

**Krebs J R.** Territory and breeding density in the great tit, *Parus major* L.  
*Ecology* 52:2-22, 1971.  
[Dept. Zoology, Animal Behaviour Research Group, Univ. Oxford, England]

The paper describes a study of the factors limiting breeding density in bird populations. The main conclusion is that density is limited by competition for territories, rather than by food shortage. Year-to-year changes in territory size and, hence, breeding density are related to changes in the intensity of competition for territories at the time when the birds settle. [The SC/® indicates that this paper has been cited in over 180 publications since 1971.]

John R. Krebs  
Department of Zoology  
University of Oxford  
Oxford OX1 3PS  
England

February 28, 1984

"In 1966, I was prospecting for a PhD project and a supervisor. I had been inspired by my undergraduate ecology teachers at the University of Oxford, especially Lack, Varley, and Southern, and the great debate among population ecologists of the early 1960s sparked off by the publication of Wynne-Edwards's famous book.<sup>1,2</sup> Wynne-Edwards espoused the view that natural populations are limited in size not by the direct action of starvation, disease, and other mortality factors, but by means of social interactions (especially territorial aggression) causing death or dispersal of some individuals. The Oxford school of ecologists was strongly opposed to Wynne-Edwards's views on both theoretical and empirical grounds and they favoured the idea of food and predators as factors limiting population size. Both Lack<sup>3</sup> and Varley<sup>4</sup> had recently summarised the results of their long-term population studies of birds and insects, respectively, in these terms.

"Against this background, I decided to study the question of whether the breeding

density of bird populations is limited by food supply (Lack's view) or by territorial competition (Wynne-Edwards's view). My supervisor at Oxford, J.M. Cullen, suggested working on the great tit *Parus major*, the species which Lack and his colleagues had been studying for 20 years. This was a fortunate choice because I could take advantage of the wealth of background data available in Oxford. My approach was experimental and straightforward. I examined the effect of food supply on numbers by adding extra food and the effect of territorial competition by removing territory holders in the spring to create vacancies which would, according to the hypothesis of territorial exclusion, be refilled by previously excluded 'surplus' birds. My results showed little or no effect of food supply, but clear exclusion by territorial behaviour. The conclusion, that territoriality limits breeding density, ran counter to the prevailing Oxford view, but was rapidly accepted by Lack and his co-worker Perrins, and is now known to apply to many species of birds.<sup>5</sup> While my results, and those of other workers, have provided some empirical support for Wynne-Edwards's thesis, the theoretical framework within which he interpreted his evidence is still not widely accepted.

"I think my work has been widely cited for three reasons. First, I was lucky enough to work on an already famous population of a well-studied species. Lack's great tit study is cited in most ecology texts as a classic population study, and my work is a small part of the whole picture. Second, I chose a timely and controversial issue, and, third, I was one of the few vertebrate ecologists at the time using field experiments rather than pure observation. It was also unusual at that time for vertebrate ecologists to adopt a 'problem oriented' rather than a 'species oriented' approach. When I went to Lack to ask about working under his supervision, he asked what species I wanted to study. I explained that I had an idea of a problem to study but had not yet chosen a species. After listening for a while, he took me to meet his current students over coffee and introduced me as 'John Krebs, who has not yet decided what he wants to work on!'"

1. Wynne-Edwards V C. *Animal dispersion in relation to social behaviour*. Edinburgh: Oliver & Boyd, 1962. 653 p.
2. .... Citation Classic. Commentary on *Animal dispersion in relation to social behaviour*.  
*Current Contents/Agriculture, Biology & Environmental Sciences* 11(25):10, 23 June 1980.
3. Lack D. *Population studies of birds*. Oxford: Clarendon Press, 1966. 341 p. (Cited 625 times.)
4. Varley G C & Gradwell G R. The interpretation of insect population changes.  
*Proc. Ceylon Assn. Advan. Sci.* 18:142-56, 1963. (Cited 35 times.)
5. Klomp H & Woldendorp J W. *The integrated study of bird populations*. Amsterdam: North-Holland, 1981. 255 p.