Foster discusses the heterogeneity of tropical forest vegetation and recommends with Diamond that tropical reserves be large and widely dispersed. With the chapters by Wilcox and by Terborgh and Winter based on the theory of island biogeography, the reader begins to suspect that ecologists do not define their terms or frame their questions carefully enough or make statistical tests. The authors do not take into account research from other sources indicating that predators are not the primary regulators of prey populations and suggesting that alternative theories explain distributions at least as well as the theory of island biogeography. And their recommendations are cast in vague, relative terms. Perhaps present ecological theory is insufficient as a basis for making decisions, at least about the design of nature reserves.

Populations of animals maintained for several generations at fewer than 50 breeding individuals lose genetic variability and suffer inbreeding depression. According to J. W. Senner, the size of the founder population is less critical than its rate of increase. This means that even the 580-square-kilometer Guatopo National Park in Venezuela is too small to provide for the long-term survival of its estimated 20 jaguars. In fact, Soulé and I. R. Franklin estimate that the minimum population size required to preserve evolutionary potential for the future is closer to 500 individuals. Given the levels of habitat destruction that have already taken place, the long-term maintenance of populations of large vertebrates on reserves is probably not possible. Goodman discusses whether careful modification of the age structure of a population could be employed to control populations without losing genetic variability and presents three applications of this method based upon data for the Pribiloff seal.

How about propagating endangered populations in captivity and then returning them to the wild? W. G. Conway and S. Campbell show that, the limited success that has been achieved with the whooping crane and the peregrine falcon notwithstanding, captive propagation is not economically feasible in most cases. According to Kleiman what is known about the management of captive populations has been learned slowly by trial and error and by sensitivity to species-specific behavioral systems.

The most comprehensive and encouraging chapter is the one by Coe on African wildlife resources. It summarizes the interactions between humans, the vegetation, the climate, and the fauna, emphasizing that if managed properly this system is still capable of renewing itself. The goal of putting conservation in a biological perspective is laudable, but Ehrlich concludes that if biologists doing basic research are going to be effective in the conservation movement more than their willingness to study the impoverished biota and make recommendations about nature reserves is needed. These efforts are only worthwhile if the larger conservation issue is also addressed. How do you get a wealthy nation to stop thinking in terms of an ever-expanding economy? The main message of this volume has to be read between the lines. Biologists are as ill prepared for the imminent resource crisis as the rest of the populace.

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Sexual Selection

Genetic Models of Sexual Selection. PETER O'DONALD. Cambridge University Press, New York, 1980. xii, 250 pp., illus. $32.50.

Darwin's theory of sexual selection, given in detail in *The Descent of Man and Selection in Relation to Sex* (1871), proved even more controversial in the scientific community than had the theory of natural selection. To explain patterns of sexual dimorphism in secondary sex characters and mating behaviors in higher animals, Darwin invoked two main selective agencies, combat or competition between individuals of one sex (usually males) for mates, and preferences exercised by the opposite sex (females) for certain characters in their mate (or mates). A major weakness in Darwin's argument was his inability to suggest why, in many species where males mate promiscuously and invest little or nothing but gametes in the next generation, females should develop sexual preferences for males with extreme characters that are apparently useless or deleterious for survival.

In species with exaggerated male characteristics, such as pheasants (most notably peacocks), birds of paradise, elephant seals, many deer and antelope, and some Hawaiian *Drosophila*, males may congregate at special localities called leks to compete and display for potential mates. In such mating systems differential mating success among males is determined in large part by female mating preferences, which are a major source of variance in male fitness. How are female mating preferences maintained in these systems? R. A. Fisher, in *The Genetical Theory of Natural Selection* (1930, 1958), provided an ingenious solution to Darwin's problem by suggesting that the evolution of mating preferences can be genetically unstable, so that "both the feature preferred and the intensity of the preference will be augmented together with ever-increasing velocity, causing a great and rapid evolution of certain conspicuous characters, until the process can be arrested by the direct or indirect effects of Natural Selection." The publication in 1972 of a Darwin centennial symposium entitled *Sexual Selection and the Descent of Man* (B. Campbell, Ed.) marked a resurgence of interest in sexual selection, which is today a subject of active research.

Peter O'Donald has developed much of the existing quantitative theory of sexual selection. In the volume under review, he summarizes and extends his work of the past several years, which has concentrated on the evolutionary importance of mating preferences. Although a synthesis of the literature on sexual selection is not attempted, whenever possible the models are motivated, illustrated, and fitted with data on mating systems in insects and birds, the emphasis being on experiments by Spiess and Ehrman on the rare-male mating advantage in *Drosophila* and observations by Davis and O'Donald on pairing and reproduction in the Arctic skua. O'Donald stresses that the evolutionary mechanisms of sexual selection are sufficiently complex that a quantitative approach using population genetics models is essential for a clear understanding of the dynamics of the process.

The book begins with a historical review of the theories of Darwin and Fisher and of misconceptions introduced by some prominent evolutionists. For example, A. R. Wallace, cofounder of the theory of natural selection, readily accepted the importance of male combat but refused for religious reasons to believe that species other than humans were capable of esthetic judgment and discrimination; and J. S. Huxley nearly eclipsed sexual selection as a legitimate subject of study for many years by confusing individual and group selection. Until recently it was not realized by many workers that under sexual selection the fitness of a trait with respect to mating success can override its value for survival, decreasing the average total fitness in a population. Further complications may arise from linkage between

genes influencing mating preferences and the preferred character or characters. Thus, popular methods based on optimality criteria, game theory, and kin selection are inadequate for the study of sexual selection and the evolution of mating systems. O'Donald's discussion of this topic (p. 58) would have benefited from a reference to the extensive work of Sewall Wright and others on frequency-dependent selection.

After summarizing the ecological and behavioral mechanisms of sexual selection, O'Donald describes three models in which all females in a population have the same (genetically fixed) type of mating preference: complete, partial, or frequency-dependent. The effect of each type of mating preference is modeled in all possible combinations with genetic variation in the male character as determined by two alleles at one locus: a dominant, codominant, or recessive trait with or without natural selection. O'Donald presents a simplified analysis of the evolutionary dynamics of the models, assuming genotypes are in Hardy-Weinberg proportions and selection is weak. An important result is that, unlike natural selection, the evolution of a recessive allele favored by sexual selection is much faster than that of a dominant allele. The chapter on monogamous species contains some of O'Donald's most original contributions and supports the theory of Darwin and Fisher that sexual selection can operate without polygamy. The final chapters are devoted to the evolution of mating preferences, using basic two-locus genetic models, and to assortative mating and sexual selection at a diallelic locus.

The major shortcoming of the book is its limitation to simple genetic systems where the fixation of an allele at one locus prevents further evolution of a trait. Although he confirmed the qualitative aspects of Fisher's theory, O'Donald claims that Fisher erred in concluding that the joint evolution of a male character and female mating preferences could result in an unstable exponential increase in both traits. With notable exceptions, such as some color polymorphisms, natural variation in quantitative characters is usually polygenic. For most dynamic systems the rate of evolution near an unstable equilibrium is approximately exponential, and when genetic variation is maintained by polygenic mutation and recombination Fisher's description may be rather accurate. It therefore appears that the qualitative theories of Darwin and Fisher are essentially correct for polygenic characters. The primary tasks for modern students of sexual selection are to develop quantitative models of these theories and to use them as conceptual tools in the empirical investigation of the behavioral and genetic mechanisms involved. *Genetic Models of Sexual Selection* is outstanding in both respects.

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Membrane Processes

Membrane Transduction Mechanisms. Papers from a symposium. RICHARD A. CONE and JOHN E. DOWLING, Eds. Raven, New York, 1979. xii, 236 pp., illus. $27. Society of General Physiologists Series, vol. 33.

Membrane Transduction Mechanisms is a collection of papers presented at the 33rd symposium of the Society of General Physiologists. The range of phenomena and experimental approaches addressed is wide, from antigen recognition to organ development, from diffraction studies to electrophysiology. This is both the volume's excitement and its weakness. The authors in general have done an excellent job of presenting their material with a broad readership in mind, but nonetheless the mental shifting of gears on moving from chapter to chapter is considerable, and one leaves the volume with an impression of a collection rather than of a unified presentation of any sort. An introductory chapter by the editors, posing general questions regarding transduction processes in membranes and tracing common motifs recurring among various specific systems, would have provided valuable cohesion and perspective.

With bacteriorhodopsin as the primary example, Henderson in a stimulating chapter suggests some generalizations regarding the structure of membrane-bound proteins: they should possess regular secondary structure such as α-helix at their interfaces with the lipid chains, and they should penetrate the bilayer completely if they penetrate it at all. Semi-integral proteins, which necessarily would have bend regions embedded in the bilayer, would therefore have unsatisfied hydrogen bonds and be energetically unfavorable. Residues believed to be involved in ion pumping, although hydrophilic, do not appear to create a domain with aqueous access, but rather a tightly knit array that would be consistent with their function in specific transport. Structural information regarding the retinal pigment rhodopsin (Hubbell and Fung), although harder to come by and of lower resolution, is consistent with these conclusions. Stoeckenius presents evidence for a light-induced isomerization of the bacteriorhodopsin prosthetic group (retinal). With the reasonable assumption that this isomerization results in a conformational change of the protein, the retinal-lysine Schiff base is postulated to be both the switch that "open-circuits" the proton conductance path in the absence of light and the pump that, by means of a pK shift energized by light, permits transport of protons against their energy gradient.

The enormous importance of calcium in communication between compartments is evident in many of the chapters. MacLennan and Klip review current knowledge and models concerning the calcium pump of the sarcoplasmic reticulum (diagrams would have made the models clearer); they emphasize that, since there does not seem to be a significant electrical potential across this membrane, flux of ions other than calcium (possibly magnesium, which is required for ATP hydrolysis by the pump) must be involved. Amino acid sequence information for a fragment essential for transport is consistent with a helix with a hydrophilic core, a structure conforming to the general predictions discussed by Henderson. However, the implied function of this region as the ionophore of the calcium pump is disputed by other workers.

The exquisite interlocking regulation of membrane transduction systems is nicely analyzed (in the context of cell activation) by Rasmussen and Clayberger. The regulation includes the activation of GTP-driven cyclase activity by hormone-bound receptor, with the simultaneous activation of GTPase activity to ensure the progressive termination of this cyclic AMP synthesis; the intimate relationship between calcium and cyclic AMP (is there special significance to cells using such disparate signals in combination?); the tuning of response by varying functional receptor concentration; and so on.

What determines the organization of actin filaments in various mechanotransducing systems such as microvilli or the acrosomal process of certain sperm? Evidence is accumulating (Tilney) that the mechanism utilizes actinin or actinin-like baseplates to originate nucleation of actin filament formation in the appropriate arrangement, with close regulation of free actin concentration at the level