

This Week's Citation Classic

CC/NUMBER 34
AUGUST 24, 1987

White T C R. The importance of a relative shortage of food in animal ecology. *Oecologia* 33:71-86, 1978.
[School of Natural Resources, University of the South Pacific, Suva, Fiji]

The abundance of animals is limited from "below" by food, not controlled from "above" by predators. This limitation operates via a relative shortage of nitrogen in the food of the very young. All animals live in a passively hostile environment, the inadequacy of which varies, often because changes in the weather alter the nutritive value of the herbivores' food plants. [The *SCI*[®] indicates that this paper has been cited in over 125 publications.]

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June 9, 1987

This paper had its genesis in the 1950s when, working with outbreaks of defoliating insects in New Zealand forests, I became increasingly dissatisfied with the accepted belief that parasites and predators controlled the abundance of their prey. I needed a new explanation for the violent changes in abundance that I was seeing.

Reading H.G. Andrewartha and L.C. Birch's now-classic book¹ crystallised all this and led eventually to my going to Australia to work with Andrewartha at the University of Adelaide, first as his postgraduate student and then as a member of his staff. I was one of a group of zoologists, each attempting to unravel the ecology of a different species, and I was working in an environment of exhilarating intellectual activity generated by Andrewartha. It was here that I developed the basic concept of the paper.

Many events and much serendipity contributed to the formulation of the hypothesis; for example, my old New Zealand boss, G.B. Rawlings, had taught me to "brainstorm" problems encountered in the field, and a farmer in South Australia pointed out blindingly obvious facts that I had not previously seen. But the key to it all was the realisation that the insect I was studying increased or decreased in abundance because more or less of its young died while still feeding on the host's sap. They died not because of disease or damage from any factor in their environment, but, rather, they starved to death on an abundance of apparently adequate food.

Later, I continued to develop this hypothesis in my teaching at the University of the South Pacific, but I was still thinking only of herbivorous insects.² The full extent of the concept did not dawn on me until I was back in Adelaide on sabbatical leave. There I happened to see on Andrewartha's desk several of A.R.E. Sinclair's papers on the Serengeti buffalo.³ And there it was: essentially the same problem faces herbivorous mammals! Towards the end of my leave, I visited A. Watson and R. Moss working on red grouse in Scotland. In their work I could see (although they may not agree!) the same story for birds. The paper was written soon after.

Why has it been cited so often? Perhaps because I gathered together evidence from seemingly unrelated fields that presented ecologists with a new way of looking at old problems. Those who do not agree with my work cite it as often as those who do; both are testing the ideas it contains. Surely that must be the major influence of the paper—that it presents ideas sufficiently exciting for people to want to test them. Only testing will tell if it is a true hypothesis. In the meantime, I continue to add my voice^{4,5} to those few—still mostly entomologists⁶—who look to the quality of food for an explanation of the success of animal populations.

1. Andrewartha H G & Birch L C. *The distribution and abundance of animals*. Chicago: University of Chicago Press. 1954. 782 p. (Cited 1,020 times since 1955.)
2. White T C R. Weather, food and plagues of locusts. *Oecologia* 22:119-34, 1976. (Cited 55 times.)
3. Sinclair A R E. The natural regulation of buffalo populations in East Africa IV. The food supply as a regulating factor, and competition. *East Afr. Wildlife J.* 12:291-311, 1974.
4. White T C R. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63:90-105, 1984.
5. ———. When is a herbivore not a herbivore? *Oecologia* 67:596-7, 1985.
6. Barbosa P & Schultz J C, eds. *Insect outbreaks: ecological and evolutionary perspectives*. Orlando, FL: Academic Press. (In press.)