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BOOK REVIEWS

Marcy F. Lawton, Editor

Evolution as entropy: toward a unified theory of biology.—D. R. Brooks and E. O. Wiley. 1986. University of Chicago Press, London and Chicago. 335 pages. Cloth: $25.00.

Since the 1920s biologists have endeavored to unite the basic concepts of physics with the laws of evolutionary and population biology. One of the most intriguing areas of physics to biologists has been thermodynamics, since all biological processes involve the transfer and changes in form of energy. The second law of thermodynamics has proved to be of considerable interest to theoretically inclined biologists, because (a) it appears to be violated (at least temporarily) by living systems, and (b) it describes a set of statistical laws that can be used to measure progress towards a state of equilibrium. R. A. Fisher argued that there are several points of resemblance between his fundamental theorem of natural selection and the second law of thermodynamics, but he also pointed out that there are profound differences, particularly since evolution tends to produce greater organization, whereas entropy should lead to reduced organization.

Evolution as entropy by Daniel Brooks and E. O. Wiley is a brave attempt to relate the concepts of evolutionary biology to the second law of thermodynamics. In this case, however, they do not apply traditional equilibrium thermodynamics, but the nonequilibrium thermodynamics of Prigogine, especially as these concepts can be applied to information theory. According to Brooks and Wiley, disorder increases in biological systems as a result of processes such as mutation and speciation, but that organization prevents the disorder in the system from reaching a maximal state. Thus living systems and biological processes such as ontogeny, evolution, and speciation are the result of entropic processes, and natural selection is at best a minor force imposing organization in the midst of increasing disorder.

Since this book attempts to present an alternative to the theory of evolution through natural selection, it is certain to be controversial, and some might view it as anti-Darwinian. For these reasons, it is essential that the authors present their material in as clear and precise a manner as possible so that the validity of their potentially important ideas can be evaluated. Unfortunately, *Evolution as entropy* is written in a turgid and convoluted style that renders many of its major points not only hard to understand, but even hard to find.

As I understand their argument, the entropy to which they refer is primarily informational, in the sense that the information contained in a system is equivalent to its entropy. Since the primary information contained in biological systems occurs in the form of macromolecules, especially DNA, Brooks and Wiley argue that random increases in variation, i.e., mutations, can be incorporated throughout the system, thereby increasing the information content (and the entropy). This rate of informational increase should diminish over time because of the accumulation of constraints, i.e., closed off developmental pathways. As a result, biological systems show the gradual decrease in entropy production predicted for open systems approaching a state of equilibrium. Therefore, evolution is driven primarily by nonequilibrium processes which increase the information content of individuals, populations, species, and even ecosystems, at varying rates.

It should be apparent at this point that a thorough comprehension of the arguments in this book requires a good understanding of information theory and its relationship to thermodynamics. Many of the criticisms of the ideas of Brooks and Wiley and their responses have bogged down in semantic exercises over the appropriateness of terms such as "entropy," "equilibrium," and "information," or of whether or not increases in "organization" are entropic or negentropic. I confess that I am not really qualified to evaluate these arguments in detail, but I also suspect that these semantic arguments are not really relevant to the ultimate reception or rejection of the ideas contained in this book.

Much more of a problem than the supposed misuse of terminology, i.e., their definition of information is different than that used by most theorists, is Brooks and Wiley's failure to explain much of their terminology, or to provide examples that would help the reader unfamiliar with difficult concepts. For example, many of the figures are excessively simplistic and provide no information beyond that already found in the text. In addition, biological systems as characterized by Brooks and Wiley show hierarchical organization which cannot be dealt with using classical (Shannon-Weaver) information theory. Brooks and Wiley attempt to deal with this issue by introducing the concepts of stored, i.e., expressed (dominant or homozygous) alleles, and potential, i.e., unexpressed (recessive heterozygous) alleles, which should allow hierarchical organization of information, but this relationship is never adequately developed or explained.

Brooks and Wiley's discussion of speciation and community ecology is basically a recapitulation of cladistic arguments and vicariance biogeography. This section of the book might have been more profitably spent discussing the origin of the large component of apparently random elements that play potentially important roles in biological systems and may be important in speciation.

As an example, are the traits that are used by taxonomists to distinguish between species adaptive in most cases? More important, are characters that conspecifics use to recognize potential mates adaptive or epiphenomena related to other traits? This can be illustrated using isolating mechanisms in birds, which are typically plumage characters, vocalizations, or other traits (e.g., bill and foot color in seabirds). Exactly which traits turn out to act as isolating mechanisms is likely to be the result of chance coupled with historical constraints, i.e., it is difficult to argue that blue is selectively favored in one group, and red or yellow in another. Such characters might well be the result of biochemical constraints in pigment production (perhaps related to diet), or in the case of vocalizations, be epiphenomena associated with bill and throat structure.

If this type of phenomenon is widespread, there may be validity to some of the arguments developed by Brooks and Wiley concerning the outcome of random changes during ontogeny. Unlike more traditional evolutionary biologists, however, cladists are not concerned with isolating mechanisms. Therefore, Brooks and Wiley never deal with some of the possible implications of their theory.

As a result, this book is both frustrating and disappointing. First, it promises more than it delivers. Although it purports to propose an alternative to evolution by selection, it never sets up testable hypotheses by which the ideas in this book could be compared to, and distinguished from, basic concepts of population genetics (i.e., genetic drift, gene flow). Second, its presentation of nonequilibrium thermodynamics is so confusing that it is difficult to determine whether the authors are correct, or even if they have the concepts from thermodynamic and information theory correct. Ultimately, Brooks and Wiley add little to our understanding of important concepts in evolutionary biology. There may be an important book to be written about the relationship between physics and evolutionary biology, but *Evolution as entropy* is not it.—RAYMOND PIEROTTI, Department of Biological Sciences, University of California, Santa Barbara, CA 93106.

An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers.—Edward H. Burtt, Jr. 1986. Ornithological Monograph No. 38, American Ornithologists' Union, Washington, DC. x + 126 p.

One of the many attractive aspects of birds is their color patterns, yet surprisingly few people have seriously investigated the subject, and virtually no one has attempted to study more than one function at a time. Burtt's monograph is a fine example of the integrative approach, which considers abrasion resistance, heat balance, glare reduction, predator visibility, and visibility to conspecifics as factors which can affect the evolution of bird coloration.

The opening chapters (1 and 2) give basic information and show that the distribution of wood-warbler colors is not random over the body. It is interesting that males have more black and less yellow-green or brown than females, while white, yellow, orange, red, and chestnut are equally common among sexes, though less saturated in females. The variation among species is also interesting, but would have been still more interesting if it had been discussed relative to the phylogenetic relationships within the Parulinae.

To me the most interesting chapter (3) was on coloration relative to durability. Very good evidence was presented that melanin in feathers significantly increases their resistance to abrasion by airborne particles. In order of decreasing abrasion resistance and increasing melanin content, the measured colors were brown, black, yellow-green, yellow, orange, and white. (It was not explained why brown is more durable than black.) This immediately predicts that feathers experiencing higher mean air velocity and wear should be darker than other feathers. This is actually the case—darker dorsum, remiges, and medial rectrices. Unfortunately, except for the rectrices, this is also predicted for counter-shading, a subject which receives insufficient attention throughout this book. These are interesting predictions, because they may bias the kinds of visual signals which can evolve in birds. For example, if the median rectrices must be stronger than the peripheral rectrices, then this biases visual signals involving the tail to evolve white or lighter outer rectrices more frequently than the reverse, as has happened in parallel in mockingbirds, meadowlarks, wagtails, gnatcatchers, and a few sparrows, warblers, and doves. It also favors spots of contrasting (nonmelanic) colors to preferentially appear in areas of less wear, as Burtt documents for colored spots on lateral rectrices. One wonders how many other evolutionary biases in signal evolution may have been caused by differential wear patterns.

Since 10 to 56% of a resting bird's heat loss occurs through the legs, Burtt's thermal analysis concentrated on leg coloration. Species with dark legs may be more cold tolerant than light-legged species, because they can maintain a higher equilibrium temperature. Examining data on times of arrival and departure in Madison, Wisconsin, and Itasca, Minnesota, which are correlated strongly with minimum temperatures, he finds that darker-legged species arrive earlier and leave later than species with lighter legs. Since there are so many other variables affecting cold tolerance (as Burtt points out), it is surprising and interesting that the correlation between phenology and color is detectable.

Glare reduction is an aspect of color patterns which has usually been neglected. Colors near the eyes and face, including the bill, should be dark to reduce glare. There is no association between color and position for eyebrow stripe, eyeline, and eye-ring, but there is a strong tendency for the upper mandible to be dark. This makes good sense as a glare-reducing adaptation but, unfortunately, is also predicted from considerations of counter-shading of the bill to reduce its visual contrast. Burtt found that time spent foraging in sunlight was greater for darker-billed species than lighter-billed species, but this is also consistent with both glare reduction and counter-shading arguments, as well as thermal arguments. To distinguish among these hypotheses on bill color it would be necessary to paint bills with *pale* nonglare paints, and see if this affects (1) foraging in sunlight, (2) mortality due to predation, or (3) heat balance. Oddly, Burtt's own experiment, where he painted *Empidonax traillii* white and found an increased foraging time in the shade, was only mentioned in a single sentence at the end of this chapter, even though it is the only solid evidence for glare reduction. This interesting possibility clearly needs more work.

The discussion of wingbars and tail spots as signals was not very convincing, but the ideas are well worth following up. Are species which fly more often during foraging or displays likely to have a greater incidence