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Smith C C & Fretwell S D. The optimal balance between size and number of offspring. *Amer. Naturalist* 108:499-506, 1974.
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A graphical model is supported by standard analytical procedures to demonstrate that for any given environmental situation there is one optimal amount of resource for a parent to expend on each of its offspring. [The *SCI*® indicates that this paper has been cited in over 210 publications.]

A Rare Agreement

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The graphical model in our paper first dawned on me during a lengthy effort to publish an earlier manuscript[1] on the coevolution of squirrels and conifers. Dan Janzen had signed a long review of that manuscript indicating that he liked my ideas but thought that seed predators often selected for smaller seed size, as he had proposed in a paper[2] analyzing the coevolution of leguminous tree seeds and bruchids. In my first semester of graduate school, Gordon Orians had patiently explained H. Jenny's[3] ideas on the distinction between independent and dependent variables in the evolution of soil ecosystems. I thought that seed size would be determined mainly by selection from the independent variable, the physical environment, as it affects germination sites. Seed predators, as a dependent variable, would influence selection for the quantity and quality of chemical or, in the case of squirrels, physical defenses of the seed kernel. But, I needed a way to express the effects of changes in seed size and parental defense on parental fitness that would convince Janzen of my view. My revision, including the model, elicited 11 single-spaced pages of comment from Dan, easily a world record for length of careful review. However, it still took Monte Lloyd another four pages of editorial sorting before we were satisfied with the paper in which the model first saw the light of day.

I joined the biology faculty at Kansas State University in 1970, a year after Steve Fretwell. Our long discussions included many of the most stimulating in my life. Because Steve's biological world view starts with population regulation and mine with shifts in gene frequency, we almost never agreed. It was, therefore, very pleasing to both of us that we could agree on the significance of the model. As Steve said in a recent phone conversation, "If we agreed on it, it had to be good." The model is based on the assumption that as a parent expends more effort on the welfare of an offspring, the fitness of the offspring increases, a view inherent to both population regulation and natural selection. That assumption leads to a convex offspring fitness set when fitness is plotted as dependent on parental effort per offspring. A straight line through the origin is tangent to the curve at the optimum effort per offspring for the parent. I had drawn the fitness set and by chance the tangent through the origin. With a ruler, I convinced myself that the point of tangency did represent the optimum parental effort per offspring, but it took Steve to prove the point analytically and make the conclusion general. We decided authorship by the flip of a nickel.

Two students whose careers took them through Kansas State University on the way to the University of Utah, Mark A. McGinley and Dave Temme, have reviewed evidence that there is considerable variation within species and individuals in the size of offspring.[4] Their models, however, still indicate that even with spatial and temporal variation in the environment there is usually one optimum offspring size for an individual.[4] Temme[5] explains some of the conflict between theory and empirical evidence on the basis of parental response to variation in genetic fitness of offspring. McGinley and Eric L. Charnov[6] argue that parent plants limited by an essential resource (i.e., nitrogen) should vary expenditure on their offspring of a nonlimiting resource (i.e., carbon) in proportion to its availability. Our manuscript seems to have gained wide attention because it is a simple and general model that gives theoretical support to J.L. Harper's[7] observation that there is far less variation in seed size than seed number among individuals in a plant species.

1. **Smith C C.** The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecol. Monogr.* 40:349-71, 1970. (Cited 90 times.)
2. **Janzen D H.** Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* 23:1-27, 1969. (Cited 205 times.)
3. **Jenny H.** *Factors of soil formation.* New York: McGraw-Hill, 1941. 281 p. (Cited 375 times since 1945.)
4. **McGinley M A, Temme D H & Geber M A.** Parental investment to offspring in variable environments: theoretical and empirical considerations. *Amer. Naturalist* 130:370-98, 1987.
5. **Temme D H.** Seed size variability: a consequence of variable genetic quality among offspring? *Evolution* 40:414-7, 1987.
6. **McGinley M A & Charnov E L.** Multiple resources and the optimal balance between size and number of offspring. *Evol. Ecol.* 2:77-84, 1988.
7. **Harper J L.** Approaches to the study of plant competition. *Symp. Soc. Exp. Biol.* 15:1-39, 1961. (Cited 155 times.)

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