

# EXPLORE THE ISSUE BEING INVESTIGATED

## 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 reproductive 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



**Barn swallow fledglings in a nest.** A similar species in the tropics would lay fewer eggs. Why?

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 that 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."*