

This Week's Citation Classic

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Brown J L. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-9, 1964. [Dept. Biology and Ctr. for Brain Res., Univ. Rochester, Rochester, NY]

A general theory of territoriality is proposed which depends upon the influence of two primary variables, competition and economic defendability, and on the adaptive value of aggressiveness under various conditions of these variables. [The *SCI*[®] indicates that this paper has been cited over 170 times since 1964.]

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"This paper was a slow starter. From 1965 to 1969 it received only ten citations; yet from 1978 to 1980 it received 82. There seem to be two main reasons for this pattern. First, in 1965, the number of persons working in the areas that today are called behavioral ecology or sociobiology was miniscule. Roughly half a dozen names spring to mind; today, perhaps 200. Second, it happened serendipitously that a basic concept that was developed in primitive form in the 1964 paper, the idea of 'economic defendability,' proved to have heuristic value for some beautiful empirical studies done later on the energetic costs and benefits of territorial behavior by Wolf, Gill, Carpenter, and others.¹⁻² These studies attracted attention to the 1964 paper. The 'economic' approach is now widely used in behavioral ecology.

"When it was written, the subject of this paper was far removed from my research interests, which then were in the new field of neuro-ethology. It would not have been written at all except for a coincidence of two events, one

scientific and one personal. In 1962, a heavy book³ appeared that misinterpreted nearly all of animal social behavior according to the theory of interdemic selection, instead of the conventional individual selection. Territorial behavior was the principal test case. Believing that a response was required because many naive readers would be swayed by the 'weight' of evidence for interdemic selection, I felt that two avenues of response were open, to reinterpret all the evidence in the book, or to present a brief and simple statement of the alternative approach. I chose the latter. Although this approach was widely known, it had not previously been set down succinctly in one publication. My version of it was, I thought, conventional and unoriginal. I suspect that others would have soon written similar thoughts had I not responded so promptly.

"I would not have troubled to write the 1964 paper had I been immersed in research in October 1962. By chance, however, I was caught in a slack period. I had just arrived at a new campus for my first academic job, and I was waiting for some electronic equipment to arrive to begin my experiments in avian neuro-ethology. I had already written up my graduate and postdoctoral work and was waiting for responses from coauthors. This left me with time to read and write about anything that came to mind.

"In graduate school, 1952-1960, I had moved from a background in evolutionary biology and systematics into the relatively new areas of ecology and behavior. My interest in the action of natural selection on territorial behavior was a logical outgrowth of this combination. An excellent review of recent work in this area has been provided by Wittenberger's new book, *Animal Social Behavior*.⁴

1. Gill F B & Wolf L L. Economics of feeding territoriality in the golden-winged sunbird. *Ecology* 56:333-45, 1975.
2. Carpenter F L & MacMillen R E. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science* 194:639-42, 1976.
3. Wynne-Edwards V C. *Animal dispersion in relation to social behavior*. New York: Hafner, 1962. 653 p. [Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 11(25):10, 23 June 1960.]
4. Wittenberger J F. *Animal social behavior*. Boston: Duxbury, 1981. 722 p.