

Schoener T W. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369-404, 1971.
[Biological Laboratories, Harvard University, Cambridge, MA]

Simple theory allows prediction of various features of an organism's feeding behavior, such as which items, from an array of encountered items, should (or should not) be selected. The theory unites a dispersed body of data and points toward numerous, highly feasible experimental tests. [The *SCI*[®] indicates that this paper has been cited in over 860 publications, making it the most-cited paper for this journal.]

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I often regretted during the last weeks of 1970 that I had let R.F. Johnston, the editor of *Annual Review of Ecology and Systematics*, persuade me to write an article on feeding-strategy theory that was due by December 31. I was suffering from a merciless flu that had worn away many of the capillary walls in my nasal passages—blood-spattered papers and books converted what had once been a rather pleasant dining space into a condemned area. My motivation for compiling the thousand-odd references read for this review was the usual hope that some entirely new pattern would emerge from an encompassing synthesis. In the last days, however, teetering piles of those references hunched like so many albatrosses, ready to pounce seriatim and grapple me from my deadline.

Somehow such reviews are written, and for me what eventually emerged was a well-over-the-ideal-length, quite compacted paper, summarizing extant theory (and creating new the-

ory) for a field begun only four years previously.^{1,2} In my paper I divided the theory into four parts to explain (1) why organisms select certain types of food from those encountered, (2) where organisms feed, (3) when organisms feed, and (4) why organisms feed solitarily rather than in groups. Questions like these quickly lit many fires, so that the literature in the area that was becoming known as "foraging strategies" (rather than "feeding strategies," as the paper attempted to christen it) exploded; growth has been steeply exponential over most of the last 20 years.^{3,4} It is certainly this latter fact that in large part accounts for the many citations to my paper; it caught the field just as it was taking off and perhaps helped the process along a bit as well.

However, my 1971 paper is often cited even now, long after its supersession by more current reviews. I imagine this is in part because of the several concepts either introduced in the paper or crystallized by it. These include a rigorous discussion of the energy-maximizer/time-minimizer dichotomy (first presented elsewhere)⁵ and the first complete algebraic formulation of the "fundamental" optimal diet model (although the essence of this model was first presented graphically by R.H. MacArthur and E.R. Pianka,¹ was first formulated algebraically in pieces scattered through an earlier one of my papers,⁶ and was eventually given its most rigorous form by E.L. Charnov⁷ and others). Other concepts such as the relation of foraging to fitness, optimal territory size, optimal group size as it contrasts costs to members vs. outsiders, and optimal foraging periods did not "take" then, although the first three of the four did later by a route that, so far as I can tell, had nothing to do with my 1971 paper. I think my 1971 presentation, however, communicated so well because terms in the equations were decomposed until biologically identifiable and measurable variables dropped out. This great strength of feeding theory, as opposed to much ecological theory at higher levels, must surely be largely responsible for the former's differentially great success.

1. MacArthur R H & Pianka E R. On optimal use of a patchy environment. *Amer. Naturalist* 100:603-9, 1966. (Cited 520 times.)
2. Emlen J M. The role of time and energy in food preference. *Amer. Naturalist* 100:611-7, 1966. (Cited 305 times.) [See also: Emlen J M. Citation Classic. *Contemporary classics in plant, animal, and environmental sciences*. Philadelphia: ISI Press, 1986. p. 196.]
3. Pyke G H. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* 15:523-75, 1984. (Cited 50 times.)
4. Schoener T W. A brief history of optimal foraging ecology. (Kamil A C, Krebs J & Pulliam H R, eds.) *Foraging behavior*. New York: Plenum, 1987. p. 5-67.
5. ———. Optimal size and specialization in constant and fluctuating environments: an energy-time approach. *Brockhaven Symp. Biol.* 22:103-14, 1969. (Cited 80 times.)
6. ———. Models of optimal size for solitary predators. *Amer. Naturalist* 103:277-313, 1969. (Cited 180 times.)
7. Charnov E L. Optimal foraging: attack strategy of a mantid. *Amer. Naturalist* 110:141-51, 1976. (Cited 210 times.)