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BOOK REVIEWS

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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 of wingbars to tail spots? No convincing pattern emerges, but specific predictions are also harder to make. For example, wingbars may always be visible, so may be dangerous for predation as well as good visual signals. Does this mean that species with wingbars should be less active and should have brighter tail spots which can be hidden until needed? (This is the opposite of Burtt's predictions.) Also, do wingbars or tail spots/bars serve as they may serve in white-tailed and mule deer—to warn a predator that the prey has spotted him, so that pursuit is less likely to result in a kill?

The chapter on quantifying color is an heroic attempt to classify colors by dominant wavelength, excitation purity, and relative luminance, and then compare animals with backgrounds to calculate overall conspicuousness. The idea of using a Euclidean distance between animal and background with respect to these three color parameters is a very good one. The calculations of these differences, and which colors are most likely to be visible or less visible on various backgrounds, are very interesting, and make sense in the field. However, the whole analysis is seriously flawed because the entire classification and analysis is based upon human color vision (the CIE curve, the notions of dominant wavelength, purity and luminance, units of lumens and lux). There is every reason to believe that bird color vision is totally different from ours, and other bird predators are likely to be still more different (for examples see G. H. Jacobs, 1981, *Comparative color vision,* Academic Press). The problem is that what is bright, pure, or a particular color to one species, genus, or order, can be extremely different from another species, and from us. So those colors predicted to be most visible to us may not be so to major bird predators, or to mates to whom the tail and wing spots may be relevant. Similarly, colors predicted on the CIE classification to be similar may be extremely different to predators or conspecifics. Burtt has reflectance spectra for the feather colors and backgrounds. It would be valuable to compare spectra directly rather than transforming them through the human visual system. Ultimately, it may be possible to transform the spectra through the warbler's visual system to estimate conspecific signal properties, and through the major predator's visual system to estimate conspicuousness to predators, but the best approximation to this is the absolute (physical) similarity of animal and background spectra rather than how they appear to a human viewer.

If a better measure of color contrast between animal and background were derived, it would be interesting to redo the analysis of which colors appear least conspicuous in which visual backgrounds. In addition, it would be very interesting to do detailed crypsis measures, for example against the actual visual backgrounds against which each species forages (canopy, subcanopy, floor; trunk, central, peripheral) instead of broad vegetation classes. It is important also not to ignore the light spectrum during cloudy weather, which can be quite different from sunny weather in a forest.

This is a valuable and thought-provoking book, and an excellent summary of the kinds of factors which bias and guide the evolution of bird color patterns. It is impossible not to come away from the book without some new insights about coloration, and birds will never appear the same again.—JOHN A. ENDLER, Department of Biological Sciences, University of California, Santa Barbara, CA 93106.

The Breeding Bird Survey: Its first fifteen years, 1965–1979.—Chandler S. Robbins, Danny Bystrak, and Paul H. Geissler. 1986. U.S. Fish and Wildlife Service Resource Publication 157. 196 pp. Available at no charge.

The publication of this volume marks a milestone in the history of North American ornithology, for it represents the coming of age of the best continent-wide bird population survey in the world. To my knowledge, it is the only continent-wide survey designed in advance by biologists and statisticians to sample bird populations in such a way as to make the data maximally comparable across time and space.

The Breeding Bird Survey was created in the mid-1960s by Chandler Robbins and his colleagues at the U.S. Fish and Wildlife Service. It consists of more than 2,000 routes stratified by degree blocks of latitude and longitude to cover most of North America north of Mexico. Routes are 24.5 miles long with 50 3-min stops 0.5 miles apart. All birds seen and heard during the 3-min stops are recorded. Most routes are run in June and begin 0.5 hr before dawn.

The major purpose of the survey is to monitor the long-term population trends of North American birds to help the Service fulfill its statutory and treaty responsibilities for migratory birds. This publication includes graphs of the population trends of 233 species. In addition, the data are useful for mapping relative abundance across the continent; the publication includes 22 maps, plus references to other published maps.

The major disappointment of the present volume is that it took 7 years to produce; there is a tremendous management need for *yearly* updates of this information. A second disappointment is that there is so little synthesis of information. My tabulation suggested that—at the continental level—61 species showed statistically significant increases and 38 species showed significant declines. Creating this tabulation was difficult because the graphs don't give any clue about statistical significance and the text doesn't always report statistical significance. I would also have appreciated a table comparing the relative stability of the populations of the species in the 15-year period.

One of the major causes of declines, well-documented in the text, was the combination of two unusually cold winters (1976–1977 and 1977–1978) in the southeastern United States late in the 15-year period. At least 18 species were shown to be sensitive to very cold winters.

A big surprise in this volume is that there is no evidence of decline among neotropical migrant passerines as a group, despite many recent claims to the contrary. For example, Western Kingbird, Great Crested Flycatcher, Barn Swallow, Cliff Swallow, Purple Martin, Wood Thrush, Red-eyed Vireo, Prothonotary Warbler, Worm-eating Warbler, Blue-winged Warbler, Tennessee Warbler, Northern Parula, Ovenbird, Bobolink, Baltimore Oriole, Rose-breasted Grosbeak, Blue Grosbeak, and Indigo Bunting all showed significant increases. Only Scissor-tailed Flycatcher, both wood-pewees, Bell's Vireo, Gray Vireo, Yellow-breasted Chat, Painted Bunting, and Dickcissel showed significant declines.

Reliable and timely information on bird population trends can serve as an important early warning system of environmental change. Knowing that a number of species are declining in a particular region should lead to follow-up studies to determine possible causes. Knowing that a species is in trouble before it is extremely rare should lead to early, and perhaps less expensive, attempts to turn the tide. The Breeding Bird Survey (BBS) should be extremely useful for these two applied purposes; it monitors 175 to 233 relatively common species well. Analysis of Christmas Bird Counts (CBC) could add 80 to 100 relatively common species to the list of species with good quantitative data. With improved coverage, about 20 species of colonial waterbirds could be monitored in some coastal areas using the Colonial Bird Register (CBR). Computerized data from both the CBC and the CBR are available from the Cornell Laboratory of Ornithology. Good quantitative surveys need to be designed for those species that are poorly covered by the BBS, CBC, and CBR. Modifications of the BBS methodology seem promising for nocturnal species (when routes are run at night) and for rarer species (when the density of routes is increased over the area of interest).

One of the reasons that the BBS covers so few species well is that it is a roadside survey and misses species that require undisturbed habitats (especially wetlands and forest interior). In addition, BBS routes are few in boreal and arctic regions of Canada and Alaska and the inland, arid regions of the west. Efforts to increase coverage in these areas, perhaps by paying travel expenses of observers, would result in dramatically improved coverage for a number of species.

Confidence in the reported results requires confidence in the techniques used to calculate the trends and the annual indices. These techniques are described in the text, in an appendix, and in P. H. Geissler and B. R. Noon, 1981, Estimates of avian population trends from the North American Breeding Bird Survey, Stud. Avian Biology 6:42–51. In the latter paper, the methods used were compared with other available methods. Minor changes have been proposed to the trend program to reduce bias, and major changes are being planned to the program to calculate annual indices (P. H. Geissler, pers. comm.). More avian population biologists should pay close attention to this vital technical area.

When deciding whether or not BBS results are expected to reflect population changes in nature, one must decide about the reliability of the observers who collect the data. A major effort has been made over the past 20 years to recruit the best field birders in North America for this project, and I have no general concern about the quality of the data. However, concerns remain because of the BBS's dependence on the ability of observers to hear birds (censuses in which a larger proportion of birds are seen may have lower variance). A number of variables are known to affect both birds and humans in ways that dramatically change an observer's likelihood of hearing and identifying a nearby bird. Many studies on this topic are cited in studies in Avian Biology 6.

Although the BBS was designed to monitor bird populations for applied reasons, there are a number of theoretical questions in avian population biology that can be addressed better with the BBS database than with any other available data set. For example, Brian Maurer and James Brown at the University of Arizona are using BBS data in a large-scale study of the biogeography of North American birds. In a series of papers, Carl Bock demonstrated the usefulness of Christmas Bird Count (CBC) data for biogeographical studies; I'm sure that Brown and Maurer are finding the BBS data equally valuable. One of the major advantages of both BBS and CBC data for biogeographical studies is that they provide information on relative abundance within a species's range, in addition to information on range boundaries.

Less work has been done with either database to explore major issues involving the population dynamics of North American birds. One exception is the work of Carl Bock, David Davis, and others using CBC data to study winter irruptions of Fringillid finches, Northern Shrikes, Snowy Owls, and other species. A number of breeding species also show highly variable populations in space and time; the BBS data provide a basis for quantifying differences in the relative stability of populations. Cedar Waxwing, Dickcissel, Evening Grosbeak, and Pine Siskin stuck out as particularly variable during a quick look through the 15-year summary. Do these and other species with variable breeding populations share any ecological characteristics that might explain their relative variability in numbers? Are there ecological events that correlate with changes in breeding numbers of these variable species?

Despite the cautions mentioned above, I remain convinced that the 15-year summary of the BBS contains the best information available to date on the long-term population dynamics of most of the 230+ species included in the volume. I urge ornithologists to take better advantage of the database. In addition, I urge ornithologists to take a more active role in ensuring that quality data continue to be collected. A number of routes lack an assigned observer. Also, if more observers were available in the west and in the north, more routes could be created. To volunteer, call your state coordinator (listed in the book) or Sam Droege, Patuxent Wildlife Research Center, Laurel, MD 20708. Also, if you need a copy of the book, contact Sam Droege.—GREGORY S. BUTCHER, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850.

BOOKS RECEIVED

KAVANAU, J. L. 1987. Lovebirds, cockatiels, budgerigars: behavior and evolution. Science Software Systems, Inc., Box 241710, Los Angeles, CA 90024. xxvi + 1,002 p. $69.

LACK, P. 1986. The atlas of wintering birds in Britain and Ireland. British Trust for Ornithology, Irish Wildbird Conservancy. Buteo Books, P.O. Box 481, Vermillion, SD 57069. 447 p. $55.

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O'CONNOR, J. O., AND M. SHRUBB. 1986. Farming