

# This Week's Citation Classic

**Fretwell S D & Lucas H L.** On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19:16-36, 1970.  
[Biomathematics Program, Dept. Experimental Statistics, North Carolina State Univ., Raleigh, NC]

An ideal free habitat distribution for birds is defined given territorial behavior that only communicates information about density and does not directly threaten pioneers choosing a place to live. This is contrasted with the ideal-despotic distribution for species that actually fight over space and a random distribution for species that select habitats without being influenced by display behavior. Distinguishing predictions are offered. [The SCI® indicates that this paper has been cited in more than 140 publications, making it the most-cited paper from this journal.]

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## Say That in Algebra

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I was actually studying earthworm brains for my doctoral thesis and only relaxing with my lifelong hobby: watching birds. But the formal research was not going well, and an undergraduate professor had made me promise to read David Lack's *The Natural Regulation of Animal Numbers*.<sup>1</sup> I was irritated by Lack's dogmatic position on territorial behavior; I did not agree with his contention that territorial behavior did not affect habitat selection but only spaced individuals within habitats. As I wandered among the many field sparrow (*Spizella pusilla*) nests that I was finding, I believed I saw a way of proving him wrong. By comparing the nesting success of individuals in different habitats, I thought I could show that some pairs had been forced into poor habitats by the territorial behavior of males in the "highly suitable" places. I began to collect data in earnest and wrote my thoughts out to my informal mentor of 10 years, Robert Haines. I was excited; proving Lack wrong was a sure way of making a name for myself. And so I was crushed when Haines wrote back that he could not understand my thinking.

Meanwhile, Henry Lucas and Rob van der Vaart, who were heading the North Carolina State Biomathematics Program in which I was enrolled, were striving to teach us an important lesson. They believed that mathematical model building was the cure to fuzzy thinking in sci-

ence and that we should always endeavor to express our ideas mathematically: "Say that in algebra!" Lucas, I now believe intentionally, was also "puzzled" by my arguments against Lack, and I spent many fruitless afternoons trying to make him understand. Finally, in desperation, I accepted his suggestion that I put it all into graphical and analytical mathematical models. As I did so, I made several wondrous discoveries.

First, I discovered that there were three sides to the territorial behavior debate, whereas only two had been mentioned before. I saw that several decades of debate were mostly based on some confused terminology.

Second, nearly everyone I talked to about my ideas understood very quickly just what I was trying to say. All I had to do was show them the models. This, it has turned out, was the most important lesson of my career.

Third, I found I had a tool that gave me insight into several other problems with bird populations. I began to understand how seasonality affects the way bird populations are regulated.

I soon dropped the earthworm research; both the worms and I were having nervous breakdowns and getting nowhere. The territorial behavior project, largely theoretical, then became my thesis, causing some anxiety among the zoologists on my committee. At my thesis defense, one concerned voice cried out, "But where will he ever publish such weakly supported arguments?" Van der Vaart, then a senior editor of *Acta Biotheoretica*, quickly offered that journal, and so I was passed for my doctorate.

Later, I presented these models to Mike Rosenzweig, who has been a champion for them<sup>2</sup> ever since. They endure simply because the ideas in them are clearly formulated. They can be corrected and added to when circumstances dictate, but are themselves still relevant to most situations where a creature must choose where to live or feed, and when to fight for space. They also were the key to my lifelong study of the population size and geographic distribution patterns in the dickcissel (*Spiza americana*).<sup>3</sup>

It is only of incidental interest to note that, through the use of these models, many cases of territorial behavior are shown to function quite differently than Lack supposed.

1. Lack D. *The natural regulation of animal numbers*. London: Oxford University Press, 1954. 343 p. (Cited 1,265 times.)
2. Rosenzweig M L. Habitat selection and evolutionary processes. *Evol. Ecol.* 1:283-417, 1987.
3. Fretwell S D. Distribution and abundance of the dickcissel. *Curr. Ornithol.* 4:211-42, 1986. (Cited 5 times.)

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