Book Reviews

The Generative Process

Gametes and Spores. Ideas about Sexual Reproduction, 1750–1914. JOHN FARLEY. Johns Hopkins University Press, Baltimore, 1982. xii, 300 pp., illus. $24.50.

Why do some animals and plants reproduce sexually whereas others do not? How does reproduction happen in both cases? And why does sex exist at all? These are some of the questions that John Farley traces from the mid-18th to the early 20th century in this informative and well-organized book. Because the problem of reproduction has been fundamental throughout the history of biology, Farley's study touches on many of the biological disciplines, techniques, and theories of the last two centuries. His narrative encompasses three periods: 1750 to the 1830's, when sexual reproduction was the principal focus of naturalists' attention; the middle decades of the 19th century, when asexual reproduction became the paradigm of generation; and the period from the 1870's to the 1910's, when sexual reproduction reemerged as a unique process and took on a new evolutionary significance.

Because there are so many topics and individuals covered in this book (nearly 300 biologists are listed in the index), only a few subjects can be highlighted here. During the 18th century, Farley recounts, most naturalists believed in the preexistence of all living things since the Creation; and controversies arose over whether the preformed organism is carried by the female parent (ovism) or the male (animalculism). Sexual reproduction was seen as universal among living things, and the vertebrate animal and flowering plant provided the model for all organisms. Much discussion, among naturalists like Linnaeus, Buffon, Haller, Bonnet, and Spallanzani—whether pro or con preexistence—centered on fecundation, that is, on the problem of what each sex contributed to the generative process. Ovism became the dominant doctrine, and by the end of the century spermatic animalcules had been demoted to the status of parasites, as von Baer's term *spermatozoa* ("animals of the semen") denotes. One impact of Schleiden and Schwann's cell theory in the 19th century was to reinstate the status of spermatozoa, principally as a trigger to initiate the egg's development.

By the 1840's and 1850's, Farley shows, asexual reproduction had been found to be widespread among lower animals and plants. Additionally, alternation of generations was discovered by Steenstrup, although it was not fully understood for decades. Asexual reproduction became so much the focus of attention that, in Farley's words, "Sex no longer occupied center stage." Schleiden's and Hoffmeister's work on plant life cycles and the research of Owen, von Siebold, and Lubbock on parthenogenesis contributed to the belief that no fundamental difference existed between sexual and asexual reproduction and that only the stimulus required—soil or sperm—separated the spore from the egg. These ideas were mirrored in the development of Charles Darwin's views on reproduction, as can be seen in his early transmutation notebooks and in his later publications.

In the final chapters of his book, Farley documents the phenomenal impact that cytology had on reproduction studies, which resulted in the chromosome theory and in the discovery of mitosis and meiosis. Such figures as O. Hertwig, Weismann, Boveri, Roux, Driesch, E. B. Wilson, Bateson, and Morgan are discussed; and the merging of evolutionary theory, cytology, and the Mendelian theory of inheritance is traced through all its complexities. The chromosomal theory of sex determination arose as the paradigm case of the cytologists' reduction of sexual reproduction to identifiable cellular events—a viewpoint, Farley notes, that is still presented to biology students even though the actual picture is much more complex both genetically and environmentally. Farley ends his study by discussing the many fundamental problems still unsolved in reproductive biology, concluding that "ninety-nine percent of the world's species reproduce sexually, and we still do not understand how that came to be."

Much of this book is taken up with the presentation and analysis of scientific material. One subtheme is the relationship between improvements in observational techniques and scientific advance, which Farley discusses in two contexts: the development of achromatic lenses in the 1820's, with subsequent claims that one could see the sperm penetrate the egg; and parallel advances in staining and fixing techniques in the 1880's that led to observations of nuclear division. Rejecting the explanation that new techniques simply enabled investigators to see unambiguous new facts that necessarily generated advances in theory, Farley stresses the interpretative context in which such new evidence was received, as well as the controversies that ensued and that in turn generated further observational investigations.

A second attempt to offer a wider framework for his study can be found in the chapter "The sexless age," where Farley correlates the biological de-emphasis on sexual reproduction in the mid-19th century with Victorian attitudes toward sex and toward the place of women in society. The argument presented here is suggestive, yet it is not pressed too far (we are shown a "reflection" of social values in science rather than a "causation" of the latter by the former). Indeed Farley's comparison of Victorian sexual attitudes with the 18th-century context might have been strengthened had he not only looked for freer attitudes toward sex in the earlier period, but also noted the social context of the hierarchical and predetermined natural world depicted by 18th-century naturalists.

Farley's study is an important contribution to the history of biology, synthesizing a subject that has generally been treated only in episodic fashion. His ability to write for scientists as well as for historians should make *Gametes and Spores* appealing to both audiences.

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An Ecological Reconstruction

Resource Competition and Community Structure. DAVID TILMAN. Princeton University Press, Princeton, N.J., 1982. xii, 298 pp., illus. Cloth, $27.50; paper, $9.95.

In this book Tilman rebuilds the equilibrium theory of competition in ecological assemblages. The reconstruction includes changes in method, in testing ground, and in starting point. Individually these improvements are not entirely novel. Collectively, though, they allow Tilman to begin from the classical hypothesis that community patterns are the result of equilibrated interactions among species but finish by predicting patterns that have been thought to show that species assemblages are not at equilibrium.

Tilman is an economist rather than a sociologist of nature. His starting point is that competition is for consumable resources, the means of production. In the production function of a given consumer, any particular pair of resources can range from separately essential to fully substitutable, and Tilman classifies kinds and degrees of substitutability or essentialness. This seems an obvious thing to do, no more than a prefatory defining of terms. But it is the critical step, which finally produces a set of predictions that distinguish Tilman's model from classical competition theory.

Tilman's arguments make sense for plants, both phytoplankton and land plants. This is a much more substantial step forward than non-ecologists might expect. Plants contribute most of the metabolic activity, and usually most of the standing crop, to the world's ecosystems. Despite this, classical models of interaction among many species are based on population models that took their methods and variables from the demography of humans. Population theory remains much easier to apply to animals than to plants. Plant ecology for decades concentrated on distribution, succession, and metabolism. Only in the last ten years has there accumulated a substantial body of measurements on demographic variables in natural plant populations. And, though these measurements have made the traditional variables seem unsuitable when applied to plants, new models are only beginning to emerge. This book shows that the plant demography revolution has begun to reach beyond life-history theory to theories of interaction among species.

Tilman's choice of testing ground has its decisive effect when he comes to competition among species for two resources. He concentrates on pairs of essential resources, defined as those which cannot be substituted for each other at all, like phosphate and silicate or nitrogen and light, and unlike grass and browse or squid and prawns. His basic theoretical device is the Zero Net Growth Isocline (written ZNGI, inescapably pronounced zingie) of a species with respect to two resources. (Or more, in principle.) The central argument of the book is that an area saturated by resource-consuming individuals can support more than two species at equilibrium provided the species grow best on different ratios of the supply of two essential resources. Classical theory, in contrast, required species to do best on different resources if they were to occur in the same area at equilibrium; thus two different resources could support at most two winning species. Animals' food resources come in packages of mixed nutrients, and so are at least partly substitutable. Since the ratio between two resources can hardly be important if they are substitutable, it is easy to see how theoreticians thinking about animals would miss this line of argument.

Tilman assumes that any area contains point-to-point variation in the supply of each resource, and hence in resource-supply ratios. This assumption complements the ZNGI approach; under Tilman's model species co-occur in an area by each being able to win competition at different places within it. This might suggest that Tilman's model does not strictly deal with coexistence of species. But what is coexistence? Classical models deal with competitive exclusion within communities; the model builders have not worried about how to decide when two species are not in the same community, so that their coexistence does not need explaining. Many animal ecologists have argued that species are able to coexist within a community by using different microhabitats, without apparently thinking it necessary to define what they mean by coexistence or by community. Plant ecology, of course, has been obsessed with the definition of community for nearly a century, but with a view to finding repeatable combinations of species, rather than aiming to circumscribe sets of species such that there is competition within but not between the sets. Tilman's model bypasses this nagging problem by accepting that no two sedentary organisms literally live in the same place and handling point-to-point variation in such a way that it is unnecessary to specify how far apart the points are. He does not emphasize this aspect of his model, but I believe it will prove a real virtue in the long run.

The last five of the monograph's nine chapters extend the central argument in various ways; these extensions are somewhat more than illustrations and somewhat less than proofs by strong inference. The first and most emphasized extension is a prediction that increased resource supply will reduce species diversity. It is easy to understand how this prediction arises. Imagine a graph plotting the supply of resource 1 against resource 2. Now the range of conditions available within an area of land or water can be represented by a patch on this graph, with diameters representing the variation that is present within the area in supply of each resource. The angle subtended from the origin by the edges of this patch measures the range of ratios of resource supply that are available, which under Tilman's model controls the number of species that can occur in the area. As resource supply increases, the patch travels away from the origin. Unless its diameters increase in proportion, the angle subtended must decrease. Tilman simply assumes that, at most, variance increases in proportion to mean resource supply, that is, standard deviation (patch diameter) in proportion to the square root of supply. He may well be right, but surely it would not be inherently implausible for the standard deviation to increase in proportion to resource supply. This is one of several places where Tilman's model suggests what data will be enlightening and how to express them. The second major extension of the central argument is the use of resource requirements, expressed as ZNGI's, of particular species to understand which species will be dominant in particular situations. The highlight of the section devoted to this effort is a detailed and plausible analysis of changes over 100 years in the Rothamsted grassland plots under different fertilizer treatments. An extension to succession says no more than that in certain successions resource-supply conditions change over time. A section on the "superspecies problem" tries but fails to relax the assumption that jacks-of-all-trades are necessarily masters of none.

Though evidence is put forward to suggest that the various extensions of the central argument make predictions that are accurate, this evidence falls short of proof because there is no systematic effort to list other models and show that their predictions are worse. This book aims to show that a viable equilibrium theory of communities can be built, rather than to prove that theory. Alternative views of what controls community patterns emphasize that competitive exclusion can be slowed to the point of ineffectiveness by disturbance and erratic recruitment, unpredictable resource supply, or predation. In some situations there is indeed direct evidence for lack of equilibrium; nevertheless, the interest in non-equilibrium models has grown up largely because classical equilibrium theory has failed to explain the world. The debate will certainly shift ground following the appearance of Tilman's system of theory which predicts from equilibrium assumptions the pattern (for instance) of maximum diversity at low-to-medium resource supply levels.

The structure of classical population genetics is grafted to traditional, animal-oriented population models; the definitions and variables assume that life histories return to zygotes at regular intervals. But the plant world is thick with species made up of clones, centuries or even millennia old, each living in several independent pieces, never reaching a stable distribution of ages or life-history stages, with recruitment of new recombinants at the lower margin of detectability, and perhaps with substantial somatic mutation rates. The treatments of selection in population genetics textbooks do not suggest sensible programs for investigating the evolutionary ecology of such plants. Plant demographers are beginning to shed the mental habits of animal ecology—an easy step, because population ecologists have never been able to agree what the questions are, never mind the answers—but have not yet got up the nerve to challenge population genetics. Tilman's book reflects plant demography as a whole in this. Throughout, he calls success "growth," a natural word to use of plant competition. But in asides he explains that growth can be strictly interpreted as "the long-term instantaneous per capita reproductive rate when a stable age or stage distribution has been reached." I should have been glad to see him dispense with this obeisance to a formal definition of fitness. Growth is a sensible measure of evolutionary success; the first imperative of success for a piece of genetic information is that tissue containing copies of it be made at least as fast as tissue containing it is lost. Whether a net profit of growth is accumulated within the individual or as multiplication of individuals all much the same size is a second-order question.

The book moves along purposefully; it is recognizably from the Princeton Monographs stable. The sequence of argument is outlined both before and after, and each chapter is clearly summarized; when sinking in a particular passage the reader knows in which direction to jump for solid ground. The method is graphical rather than algebraic. More ecologists will believe the argument as a result, because we can tell at a glance whether a conclusion changes when a line has a bend put in it. Tilman brings plants to stage front, where they belong. He strips away peripherals and concentrates on the basis of evolutionary success: use of energy and materials to build tissue containing one's genes at a rate no slower, on average, than such tissue is lost. His model makes many predictions, plenty of them quite testable. His book deserves to be widely read.

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Embryonic Development

Cell Interactions and Development. Molecular Mechanisms. KENNETH M. YAMADA, Ed. Wiley-Interscience, New York, 1982. xii, 288 pp., illus. $39.95.

This collection of ten reviews by well-chosen authors summarizes and evaluates current knowledge of the molecular mechanisms underlying some of the cell interactions occurring during development. It was designed for advanced undergraduate and graduate students and for scientists who are not specialists in the subject. The intent of the editor and authors to create a thoroughly readable treatment of the subject is eminently achieved, for the papers provide current, understandable, and sometimes simplified accounts of research progress.

The first paper, by Wassarman, reviews sperm-egg interactions during fertilization, with special attention to the sea urchin and to studies by the author of the mouse zona pellucida. The paper is complemented by a treatment of the mating processes of yeast and of *Chlamydomonas* by Goodenough and Thorner. This paper contains a more detailed and comprehensive treatment of a narrower subject than any of the other papers does.

Roth gives a relatively brief but insightful account of the biochemistry of cell adhesion among vertebrate cells, and Barondes adds a discussion of developmentally regulated lectins and their possible roles in both intracellular and intercellular recognition. An interesting addition on a subject too often omitted in discussions of cell interactions is a paper by Dazzo on recognition involving plant cells. He reviews the mechanisms underlying selectivity in the fertilization process and those responsible for recognition and rejection of grafts. The emphasis of the paper, however, is on recognition between plants and microbes, including both pathogenic bacterial infections and the symbiosis between nitrogen-fixing *Rhizobium* and legumes.

Four papers deal with migrating cells and their interactions with the extracellular matrix. Harris reviews cell migration and its directional guidance. He gives only a superficial account of the proteins responsible for movement but thoughtfully discusses chemotaxis and the molecular mechanisms underlying contact guidance. The composition and morphogenetic roles of the pericellular matrix are discussed by Toole and Underhill, and Yamada reviews the structure and functions of fibronectin. The information presented in these three papers is integrated into the life history of a single group of cells in Weston's account of the migration of the neural crest cells. Weston's paper also includes an enlightening discussion of the roles of environmental influences in determining the phenotypes expressed by crest cells and of the prospects for analysis of the "conversation" between crest cells and their surroundings. This theme is further explored by Kratochwil in an excellent review of embryonic induction.

The strength of this collection comes from its coherence and from the authors' success in promoting understanding. The authors are aided in this endeavor by a wealth of superior illustrations and a substantial index. The book could serve well as the basis for a seminar or as a supplemental textbook in developmental biology courses, since many of the widely used textbooks are deficient in precisely the subjects covered by the book. The sole drawback to its wide use in this role is the book's price, which, if added to the price of a classical textbook, would make for an expensive, though exciting, course.

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Books Received

Geochemical Exploration in Deeply Weathered Terrain. Papers from a workshop, Floreat Park, Western Australia, June 1982. Raymond E. Smith, Ed. CSIRO Division of Mineralogy, Wembley, W.A., Australia, 1982. vi, 190 pp., illus. Paper, $A12.

Handbook of Stress. Theoretical and Clinical Aspects. Leo Goldberger and Shlomo Breznitz, Eds. Free Press (Macmillan), New York, and Collier Macmillan, London, 1982. xxii, 804 pp. $49.95.

Hankel and Toeplitz Matrices and Forms. Algebraic Theory. I. S. Iohvidov. Translated from the Russian edition (1974) by G. Philip A. Thijsse. Birkhäuser, Boston, 1982. xiv, 232 pp. $24.95.

Health and the Law. A Handbook for Health Professionals. Tom Christoffel. Free Press (Macmillan), New York, and Collier Macmillan, London, 1982. xiv, 450 pp. $29.95.

Heat Pipes. P. Dunn and D. A. Reay. Pergamon, New York, ed. 3, 1982. x, 308 pp., illus. Paper, $20.

Heat Pipes and Thermosyphons for Heat Recovery. Papers from a conference, London. D. A. Reay, Ed. Pergamon, New York, 1982. iv pp. + pp. 259–348, illus. Paper, $64. *Journal of Heat Recovery Systems*, vol. 1, No. 4.

Insect Behavior. A Sourcebook of Laboratory and Field Exercises. Janice R. Matthews and Robert W.

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