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This Week's Citation Classic

Krebs C J, Keller B L & Tamarin R H. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology* **50**:587-607, 1969.
[Dept. Zoology, Indiana Univ., Bloomington, IN]

Vole populations enclosed by a mouse-proof fence in grassland increased in density to two to five times the density of unfenced control populations, destroyed their habitat, and declined from starvation. The 'fence effect' shows that *dispersal* is necessary for normal population regulation. [The *SCI*® indicates that this paper has been cited in over 175 publications since 1969.]

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"In September 1964, I began teaching at Indiana University, and Barry Keller joined me immediately to do PhD work. Robert Tamarin had just arrived from Brooklyn College to work with Tracey Sonneborn in genetics but fortunately Sonneborn had an excess of students and we enticed him to begin looking at the population genetics of voles. We knew we had to study field rather than laboratory populations, but we wanted the control that laboratory populations offered. We compromised by deciding to build large field enclosures, and during the hot summer of 1965 the three of us with some local help built three enclosures on an abandoned farm seven miles east of Bloomington. Each enclosure was 0.8 hectare, approximately 90 metres on a side. These enclosures were about ten times larger than any previously used. We assumed they would be a universe to a vole population, and we could therefore use them to study populations of specific genetic composition in the field. Before we could do this, however, we thought we should check whether the fencing itself affected the dynamics of the vole population. We had no reason to expect that it would, and the results we obtained were completely unexpected. The 'fence effect' was stunning: grasses in midsummer mowed right to the ground, voles like walking pencils, starving to death. We have never seen these symptoms in natural, unfenced populations. What had we changed by the simple act of fencing? We suggested that we changed only *dispersal*, and that this single experiment was sufficient to cause one to reject most of the competing explanations for vole population regulation: predation, food shortage, and stress.

"MacArthur[1] called this the 'Krebs effect,' and noted that it might be an explanation of why some island populations existed at a higher density than adjacent mainland populations. There has also been some argument as to whether this effect occurs in big mammals in national parks.

"The 'fence effect' (we prefer the more descriptive term) has been shown experimentally in *Microtus townsendii* by Boonstra and myself.[2] Beacham[3] showed that, if one provides a 'dispersal-sink' inside a fenced area, the fence effect disappears. Abramsky and Tracy[4] in a brilliant experiment showed that in *Microtus ochrogaster* emigration was important in regulating population density while immigration was critical for producing three- to four-year cycles in density.

"We still do not understand the mechanisms of social behavior which underlie the 'fence effect.' Nor do we know at what spatial scale the fence effect disappears. Island populations need more study and fencing experiments should be attempted on a broader range of species.

"This paper has been widely cited because of the increasing experimental orientation of small mammal research and the general appreciation that *dispersal* is a major unstudied force in population dynamics."

1. **MacArthur R H.** *Geographical ecology*. New York: Harper & Row, 1972. p. 118.
2. **Boonstra R & Krebs C J.** A fencing experiment on a high-density population of *Microtus townsendii*. *Can. J. Zool.* 55:1166-75, 1977.
3. **Beacham T D.** Dispersal during population fluctuations of the vole, *Microtus townsendii*. *J. Anim. Ecol.* 49:867-77, 1980.
4. **Abramsky Z & Tracy C R.** Population biology of a "noncycling" population of prairie voles and a hypothesis on the role of migration in regulating microtine cycles. *Ecology* 60:349-61, 1979.