

## BOOK REVIEWS

MARCY F. LAWTON, EDITOR

**Connie Hagar: The life history of a Texas birdwatcher.**—Karen Harden McCracken. Texas A&M. University Press, College Station. xvi + 296 p. \$18.95.

This is the biography of a remarkable woman, an amateur who contributed substantially to ornithology and conservation. Martha Conger Neblett, who later became Connie Hagar, was born on 14 June 1886, in Corsicana, Texas. From her father, an attorney and mayor of the small town, she learned the names of native trees, shrubs, and wild flowers. Her mother identified the butterflies that frequented her flower garden. At night she pointed out the constellations, not as first lessons in astronomy, but to teach her daughters to appreciate references to them in poetry and mythology. Despite this early introduction to nature, music was Connie's chief interest. She early learned to play the piano, and from Forest Park College in Saint Louis she received a diploma in voice. Until an advanced age, she sang and played for churches.

After the dissolution of her first marriage, Connie returned to Corsicana and, with her younger sister, became more interested in nature. They decided to learn the names of constellations, butterflies, wild flowers, and all the birds in Navarro County. In 1923 the sisters helped to organize a nature club which they affiliated with the National Audubon Society. After marrying her second husband, Jack Hagar, when nearly 40, Connie started to band birds for the U.S. Biological Survey. In 1928 she began, in a blank ledger that she found in the family library, a "Nature Calendar" which, in a succession of miscellaneous notebooks, often pocket-sized engagement booklets, she would continue for more than 35 years, jotting down her daily observations, chiefly of birds; she kept no other records. Handicapped by lack of contacts with more advanced birdwatchers, she did not use a binocular until given one by her husband when she was 48 years of age.

In the summer of 1933, Connie and her sister, both of whom suffered from arthritis, went on their doctor's advice to spend a month at Rockport, a resort village on the Texas Coastal Bend. After a second visit the following summer, Connie, enchanted by the abundance of birds, wished to live there permanently and study them. Readily agreeing, Jack Hagar bought Rockport cottages—eight cabins with simple accommodations for visitors. Thus, late in life, began a happy partnership of birdwatching wife and cabin-managing husband that was to continue until he died 27 years later.

As Connie's competence in field identification increased and Rockport became famous as a spot for watching migrating birds and finding rarities, birders came in increasing numbers. Among guests at the Cottages were many leaders in ornithology and conservation. Always generous of her time and eager to learn as well as to teach, Connie, on almost daily trips afield, guided a succession of amateurs and professionals.

Harry C. Oberholser, then gathering information for his posthumously published *The Bird Life of Texas*, Ludlow Griscom, leading authority on field identification, and other experts were understandably skeptical of her many reports of birds far from their recorded ranges, but nearly always she managed to convince them of the accuracy of her identifications, often by showing them the very birds whose presence in her part of Texas they doubted.

Mrs. Hagar published only articles in local newspapers and periodicals and short notes in ornithological journals. The *Checklist of Birds of the Central Coast of Texas*, by Hagar and Packard, was written by Fred M. Packard, using Connie's Nature Calendar. She is frequently mentioned in Peterson's *A Field Guide to the Birds of Texas*, especially in the list of accidentals. Connie probably contributed more to ornithology and conservation directly through her contacts with people than through her writings. Until the infirmities of age overtook her, she continued to give frequent talks to schools, local Audubon Societies, and other groups. She promoted conservation in Rockport, where a wildlife sanctuary was named for her. She received many honors, including a plaque from the National Audubon Society. After a lingering illness, she died on 24 November 1973.

Karen McCracken, herself a birdwatcher of wide experience, was long intimate with Connie Hagar. To gather information for this Boswellian biography of a woman as unique in her own way as Dr. Johnson was in his, she spent two hours daily, five days a week for a number of years, interviewing her subject, impressed by Connie's extraordinary memory. She also consulted the 25 volumes of the Nature Calendar, letters, newspaper clippings, and photographs. The result is a well-written, leisurely story that endears an exceptionally dedicated birdwatcher. At times the year-by-year listing of the multitudes of migrants that passed through Rockport or remained to nest tends to tire the reader who has no prospect of seeing them; some of this information might have been condensed. Intimate glimpses of prominent ornithologists and amusing episodes enliven the narrative. A photographer, sent by *Life* magazine to take pictures for a story about famous amateur naturalists, was dismayed when Connie appeared, ready to accompany him afield, attired as though for a fashionable tea party. He thought that she should be roughly clad for the outdoors, but she assured him that she always watched birds in conventional feminine dresses. After seeing a snapshot of herself in boots and baggy denim trousers, she decided that birdwatching did not require "such desperate measures."

Despite the lack of mathematics other than simple counting of birds, I recommend this book to ornithologists and birdwatchers. It shows how, without shooting a single specimen but giving conscientious attention to field marks, and freely communicating one's

knowledge and enthusiasm to others, one can contribute to a science that has been enriched by men and women of diverse temperaments and approaches.—ALEXANDER F. SKUTCH, Quizarrá, 8000 San Isidro de El General, Costa Rica.

**Unfinished synthesis.**—Niles Eldredge. 1985. Oxford University Press, New York. vii + 237 p. ISBN 0-19-503633-6.

In this book, Eldredge outlines what he believes to be the content of the “neoDarwinian synthesis” of evolutionary theory, explains why he thinks it is incomplete, and suggests remedies. To avoid setting up a “straw man,” he begins by discussing the four books which, in his opinion, established the synthesis, to wit, Dobzhansky (1937, 1941), Mayr (1942), and Simpson (1944). He outlines the further development of the synthesis, describing its growing emphasis on natural selection within populations as the only significant cause of evolutionary change, which he rightly feels unduly narrowed the scope of evolutionary thought. He sees the climax of this trend in Dawkins’s (1976) *The Selfish Gene*, and quite reasonably wonders how evolutionary theorists could possibly treat genes as the only significant units of selection, or discuss evolution as if paleontology were an irrelevance. Finally, Eldredge sketches a hierarchical view of evolution. He envisions a hierarchy of replicators (genes, organisms, species, monophyletic lineages of species), and a hierarchy of interactors (cells, organisms, populations, communities); relationships between interactors cause differential replication of replicators.

Eldredge was perhaps mistaken to base this book on a critique of the neoDarwinian synthesis. A critique of an articulate and coherent body of thought can be very stimulating. The neoDarwinian synthesis, however, has no such coherence: indeed, the phrase means something different to everyone who would talk about it. Unavoidably, criticisms of some representatives of the synthesis are grossly unfair to others. In turn, reaction to such criticisms can distract one ever further from the proper subject of evolutionary theory, the actual processes involved in “descent with modification” and the diversity of forms they yield.

Eldredge’s critique, moreover, is based on assumptions which guarantee that he can neither understand the synthesis nor convince its proponents of its flaws. Eldredge remarks (p. 184) that “. . . perhaps the major problem with the synthesis has been that adaptation was seen as the fundamental theme of the entire evolutionary process.” Of course the makers of the synthesis focussed on adaptation! . . . however much they differed in other respects. After all, the apparent purposiveness of living things, and the aura of design in their morphology, are their most characteristic features, as Aristotle well knew. Darwin’s argument that these features are an automatic consequence of differential replication with heritable variation, and its implication that adaptation and diversity can be accounted for without appeal to miracle or mystery, has not ceased to astonish or even outrage laymen (and many biologists as well). To this day, Darwin’s idea is the most astonishing to have emerged from biology: this

idea provides biology with its central theme, and biologists with their strongest reason for hoping that their subject will eventually be comprehended among the exact sciences. Especially after Fisher (1930) reconstructed Darwin’s theory in terms of Mendelian genetics and showed that it was eminently reasonable, evolutionary theorists were anxious to test it further, and to explore its implications. Why does Eldredge wish to displace adaptation from the center of the stage?

Eldredge believes (p. 184) that the origin of adaptation is relatively well understood, and traces exclusively to natural selection within populations. As paleontology deals with changes in higher levels of his hierarchies, the replacement of one phylad by another and the like, Eldredge appears to conclude that paleontology cannot reveal anything about the origin of adaptation, so that a paleontological theory of evolution must center on a different theme. Of all the slurs I have ever heard on paleontology, and they have been many and odious, this one takes the cake. To begin with, it is news to me that the origin of adaptation is a solved problem. Considering all the chaos of selfish genes, molecular drives, multiplication of transposable elements, and the like, it remains to discover just how selection within populations manages to produce such marvels of organismic adaptation. This question retains its urgency regardless of whether these marvels are “optimal.” It also remains to learn what role this molecular chaos plays in creating suitable “raw material” for natural selection. It surprises me rather more to hear that paleontology has nothing to contribute to understanding the origin of adaptation. I believe that Eldredge himself remarked on the essential role of biotic crises, those widespread extinctions which punctuate the great eras of the fossil record, in facilitating evolutionary progress. On a more theoretical plane, the outcomes of natural selection within populations are unpredictable, and some are better for the species than others. Presumably, those species where individual advantage most nearly coincides with the good of the species (in terms of higher speciation rate or lower extinction rate: Stanley 1979) are the ones whose descendants populate later geologic strata. If so, selection between species plays an integral role in shaping adaptation (Leigh 1977), and evolutionary theorists cannot afford to neglect the fossil record.

What comes of displacing adaptation from the center of evolutionary theory? Eldredge’s logic has nudged him toward an elaborate and sterile formalism, which divorces his evolutionary patterns from the processes which might explain them. Sometimes the problem is merely overmuch faith in the tidiness of his hierarchy. Eldredge posits organisms as the fundamental units of natural selection (p. 184), but what are organisms? Consider the implications of the challenge clonal reproduction poses for Weismann’s doctrine of the sequestration of the germ line (Buss 1983). In organisms capable of clonal reproduction, somatic cells can give rise to reproductive tissue, so their contribution to the genetics of future generations is no longer identified with the well-being of the individuals of which they are now part. A similar conflict arises in colonies of social insects: if workers can lay eggs of their own, their evolutionary future is no longer absolutely linked to

that of the colonies to which they belong, and colonies may cease to be the primary units of selection. Constructing hierarchies, however plausible, provides no license for ignoring how natural selection actually works.

A more damaging instance of logic run wild is Eldredge's criticism (p. 158f) of Ghiselin's (1974) analogy of species with business firms. Eldredge argues that species are not "interactors" because one species may live in several different communities, and thus may not be decisively affected by events in any one of them. Yet firms may also operate in several different markets, perhaps because the factors which make for success in one market presumably enhance the prospects of success in others where the firm has established itself. Correspondingly, sufficiently widespread crises may extinguish widely ranging species, or multinational firms, as the case may be, favoring the more adaptable entities. Possibly because his formalism divorces species from communities, Eldredge argues (p. 196) that

"... if the notions of species selection are falsified by the observations that (1) economic adaptations, at least, solely involve organismic attributes, not species-level properties, rendering species selection meaningless... and (2) in any case, species do not seem to be active interactors in the ecological arena, then *so too is the entire adaptive landscape metaphor of adaptive evolution simultaneously falsified*—provided, of course, that species are construed as individuals and the literal truth of the two observations above is agreed upon."

There are many potential conflicts between individual advantage and the good of the species—dispersal rate, mutation rate, sex ratio, and sexuality itself being among the better known. As I mentioned earlier, the resolution of such conflicts is probably a major feature of evolution. A formalism that complicates or hinders their discussion will inevitably obstruct a deeper understanding of the origin of adaptation. In sum, an overly formalistic approach to evolution and phylogeny is dangerously constricting, as Ghiselin (1984) so eloquently warned.

Given the controversy between population geneticists and paleontologists, I had best remark that positing the origin of adaptation as the central problem of evolutionary theory (Pittendrigh 1958) does not imply that natural selection within populations is the only relevant cause of evolutionary change. Whatever fault I may find with his book, Eldredge is quite right to insist on the incompleteness of modern evolutionary thought and to associate this incompleteness with neglect of the various possible levels of evolution, which can in turn be blamed partly on ignorance of paleontology. Those who think we know all we need to about evolution are welcome to explain (1) how a scientific team from another galaxy, with full access to Earth's fossil record in proper stratigraphic order, but no access to living or recently dead organisms, could deduce the principles of inheritance from the fossil record, and (2), how large, and how subdivided, a landmass was required to allow evolution of mammals from reptiles. The absence of an answer to the first question suggests that the relevance of genetics to paleontology, and therefore to evolution, is not fully established; the an-

swer to the second question will undoubtedly involve selection between species.

Although evolutionary theory needs to be reformed, to attempt this reform by abandoning the quest to understand the origin of adaptation is to make the subject fearfully dull, indeed, to cut the heart out of it. Eldredge's book suffers grievously by abandoning the theme that would have lent interest and unity to its subject.—E. G. LEIGH, Smithsonian Tropical Research Institute, Panama.

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**Phenetics: evolution, population, trait.**—A. V. Yablokov (trans. M. J. Hall). 1986. Columbia University Press, New York. xi + 171 p.

This work is the third edition, heavily revised, of the well-known Russian book *Fenetika* by Alexey V. Yablokov, a leading Soviet evolutionist and ecologist. "Phenetics" for Yablokov is not the "phenetics" of numerical taxonomists, who applied the term loosely to a group of numerical methods. Rather, it is the study of "phenes." Phenets are alternative variants of genetically determined traits, though the underlying genetics may involve such complexities as pleiotropy and polygenes. The variation can be continuous, as for size and color, so long as each individual can be assigned unambiguously to one phene-class.

One should not worry about the introduction of new jargon, since "phene" was first defined, very similarly to Yablokov's definition, in 1909 by Johannsen, the Dane who also defined "gene," "genotype," and "phenotype." In a brief historical chapter, Yablokov dis-

cusses why study of genes and genotypes rapidly surpassed study of phenes and phenotypes. The essential reason was that the gene was the central unit of genetics, a science that quickly became exciting and productive as the physical nature of genes and chromosomes was elucidated and the rather simple genetic basis of some traits become manifest. However, these latter were exceptional and the general picture was of a complicated path from gene to phene. This complication was the spur to a focus on genes and neglect of phenes—it seemed as if fruitful study of phenes would require a clearer understanding of their genetic bases.

Why resurrect the study of phenes now? What insights can they yield, especially if the underlying genetics have not been elaborated? In fact, as Yablokov demonstrates, phenes have not really been buried from 1909 until the present and much evolutionary and ecological research is actually phenetic: phenotypic traits are assumed to have a genetic basis but the underlying genetics are not worked out. Instead, evolutionary deductions have often been based directly on phenotypic patterns. One example presented in detail (studied phenetically by Timofeeff-Ressovsky and Yablokov in 1973 in an untranslated Russian paper) is the relation between precipitation and clinal variation in the hybrid zone between the Baltimore and Bullock orioles described by Rising in 1970. Many other examples, often from the eastern European literature, make the same point.

The first goal of *Phenetics* is to formalize methods for detecting phenes, assigning individuals to pheneclasses, and analyzing resulting phenetic patterns. Yablokov gives examples of several graphical and statistical methods of presenting phenetic data to facilitate detecting patterns and also treats the problem of analyzing several phenes (say, color and size) simultaneously for the same group of populations.

One might have expected that the growth of genetics and concomitant better understanding of some gene-to-phene pathways would cause phenetics to be subsumed into genetics. In other words, for what specific questions is analysis of phenes likely to provide an answer? Yablokov argues convincingly that there are only a handful of cases for which sufficient genetic understanding exists so that study of phenotypic traits (phenes) will still be important for years to come in addressing many evolutionary questions: the nature of natural selection, the importance of gene flow, mutations, and population fluctuations, the evolutionary relationships of different populations and species, etc. Ontogenetic noise and phenotypic plasticity bedevil phenetics, just as they bedevil genetics. However, Yablokov is concerned that we not overestimate the difficulties posed by this indeterminacy. His key argument here is that the complexity of interaction of external factors during ontogeny is so great that their effects must somehow cancel one another out, much as do the movements of particles in Brownian motion. The evidence he marshals in support of this proposition is quite meagre, given its importance in justifying the study of phenes. However, the many cogent phenetic examples he presents suggest that this defect may not be crucially debilitating, but rather a point to be argued and perhaps remedied.

Yablokov conceives of phenetics as primarily a pointer to interesting situations for further genetic and ecological research. Most insights to date and for the near future rest on the geographical distribution of various phene-classes so it is fitting that by far the largest chapter is on "phenogeography." Usually one is seeking regions of abrupt changes in the distribution of frequencies of phene-classes. For example, an early study by Serebrovskii focussed on the phenes of color and comb shape in semiwild chickens in Dagestan (North Caucasus). Phenetic frequencies changed abruptly at the Avarskoe Koisu River, which flows in a gorge several hundred meters wide. Apparently chickens cannot cross the gorge, though other gorges do not constitute regions of phenetic frequency change and, by implication, barriers to dispersal. A similar example for a much more widely distributed bird, the yellow wagtail, is presented from untranslated research by Timofeeff-Ressovsky et al.

In addition to taxonomic uses, such as the delineation of infraspecific categories, phenogeographic data can lead to interesting ecological questions. A featured example is color variation in the rustic autumnal moth in the Shetland Islands, which has a melanistic and a non-melanistic form that were studied by Kettlewell and Berry. A small valley on Shetland Mainland marks an abrupt shift from predominantly melanistic moths in the north to predominantly non-melanics in the south. Mark-and-recapture experiments showed that individual moths frequently flew far enough to cross the valley but very rarely did so. Exactly why they do not cross the valley, and why melanistic moths are favored north of the valley, are unanswered questions though several hypotheses have been proposed in the wake of the phenogeographic observations.

Probably the American edition of *Phenetics* will generate most interest in two ways. First, the focus on the relationship between geographic pattern and microevolutionary processes will help to strengthen interest in the populational aspects of biogeography, such as the significance of clines and stepped clines. Though far from moribund, this branch of biogeography has taken a distinct back seat for two decades to the multispecies questions associated with the equilibrium theory of island biogeography and with variants of vicariance biogeography. New methods such as those proposed by Yablokov and greatly increased data suggest that population-oriented biogeography may be an extremely fruitful area of research even though it is an old field. Second, a comprehensive (though short) work by a respected Russian scientist must intrigue thoughtful western readers. Especially in evolution and ecology the traditions have grown sufficiently apart that there are somewhat different problems, different perspectives on common problems, and a separate (and usually untranslated) literature. Any American who has worked in an active foreign (especially non-anglophone) laboratory knows the excitement and novel insights derived from discussions with critical and dedicated scientists working on problems similar to one's own. *Phenetics* conveys much the same feeling without one's having to travel to Moscow.—DANIEL SIMBERLOFF, Department of Biological Science, Florida State University, Tallahassee, FL 32306.