GAIA OUT OF EQUILIBRIUM?

Author: MARTIN, RONALD E.

Source: BioScience, 55(9) : 799-801

Published By: American Institute of Biological Sciences

URL: https://doi.org/10.1641/0006-3568(2005)055[0799:GOOE]2.0.CO;2

Walking Back through Evolutionary Time

The Ancestor's Tale: A Pilgrimage to the Dawn of Evolution. Richard Dawkins. Houghton Mifflin, Boston, 2004. 673 pp., illus. $28.00 (ISBN 0618005838 cloth).

Richard Dawkins, the Charles Simonyi Professor of the Public Understanding at Oxford University, has written his best book—a large claim, given its many excellent predecessors. It is also the best book available if one really wants to "get" evolution, in contrast to being lucidly informed about it (which other books accomplish), because Dawkins, using a brilliant structural device, enables his readers to participate in the evolutionary process.

After a few introductory chapters in which Dawkins carefully explains what is meant by "common ancestry" and explores the common ancestry of humankind, we then set out, as a pack of all the humans alive today, on a backward journey through time. After traveling for 6 million years, we meet up with a pack of all the chimps and bonobos alive today (alas, a very much smaller pack than ours). They have also been walking for 6 million years since the present, and we meet at our first rendezvous site, the time of our common ancestor ("concestor"). Here we pause for some commentary on chimps and bonobos, and then the humans, chimps, and bonobos join together and walk for another million years until we meet, at the next concestor rendezvous, all the gorillas alive today. After some gorilla commentary, we all join up until we meet with the pack of orangutans 14 million years ago. They join us, and next we hook up with the marching gibbons at the 18-million-year mark.

The meetings continue with the various living families of the primate order, and then become more coarsely grained, as we join with groups of related mammalian orders, then with birds and reptiles, fish, fungi, plants, and the various unicells. The final (40th) rendezvous, more than three billion years ago, is with the concestor of us all, that DNA-bearing creature with whom bacteria, archeans, and eukaryotes all share common descent. Many of the creatures that join us—like the lungfish, lancets, and sea squirts—have only one group of living representatives; their tenacity reminds us of the countless creatures who fail to join us at all—like the dinosaurs and trilobites—because they are not alive today. Others have radiated since our shared ancestry into forms that startle us with their diversity, like cats, dogs, bears, weasels, hyenas, seals, and walruses, which all evolved from a root concestor that lived 75 million years ago.

This backward chronology is immensely effective. Each chapter opens with the same simple diagram that shows the next group to join, with the relevant dates and geological eras. I found myself turning a page, taking in the diagram, and gasping, "Holy cow! Here come the rodents!" or "Wow, here come the insects!" It's also a most effective antidote to forward chronologies that so readily convey the sense, however unintentionally, that other species in the diagram are lower or more primitive, while humans are the apex and hence the point. Going backward drives home the fact that all present-day creatures are equipositioned in the present and that biological diversity is the consequence of planetary circumstances, and adaptations to those circumstances, in the past.

Going backward also allows us to experience, rather than just know about, the deep time involved. At the outset we are appropriately impressed by concestors encountered 20 million or 75 million years ago, but as we continue to trudge, the time intervals are measured in the hundreds of millions, and the diagram shrinks in scale until the rendezvous points that were once widely spaced are layered on top of one another. By the time we get to the archeal and bacterial concestors, there's the palpable sense of peering into some dark, roiling deep-sea vent on some mysterious planet that is nonetheless this planet. I came away feeling as though I had come to understand the word *ancient* for the first time.

In less skillful hands, a template like this could become tedious: by the 20th rendezvous, the format could sag. Happily, Dawkins is the consummate tour guide, embellishing the journey at every turn, sometimes pausing to offer a clear and trenchant explanation of cladistics or geological dating, sometimes commenting on the configuration of the continental plates in that period, sometimes telling us of the marvelous ways that particular creatures go about their lives (as a teller of natural history, Dawkins is right up there with Stephen J. Gould). There's a photograph here, an amusing anecdote there, an account of a blistering scientific controversy about phylogeny somewhere else. Dawkins is always with us, letting us know when an idea or a dating is controversial or speculative and how he made the call, sharing his awe with us at everything we encounter. The scholarship involved in pulling this book off quite boggles the mind, yet there's nary a whiff of pedantry. Although I came to this book with a more substantial understanding of evolution than the generic "average reader," I am confident that it is accessible to anyone with some science background and a sense of adventure.

Those interested in Dawkins's more theoretical perspectives on evolution will find much excellent thinking to consider in his concluding chapters. Since the 1976 publication of *The Selfish Gene* (Oxford University Press), Dawkins has served as the poster child, not to mention the whipping boy, for a gene-centered view of life and evolution, despite the more inclusive perspectives offered in his later books. In *The Ancestor's Tale,* he appears to be incorporating the valuable thinking of complexity theorists like Stuart Kauffman into his framework, lifting up the centrality of autocatalytic cycles in biology and mentioning the concept of emergence ("No extra ingredient needs to be added at the micro level to explain the macro level. Rather, an extra level of explanation *emerges* at the macro level as a *consequence* of events at the microlevel"; p. 605). He also takes on the now-classic Gould question, sharpened by Kauffman, as to whether, if the clock were rewound, evolution would produce the same outcomes. Dawkins argues persuasively that yes, the same *kinds* of adaptations—vision, audition, flight, and intelligence—keep popping through, because niches that render such adaptations useful are continuously available.

Particularly important is his consideration, regrettably brief, of the concept of evolvability, a concept he first proposed in a paper in 1987 and one that, to my mind, is likely to have a far more enduring legacy than the concept of the selfish gene. The basic notion is that the capacity to evolve is a feature of a lineage, a capacity that is itself subject to both variation and selection. Organisms with evolvable features are more likely to diversify; hence their lineages are more likely to radiate into new niches; and hence the lineages are more likely to be represented in an inventory of present-day organisms. An example of an evolvable trait is the segmented animal body plan, ab initio a fairly simple scheme involving differential *Hox* gene expression. Once set up, it is also fairly simple to add or subtract segments in the embryo, and for particular segments to acquire particular features, the outcome being the spectacular diversity of animal forms. Evolvability is fast becoming a central feature of evolutionary theory, and it would be exciting if it were the centerpiece of Dawkins's next book.

URSULA GOODENOUGH
Department of Biology
Washington University
St. Louis, MO 63130

GAIA OUT OF EQUILIBRIUM?

Scientists Debate Gaia: The Next Century. Stephen H. Schneider, James R. Miller, Eileen Crist, and Penelope J. Boston, eds. MIT Press, Cambridge, MA, 2004. 377 pp., illus. $50.00 (ISBN 0262194988 cloth).

Since its appearance, the Gaia hypothesis has attracted criticism, skepticism, and outright hostility, for a number of reasons. First, the name "Gaia" (meaning goddess of the earth) implied to some that Earth was alive and also goal-directed (i.e., teleological). The alternative "weak Gaia" hypothesis, which held that Earth was self-regulating (i.e., homeostatic through feedback mechanisms), was more palatable to a larger number of scientists. However, many scientists still believed this version of Gaia was merely a metaphor that explained relatively little that was (presumably) not already understood. Finally, there was no consistent statement or definition of the Gaia hypothesis.

Nevertheless, the Gaia hypothesis is widely credited with having stimulated the development of the science of Earth systems. The Gaia hypothesis challenged the then prevalent reductionist approach of most science, because it required multidisciplinary approaches to understanding Earth's biological and geophysical realms and their interactions. The science of Earth systems received a further boost with the growing realization in the late 20th century that Earth's environment has affected civilization in the past, and that anthropogenic activities are now affecting art and civilization. The current surge of studies aimed at detecting life on other planets also stems in part from the Gaia hypothesis.

So what is the current status of Gaia? *Scientists Debate Gaia: The Next Century* attempts to answer the question by building on an earlier (1988) Gaia symposium. For one thing, in the authors' view, Gaia has been upgraded from hypothesis to theory. Gaia is certainly a theory at some stage of development, because it is an innovative way of viewing Earth itself (see the introduction, by James Lovelock). Despite the blossoming of Earth systems science, however, there is still no clear definition of the Gaia theory. One author (Lenton, chapter 1) equates Gaia to the "Earth system with abundant life." This definition implies that Earth cannot function as a system without life. Perhaps this is true for Earth as we know it, but physicochemical systems can exhibit emergent properties such as feedback and self-regulation, and there is no reason to think that such systems could not function on other planets without life, given suitable conditions. Otherwise, how could simple nonliving systems have given rise to life on Earth? Another definition restricts Gaia to the biosphere alone (Volk, chapter 2). Why then do we need the term "Gaia"? "Biosphere" is much more widely accepted and used in the literature.

Second, Gaia theory states that Earth is in equilibrium (steady state) as a result of feedback and self-regulation (homeostasis). The concept of Earth in homeostasis is based on the notion of the uniformity of nature. Early in the 19th century, Charles Lyell (on the basis of observations of modern processes and their rates of change) formulated what came to be called the principle of uniformitarianism. This principle is usually blithely stated in textbooks as "the present is the key to the past," but it meant far more than this to Lyell. According to him, Earth's behavior was cyclic, so that Earth exhibited no net change (Gould 1987). In Lyell's view, for example, as mountains were slowly uplifted in one place, they were slowly eroded elsewhere, resulting in no net change (i.e., in equilibrium). Geologists are proud to claim this principle as their own, because they infer the existence of past processes and events on the basis of modern analogs. However, uniformitarianism really underlies all scientific inquiry. Indeed, the concept of equilibrium oozes all through modern science. It allows us, for example, to study rates of change for systems that are presumably in steady state. Such studies indicate that Earth's systems do indeed exhibit equilibrium behavior, because they typically move back toward their original state when disturbed. Nevertheless, the feedback mechanisms may not be as tightly coupled as Gaia theory would seem to predict, because feedbacks have had to evolve, and time lags occur between stimulus and response (Föllmi et al., chapter 7; Kump, chapter 8).

Moreover, Earth's geologic record is rife with evidence of directional (secular, noncyclic) changes. Directional changes may be so slow that the systems *appear* to be in equilibrium, when in fact the systems are changing on geologic scales of time. In their early papers, Lovelock and Margulis pointed to the presence of an atmosphere in disequilibrium (i.e., the presence of oxygen) as evidence for life. Early critics countered by pointing out that the presence of oxygen contradicted the Gaia hypothesis of global homeostasis. A similar theme resurfaces several times in the current volume. Volk, for example, argues for a nonteleological view of the Earth as "a waste-world: a system of by-products (and their effects).... Organisms make metabolic products aimed to ensure their success at living and reproducing, not aimed at transforming or controlling the global environment" (p. 27).

Thus, the processes that occurred during the ancient past have also varied with historical circumstances, or contingency (Gould 1987). One cannot truly understand the behavior of Earth's systems (Gaia) without examining the geologic record, because processes observable on human time scales do not necessarily scale upward to geologic time scales (as Lyell inferred they did), nor do historical constraints remain the same (Martin 1998). (Indeed, the words *geology* and *Gaia* share a common etymological derivation.) Chemical elements have always reacted in the same (uniformitarian) manner, to be sure, but the historical constraints under which they have reacted have changed through time. For example, the cooling of the earth led to the formation of continents and the appearance of continental shelves. Continental shelves, in turn, provided widespread (photic) habitat for early photosynthesizing cyanobacteria, the metabolic by-product of which (oxygen) led to eukaryotes. Various branches of photosynthetic eukaryotes eventually led to eukaryotic plankton in the seas and terrestrial forests on land, forming the base of early food chains (Martin 1998).

Paradoxically, then, in helping to maintain equilibrium (homeostasis), Gaia may be slowly driving Earth away from equilibrium because Earth's systems require the flow of matter and energy (including the metabolic products and structures of other creatures) to function (Schwartzman and Volk, chapter 11). Could Gaia therefore be out of equilibrium on geologic scales of time because it obeys the laws of thermodynamics? In the case of the biosphere, natural selection acts to increase the total mass and energy flux through a system, so long as there is unutilized matter and energy made available (Lotka 1925). Through natural selection, species possessing superior energy-capturing and energy-directing devices direct more energy and matter into their biomass than other species, causing the total biomass of the system (ecosystem, biosphere) to increase. Improved energy acquisition and accumulation in one species reduces the total energy available to other species by sequestering nutrients in biomass; to survive, the other species must improve their acquisition of energy. As a result, there has been a "ratchet effect" on the biosphere in terms of energy flow and diversity (Martin 1998). It is precisely this kind of behavior that accounts for the seemingly teleological behavior of Earth's systems and counters the criticisms of evolutionary biologists about what is selected in Gaia (Schneider, chapter 4; Sagan and Whiteside, chapter 15).

Of course, computer models provide a way to effect long-term change on human time scales. Most of the models presented in this volume are based on Lovelock's "Daisyworld," which was intended only to demonstrate the feasibility of feedback and self-regulation by a system (in Daisyworld, life regulates Earth's surface temperature by regulating the planet's albedo). Daisyworld was never meant to be more than this, but a number of Gaia models are based on Daisyworld because it provides a convenient starting point. Two chapters in this volume point out flaws in the original Daisyworld model and present more realistic models (Weber and Robinson, chapter 20; Nordstrom et al., chapter 21). Although one can test models using sensitivity experiments, the best way to test them is to evaluate them against geologic and climatic data sets. Unfortunately, there are few attempts in this volume to evaluate models against data.

Specific case studies (which might make more scientists willing to view Gaia with less skepticism) are also few in this volume. Besides the chapter by Föllmi and colleagues on phosphorus and carbon cycling, two of the most intriguing are those by Kleidon (chapter 25) on the response of Amazonian forests to aridity in the tropics during glacial intervals, and by Gómez and colleagues (chapter 28) on the bacterial flora of extreme (low-pH) environments of the Tinto River (Spain), which has obvious implications for finding life on other planets.

To sum up, this volume does indeed demonstrate that Gaia is an innovative way of viewing the earth. Like Gaia itself, Gaia theory is also evolving. But, in order to evolve as more than a way of thinking, Gaia theory must continue to test its predictions against historical records on different time scales. It is in this way that Gaia will gain broader acceptance among scientists in the next century.

RONALD E. MARTIN
Department of Geology
University of Delaware
Newark, DE 19716

References cited

Gould SJ. 1987. Time's Arrow, Time's Cycle: Myth and Metaphor in the Discovery of Geological Time. Cambridge (MA): Harvard University Press.

Lotka AJ. 1925. Elements of Physical Biology. New York: Williams and Wilkins.

Martin RE. 1998. One Long Experiment: Scale and Process in Earth History. New York: Columbia University Press.

LIFE: THE SHORT(ER) VERSION

Evolution. Douglas J. Futuyma. Sinauer, Sunderland, MA, 2005. 603 pp., illus. $89.95 (ISBN 0878931872 cloth).

As all evolutionists know, Douglas J. Futuyma, a professor at the State University of New York at Stony Brook, is the author of a successful textbook about evolution. The third edition of

Evolutionary Biology (Sunderland, MA: Sinauer) appeared in 1998, weighing in at nearly 1000 large-format pages, including references and other subsidiary material. *Evolution* is Futuyma's update of the earlier text, with a welcome 40 percent reduction in length. It includes two chapters written by other authors, "Evolution of Genes and Genomes" (chapter 19), by Harvard's Scott V. Edwards, and "Evolution and Development" (chapter 20), by John R. True, Futuyma's colleague at Stony Brook. Evolutionary studies have advanced at a fast pace in the last seven years. The new book fittingly incorporates recent knowledge from molecular biology, genomics, population genetics, paleontology, ecology, and animal behavior, although these terms do not appear in any of the chapters' titles. There is no separate chapter on human evolution and variation, which was the subject of the final chapter in *Evolutionary Biology;* much of what was in that chapter appears dispersed throughout the new book.

"Evolutionary Science, Creationism, and Society" is the final chapter of *Evolution*, and at 20 pages is a useful expansion of the 5-page appendix, "Contending with Creationism," in the previous textbook. More than 40 percent of Americans, including many college students and college-educated citizens, believe that *Homo sapiens* was directly created by God rather than having evolved, through several hominid species, from nonhuman ancestors shared with other primates and, ultimately, from very remote and very different sorts of organisms that are also ancestral to many other species on Earth. Some creationists believe that our planet is less than 10,000 years old, while others accept Earth's old age but claim that God's special action is required to account for the different kinds of organisms. A recently revived version of this view is known as intelligent design (ID).

The argument from design was articulated by the English theologian William Paley in his book *Natural Theology* in 1802, with greater cogency and more extensive knowledge of biological detail than has been shown by any other creationist author before or since, although modern authors adduce biochemical or mathematical considerations that were unknown in Paley's time. Paley's argument derives from a notion akin to what some contemporary authors have named "irreducible complexity," which he calls "relation": the presence of several parts interacting with each other to produce an effect that cannot be accomplished if any of the parts is missing. This argument is fallacious and has been refuted with evolutionary evidence. As Futuyma writes in *Evolution,* "an adaptation that we see today may indeed require precise coordination of many components in order to perform its current function, but the earlier states, performing different or less demanding functions, and performing them less efficiently, are likely to have been an improvement on the ancestral feature" (p. 534).

A telling example is the presence among living species of molluscs of a gradation from very simple "eyes" consisting of just a few contiguous pigmented, light-sensitive cells, as in the limpet *Patella,* to the eye of the octopus, as complex and effective an organ of vision as the human eye. Between these extremes are several intermediate conditions, such as the "pinhole-lens" eye of *Nautilus,* with a full array of light-sensitive cells forming an optic cup around a small opening for the entrance of light, and the eye of the marine snail *Murex,* with a single, primitive refractive lens and an optic nerve, although lacking the iris and cornea present in the octopus (see "Evolution, the theory of," *Encyclopaedia Britannica,* 15th ed.).

Intelligent design does not belong in science because it postulates an extranatural or supernatural agent and because it cannot be scientifically tested. This is because, as proponents of ID state when confronted with contradictory evidence, we cannot know what the intentions of a supernatural designer are, or whether they may have allowed for a less than perfect design. Moreover, beyond scientific considerations, ID is theologically problematic: it is not simply that organisms are less than perfect, but also that the dysfunctions, oddities, waste, and cruelty pervasive in the living world are difficult to reconcile with the special action of an intelligent designer who is also benevolent. Many theologians, therefore, have rejected ID, preferring to see dysfunction, waste, and cruelty as results of a natural process—evolution—rather than as direct consequences of special action by an omnipotent and benevolent creator.

Futuyma effectively disposes of various red herrings adduced by creationists, such as the argument that evolution is only a theory. "A theory, as the word is used in science, doesn't mean an unsupported speculation or hypothesis.... A theory is instead a big idea that encompasses other ideas and hypotheses and weaves them into a coherent fabric" (*Evolution,* p. 527; see also p. 13). The modern theory of evolution embodies a complex array of knowedge from biology and other sciences, centered around Darwin's theory of evolution by natural selection and couched in genetic terms. It is not a single, simple theory with its corroborating evidence, but a multidisciplinary body of knowledge bearing on biological evolution, an amalgam of well-established theories and working hypotheses together with the observations and experiments that support accepted hypotheses (and falsify rejected ones), which jointly seek to explain the evolutionary process and its outcomes. Indeed, *Evolution* is an excellent compendium of the modern theory of evolution, although surely not a complete one, as no single book could possibly be.

Evolution's first chapter is a brief history of evolutionary ideas, from Lamarck through Darwin to the mid-20th-century authors of the "modern synthesis," Theodosius Dobzhansky, Ernst Mayr, George Gaylord Simpson, and others. It also makes passing reference to Motoo Kimura's neutral theory of molecular evolution, and mentions molecular biology, developmental biology, and genomics as subdisciplines that recently have greatly contributed to evolutionary theory.

Treatment of the subject matter starts in earnest with several chapters (chapters 2–7) dedicated to the reconstruction of evolutionary history, including macroevolutionary patterns and biogeographical diversity. Futuyma's treatment of the various methods available for inferring phylogenetic relationships is exemplary: clear, focused, and informative, with telling examples and illustrations. The discussion of molecular clocks, however, is much too brief and incomplete. There is only casual reference to the works and accomplishments of the last quarter-century. The relative-rate test is introduced without pointing out that it is of little value when the reference species is far removed from the subject species; nor is there any discussion of other pitfalls of the molecular clock, nor of why molecular clocks often yield older ages than paleontological data. The discussion of gene trees and gene genealogies is brief, but a few pages later, Futuyma clearly explains why an accurate gene tree may yield an inaccurate species phylogeny (because of preexisting and differential extinction of polymorphic alleles).

The chapters covering population genetics (chapters 8–12), phenotypic evolution (chapter 13), and sexual and social behavior (chapter 14) helpfully minimize the use of equations and mathematical symbols, while being profound and well balanced, and displaying the characteristic clarity of Futuyma's style. The discussion of molecular population variation, however, is surprisingly scant, all but ignoring the enormous amount of evidence gathered since the initial papers published in 1966 and 1983, respectively, on protein and DNA polymorphisms.

Chapters on species concepts and speciation, on life history evolution, and on species coevolution are delightful. Futuyma is thoroughly at home when describing reproductive isolating barriers and their genetic basis, the ascendancy of the biological species concept, interspecies competition, predator–prey coevolution, and related topics. The discussion of mimicry rings as an instance of multispecies interactions is suitably brief, but masterfully done.

The two guest chapters by Scott V. Edwards and John R. True are magnificent, remarkably comprehensive, clearly written, and beautifully illustrated. (I found the acknowledgment of these two authors' work surprisingly meager: their contributions are noted on the book's title page and credited in the preface, but their names do not appear in the table of contents or in the text of the chapters.)

Edwards begins "Evolution of Genes and Genomes" (chapter 19) with a fast-paced introduction to genome sequencing, microarray tests of gene expression, protein interaction networks (exemplified with a display of 20,405 interactions among 7048 *Drosophila* proteins), and adaptive molecular evolution in primates. Other topics in this chapter include the evolution of genome size, the processes by which new genes and gene families come about, and the adaptive diversification of gene families.

In his chapter ("Evolution and Development," chapter 20), True engagingly summarizes the remarkable advances of evo-devo, with the *Drosophila Hox* genes serving both as a model of development and as a means of reconstructing the metazoan evolution of the *Hox* gene complex, from jellyfish and flatworm to mollusc and mammal. Gene regulation is introduced as the keystone of developmental evolution. The topics of homology, allometry, developmental constraints, and morphological evolution are presented with clarity and precision, and illustrated with beautiful photographs and still more beautiful (and more informative) graphics.

Evolution is a shorter book than the third edition of *Evolutionary Biology*, a change that represents (in my opinion) an improvement, but this is not the only or the most important improvement of the new over the old book. *Evolution* will serve well for undergraduate or graduate courses on evolution, and it has also served me well, and will serve other scientists, for reviewing the subject.

FRANCISCO J. AYALA
Department of Ecology and Evolutionary Biology
University of California, Irvine
Irvine, CA 92697

THE GENETICS OF GROUPS, FOR GROUP READING

Genetic Structure and Selection in Subdivided Populations. François Rousset. Princeton University Press, Princeton, NJ, 2004. 288 pp. $85.00 (0691088160 cloth).

In the first half of the 20th century, the eminent founders of quantitative population genetics—R. A. Fisher, J. B. S. Haldane, and Sewall Wright—established a foundation of mathematical methods of analysis that, with further development by others, serves researchers so well in our quest to understand how patterns of biological adaptations in time and space, and ultimately speciation events, are generated and maintained by natural selection. Among the other contributors to the development of the field are Gustave Malécot, W. D. Hamilton, John Maynard Smith, Motoo Kimura, Thomas Nagylaki, and Monty Slatkin, all of whose work François Rousset ably reviews and synthesizes in his new monograph on genetic structure and selection in group-structured populations.

In the preface, Rousset opens a section entitled "Assumed Background" by stating, "I assume the reader has some basic interest in population biology and some knowledge of the population genetics of panmictic populations.... I have used only a minimum set of mathematical techniques that are already well-established among population biologists" (p. xv). Lest this lull you into thinking that this monograph is going to be a breeze to read, let me immediately disabuse you of that notion. This book will be tough going for all but a small handful of the leading mathematical population geneticists.

Much background material on the fundamental notions and assumptions underlying the formulation of models in population genetics is either absent or skimmed over in this book. Furthermore, empirical examples that would help illustrate concepts and ground the reader's intuition are absent. The work is like a pictureless recipe book of formulas that can be used to compute the frequencies of genes under selection in structured populations. Thus, the best way to break the back of the material is through participation in a reading group or seminar led by someone steeped in the conceptual foundations of the field and familiar with illustrative empirical examples. The mathematical tools needed to read this book are not beyond the basics of calculus and linear algebra, but the derived formulas presented throughout the text increasingly tax the ability of the noncognoscenti to conceptually interpret their meaning in the context of the common origins (coalescence) of genes found in different subgroups of the population.

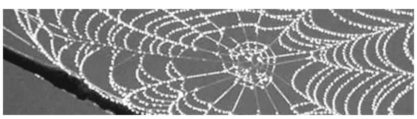
In concluding a short introductory chapter, Rousset advises the reader that "this book aims to show how a range of questions can be efficiently addressed using a limited number of concepts and technical tools, and to provide a self-contained account of the basic models of the genetic structure of populations"—an aim that is certainly fulfilled. He further advises that one can either read chapters 3 and 4, reviewing neutral theory of population structure, or jump straight from chapter 2, which covers the basics of influence of selection and drift on changes in allele frequencies from one generation to the next, to chapters 5 and beyond, where the real meat of the book resides.

Chapter 5, followed by the more technical chapter 6, signals the modernity of Rousset's approach by developing an excellent exposition of the dynamical concepts underpinning "evolutionarily stable strategy theory," an approach introduced by Maynard Smith and his collaborators in the 1970s. This modern treatment is continued in chapter 7, where the ideas of W. D. Hamilton on inclusive fitness, cooperation, and altruism are presented in the mathematical framework developed in the early chapters. Rousset takes considerable care in this chapter to clarify the essential differences between inclusive and direct fitness, as well as unify these two views of selection. Of particular note in this chapter is an insightful diagram (figure 7.2) that clarifies, in the context of Hamilton's famous identity of evolutionarily favored acts (involving costs, benefits, and relatedness of actors and recipients), when such acts should be interpreted as cooperation, altruism, spite, or selfishness.

The remaining four substantive chapters of the book deal with diploid and sex-structured populations (chapter 8), effective population size (chapter 9), and the generalization of the analysis to account for fluctuating (chapter 10) and class-structured (chapter 11) populations. A short chapter offering an overview and perspectives concludes the book.

In the final paragraph of the last chapter, Rousset raises the issue that a common problem in the field of population dynamics (from both an evolutionary and an ecological perspective) is how to make theoretical models simpler. The trap here is that, although we may find more effective ways to encapsulate our understanding of the commonalities of a broad spectrum of processes in relatively simple equations, the ideas behind those equations are neither simple nor easy to master. It takes about six years of slogging through mathematical physics to understand the real implications of the fundamental equations of physics so elegantly represented by a set of symbols that I have seen printed on a T-shirt. In the same way, Rousset has done a fine job of unifying seemingly disparate ideas in population genetics under the rubric of rather compact-looking "gene coalescence" equations. From his concluding statement, it is clear that Rousset would like to make his equations even more compact. But for most of us reading his book, our task is to master the concepts behind the elegant equations presented in Rousset's monograph, if we are to have any hope of keeping up with future developments in the field of mathematical population genetics.

WAYNE M. GETZ
Department of Environmental Science, Policy, and Management
University of California
Berkeley, CA 94720



AN ECOSYSTEM OF SUPERLATIVES

Under Antarctic Ice: The Photographs of Norbert Wu. Text by Jim Mastro, photographic notes by Norbert Wu. University of California Press, Berkeley, 2004. 176 pp., illus. $39.95 (ISBN 0520235045 cloth).

This book presents the reader with a view that few ever experience: the underwater world beneath the annual sea ice in McMurdo Sound, Antarctica. This view is presented through the lens of internationally renowned photographer Norbert Wu, who, under the auspices of the National Science Foundation (NSF), spent three years photographing the icy waters in the region. The book includes more than 100 full-color images that take the reader on a tour of the higher life forms and their sub-ice habitats in this unique ecosystem.

Wu also focuses his lens on the conditions that scientists and support staff have to face to work in one of the harshest environments on our planet. His remarkable images show the novel habitats frequented by tiny notothenioid fishes, which produce glycopeptide antifreeze molecules that inhibit the growth of ice crystals in the body; the graceful movement of penguins swimming under the ice; and minke whales trapped in ice-locked pools, to list just a few examples. Each individual image is accompanied by photographic notes by Wu that reveal his fascination with this underwater world, where visibility can reach 180 meters, and detail the obstacles that a photographer must endure to work in this environment. Wu graciously provides detailed descriptions of the equipment and printing processes that have yielded the one-of-a-kind images included in this book.

A real bonus is the narrative provided by Jim Mastro, who worked in Antarctica from 1982 to 1996, during which he served for five years as manager of the US scientific diving program for the NSF Office of Polar Programs. Mastro is a consummate science writer who has published feature articles in *International Wildlife* and is the author and photographer of *Antarctica: A Year at the Bottom of the World* (Boston: Little, Brown, 2002). Mastro's eloquent introductory text combines the history of exploration in this region with an overview of the history of Antarctica, bringing us to the icy continent we see today. With this backdrop, the reader is introduced to the physical and chemical differences that are present within McMurdo Sound, an arrangement that dovetails perfectly with Wu's photographs.

Beginning with Carsten Borchgrevink's 1899 winter expedition, and continuing through Robert F. Scott's unsuccessful attempts to reach the South Pole during his 1901 and 1910 expeditions and, later, Ernest Shackleton's 1914 voyage in the *Endurance,* the southernmost continent has lured explorers and scientists to its virgin land. The early explorers' diaries often depict Antarctica as a harsh, barren landscape devoid of life. I can attest to having had this feeling as a young scientist in the mid-1980s studying the microalgae living in sea ice in McMurdo Sound. While traveling by snowmobile to a dive site near Cape Evans, the site of Scott's 1910 base camp, I could not help but think how lifeless the place was. It was not until I squeezed into my dry suit and shimmied through a hole 1 meter in diameter, drilled through sea ice 2 meters thick, that I realized the environment under the ice offered a clement refuge from the dry, cold, and windy surface. My haunting memories of the stark surface environment were immediately left behind as I witnessed the biotic diversity and abundance offered by the colorful sub-ice world. The hazards of working in such an environment also became vividly clear as my air regulator froze shut during my ascent, forcing me to reach the surface on a final gasp of air.

The Antarctic continent itself covers more than 13 million square kilometers (roughly 1.5 times the size of the United States), and during winter, the sea ice surrounding the continent nearly doubles its extent. How did Antarctica become the icy continent we know today? A model of Earth some 250 million years ago would show the continent in the center of the vast supercontinent Pangaea. Major rifting events then occurred, fragmenting the supercontinent until Antarctica developed its present shape. The rifting opened seaways between major oceans and changed the ocean circulation around the Antarctic continent. Throughout this time, Antarctica remained in the low southern latitudes and has been in a near-polar position for about 100 million years.

Despite its near-polar position, Antarctica's climate was initially warm. Seas surrounding the continent at this time had bottom-water temperatures ranging from 12 to 16 degrees Celsius and supported a complex fauna typical of contemporary temperate oceans, while temperate vegetation flourished on land. These temperate climatic conditions ended dramatically when rifting opened crucial oceanic passages, including the Tasmanian Seaway and the Drake Passage.

This rifting combined with declining atmospheric carbon dioxide levels to trigger dramatic cooling and the onset of rapid glaciation. Continued cooling shifted eastern Antarctica into a state of permanent glaciation and allowed the growth of the more dynamic West Antarctic ice sheet. Despite several climate reversals since Antarctica became perennially glaciated, the present polar ocean surrounding the continent is Earth's most severely and consistently cold marine environment.

The marine species that are depicted so eloquently in Wu's book have been shaped by evolution driven by a long period of stable, low temperatures; they illustrate Jared Diamond's comment that "unplanned natural experiments create ecological communities that we would have never dreamed of creating" (*Science* 294: 1848). Indeed, Darwin, if he could have peered beneath the Antarctic sea ice, would have found another powerful example of evolutionary divergence to support his theory of evolution. The rapid onset of extreme conditions in this isolated polar marine environment has clearly driven the rapid evolution of the species present, yielding a hotbed of evolutionary change in a cold portion of Earth.

Wu's photographs reveal vividly the contemporary result of evolution in a cold, insular environment. His images depict fish that, unique among vertebrates, lack red blood cells; microalgae that persist in brine channels within sea ice; fishes whose blood remains in the liquid state at subzero temperatures because of the presence of novel biological antifreeze proteins; giant jellyfish with tentacles 9 meters long; sea spiders the size of a human hand; and sponges that tower above the surface of the sediments.

Implicit in the images and accompanying text is the highly sensitive nature of sub-ice life to environmental change. Although highly adapted to the icy world, polar organisms are acutely sensitive to anthropogenic perturbation, such as the production of greenhouse gases and ozone-destroying chemicals. Human activities are already affecting polar ecosystems dramatically, and these effects are likely to increase in the future. This book provides important background to our understanding of the delicate life forms and behavioral patterns associated with Antarctic sea ice. The organisms pictured in the volume may well serve as "canaries in the coal mine" and provide warnings about the effects of climate change worldwide.

The fascination that polar ecosystems hold for scientists and nonscientists alike is not difficult to understand, given the key role of these ecosystems in many aspects of the Earth system. Though *Under Antarctic Ice: The Photographs of Norbert Wu* serves appropriately as a coffee table book, it goes well beyond this use. The informed reader should have no problem linking Jim Mastro's informative text with Wu's images to gain a scientific understanding of the complexity and sensitivity of the icy ecosystem depicted. After my initial reading of the book, I could not help but think of it as a beautifully illustrated introductory textbook on Antarctic nearshore marine life.

One final aspect that cannot be overlooked is the collection of photographic notes near the end of the volume. Any serious outdoor photographer can glean an enormous amount of information from the technical details Wu provides. Although the images alone are worth the cost of the book, there is also a plethora of information that will be of interest to the general public, to polar and nonpolar scientists, and to wildlife photographers. This book will remain a staple on my coffee table and on my scientific bookshelf for many years to come.

JOHN C. PRISCU
Department of Land Resources and Environmental Sciences
Montana State University
Bozeman, MT 59717

SIMPLER, BUT STILL NOT SIMPLE

Complex Worlds from Simpler Nervous Systems. Frederick R. Prete, ed. MIT Press, Cambridge, MA, 2004. 436 pp., illus. $40.00 (ISBN 0262661748 paper).

Not many years ago I gave a talk to an audience, consisting largely of engineers, on what the field of neuroethology had to offer to their efforts to design "biologically inspired" computer chips. I introduced them to what is arguably the best-understood part of any nervous system on this planet, the crustacean stomatogastric ganglion (STG). I told them we had a complete wiring diagram for its 30-odd neurons, could record simultaneously from up to eight of these cells to describe their circuit interactions, knew all of the neurotransmitters and most of the neuromodulators they used, had constructed detailed biophysical models of the individual neurons, and were only now beginning to figure out how this circuit actually worked. But the jaw-dropping moment came when I told them that this level of knowledge had required an investment of something on the order of 1000 person-years, and that the behavior the STG produces is *movement of the animal's stomach.* Even the simplest neural systems have turned out to be dauntingly complex.

Against this sobering background comes *Complex Worlds from Simpler Nervous Systems.* In this volume, Frederick Prete (of Visuo Technologies) has assembled a collection of papers that look at how "simpler" organisms (grant-speak for "not a bird or mammal") construct their *Umwelt*—their self-world. We owe the word to Jakob von Uexküll, who emphasized that organisms construct their *Umwelt* through the interaction between their physical environment and their own behavior, sensory capabilities, and internal states. Prete's self-stated goal is to move away from the misconception that animals such as spiders, insects, and molluscs are simple reflex machines, and to appreciate the complex perceptual models they construct of their environments. While this is not a view that will surprise those who study the neural bases of behavior in these simpler systems, it is a case worth making. In particular, in an era of funding agencies focusing ever more tightly on a small number of model systems, it is good to be reminded of the advantages of diversity, and of curiosity-driven research.

After a typically delightful foreword by Mike Land, the book is organized into three sections: "Creating Visual Worlds: Using Abstract Representations and Algorithms" (four chapters), "Enhancing the Visual Basics: Using Color and Polarization" (five chapters), and "Out of Sight: Creating Extravisual Worlds" (two chapters). The reader will immediately note that this is very much a book about vision. This is not surprising, given Prete's research background in vision in mantises. However, it is unfortunate that there are no chapters on olfaction, particularly given the large number of active laboratories investigating problems in olfaction in nontraditional model systems, and the fact that so many animal behaviors are guided by olfaction rather than by vision.

Nonetheless, this is a highly readable and worthwhile book. Several chapters stand out both for the wonderful behaviors described and for their careful attention to detail. I was particularly impressed by Harland and Jackson's chapter on spider-hunting spiders of the genus *Portia.* These authors actually succeed in drawing the reader into the spider's *Umwelt.* Opening with descriptions of sophisticated and flexible hunting behavior that would be surprising enough coming from a primate, let alone an arthropod, they move on to a thorough description of the known sensory capabilities of these marvelous animals. They conclude with a laudable attempt at understanding how an organism integrates disparate sensory modalities into its own view of the world. This chapter alone is worth the price of the book, but I warn principal investigators that graduate students who read it will want to change their projects!

Equally impressive from the standpoint of cognitive abilities is visual pattern recognition and maze learning in honeybees, reviewed by Zhang and Srinivasan. These authors thoroughly review the excellent work that has come out of their own laboratory, but I was a little disappointed to find, in a chapter on cognition in bees, so little mention of olfactory learning, particularly when this is an area in which researchers are beginning to understand the cellular mechanisms involved.

Perhaps the most ambitious chapter in the book is Comer and Leung's attempt to understand the integration of multimodal inputs in the escape systems of insects. In large part because of the wealth of information on escape circuitry in crickets and cockroaches, this chapter offered the most complete description of how an animal uses its *Umwelt* to direct its behavior.

The chapters on vision in bees (Chittka and Wells), butterflies (Arikawa and colleagues), and mantis shrimps (Cronin and Marshall) are all excellent critical reviews of the current state of knowledge, and would be a superb introduction for workers new to these fields, or for those looking to catch up on recent findings. I was also gratified to learn about an animal communication system I had never encountered before: auditory signaling in bladder grasshoppers (van Staaden and colleagues). Each of these chapters contains numerous suggestions for important work that needs to be done (i.e., good thesis topics).

Unfortunately, I found the remaining chapters rather uneven. While Ewert's chapter on the visual world of frogs and toads was thorough and authoritative, it also seemed somewhat aimless at times. I suspect this is simply a case of trying to stuff too much of the several decades of beautiful work that has come from his lab into one small review. There was also an unfortunate lack of scholarship in Kral and Prete's chapter on vision in the praying mantis: it's difficult to understand how the authors could review mantis vision without discussing Samuel Rossel's work on binocular stereopsis. Although this appears to be a case of tit for tat (authors ignoring each other's work), it is a behavior that does not help the field.

While reading this book, I was frequently reminded of Ken Roeder's *Nerve Cells and Insect Behavior* (Cambridge, MA: Harvard University Press, 1963). This is high praise, as Roeder's book is the first I put into the hands of any student interested in neurobiology and behavior. Roeder emphasized that it is important to understand neurobiology from the perspective of the organism, and that important general principles are often first learned from relatively obscure organisms. Prete's book continues this tradition, and will be of interest to engineers looking for biological inspirations, to biologists looking into new fields, and to anyone who is interested in how amazing the behavior of even "simpler" animals can be.

JIM BELANGER
Department of Biological Sciences
Louisiana State University
Baton Rouge, LA 70803

NEW TITLES

Aquatic Food Webs: An Ecosystem Approach. Andrea Belgrano, Ursula M. Scharler, Jennifer Dunne, and Robert E. Ulanowicz, eds. Oxford University Press, New York, 2005. 272 pp., illus. $74.50 (ISBN 019856483X paper).

Bacterial Ion Channels and Their Eukaryotic Homologs. Andrzej Kubalski and Boris Martinac, eds. ASM Press, Washington, DC, 2005. 358 pp., illus. $115.95 (ISBN 1555813283 cloth).

Bioethics and the New Embryology: Springboards for Debate. Scott F. Gilbert, Anna L. Tyler, and Emily J. Zackin, eds. Sinauer, Sunderland, MA, 2005. 261 pp., illus. $14.95 (ISBN 0716773457 paper).

Bioindustry Ethics. David L. Finegold, Cécile M. Bensimon, Abdallah S. Daar, Margaret L. Eaton, Béatrice Godard, Bartha Maria Knoppers, Jocelyn E. Mackie, and Peter A. Singer. Elsevier, Burlington, MA, 2005. 378 pp., illus. $34.95 (ISBN 0123693705 paper).

Biology and Biotechnology: Science, Applications, and Issues. Helen Kreuzer and Adrianne Massey. ASM Press, Washington, DC, 2005. 686 pp., illus. $79.95 (ISBN 1555813046 paper).

Biology of Gila Monsters and Beaded Lizards. Daniel D. Beck. University of California Press, Berkeley, 2005.

247 pp., illus. $49.95 (ISBN 0520243579 cloth).

Black Carp: Biological Synopsis and Risk Assessment of an Introduced Fish. Leo G. Nico, James D. Williams, and Howard L. Jelks. American Fisheries Society, Bethesda, MD, 2005. 337 pp., illus. $60.00 (ISBN 1888569689 cloth).

Branching Processes: Variation, Growth, and Extinction of Populations. Patsy Haccou, Peter Jagers, and Vladimir A. Vatutin. Cambridge University Press, New York, 2005. 336 pp., illus. $95.00 (ISBN 0521832209 cloth).

The Cambridge Dictionary of Human Biology and Evolution. Larry L. Mai, Marcus Young Owl, and M. Patricia Kersting, eds. Cambridge University Press, New York, 2005. 672 pp. $60.00 (ISBN 0521664861 paper).

Campylobacter: Molecular and Cellular Biology. Julian M. Ketley and Michael E. Konkel, eds. Horizon Scientific Press, New York, 2005. 464 pp., illus. $175.00 (ISBN 190493305X cloth).

Charles Darwin, Geologist. Sandra Herbert. Cornell University Press, Ithaca, NY, 2005. 485 pp., illus. $39.95 (ISBN 0801443482 cloth).

Culture of Animal Cells: A Manual of Basic Technique. 5th ed. R. Ian Freshney, ed. Wiley, Hoboken, NJ, 2005. 668 pp., illus. $79.95 (ISBN 0471453293 cloth).

Darwin: The Indelible Stamp. James D. Watson, ed. Running Press, Philadelphia, 2005. 1200 pp., illus. $29.95 (ISBN 0762421363 cloth).

Ecological Paradigms Lost: Routes of Theory Change. Kim Cuddington and Beatrix E. Beisner, eds. Elsevier, Burlington, MA, 2005. 464 pp., illus. $79.95 (ISBN 0120884593 cloth).

Eugenic Nation: Faults and Frontiers of Better Breeding in Modern America. Alexandra Minna Stern. University of California Press, Berkeley, 2005. 368 pp., illus. $24.95 (ISBN 0520244443 paper).

Hormones and Animal Social Behavior. Elizabeth Adkins-Regan. Princeton University Press, Princeton, NJ, 2005. 416 pp., illus. $45.00 (ISBN 0691092478 paper).

Life Itself: A Comprehensive Inquiry into the Nature, Origin, and Fabrication of Life. Robert Rosen. Columbia University Press, New York, 2005. 285 pp., illus. $22.50 (ISBN 0231075650 paper).

The Microstructure of Dinosaur Bone: Deciphering Biology with Fine-scale Techniques. Anusuya Chinsamy-Turan. Johns Hopkins University Press, Baltimore, 2005. 216 pp., illus. $85.00 (ISBN 080188120X cloth).

Molecular Pathogenesis of Virus Infections. Paul Digard, Anthony A. Nash, and R. E. Randall, eds. Cambridge University Press, New York, 2005. 360 pp., illus. $125.00 (ISBN 0521832489 cloth).

Parsimony, Phylogeny, and Genomics. Victor A. Albert, ed. Oxford University Press, New York, 2005. 240 pp., illus. $99.50 (ISBN 0198564937 cloth).

Robustness and Evolvability in Living Systems. Andreas Wagner. Princeton University Press, Princeton, NJ, 2005. 408 pp., illus. $49.50 (ISBN 0691122407 cloth).

Tropical Rainforests: Past, Present, and Future. Eldredge Bermingham, Christopher Dick, and Craig Moritz, eds. University of Chicago Press, Chicago, 2005. 672 pp., illus. $45.00 (ISBN 0226044688 paper).