

# This Week's Citation Classic

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Cody M L. A general theory of clutch size. *Evolution* 20:174-84, 1966.  
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**Natural selection effects compromises among alternative complementary time and energy drains, and birds cannot simultaneously maintain high reproductive rates, be good competitors, and successfully avoid predation. In different environments different compromises are reached, and clutch size varies accordingly. [The SCI® indicates that this paper has been cited over 135 times since 1966.]**

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"Biology graduate students at the University of Pennsylvania were required to attend seminars and present review papers in four major areas of their subject. Robert MacArthur conducted the seminar in population biology, for which I discussed the evolution of reproductive rates in birds. With his encouragement, I submitted a version of my seminar paper to the sympathetic editors of *Evolution* and the paper became, evidently, a *Citation Classic*. I introduced the seminar with some lines by Robert Frost about the 'chain of beaded birth' which seemed appropriate at the time. Like many neophyte graduate students I thought I could see quite clearly how everything, from poetry to biology, fit together in the continuum of life, and the title of my paper reflects this confidence. In subsequent work on this and related ecological questions, I have tried to preserve a holistic approach and reach generalities that extend beyond taxonomic as well as time and place specifics. This, it seems to me, is what ecology is all about; only thus can one keep one's nose above

water in the seas of experimental reductionism and secular pedantry that currently threaten to swamp the field.

"In the mid-1960s the dominant view of the regulation of clutch size was that of David Lack,<sup>1</sup> conditioned by temperate England, who believed birds reared as many young as they could, food supplies permitting. Lack seemed to be right most of the time, especially since most bird studies were from temperate latitudes in which bird populations show high turnover rates and thus selection favors the phenotype that produces the most offspring. But in tropical America, Alexander Skutch<sup>2</sup> accumulated information that suggested that factors other than food supply might limit clutch size, and he implicated predation rate on nests as a likely alternative. This too seemed reasonable, in that stable populations with low turnover rates favor phenotypes that rear a few well-nourished and well-protected young. Such offspring would stand a better chance of attaining reproductive status in the competitive environments of populations at saturation density.

"My paper showed a way in which both Lack and Skutch might be right. As R.A. Fisher<sup>3</sup> first pointed out, a bird living in a low-predation environment at low or unpredictable population density cannot improve on the strategy of producing many young as fast as possible. However, I argued, in a high-predation environment the bird that slows its reproductive schedule and adjusts its behavior to counter the threat of predators might ultimately leave more offspring than the all-out fast breeder. See, for example, Rickleff for a more recent treatment.<sup>4</sup> Similarly, stable populations at carrying capacity are better broached by a few well-prepared offspring than larger broods of lower quality. These arguments are simple, logical, general, realistic, and in general accord with the evidence; I like to think that this explains why the paper has been so often cited."

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1. Lack D L. *The natural regulation of animal numbers*. Oxford: Clarendon Press, 1954. 343 p.
  2. Skutch A. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430-55, 1949.
  3. Fisher R A. *Genetical theory of natural selection*. New York: Oxford University Press, 1929. 272 p.
  4. Rickleff R E. On the evolution of reproductive strategies in birds: reproductive effort. *Amer. Naturalist* 111:453-78, 1977.