"closest comrades and colleagues in pursuit of the Arctic's frozen fauna." At the end of the Blue Babe project, the latter two enjoyed a bison stew in Fairbanks, despite its "strong Pleistocene aroma."

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Muller's Ratchet

Sex and Death in Protozoa. The History of an Obsession. GRAHAM BELL. Cambridge University Press, New York, 1989. xiv, 199 pp., illus. $44.50.

The obsession to which Graham Bell refers in the subtitle of this book is that of protozoologists, who, from about 1900 to 1930, collectively produced a great volume of work seeking to determine whether protozoan lineages are potentially immortal or inevitably senesce, as do individual metazoans. Bell (p. xiii) states that his initial reaction was that this work indicated "the futility of research unguided by adequate theoretical understanding." It is also fair to say that present-day evolutionists are obsessed with sex, in particular with identifying the processes responsible for the origin and maintenance of sexual recombination, or mixis. Although there exists a wealth of alternative theories, which are discussed in *The Evolution of Sex: An Examination of Current Ideas* (R. E. Michod and B. R. Levin, Eds., Sinauer, 1987), there is a dearth of empirical data suitable for choosing among them.

Bell brings these two obsessions together in his book, which provides a stimulating blend of theory and experiment. He clearly presents the essential elements of ciliate reproduction and sexuality, as well as the technique of isolation culture, which allows an investigator to follow an asexual line of descent consisting of only one to a few of these unicellular organisms. Bell then analyzes the temporal trends in rates of fission in these lines, some maintained for thousands of generations, which he has compiled from dozens of old papers. His analyses indicate that isolated protozoan lineages do indeed typically decline in vitality, with extinction often resulting.

But Bell argues forcefully that this loss of vitality has little to do with somatic senescence in multicellular organisms; instead, it indicates the decay of the germ line in the absence of mixis between lines of descent. Again using data from these old papers, he shows that occasional conjugation (which, in ciliates, involves the reciprocal exchange of haploid "gametic pronuclei") permits indefinite maintenance of the lines.

Without mixis, deleterious mutations cannot be removed from a line of descent, but instead will accumulate in a ratchet-like manner first described by H. J. Muller. In large asexual populations, consisting of many different lines of descent, selection against those lines with the greatest load of deleterious mutations can be effective in opposing Muller's ratchet. However, in small asexual populations, such as protozoan lines maintained by isolation culture, random genetic drift causes the fixation of deleterious mutations and the ratchet advances inexorably. Mixis between lines of descent produces variation in the genetic load carried by individual organisms. While some sexual recombinants will carry more than the expected number of deleterious mutations, others will have fewer, thereby reversing the ratchet. Thus, Bell (p. 117) concludes that "conjugation rejuvenates ciliate lineages [by] bringing together deleterious mutations that have arisen in different lines of descent, so that the death of a few heavily-laden scapegoats can cleanse a whole community of its sins."

The rate at which Muller's ratchet advances is highly sensitive to population size because each advance reflects the subordination of natural selection to random genetic drift. The loss of vitality in isolation cultures of protozoans over mere hundreds of generations is therefore an extreme illustration of the effect of the ratchet, since "real" populations do not normally consist of only one to a few individuals. But Bell argues from theoretical models and scant data that, over much longer time scales, the accumulation of deleterious mutations presents a serious problem for any asexual organisms, except those with enormous population sizes or very small genomes (such as bacteria).

Bell admits, however, that the effect of mixis in opposing the ratchet could not easily account for the *origin* of sexual recombination, because the selective advantage accrues to a group, in the form of differential extinction of sexual and asexual populations; the individual protozoan apparently experiences a short-term reduction in fitness due to mixis (p. 132), and reciprocal genetic exchange is just as likely to increase an individual's mutational load as to decrease it. Nor does Bell suggest that the maintenance of sexuality is due solely to its beneficial effects in opposing Muller's ratchet. Rather, he observes that the ecological distribution of sexuality also supports the more traditional view that mixis is advantageous because the resulting genetic variation permits more efficient exploitation of variable environments.

In summary, Bell has presented compelling experimental evidence that occasional mixis is necessary to avoid extinction due to the accumulation of deleterious mutations, at least in extremely small populations. It remains to be seen whether this advantage of mixis is as ubiquitous as he asserts. I hope that this book will stimulate further experiments on the evolution of genetic systems in protozoa. In any case, Bell has clearly shown that a senescent body of data can be rejuvenated when it is mixed with fresh new ideas.

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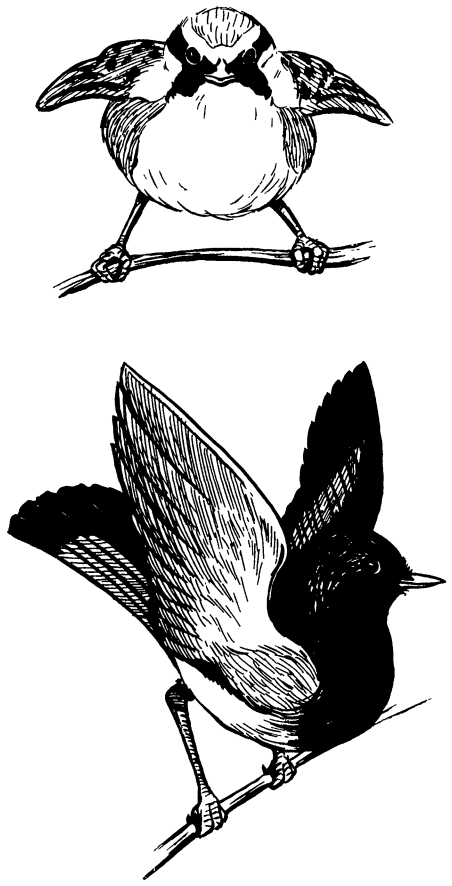
Feathered Models

American Warblers. An Ecological and Behavioral Perspective. DOUGLASS H. MORSE. Harvard University Press, Cambridge, MA, 1989. xiv, 406 pp., illus. $30.

In a recent issue of *Science* (**246**, 465–472 [1989]), Konishi *et al.* documented the many ways in which studies of birds have contributed to the understanding of biological processes and concepts. One group of birds in particular that has influenced the development of ecological, behavioral, and evolutionary theory is the Parulinae (family Emberizidae)—the New World warblers. Starting largely with the contributions of Robert H. MacArthur and his associates, studies of warblers have provided insight into topics such as species diversity, niche partitioning, habitat selection, mating systems, territoriality, population regulation, vocal and display repertoires, and speciation patterns.

In this book, Douglass H. Morse, a long-term student of the Parulinae, provides an interesting and often penetrating review of the ecology and behavior of this group of birds. On the basis of his own research and thorough and critical analysis of the literature, Morse considers warbler distribution and evolutionary history, breeding biology, migration, and wintering season ecology. In addition, he covers special topics such as predators and parasites, population limitation, plumages, and hybridization. Although his emphasis is on species that breed in the temperate zone and winter in the neotropics, Morse also devotes a chapter to species that are continuously resident in the tropics. He compares the Parulinae with Old World sylviine warblers and other passerine birds to illustrate important differences that provide insight into the evolu-



Displays of male warblers. *Top*, "wings out" display of chestnut-sided warbler (*Dendroica pennsylvanica*). *Bottom*, courtship display of American redstart (*Setophaga ruticilla*). [From *American Warblers*; redrawn by Brian Regal from painting by Dilger in M. S. Ficken and R. W. Ficken, *Living Bird* **1**, 103–122 (1962)]

tion and ecology of these animals.

Themes that recur through the book include species diversity, resource exploitation patterns, habitat selection, and population limitation. The last is discussed in terms of whether such limitation occurs on the summer breeding grounds, or in winter, or both. Although the available information on winter season ecology of these warblers is limited, Morse presents a good overview of what is known. I find his discussion of warbler population dynamics in winter rather superficial and, in contrast to other parts of the book, lacking in insight or suggestions for further research. As Morse points out, understanding the habitat relations, patterns of resource use, and especially the factors affecting the population sizes of such species, which must include studies of populations in both summer and winter, is both timely and crucial to conservation efforts. The accelerating effects of human modification of habitats in both temperate and tropical zones will inevitably have an impact on populations of many migratory birds, including Paruline species.

One of the central issues that appears in nearly all chapters is the potential importance of food resources. Morse, as do many other ecologists, consistently invokes resource limitation as the underlying cause for many phenomena, including niche and habitat partitioning, species packing, territoriality, and population regulation. Yet, as Morse acknowledges (but doesn't emphasize sufficiently, in my opinion), there are few, if any, quantitative or experimental studies of warbler or other migratory songbird populations that provide adequate measures of resource availability, not to mention resource limitation. If indeed food resources are as important as Morse and many others suggest, it is essential that avian ecologists tackle this problem and develop methodologies for measuring food availability and for testing food limitation.

Morse's call for more experimental manipulations in the studies of warbler and other bird populations is laudable. Despite their inherent difficulties, field manipulations, with appropriate replications, of habitat structure, food supplies, predators, and the warbler populations themselves may be the only way to tease apart the ecological and evolutionary processes that affect bird populations and communities.

I think some of Morse's most useful contributions in *American Warblers* are the many ideas and suggestions he makes for further research. Besides having a final chapter that explicitly describes ten areas in which research is clearly needed, he suggests numerous other hypotheses throughout the book. On a quick tally, I noted at least 40 such ideas that could lead to productive research projects, some of which would be short-term, perhaps done in a few weeks or a single season, and others of which would require many seasons and a large research budget. These should be of interest to both undergraduates and Ph.D. candidates looking for thesis projects, not to mention seasoned researchers.

This book clearly demonstrates that Paruline warblers are a fascinating group of organisms—they are diverse, colorful, and widely distributed and exploit their environments for breeding, wintering, and migrating in a variety of ways. Morse makes a convincing case for using them as a model avian system for further studies of ecological, behavioral, and evolutionary processes. Overall, this is an important book that will be of interest to field biologists and the general reader, as well as to avian ecologists and behaviorists.

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Foundations of Planktology

Biological Oceanography. An Early History, 1870–1960. ERIC L. MILLS. Cornell University Press, Ithaca, NY, 1989. xx, 378 pp., illus. $47.95.

Given a sufficient supply of nutrients and light, photosynthesizing plankton will grow at their intrinsic rates until nutrients become limiting, light is reduced by shading, and grazing organisms become abundant enough to check the increase and reduce the standing stocks. What kinds of organisms are involved in this process presumably depends on the seed populations and their adaptations to the particular physical conditions prevalent at the sites and periods studied (temperature and salinity distribution and the mix of nutrients and trace substances).

According to Mills, the investigation of this system constitutes the core of biological oceanography. He traces the history of the fieldwork, the experiments, and the concepts invented to elucidate the workings of the productivity machine of the ocean, beginning in the late 19th century and ending in the middle of the 20th, prior to the advent of "big science and the one-track strategy of the research grant." He does this with an eye to the sociopolitical setting within which the research takes place. His focus is on the stages of emergence of a quantitative theory of plankton dynamics in the 70 years between Victor Hensen's plankton surveys and Gordon Riley's equations describing growth rates of phytoplankton as a function of environmental variables and of intrinsic population properties.

The first part of the book, a little more than half of it, is devoted to the origin of biological oceanography in Germany and Scandinavia, in the late 19th and early 20th centuries. The heroes are Victor Hensen (1835–1924) and Karl Brandt (1854–1931), who founded the "Kiel school" of planktology, and H. H. Gran (1870–1955) of Oslo, who made a major effort to integrate plankton biology and physical oceanography. Other major players are Hans Lohmann ("nannoplankton"), Emil Raben (nutrient distributions), Alexander Nathanson (importance of upward mixing of nutri-