring that studies of anuran social behaviour were carried out in a rigorous manner and with a concentrated focus on testing hypotheses of interest in behavioural ecology. In turn, this has resulted in the current status of anurans as focal taxa in numerous classic and ongoing studies in the field. Wells's (1977a) review provided the ultimate roadmap for anuran behavioural ecology at its inception. His 2007 magnum opus is truly a tour de force that both reflects on progress in the previous three decades and looks forward to where the field should be going in the future. It would be only a slight exaggeration to claim we could have written this entire essay citing only these two reviews. We conclude by turning once again to the text of Wells's (1977a) review. In outlining directions for future research in his own Conclusion section, he wrote:

Problems that require special attention include the relative importance of vocal signalling and searching in mate acquisition, changes in mate locating behaviour with changes in male density, competitive strategies of individual males in choruses, the adaptive significance of aggression and territoriality, the relative importance of female choice in different social systems and the criteria used by females to select mates, the development of complex courtship interactions between males and females, ecological factors governing the evolution of parental investment patterns, and the

influence of parental investment on mating systems and sexual selection. (Wells 1977a, page 683)

In reflecting on these words some 36 years after they were published, there is significant cause for celebration. The field of anuran behavioural ecology has made magnificent progress addressing some of Wells's *problems of special attention*. Yet, some problems (e.g. female choice, aggression, chorusing, parental care) have received far more attention than others, so there is still plenty of work to do. Even within these well-studied problems, many new discoveries remain to be made, and we have laid out some of the future research directions we believe will lead to these discoveries. Given the number of open questions to answer amid tightening research budgets and declining amphibian populations, it is imperative that researchers marshal the scientific tractability of frogs and their charismatic appeal among the general public to ensure there are both biological and financial resources to continue this work in the future.

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