CC/NUMBER 27 JULY 7, 1980

This Week's Citation Classic

Emlen J M. The role of time and energy in food preference. *Amer. Naturalist* **100**:611-17, 1966. [Dept. Zoology, Univ. Washington, Seattle, WA]

A simple, probabilistic model of food preference allows prediction of the proportions of food types in the diet as a function of relative and absolute availabilities, caloric values, and handling times of the various potential foods in an animal's habitat. [The SCI^{\circledast} indicates that this paper has been cited over 160 times since 1966.]

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> > January 29, 1980

"When this paper was written there were few researchers interested in applying mathematics to problems in behavioral ecology. I had just come to biology from a very mixed, incomplete, but seductive background in physics and math, so it was natural that I dive into the vacuum. My hero at the time, though I'd never met him, was Robert MacArthur, the instigator of modern mathematical ecology. At that time almost any theoretical foray involving computations beyond the ninth-grade level in algebra was novel, impressive, and likely destined to open new fields of research. It is interesting in this light that the paper discussed here, although flawed (see Schoener's excellent review of the literature on feeding strategies¹), has reached the pages of 'Citation Classics,' while a later, more accurate, and generally applicable account² almost never appears in bibliographies.

"I was a graduate student at the University of Washington, working on intertidal ecology, and struggling to explain food preference patterns in carnivorous snails. Certain causes of food preference in animals were intuitively well known and accepted, but none had been discussed in a manner amenable to making quantitative predictions. I had been reading MacArthur, however, and listening to Gordan Orians' discussions of natural selection as an 'efficiency expert,' so the evolutionary model eventually produced was a logical and straightforward response to the problem of my snails' predilections. It was simply a matter of supposing that these seemingly innocuous animals were really adaptive dynamos, that their agile intellects enabled them to assess the net energetic value of each potential food item encountered and, figuratively speaking, to ask themselves whether or not it was in their best interests to indulge or to move on and wait for something better. Basic probability theory was more than adequate to the task and, though the calculations are simplistic and restrictive in application to the real world, they led to a number of predictive conclusions that have since been augmented by theory and, for the most part, corroborated by data.

"As a postscript to this story, I met MacArthur shortly after publication of the paper and discovered that he had been working on a similar model at the same time. A year later I intersected him again, unexpectedly, in Kennedy Airport, and described to him the ideas which became my 1968 paper. Again, our thoughts had been parallel, and this time he was in the lead. I discovered only later that he had already produced a rough manuscript. But he withheld his manuscript and I, unaware of his generosity, received credit for our ideas."

^{1.} Schoener T W. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369-404, 1971.

^{2.} Emlen J M. Optimal choice in animals. Amer. Naturalist 102:385-9, 1968.