

Wells K D. The social behaviour of anuran amphibians. *Anim. Behav.* 25:666-93, 1977.  
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Many aspects of anuran mating systems are affected by the length of the breeding period and the density of mating aggregations. Males of explosive-breeding species often acquire mates by active searching and aggressive competition. Males of prolonged breeders usually are territorial, and females can select their mates. Density-dependent shifts in mating tactics are common in many species. [The SCJ® indicates that this paper has been cited in more than 235 publications.]

## Mating Systems of Frogs and Toads

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I finished writing this paper during the summer of 1975, when I was completing my final year of PhD research on the territorial behavior of frogs under the direction of Harvey Pough at Cornell University, Ithaca, New York. This was an exciting time for students of social behavior, for the fields we now call behavioral ecology and sociobiology were in their infancy. Jerram Brown's book on *The Evolution of Behavior* (W.W. Norton & Co.) and E.O. Wilson's now classic *Sociobiology: The New Synthesis* (Harvard University Press) were both published that year, revealing new ways of understanding social behavior in an evolutionary and ecological context. However, studies of amphibians had not had much impact on this developing field.

My paper was inspired in part by ideas presented in Steve T. Emlen's graduate course on ecological aspects of social behavior. In the 1960s, work by behavioral ecologists, such as Brown, Gordon Orians, and John Hurrell Crook, had shown how the temporal and spatial distribution of resources profoundly affect the evolution of aggressive interactions, territorial behavior, and mating systems in birds and mammals.

I decided to apply these ideas to anuran amphibians and began a survey of the natural history literature on frogs and toads. I found that the mating systems of these animals are determined in part by the temporal availability of females. In explosive breeding aggregations, a form of scramble competition among males predominates, with few opportunities for females to

choose their mates. In contrast, when the arrival of females is less synchronized, males generally call to attract them from fixed sites that may be defended as territories, and females have more opportunities to choose their mates. Changes in chorus density often result in males switching from calling to searching, or to alternative mating tactics such as satellite behavior.

I wrote this review at a time when quantitative studies of anuran mating systems were nonexistent, so I had to rely on descriptive and even anecdotal papers for information. Fortunately, two of the best early studies of territorial behavior in frogs had been done by Emlen,<sup>1</sup> who served on my graduate committee, and Tom A. Wiewandt,<sup>2</sup> one of my office mates in graduate school, so I was able to kick ideas around with them as the paper developed. At the same time, I continued my own field studies of the resource-based mating system of green frogs, which eventually produced some of the first detailed information on factors influencing male mating success in an anuran species.<sup>3</sup> This was soon followed by Richard D. Howard's study of a very similar mating system in bullfrogs.<sup>4</sup>

Studies of anuran mating systems proliferated in the 1980s, and we now have dozens of detailed investigations of male-male competition, territoriality, female choice, alternative mating tactics, vocal interactions among chorusing males, parental behavior, and the evolution of sexual dimorphism, all topics that were touched upon in my review.<sup>5,6</sup> Fortunately, many of my speculative conclusions derived from descriptive studies have been confirmed, although the variability of mating systems, even among populations of the same species, is greater than was apparent at the time.

I think there are several reasons why the paper has been influential in shaping subsequent work in this field. First, the question of how ecological variables influence the structure of mating systems was a hot topic when the paper appeared. Second, the paper brought together a body of information that had been scattered through the herpetological literature, making it available for the first time to a broader audience of animal behaviorists. Finally, I was able to identify a number of general patterns in anuran mating systems that provided a conceptual framework for future studies.

1. Emlen S T. Territoriality in the bullfrog, *Rana catesbeiana*. *Copeia* 1968:240-3, 1968.

2. Wiewandt T A. Vocalization, aggressive behavior, and territoriality in the bullfrog, *Rana catesbeiana*. *Copeia* 1969:276-85, 1968.

3. Wells K D. Territoriality and male mating success in the green frog (*Rana clamitans*). *Ecology* 58:750-62, 1977.

4. Howard R D. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* 32:850-71, 1978.  
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5. Arak A. Male-male competition and mate choice in anuran amphibians. (Bateson P, ed.) *Mate choice*. New York: Cambridge University Press, 1983. p. 181-210.

6. Ryan M J. Sexual selection and communication in frogs. *Trend. Ecol. Evol.* 6:351-5, 1991.

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