"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-