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This Week's Citation Classic™

Healey M C. Aggression and self-regulation of population size in deermice. *Ecology* **48**:377-92, 1967.
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Litters born to deermice early in the breeding season survive poorly while those born late survive well. By creating free-living populations differing in aggressiveness, and by other manipulations of natural populations, I demonstrated that male aggressiveness was a sufficient cause of poor litter survival and an important population regulating mechanism. [The *SCI*® indicates that this paper has been cited in over 130 publications since 1967.]

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"The mid-1960s was an exciting time to be doing graduate work in ecology. Whether or not intrinsic mechanisms of population regulation existed was still a burning question. Don Chapman[1] had recently published data which apparently demonstrated that the density of young coho salmon in streams was regulated by territorial behavior. The exciting work of David Jenkins and Adam Watson on regulation of population size in red grouse was being talked about.[2] Dennis Chitty's important ideas (recently reviewed by Charles Krebs[3]) were hotly debated. Several of us at the University of British Columbia were investigating behavioral regulation of population size, Frank Tompa with song sparrows, Fred Zwickel with blue grouse, and Richard Sadleir and I with deermice. Although we all came to similar conclusions regarding the importance of behavior in limiting population size, perhaps the most conclusive and enduring results were Richard's and mine. We were both students of Dennis and he was anxious that we find some way to test, critically, his idea that cyclic changes in small mammal abundance were a consequence of density-induced alternations in the fitness of aggressive and docile genotypes. Voles, Dennis's favorite animal, were proving uncooperative, so Richard began studying deermouse populations in wooded areas of the university campus.

"Deermouse populations were rather stable from year to year. They did, however, show a curious annual fluctuation, declining dramatically in abundance at the onset of breeding in the spring and remaining scarce, despite impressive production of litters, until fall when good survival of the final litters doubled or trebled population size. The spring decline in numbers and subsequent poor litter survival, Richard found, were associated with high aggressiveness among resident males, and the good survival of late litters coincided with a postbreeding decline in male aggressiveness. My research involved confirming with captive mice the seasonal cycle in male aggressiveness and demonstrating the bad effects of aggressive males upon young deermice. With these results in hand, I went on to design a series of manipulations of mouse populations in their natural habitat and at their natural density. These manipulations showed that young mice readily colonized the habitat from which the aggressive adults had been removed, or which was populated with docile males. The aggressiveness of resident breeding males proved to be a sufficient cause of both the spring decline in mouse numbers and the poor survival of early litters.

"Population and community ecology now have an almost 20-year tradition of creative manipulation of natural systems to test ecological hypotheses. In the mid-1960s, however, such manipulations were a novel departure from traditional, descriptive field ecology. One reason this paper is cited so often is because it was one of the first attempts at fairly rigorous falsification of an ecological hypothesis. Another reason is that the work still left many questions unanswered. The students who followed Richard and me have built on the foundation we laid and have generously referred to our work."

1. **Chapman D W.** Aggressive behavior in juvenile coho salmon as a cause of migration. *J. Fish. Res. Board Canada* **19**:1047-80, 1962. (Cited 60 times.)
2. **Jenkins D, Watson A & Miller G R.** Population fluctuations in the red grouse, *Lagopus lagopus scoticus*. *J. Anim. Ecol.* **36**:97-122, 1967. (Cited 60 times.)
3. **Krebs C J.** A review of the Chitty hypothesis of population regulation. *Can. J. Zool.* **56**:2463-80, 1978.

