

## BOOK REVIEWS

RAYMOND PIEROTTI, EDITOR

### INDIVIDUAL VARIATION AND THE COSTS OF REPRODUCTION

**Lifetime Reproduction in Birds.**—Ian Newton [Ed.]. 1989. Academic Press, New York, NY. x, 479 p. ISBN 0-12-517370-9. \$42.50, cloth.

In population ecology, the 1980s might be characterized as the LRS decade, because of the large number of studies of long-term (or lifetime) reproductive success. Many of these were summarized in Clutton-Brock's 1988 *Reproductive Success* (University of Chicago Press), and Ian Newton has quickly followed with the publication of *Lifetime Reproduction in Birds* (henceforth LRIB), which includes data on 23 studies of individual variation in breeding performance in birds.

One of the strengths of LRIB is the breadth of its coverage. The book is divided into five sections: (1) short-lived hole nesters, (2) short-lived open nesters, (3) cooperatively breeding species, (4) birds of prey, and (5) long-lived waterfowl and seabirds. A few chapters show some apparent overlap with Clutton-Brock's book, notably those chapters on Great Tits, Song Sparrows, and Florida Scrub Jays, but these are all classic studies with excellent data sets, and the emphasis in these chapters is different. As a result, LRIB stands by itself as a major reference work on avian life histories. Even more important, the data contained in these chapters may be instrumental in generating a new approach to population biology and life history evolution.

Perhaps the most significant legacy of the socio-biology furor to the study of population ecology was the recognition that, if it was important to study how specific behavioral tactics (or strategies) contributed to fitness, it was necessary to monitor specific, recognizable individuals. Ornithologists had a considerable head start in this area, because several long-term banding projects had been in existence since the 1940s. Until the late 1980s, however, the results of these studies were characteristically interpreted at the level of the population, rather than the individual, and led to the development of hypotheses and models based upon the mean performance averaged over the entire population. The historical antecedent of Newton's book from this perspective is David Lack's 1966 *Population Studies of Birds* (Clarendon Press, Oxford).

Another strength of LRIB is its emphasis on individual variation in lifetime breeding performance, and the general pattern that is yielded by these varied studies. In every study, a similar set of results is found, regardless of the size or longevity of the species involved. First, the majority of fledged offspring die before they even have a chance to breed. Second, a variable percentage of individuals that do breed produce no fledged offspring during their lifetimes. This percentage ranges from around 5% of tits, flycatchers, martins, and kittiwakes to around 40–50% of magpies, fairy wrens, geese, and gulls. Third, 50% or more of the fledged offspring are produced by only 15–30% of the

breeding adults, and a few individuals, typically only 1–2% of any given cohort, reproduce themselves many times over. Finally, the overall best predictor of the number of fledglings, and recruits, produced by an individual, or a pair, is the length of the individual's lifetime; i.e., individuals that live the longest have the highest LRS. (This result may alter, at least in part, our concept of what "short-lived" means in birds since the most successful "short-lived birds" typically survive to 6–7 years, which is greater than the average lifespan of many "long-lived" species.)

These results have significant, but not widely recognized, implications for population ecology. First, the mean, or typical, individual that is assumed to replace itself in the population over its reproductive lifetime does not, for all practical purposes, exist. The actual average individual in a population or cohort probably fails to leave any surviving offspring in most species. Second, the strong correlation between longevity and LRS calls into question the idea of a tradeoff between reproduction and survival (see below). In fact, most studies showed that successfully breeding individuals, which might have been expected to show reduced survival, actually showed higher rates of survival than unsuccessfully reproducing individuals. Finally, the high level of individual variation in lifetime breeding performance appears to be heavily influenced by stochastic environmental factors. For example, one of the best predictors of survival, longevity and LRS in Great Tits was fledging in a year in which beech mast crop was high.

Given the generality of these results (most of the studies in Clutton-Brock's *Reproductive Success* yielded similar patterns), it is appropriate to consider whether tradeoffs between survival and fecundity (costs of reproduction) actually exist in natural populations. Linda Partridge addresses this topic in a summary chapter on "Lifetime reproductive success and life-history evolution." Partridge opens with a discussion of optimal life history models, which are based on the idea that costs of reproduction generate tradeoffs between reproduction in the present and future survival and reproduction. The centerpiece of this section is the cost-based Charnov-Krebs model for the evolution of reproductive rates which argues that increases in clutch size above some optimum lowers survival of both adults and immatures. Unstated, however, is the underlying assumption of this model (and numerous similar models) that all individuals in a population are identical in quality and therefore any increase in clutch size will generate physiological stress. This is a general problem with evolutionary "arguments from design" which assume that all individuals in a population are equivalent from an evolutionary perspective. In reality, individuals are likely to differ in quality (e.g., physiological condition or amounts of stored energy reserves), with some individuals being in extremely good condition and most being in intermediate to poor condition.

Where costs of reproduction exist, they are almost certainly borne primarily or exclusively by these latter individuals, which probably have low LRS and make little or no contribution to future generations.

This variation in phenotypes with regard to individual quality is also relevant to Partridge's discussion of how costs of reproduction should be measured. This has become a controversial issue, with one school arguing that the best way to look for costs is to allow organisms to reproduce at the rate of which they are capable and see if there is a positive or negative correlation between current rates of reproduction and future survival or fecundity. If there is a negative correlation, costs are presumed to exist, whereas if the relationship is either zero or positive, costs are presumed to be unimportant. The alternative school, of which Partridge is a member, argues that these studies do not control for important confounding variables, and the only way to really look for costs is to manipulate the apparent rate of reproduction. These manipulative studies typically do show "costs of reproduction," but they achieve these results by ignoring underlying phenotypic variation.

For example, in birds the typical manipulative approach is to exchange eggs or nestlings among nests. This can be done according to strict protocols that allocate individuals randomly to experimental groups. However, the problem still remains that it is virtually inevitable given the results of the empirical studies in LRIB that most individuals in breeding populations are not in prime physical condition. As a result, many individuals are allocated a higher apparent rate of reproduction (i.e., more eggs or nestlings) than they are capable of sustaining. As a consequence, when results are averaged across these groups it is not unexpected that an apparent cost is shown. No one doubts that if individuals are given ever increasing numbers of eggs or nestlings to rear, even individuals in the best condition can be stressed. However, in all eleven manipulative studies reported by Partridge, breeding individuals had their broods enlarged above that which they produced on their own, and in some cases (most

notably Reid's work on Glaucous-winged Gulls) broods were enlarged beyond the achievable range of the species itself.

The important question that needs to be addressed is not whether it is possible to generate costs experimentally, but whether such costs are an important component of the evolved life history of a species. This returns us to the most important result of this book, the high level of individual variation in LRS among individuals. This variation, and especially the low numbers of highly successful individuals, could lead us to reevaluate our basic understanding of population dynamics. For example, what sort of fluctuations in population size might result from this variation in individual performance? Where exploited populations are concerned, how can we minimize negative impacts on our prime breeders? (One way might be to stop exploitation of trophy-size individuals.) Alternatively, have human beings created this variation by forcing species to live in abnormally high densities in a few habitat fragments?

A final question is whether this great variation in individual LRS shows the workings of powerful selection that could lead to reduce genetic diversity. The answer is probably not, because most of the traits associated with LRS (longevity, survival rate, age of first reproduction) seem to show low heritability. Thus, the plasticity in phenotypic abilities appears to be primarily the result of environmental variation.

To conclude, *Lifetime Reproduction in Birds* is an important book for population biologists, evolutionary biologists, and ornithologists in general. It would make an excellent basis for a graduate seminar or a discussion group. Along with Clutton-Brock's *Reproductive Success*, it provides raw material in its data sets that should lead to a rethinking of how we view population dynamics and fitness in birds. Finally, for a hard bound book produced by Academic Press, it is reasonably priced. —RAYMOND PIEROTTI, Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701.