This Week's Citation Classic® CC/NUMBER 8 FEBRUARY 22, 1988

Emlen S T & Oring L W. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-23, 1977.
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In this paper we extended Jerram L. Brown's concept of economic defendability to encompass *monopolizability*, recognized that receptive mates (usually females) were the critical resource for understanding mating systems, and applied the approach to develop an ecological classification of mating-system types. [The *SCI*® and *SSCI*® indicate that this paper has been cited in over 570 publications.]

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November 30, 1987

In the early 1970s the major focus of animal mating-systems research was avian polygyny. Gordon H. Orians,[1] Jared Verner, and Mary F. Willson[2] had realized the importance of environmental resources in their now-classic polygyny threshold model, which emphasized the role of the female in choosing between mating with an already mated male on a high-quality territory (polygynous bonding) versus pairing with an unmated male occupying a lower quality territory (monogamous bonding).

At this time we were working independently. Stephen T. Emlen was thinking about the evolution of amphibian mating systems and had just written an article about lek mating in bullfrogs.[3] That study made him appreciate the strong role that several environmental factors played in shaping mating systems. These factors included the length of the breeding season, the temporal pattern of receptivity of individual females, and the defendability of resources important for successful reproduction. He felt that these three factors were important predictors of the full spectrum of anuran mating systems. Since he was primarily an *avian* behaviorist, however, he was struggling to recast these thoughts in a broader framework that would have relevance for birds as well as amphibians.

Lewis W. Oring had studied birds with a variety of mating systems and had recently published a paper with M.L. Knudson on polyandry in the spotted sandpiper.[4] That study also brought about the realization that the earlier mentioned environmental factors shaped mating-system evolution and expression, and Oring initiated a study to tease apart these factors as determinants of polyandry. Still, he was grasping for a unifying set of principles that would describe the full spectrum of avian mating systems.

From 1975 to 1976 we joined forces when Oring came to Cornell for a sabbatical leave. Together we fleshed out a preliminary framework on the role that various environmental factors might play in shaping animal mating systems. We believed that a male's ability to control access to females was strongly influenced by the "operational sex ratio" (defined as the ratio of sexually active males to sexually receptive females at any one time[5]) and by the spatial and temporal distribution of receptive females. Polygamy occurs only when some individuals can monopolize an uneven share of mates. The greater the potential for such monopolization, the greater the "environmental potential for polygamy." The precise form of the resulting mating system depends on which sex is limiting and on the manner in which the limited sex controls access to mates.

Our ideas were a logical extension of Jerram L. Brown's concept of economic defendability.[5] He had argued that the distribution pattern of a resource determined the benefit-to-cost ratio of defending that resource, and he used this approach to model the evolution of territorial behavior.

During the fall semester of 1975 we organized a graduate seminar around this topic and used it as a testing ground for our ideas. We were joined by Donald Jenni (another bird polyandry expert who was spending a sabbatical semester at Cornell). Together we reviewed the literature from as many groups of organisms as possible. As the semester progressed, we grew more confident that our ideas had broad generality. We worked on writing the article throughout the spring term. We wanted to publish it in a journal with a broad readership. Emlen had been invited by *Science* magazine to submit an article on a different topic (the evolution of coloniality in swallows); we decided to submit the mating-system manuscript instead.

This paper is probably cited frequently because it identified a simple set of variables that influence the mating options of individual organisms. These variables, and the interactions among them, have proven to be strong predictors of mating systems, not only for amphibians and birds, but for many other taxa as well.[6,7] Because of this work, ecological classifications of mating systems are now widely employed.

In the decade since our paper was published, there have been tremendous advances in the modeling of mating systems. Optimality theory has refined the economic approach to behavior and has brought with it a more rigorous measuring of the costs and benefits of monopolization. Game theory has advanced our understanding of the conflicts of interest between male and female "players" in the mating game. And new field studies have increased the power of comparative "tests" of hypotheses.

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2. **Verner J & Willson M F.** The influence of habitats on mating systems of North American passerine birds. *Ecology* 47:143-7, 1966. (Cited 155 times.)
3. **Emlen S T.** Lek organization and mating strategies in the bullfrog. *Behav. Ecol. Sociobiol.* 1:283-313, 1976. (Cited 80 times.)
4. **Oring L W & Knudson M L.** Monogamy and polyandry in the spotted sandpiper. *Living Bird* 11:59-73, 1972.
5. **Brown J L.** The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-9, 1964. (Cited 310 times.)
6. **Thornhill R & Alcock J.** *The evolution of insect mating systems*. Cambridge, MA: Harvard University Press, 1983. 547 p. (Cited 180 times.)
7. **Rubenstein D I & Wrangham R W,** eds. *Ecological aspects of social evolution: birds and mammals*. Princeton, NJ: Princeton University Press, 1987. 551 p.

