This Week's Citation Classic®

Huffaker C B. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343-83, 1958.
[California Agricultural Experiment Station, Berkeley, CA]

This paper is the second covering a series of experiments designed to shed light on the fundamental nature of predator-prey interaction, in particular, and the interrelations of this interaction with other important parameters of population changes, in general. [The *SCI*® indicates that this paper has been cited in more than 270 publications.]

Continuity in Natural Environments

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Work by G.F. Gause[1,2] had theorized that predator-prey systems are inherently self-annihilative; that continuity depends on two stipulations: (1) immigrations into the depopulated areas or (2) existence of definite prey refuges restrictive to the predators. My work suggests that, in a sufficiently natural environment (of reasonable size for meaningful interaction), continuity is possible without stipulation (1) or (2).

An earlier work of mine with C.E. Kennett[3] showed that a continuing interaction of a predatory and a prey mite species in field strawberries seemed natural even on only a half-dozen strawberry plants. But in this situation the predatory mite was excluded for a brief interval from entering the still unopened leaflets, whereas the prey mite could enter a few days sooner.

So, in the currently reported experiments, I devised artificial systems that allowed for no such specific exclusion.[4,5] I used the prey mite *Eotetranychus sexmaculatus* and the predator *Typhlodromus occidentalis*. Heterogeneity of the laboratory environments was established by using oranges as food and dispersing it in widely different patterns for comparisons. The positions in the system and the amounts of accessible orange peel were also varied greatly by interspersing these units among waxed rubber balls. In the universe employing the greatest dispersion and complexity, the interaction continued for three distinct oscillations. On a single orange, the predator invariably exterminated the prey and then, of course, itself; but, as the universe's size and complexity was increased, there was increasing chance of some prey being missed and reproducing a cluster of population available for a later use of predators encountering them. In the most heterogeneous physical universe, the predator-prey populations passed through three distinct oscillations before interaction was terminated.

Later similar studies[6-8] produced results that continued for five oscillations and were terminated then by an outside disturbing factor—a disease of the prey mite. Moreover, it was shown that trebling the quantity of food while not increasing heterogeneity created imbalance between numbers of predators generated and the hazards they faced in searching—they overexploited in each case and no second wave ever occurred.

1. **Gause G F.** *The struggle for existence.* Baltimore, MD: Williams & Wilkins, 1934. 163 p. (Cited 550 times since 1945.)
2. **Gause G F, Smaragdova N P & Witt A A.** Further studies of interaction between predators and prey. *J. Anim. Ecol.* 5:1-18, 1936. (Cited 35 times since 1945.)
3. **Huffaker C B & Kennett C E.** Experimental studies on predation: predation and cyclamen-mite populations on strawberries in California. *Hilgardia* 26:191-222, 1956. (Cited 60 times.)
4. **Nicholson A J.** The balance of animal populations. *J. Anim. Ecol.* 2(Supp.):132-78, 1933. (Cited 270 times since 1945.)
5. -------. An outline of the dynamics of animal populations. *Aust. J. Zool.* 2:9-65, 1954. (Cited 280 times.)
6. **Huffaker C B, Shea K P & Herman S G.** Experimental studies on predation. Complex dispersion and levels of food in an acarine predator-prey interaction. *Hilgardia* 34:305-30, 1963. (Cited 80 times.)
7. **Huffaker C B.** Competition for food by a phytophagous mite. Dispersion and superimposed density-independent mortality. *Hilgardia* 37:533-61, 1966. (Cited 5 times.)
8. -------. A note on competition. *Hilgardia* 37:563-7, 1966.

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