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
[Zoology Department, Michigan State University, East Lansing, MI]

This paper develops a cost/benefit model that predicts the optimal array of prey sizes a predator should choose from a given environmental distribution, i e, the array that maximizes return/effort All elements of the model are estimated from laboratory experiments with the bluegill sunfish (*Lepomis macrochirus*) Changes in prey size-selection by the bluegill with changes in prey density are shown to be in agreement with the predictions of the model [The *SCI*® indicates that this paper has been cited in over 205 publications since 1974]

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In 1967, as a beginning graduate student at Michigan State University, I was invited by Bill Cooper and Don Hall to collaborate with them in working up the data from a massive field experiment on the animal communities of small ponds I analyzed the response of the fish populations (bluegills) in these experiments while they concentrated on the invertebrates This turns out to have been a fertile experiment The report of that study was recently named a *Citation Classic*[1] and the patterns in prey selection exhibited by the fish motivated my thesis work, which resulted in the presently cited paper.

I discovered that, despite its catholic tastes for different prey species, the bluegill was very particular about the sizes of prey it chose In an attempt to account for this pattern, I developed a model of the costs and benefits associated with consuming different prey sizes and suggested that the fish selected an "optimal" array of prey sizes that maximized their return for effort It turns out that MacArthur and Pianka[2] and Emlen[3] had recently published similar models, but I was only vaguely aware of their work I had been more influenced by the work of Holling[4] on the components of predation, and the economic analogy was motivated by some reading in microeconomic and price theory. At this point, I again teamed up with Hall to test the theory experimentally in the laboratory.

This paper's popularity was certainly not evidenced early in its life history An initial version containing the theory was rejected by the *American Naturalist*, though similar papers were to appear there subsequently. We then combined the theory and experimental work and sent the paper to *Ecology*. Results there were only marginally more positive. First one, then a second set of reviewers expressed diametrically opposing views of the paper. Only because of the editorial wisdom of Bob Paine was the paper eventually published.

There appear to be several reasons the paper has been so widely cited. First, the work was timely Our study represented the first attempt to test quantitatively optimal foraging theory, and this area has grown enormously since the early 1970s (by 1981, papers on optimal foraging theory comprised 8 percent of the literature in the *American Naturalist*, *Ecology*, *Journal of Animal Ecology*, and *Animal Behavior*[5]). Moreover, the system was relatively simple, the phenomenon abundantly documented in the field, and the results in good agreement with the theory All of these factors appeared to contribute to the impact of the paper and it thus became part of the mandatory litany of citations found in the introductions of many foraging studies.

Second, the paper has been cited because of the minor controversy it created. Alternative explanations were offered to account for our results,[6] and attempts to resolve these views have led to a sizable literature exploring the size-selection of prey by fish The fact that this work was stimulated by our ideas has certainly been one of the more satisfying aspects of the response to our paper.

The hypothesis set out in this paper remains an open question, and it is transparent that such simple models cannot account for all of the complexities involved in food choice by animals. Yet what these models lack in precision seems to be compensated for by their generality as the ideas have now survived a least-qualitative test with a very wide variety of taxa, and attempts to build more realism into the models is an active area of research.[5]

1 **Hall D J, Cooper W E & Werner E E.** An experimental approach to the production dynamics and structure of freshwater animal communities *Limnol Oceanogr* 15 839-928, 1970 [See also **Hall D J.** Citation Classic *Current Contents/Agriculture Biology & Environmental Sciences* 12(44) 24, 2 November 1981]
2 **MacArthur R H & Pianka E.** On optimal use of a patchy environment *Amer Naturalist* 100 603-9, 1966 (Cited 425 times)
3 **Emlen J M.** The role of time and energy in food preference *Amer Naturalist* 100 611-17, 1966 [See also **Emlen J M** Citation Classic *Current Contents/Agriculture Biology & Environmental Sciences* 11(27) 10, 7 July 1980]
4 **Holling C S.** The functional response of invertebrate predators to prey density *Mem Entomol Soc Can* 48 1-86, 1966 (Cited 210 times)
5 **Krebs J R, Stephens D W & Sutherland W J.** Perspectives in optimal foraging (Brush A H & Clark G A, Jr, eds) *Perspectives in ornithology* Cambridge England Cambridge University Press, 1983 p 165-216
6 **O'Brien W J, Slade N A & Vinyard G L.** Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*) *Ecology* 57 1304-10 1976 (Cited 70 times)

