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This Week's Citation Classic®

Schoener T W. Models of optimal size for solitary predators.
Amer. Naturalist 103:277-313, 1969.
[Biological Laboratories, Harvard University, Cambridge, MA]

Models predicting optimal body size as a function of prey density, feeding style, and other properties of predators and prey are constructed from submodels, including one on diet selectivity. This theory helps understanding of such diverse phenomena as prey-size distributions, sexual dimorphism, and character convergence. [The *SCI*® indicates that this paper has been cited in over 200 publications.]

How Feeding Relations Affect Body Size

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In the mid-1960s, I was trying to understand the body-size patterns of the lizard genus *Anolis* generated from thousands of museum specimens whose measurements I had just completed. Some of these were not-so-obviously explained by the then-conventional character-displacement theory, e.g., one species sometimes converged in size toward a second species in the overlapping part of their geographic ranges; this nearly always involved the larger of the pair. I felt such patterns might be related to food availability and feeding selectivity, so I set out to make the connection between these characteristics and body size. First, I constructed several submodels that computed the optimal diet for a given predator body size and size distribution of prey. Then I constructed a second kind of submodel that gave the optimum from a set of body sizes, that predator size able to obtain energy requirements in the least feeding time. The entire model showed how optimal body size varied as a function of food density and feeding style (sit-and-wait vs. actively searching, or Type I vs. Type II, as I uncolorfully called them then).

I presented the details to Robert MacArthur and Henry Horn at Princeton University one very extended day, and MacArthur summarized the proceedings by saying that I had now developed a theory of optimal size but that it should take up no more than 12 pages in *American Naturalist*. In major disregard of this, I wrote a very long paper and sent it out for comment; my covering letter to Ed Wilson, one of my PhD advisers, began, "Just to remind you why you are on a leave of absence I am sending you a 42-page manuscript on optimal predator size." Buzz Holling, who was one of the reviewers, wanted still more information than I gave, and I eventually ended up with 36 printed pages, a compromise between the two prevailing styles of theoretical ecology at the time, but rather closer to Holling's than to MacArthur's.

This paper was in no sense a review paper, so that the citations it received must have resulted mostly from its original aspects, for example, the shape of the function relating mean prey size to predator size or the way in which food sizes selected vary with pursuit or provisioning distance, which was interesting enough to lead to a major elaboration.[1] Interestingly, the paper is almost never cited for perhaps its most important contribution: the first algebraic formulation of the by-now-standard optimal diet model (the contingency model, called "Type II" here). Rather, my 1971 paper,[2] along with papers by Ric Charnov,[3] Ron Pulliam,[4] and others, is cited instead. This probably results from the clumsy, FORTRAN-like manner in which the mathematics was presented; indeed, Charnov wrote, "I really did not understand the [optimal foraging theory] until I derived a lot for myself and then went back. Your '69 *American Naturalist* paper was impossible to me!"

Although other papers on optimal size as related to feeding later appeared, most notably those of Graham H. Pyke[5] and Gary E. Belovsky,[6] interest in this topic subsided somewhat, perhaps because it was realized (or realized again) that body size has a plethora of possible factors affecting it, only one set of which involves trophic considerations. Nonetheless, the model generates precise hypotheses that can be evaluated along with hypotheses concerning thermoregulation, sexual selection, and offspring-bearing capacity, among others, toward a full understanding of the determinants of body size. And the number of studies on a principal component of the model, optimal diet, have been truly enormous.[7]

1. **Schoener T W.** Generality of the size-distance relation in models of optimal foraging. *Amer. Naturalist* 114:902-14, 1979. (Cited 55 times.)
2. ————. 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.]
3. **Charnov E L.** Optimal foraging: attack strategy of a mantid. *Amer. Naturalist* 110:141-51, 1976. (Cited 240 times.)
4. **Pulliam H R.** On the theory of optimal diets. *Amer. Naturalist* 108:59-74, 1974. (Cited 220 times.)
5. **Pyke G H.** Optimal body size in bumblebees. *Oecologia* 34:255-66, 1978. (Cited 25 times.)
6. **Belovsky G E.** Diet optimization in a generalist herbivore: the moose. *Theor. Pop. Biol.* 14:105-34, 1978. (Cited 110 times.)
7. **Stephens D W & Krebs J R.** *Foraging theory*. Princeton, NJ: Princeton University Press, 1986. 247 p. (Cited 60 times.)

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