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# This Week's Citation Classic®

**Pulliam H R.** On the theory of optimal diets. *Amer. Naturalist* 108:59-74, 1974.
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Optimal foraging theory attempts to predict various aspects of the foraging behavior of animals based on the assumption that animals behave as if attempting to maximize their survival and reproductive success. The theory of optimal diets uses this approach to predict the dietary choices of a mobile forager searching for stationary prey. [The *SCI*® indicates that this paper has been cited in over 220 publications.]

## Theory of Optimal Diets

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In 1966 R.H. MacArthur and E.R. Pianka published a short paper[1] containing a graphical model of how the diet of a resident species might change in response to invasion by a competitor species. The logic was based on the assumptions that the invading species would alter the availability of food and each species would attempt to maximize its own rate of intake given the availability of its preferred food types. Though the model was motivated by a consideration of interspecific competition, it made explicit predictions about how diets might change in response to a change in prey availability without regard to the cause of the change in availability. My 1974 paper on the theory of optimal diets was one of several attempts to generalize MacArthur and Pianka's model and to make the model more mathematically explicit.

As noted by T.W. Schoener[2] and others, between 1971 and 1974, no fewer than six authors derived or rederived the same basic result, later known as the contingency model. This model, based on the original graphical model and assumptions of MacArthur and Emlen, was an explicit formulation of how the rate of food or energy intake should depend on the abundances of prey of various kinds, their energy content, and the time required to find and consume or handle each prey item. Among the predictions of the contingency model are that prey should be ranked (or preferred) according to the ratio of energy content to handling time and that diets should expand to include more prey types or contract according to the abundance of the most preferred types.

The various derivations of this model were mostly "rediscoveries of the wheel" based on "partial or total ignorance of earlier algebraic formulations";[2] however, some, including my 1974 paper and E.L. Charnov's 1973 dissertation,[3] were attempts to expand earlier deterministic treatments to include the stochastic nature of the search process. In fact, Charnov and I first learned of each other's work when my manuscript, submitted to the *American Naturalist*, was sent to Charnov's major professor for review. Ironically, Charnov's thesis, though still frequently quoted, was never published even though it presents a much more detailed stochastic model than my 1974 paper.

Despite the fact that my paper was viewed as an advance over earlier models because it was explicitly based on stochastic theory, both Charnov and I were later accused of committing the "fallacy of the averages."[4] This fallacy, according to A.R. Templeton and L.R. Lawlor, is the erroneous belief that the expected value of the ratio of two random variables is equal to the ratio of their separate expected values. As later pointed out by M. Turelli *et al.*,[5] a careful reading of my paper shows that I did not explicitly make this mistake though I may have implicitly done so by failing to make all of the assumptions of the model clear. Turelli *et al.* conclude that my results were indeed correct and that rather than my committing the fallacy of the averages, Templeton and Lawlor had committed "the fallacy of the fallacy of the averages," which is the false accusation that the fallacy of averages has been committed. Fortunately, the Turelli paper was the last of this series of accusations, which could have led to an endless regress of fallacies.

Since the initial flurry of theoretical papers in the early 1970s, no fewer than 200 papers have been published claiming to test some aspect of optimal foraging theory,[6] and a number of these have been direct, experimental tests of the predictions of the contingency model. The G.H. Pyke review[6] and the above mentioned review by Schoener[2] both conclude that the qualitative predictions of the model have largely been supported by these tests, though the model sometimes fails to predict the quantitative details of dietary choice. In my opinion the contingency model has been very successful in that it has been a useful guide to experimentation and the basis for a new generation of more sophisticated foraging models.

1. **MacArthur R H & Pianka E R.** On the optimal use of a patchy environment. *Amer. Naturalist* 100:603-9, 1966. (Cited 585 times.) [See also: **Pianka E R.** Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 19(31):16, 1 August 1988; *CC/Arts & Humanities* 10(31):16, 1 August 1988; and *CC/Social & Behavioral Sciences* 20(31):16, 1 August 1988.]
2. **Schoener T W.** A brief history of optimal foraging ecology. (Kamil A C, Krebs J R & Pulliam H R, eds.) *Foraging behavior.* New York: Plenum Press, 1987. p. 5-67. (Cited 10 times.)
3. **Charnov E L.** *Optimal foraging: some theoretical explorations.* PhD dissertation, University of Washington, 1973. (Cited 80 times.)
4. **Templeton A R & Lawlor L R.** The fallacy of the averages in ecological optimization theory. *Amer. Naturalist* 117:390-3, 1981. (Cited 15 times.)
5. **Turelli M, Gillespie J H & Schoener T W.** The fallacy of the fallacy of the averages in ecological optimization theory. *Amer. Naturalist* 119:879-84, 1982. (Cited 10 times.)
6. **Pyke G H.** Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* 15:523-7, 1984. (Cited 145 times.)

 

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