

Ecology and Behavior

Why do tropical songbirds lay fewer eggs?

Sometimes odd generalizations in science lead to unexpected places. Take, for example, a long obscure monograph published in 1944 by British ornithologist (bird expert) Reginald Moreau in the journal *Ibis* on bird eggs. Moreau had worked in Africa for many years before moving to a professorship in England in the early 1940s. He was not in England long before noting that the British songbirds seemed to lay more eggs than he was accustomed to seeing in nests in Africa. He set out to gather information on songbird clutch size (that is, the number of eggs in a nest) all over the world.

Wading through a mountain of data (his *Ibis* paper is 51 pages long!), Moreau came to one of these odd generalizations: songbirds in the tropics lay fewer eggs than their counterparts at higher latitudes (see above *right*). Tropical songbirds typically lay a clutch of 2 or 3 eggs, on average, while songbirds in temperate and subarctic regions generally lay clutches of 4 to 6 eggs, and some species as many as 10. The trend is general, affecting all groups of songbirds in all regions of the world.

What is a biologist to make of such a generalization? At first glance, we would expect natural selection to maximize evolutionary fitness—that is, songbirds the world over should have evolved to produce as many eggs as possible. Clearly, the birds living in the tropics have not read Darwin, as they are producing only half as many eggs as they are capable of doing.

A way out of this quandary was proposed by ornithologist Alexander Skutch in 1949. He argued that birds produced just enough offspring to offset deaths in the population. Any extra offspring would be wasteful of individuals, and so minimized by natural selection. An interesting idea, but it didn't hold water. Bird populations are not smaller in the tropics, or related to the size of the populations there.

A second idea, put forward a few years earlier in 1947 by a colleague of Moreau's, David Lack, was more promising. Lack, one of the twentieth-century's great biologists, argued that few if any birds ever produce as many eggs as they might under ideal conditions, for the simple reason that conditions in nature are rarely ideal. Natural selection will indeed tend to maximize reproduc-



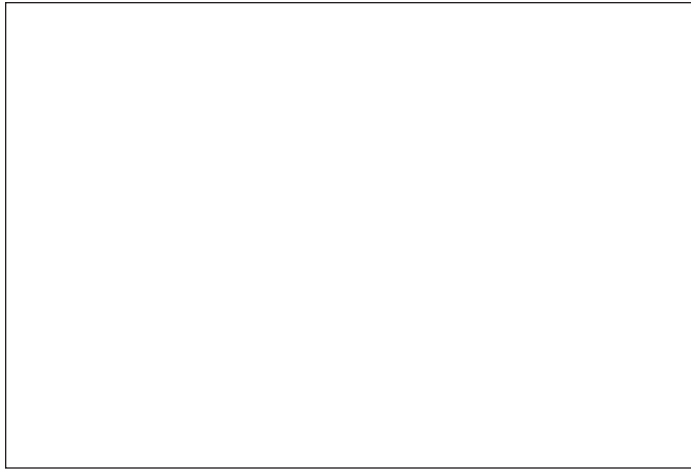
This Kentucky warbler is tending her nest of eggs. A similar species in the tropics would lay fewer eggs. Why?

tive rate (that is, the number of eggs laid in clutches) as Darwin predicted, but only to the greatest level possible within the limits of resources. There is nothing here that would have surprised Darwin. Birds lay fewer eggs in the tropics simply because parents can gather fewer resources to provide their young there—competition is just too fierce, resources too scanty.

Lack went on to construct a general theory of clutch size in birds. He started with the sensible assumption that in a resource-limited environment birds can supply only so much food to their young. Thus, the more offspring they have, the less they can feed each nestling. As a result, Lack proposed that natural selection will favor a compromise between offspring number and investment in each offspring, which maximizes the number of offspring which are fed enough to survive to maturity.

The driving force behind Lack's theory of optimal clutch size is his idea that broods with too many offspring would be undernourished, reducing the probability that the chicks would survive. In Lack's own words:

"The average clutch-size is ultimately determined by the average maximum number of young which the parents can successfully raise in the region and at the season in question, i.e. ... natural selection eliminates a disproportionately large number of young in those clutches which are higher than the average, through the inability of the parents to get enough food for their young, so that some or all of the brood die before or soon after fledging (leaving the nest), with the result that few or no descendants are left with their parent's propensity to lay a larger clutch."



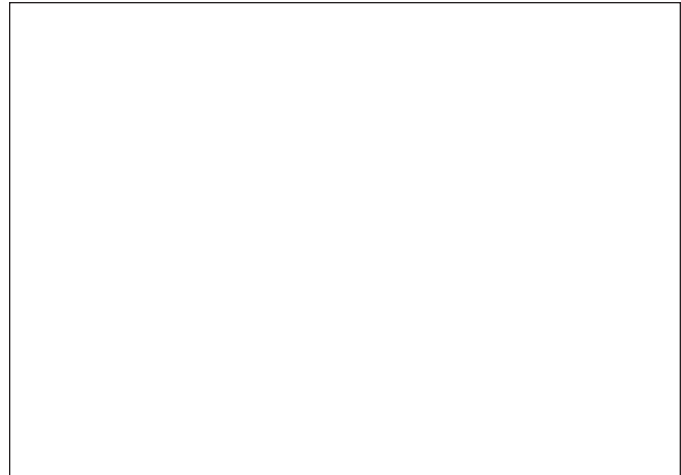
Testing Lack's theory of optimum clutch size. In this study from woods near Oxford, England, researchers found that the most common clutch size was 8, even though clutches of 12 produced the greatest number of surviving offspring. (After Boyce and Perrins, 1987.)

The Experiment

Lack's theory is attractive because of its simplicity and common sense—but is it right? Many studies have been conducted to examine this hypothesis. Typically, experimenters would remove eggs from nests, and look to see if this improved the survivorship of the remaining offspring. If Lack is right, then it should, as the remaining offspring will have access to a larger share of what the parents can provide. Usually, however, removal of eggs did not seem to make any difference. Parents just adjusted down the amount of food they provided. The situation was clearly more complicated than Lack's simple theory envisioned.

One can always argue with tests such as these, however, as they involve direct interference with the nests, potentially having a major influence on how the birds behave. It is hard to believe that a bird caring for a nest of six eggs would not notice when one turned up missing. A clear test of Lack's theory would require avoiding all intervention.

Just such a test was completed in 1987 in the woods near Oxford, England. Over many years, Oxford University researchers led by Professor Mark Boyce (now at the University of Wyoming, Laramie) carefully monitored nests of a songbird, the greater tit, very common in the English countryside. They counted the number of eggs laid in each nest (the clutch size) and then watched to see how many of the offspring survived to fly away from the nest. Nothing was done to interfere with the birds. Over 22 years, they patiently examined 4489 nests.



Two theories of optimum clutch size. David Lack's theory predicts that optimum clutch size will be where reproductive success of the clutch is greatest. George Williams's theory predicts that optimum clutch size will be where the *net* benefit is greatest—that is, where the difference between the cost of reproduction and the reproductive success of the clutch is greatest.

The Results

The Oxford researchers found that the average clutch size was 8 eggs, but that nests with the greatest number of surviving offspring had not 8 but 12 eggs in them! Clearly, Lack's theory is wrong. These birds are not producing as many offspring as natural selection to maximize fitness (that is, number of surviving offspring) would predict (see above *left*).

Lack's proposal had seemed eminently sensible. What was wrong? In 1966 the evolutionary theorist George Williams suggested the problem was that Lack's theory ignores the cost of reproduction (see above). If a bird spends too much energy feeding one brood, then it may not survive to raise another. Looking after a large clutch may extract too high a price in terms of future reproductive success of the parent. The clutch size actually favored by natural selection is adjusted for the wear-and-tear on the parents, so that it is almost always smaller than the number which would produce the most offspring in that nest—just what the Oxford researchers observed.

However, even William's "cost-of-reproduction" is not enough to completely explain Boyce's greater tit data. There were marked fluctuations in the weather over the years that the Oxford researchers gathered their data, and they observed that harsh years decreased survival of the young in large nests more than in small ones. This "bad-year" effect reduces the fitness of individuals laying larger clutches, and Boyce argues that it probably contributes at least as much as cost-of-reproduction in making it more advantageous, in the long term, for birds to lay clutches smaller than the Lack optimum.