

On the other hand, because Brown distorts so much of the development of the field as a conceptual framework for empirical study and because he fails to present the reader with a solid body of his own empirical data, this book may well be selected against.—MARCY F. LAWTON, Dept. Biological Sciences, The University of Alabama, in Huntsville, Huntsville, AL 35899.

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**Reproductive success: studies of individual variation in contrasting breeding systems.**—T. H. Clutton-Brock, ed. 1988. University of Chicago Press. ix + 538p. \$75.00 cloth, \$29.95 paper.

Variation in individual reproductive performance is the raw material upon which Darwinian selection must act, yet most models and theory in evolutionary biology concern themselves primarily with mean, or average, reproductive performance. This focus on mean performance, while useful from a theoretical point of view, may actually obscure useful patterns and information that could allow us to understand the action of selection, both natural and sexual, and the dynamics of populations. *Reproductive success* is the first book to collect and evaluate numerous studies of variation in reproductive performance over the lifetimes of recognizable individuals. Clutton-Brock has made an attempt to draw examples from as wide an array of taxonomic groups as available, yet the results come primarily from three groups: insects, birds, and mammals, with a single chapter on frogs. Even within these few groups, the quality of the data are highly variable. There is good news for ornithologists, however, since nine of the 10 best data sets are from long-term studies of birds.

Despite the variability in the quality of the data, a number of general trends and numerous useful insights can be discerned. First, male reproductive success (RS) generally varies more than female RS, but the variation in female performance is far greater than is traditionally assumed. Second, in most species where data exists, the best predictor of lifetime reproductive performance is survival. The major exception to this pattern may be in highly polygynous species where male mating success may be a better predictor, but the data supporting this argument are fairly weak (for reasons described below). Third, if the individuals with the longest lifespans also show the highest rates of reproduction, this calls into question the general concept of tradeoffs between survival and reproduction, especially for female organisms. This finally leads to the conclusion that in most populations, the bulk of successful reproduction may be performed by only a small per-

centage of the total population, and that these "superior" phenotypes show little or no cost of reproduction.

The putative existence of these superphenotypes has possible implications for both the study of selection and adaptation, especially if traits can be identified that contribute strongly to this high rate of RS. For this reason, one of the most stimulating chapters in the book is Grafen (chapter 28) "On the uses of data on lifetime reproductive success." At first, this chapter appears anomalous because Grafen's basic argument is that most of the data in this book are of limited use in studying adaptation, although they may be useful for examining selection in progress. Grafen is a disciple of the British "argument from design" school, and advocates the use of experiments that demonstrate current "function" as being the way to study adaptation. Despite Grafen's arguments, however, if variation in traits, either behavioral, morphological, or physiological, can be found that correlate with the variation in reproductive performance, they may well be useful in elucidating phenomena related to adaptation.

Grafen is correct, however, in pointing out that simply measuring RS tells us little or nothing about either selection or adaptation. One general weakness of most of the studies in this book is, in fact, that although they do an admirable job of describing variation in individual performance in some detail, they do little to examine the underlying factors that might contribute to this variation. Notable exceptions to this rule are chapters on *Polistes* wasps by Queller and Silk, on red deer by Clutton-Brock et al., and several of the chapters on birds.

One result that seems apparent from reading this book is that if you want to obtain a strong data set on lifetime RS, study birds, especially monogamous ones. Excellent results are provided by both van Noordwijk and van Balen, and McLeery and Perrins on Great Tits (*Parus major*), on Song Sparrows (*Melospiza melodia*) by J.N.M. Smith, on House Martins (*Progne* sp.) by Bryant, on sparrowhawks by Newton, on kittiwakes by Thomas and Coulson, on fulmars by Ollason and Dunnett, and on Florida Scrub Jays (*Aphelocoma coerulescens*) by Fitzpatrick and Woolfenden. The only weak chapter on birds is by Harvey et al. on Pied Flycatchers

(*Ficedula hypoleuca*) which presents no data on individual variance in RS and little data on any other topic.

The mammalian studies are all on polygynous species and run the gamut from excellent to weak. The chapter on red deer by Clutton-Brock et al. presents an excellent data set combined with a thought provoking discussion of the factors that contribute to variation in individual RS. At the other extreme is a chapter on northern elephant seals by LeBoeuf and Reiter, which uses data from male and female cohorts born 10 years apart to compare male and female lifetime RS. Since the male cohort was part of an expanding population whereas the female cohort was part of a stable or declining population the results are not at all comparable, and in fact LeBoeuf and Reiter obtain the unlikely result that *mean* male RS (2.95) was more than three times that of *mean* female RS (0.75). This demonstrates why comparisons of male and female lifetime RS should be drawn from the same cohort.

Another general observation that one gathers from this book is that data on reproductive success, whether seasonal, annual, or lifetime, should always be presented as histograms or frequency distributions. Reproductive data presented as means, even with standard errors or deviations appended, obscure too much information and patterns that allow us to understand the dynamics of a cohort or population.

Overall, I regard *Reproductive success* to be a successful book. It would be an excellent text for a graduate seminar, since it covers a reasonable taxonomic array, discusses a number of salient issues in evolutionary biology, and even presents a very intriguing way of evaluating the contribution of various components to total variation in reproductive output by David Brown. Strengths and weaknesses of various approaches and viewpoints are presented in the chapters on general issues by Brown, Grafen, and Clutton-Brock. *Reproductive success* demonstrates that we have come a long way in our understanding of population biology and reproductive success, but perhaps even more important, it demonstrates that we still have a long way to go and points us firmly in the right direction.—RAYMOND PIEROTTI, Department of Biology, University of New Mexico, Albuquerque, NM 87131.