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Charnov E L. Optimal foraging, the marginal value theorem. *Theor. Pop. Biol.* 9:129-36, 1976.
[Ctr. Quantitative Science in Forestry, Fisheries, and Wildlife, Univ. Washington, Seattle, WA and Inst. Animal Resource Ecology, Univ. British Columbia, Vancouver, Canada]

Natural selection is used to justify an economic approach to foraging behavior. A predator visiting a series of patches, where its own presence depresses the local food availability, should leave each patch when the intake rate within the patch drops to the average rate over all patches. [The *SCI*® indicates that this paper has been cited in over 400 publications.]

Foraging Decisions in a Patchy Environment

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My involvement with foraging decision theory was motivated by Gordon H. Orians; the specific catalyst was a lecture he gave in his advanced ecology class in the winter of 1971 at the University of Washington. Orians lectured about the pioneering work by J.M. Emlen[1] and R.H. MacArthur and E.R. Pianka[2] done five years before: the treatment of predatory decisions in an economic framework. The form of the question intrigued me. Although I found the original papers fairly difficult to understand, Orians's response was to challenge me to go beyond them. My association at that time with both Orians and John R. Krebs provided the necessary impetus. Krebs criticized the classical work from the viewpoint of an experimental animal behaviorist; in short, he said that the concepts must make predictions that are both interesting and experimentally testable. He claimed that the earlier work failed to meet these criteria.

My resulting 1973 doctoral thesis dealt with several questions in predator economics; use of a patchy environment (this paper) and diet breadth were the main areas. A simplified version of the "marginal value" result (tied to some experiments with J. Ryan and Krebs, the results of which were "just good enough" to suggest that we were on the right track) was published in 1974.[3] A later paper with Orians[4] explored in greater detail the possible reasons prey may become less locally available the longer a predator stays in any fixed location. I think these papers were widely cited because they satisfied Krebs's dictum of making interesting, testable, experimental predictions. The diet breadth theory[5,6] did likewise and again involved early experiments with Krebs.[7] Interestingly, Earl E. Werner, in his PhD thesis, formulated independently a version of the diet breadth theory for size selection of prey in fish. He provided experimental tests,[8] and his work has had an immense impact in the field of aquatic ecology.

The most highly cited papers in foraging ecology tend to fall into one or more of three classes; the originals that put new questions on the table,[1,2,5,6,9-11] early work that blended theory with hard data and suggested that the exercise was worth pursuing,[3-5,7,8] and a few overview (not just review) papers that discussed the broad implications of the economic approach.[10,11] Any scientific work that profoundly stimulates a field is bound to become quickly dated, and all the above-mentioned works are no exceptions. The recent book by D.W. Stephens and Krebs[12] shows what these early formulations got turned into.

1. **Emlen J M.** The role of time and energy in food preference. *Amer. Naturalist* 100:611-7, 1966. (Cited 335 times.) [See also: **Emlen J M.** Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences.* Philadelphia: ISI Press, 1986. p. 196.]
2. **MacArthur R H & Pianka E R.** On 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.]
3. **Krebs J R, Ryan J & Charnov E L.** Hunting by expectation or optimal foraging: a study of patch use by chickadees. *Anim. Behav.* 22:953-64, 1974. (Cited 185 times.)
4. **Charnov E L, Orians G H & Hyatt K.** Ecological implications of resource depression. *Amer. Naturalist* 110:247-59, 1976. (Cited 165 times.)
5. **Charnov E L.** Optimal foraging: attack strategy of a mantid. *Amer. Naturalist* 110:141-51, 1976. (Cited 240 times.)
6. **Pulliam H R.** On the theory of optimal diets. *Amer. Naturalist* 108:59-75, 1974. (Cited 220 times.)
7. **Krebs J R, Ericksen J, Webber M & Charnov E L.** Optimal prey selection in the Great Tit (*Parus major*). *Anim. Behav.* 25:30-8, 1977. (Cited 155 times.)
8. **Werner E E & Hall D J.** Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042-52, 1974. (Cited 320 times.) [See also: **Werner E E.** Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 16(8):18, 25 February 1985.]
9. **Pulliam H R.** Diet optimization with nutrient constraints. *Amer. Naturalist* 109:765-8, 1975. (Cited 110 times.)
10. **Schoener T W.** Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369-404, 1971. (Cited 930 times.) [See also: **Schoener T W.** Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 18(37):16, 14 September 1987.]
11. **Pyke G H, Pulliam H R & Charnov E L.** Optimal foraging: a selective review of theory and tests. *Quart. Rev. Biol.* 52:137-54, 1977. (Cited 860 times.) [See also: **Pyke G H.** Citation Classic. *Op cit.* p. 194.]
12. **Stephens D W & Krebs J R.** *Foraging theory.* Princeton, NJ: Princeton University Press, 1986. 247 p. (Cited 60 times.)

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