

# This Week's Citation Classic

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Miller R S. Pattern and process in competition. *Advan. Ecol. Res.* 4:1-74, 1967.  
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This paper reviews the history and development of competition theory, and describes a set of patterns within which the central problems of competition can be understood and tested. It shows that different patterns and mechanisms of competition can lead to different results within the general model of 'the competitive exclusion principle.' [The SCI® indicates that this paper has been cited over 195 times since 1967.]

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"James B. Cragg, the editor of *Advances in Ecological Research*, had invited me to his favorite pub in northern Lancashire, England, to sample a particularly good draft bitters. Over a second pint he invited me to write a review article on competition and I accepted. It was a chance for me to finally organize a series of thoughts which had begun to be formed when I went to Oxford in 1949 to begin my D.Phil. dissertation research with Charles Elton.

"At Oxford I became aware of the controversy over the factors which control the size of animal populations and the role of competition in what Darwin called 'the economy of nature.' The Lotka-Volterra logistic equation predicted that two species using the same resources cannot coexist indefinitely, and experimental verification of the model was provided by G.F. Gause<sup>1</sup> in the 1930s and, most convincingly, by a long series of experiments by T. Park<sup>2</sup> with laboratory populations of two species of flour beetles, *Tribolium confusum* and *T. castaneum*. However, although these and other

experiments showed that species A will eliminate species B, the actual mechanisms of the interactions were not understood, and there was considerable disagreement over the actual role of competition in natural populations. It seemed to me that the proponents of different views were strongly biased by whether their research was with birds, small mammals, or laboratory populations of insects, and that competition tended to be viewed, wrongly I thought, as an abstract term in the Lotka-Volterra model. It also seemed that progress toward a set of unifying principles in competition theory must come through a comparative approach, which subsequently led me to a series of studies with laboratory populations of two sibling species of *Drosophila*, and field studies of four species of geomyid rodents and two closely related birds, the redwing and the yellow-headed blackbirds.

"During my research on the Geomyidae, Hutchinson<sup>3</sup> published a classic paper on niche theory. One of his cases, which I termed 'the included niche,' was not only the solution to the geomyid problem, and provided a model which I could test with the blackbirds, but also allowed us to begin to describe patterns of competition within which we could define and describe different processes. It became clear that competition through 'exploitation,' in which two nonterritorial species have equal access to a resource (e.g., *Drosophila*) is a different process with different results from 'interference competition,' in which one species prevents access of the other to the resource (e.g., territorial birds).

"By the 1960s, it was possible to synthesize the results of several important studies of competition in natural populations and to define the patterns and processes of competition in such a way that the problems for future research could be seen more clearly.

"The reason this paper has been so frequently cited is that it still appears to provide a testable set of definitions and models for meaningful research on both the pattern and process of competition."<sup>4</sup>

1. Gause G F. *The struggle for existence*. Baltimore, MD: Williams and Wilkins, 1934. 163 p.
2. Park T. Experimental studies of interspecies competition: I. Competition between populations of the flour beetles *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecol. Monogr.* 18:265-307, 1948.
3. Hutchinson G E. Concluding remarks. (Population studies: animal ecology and demography.) *Cold Spring Harbor Symp.* 22:415-27, 1957.
4. ----- . *An introduction to population ecology*. New Haven, CT: Yale University Press, 1978. 260 p.