

BOOK REVIEWS

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Natural selection in the wild.—John A. Endler. 1986. Princeton University Press, Princeton, NJ. xiii + 336 p. ISBN 0-691-08386-X cloth, 0-691-08387-8 paper.

Natural selection is the idea which, in Darwin's hands, expelled supernatural explanations of adaptation from scientific discourse and opened the possibility of bringing all biology within the realm of mechanism. Unfortunately, in replacing a purposeful Designer, natural selection sometimes acquires the attributes of a *Deus ex Machina*. As D'Arcy Thompson (1942, p. 960) remarked, "To buttress the theory of natural selection, the same instances of adaptation (and many more) are used, as in an earlier but not distant age testified to the wisdom of the Creator and revealed to simple piety the immediate finger of God."

In this book, Endler seeks to restore natural selection to the realm of science. He begins by defining natural selection and related terms, discussing other meanings which have threatened to usurp these terms, and identifying various misconceptions of how selection works or what it implies. Then, in the heart of the book, he suggests 10 methods for recognizing natural selection in wild populations and shows how to measure its rate. He tabulates what he accepts as valid examples of natural selection in the wild, and figures frequency distributions of the intensity of selection. Finally, he reflects on the implications of all this, and considers where evolutionary theory should now be going. This is an ambitious project, and Endler's handling of it is most interesting.

Endler defines natural selection as a mechanism occurring among replicating units which possess heritable variation in replication rate or survival prospects. This definition reflects a stable and reasonable modern consensus. In abstracting the essence of Darwin's idea, however, it obscures a definition which Darwin considered essential. Unlike Endler, Darwin (1871, pp. 261, 262) distinguished natural from sexual selection in a manner which suggested that natural selection worked for the good of the species while sexual selection did not. Specifically, he asserted that if male oceanic crustaceans needed claspers to propagate their kind, the development of these claspers should be ascribed to natural selection, but if these claspers only served to give one male an advantage over another in the competition for mates, they must be ascribed to sexual selection. Even good definitions occasionally obscure important distinctions.

Language is slippery, and sometimes Endler trips. To avoid "personifying" natural selection, Endler eschews treating it as a "force," "speaking of it as "acting," or referring to its "intensity." This seems unnecessary. Haldane (1932) defined the "intensity of selection" without misunderstanding the process. Endler also argues (p. 30) that "Since natural selection does not 'act,' it is meaningless to speak of a 'unit' of selection, except possibly as an entity whose *relationships* with other such entities are *affected* by selection." It is difficult to

see the point of this remark: the standard definition (Lewontin 1970) of units of selection as replicators that vary heritably in fitness, such as genes or species, obviously satisfy Endler's proviso. Moreover, neglect of these units obscures potential conflicts between selection within populations and selection between species. For example, Darwin's belief that natural (as opposed to sexual) selection works for the good of the species, may be empirically justified only because species for which selection within populations was disruptive tended to go extinct in consequence (cf. Alexander and Borgia 1978).

Endler's definition of an allele's fitness as its expected time to extinction may also prove confusing. He asserts, in effect, that this definition is the Platonic ideal of fitness, of which others are but shadows. This definition is ambiguous because, unlike the ordinary measure of allelic fitness (the number of offspring alleles per parent, divided by the mean for all alleles at its locus), an allele's expected time to extinction necessarily depends on the number of copies of that allele now in the population. This definition is also unworkable: calculating expected time to extinction requires knowledge of the allele's fitness (in the ordinary sense) far into the future. And, in fact, Endler uses ordinary measures of fitness throughout the rest of the book.

The most striking confusion of language in Endler's whole book, however, masquerades as an empirical observation: "There are almost no examples showing competition . . . among phenotypes." Darwin and his successors viewed sexual selection as an explicit consequence of competition for mates, and Darwin's phrase, "the struggle for existence," also suggests an intimate connection between intraspecific competition and natural selection. One would think Endler's book is largely devoted to documenting . . . intraspecific competition.

Endler's 10 methods for detecting natural selection are quite interesting. The first three are designed to detect adaptation rather than its origins. Since, in fact, we expect adaptation to reflect natural selection, these methods do suggest where to look for selection. Endler's favored means for detecting natural selection is to simultaneously follow cohorts of different genotype from birth to death, comparing their reproduction and mortality at each age to learn whether the genotypes differ. He also considers change in genetic composition after an artificially imposed environmental perturbation to be good evidence, if a suitable control population is monitored simultaneously. Endler does not consider it adequate proof to identify characteristics whose optima under natural selection are predictable, even if the optima vary predictably with environmental circumstances, as with "sex allocation" (Charnov 1982). Granted, one must understand the genetics of such characteristics to conclude that natural selection currently affects them. On the other hand, the mere fact that characters vary in sufficiently precise coincidence with a complex and unexpected prediction of

selective optima, testifies to the importance of being in compliance with what selection favors, and may also suggest what units are being selected (Leigh 1986).

In measuring the directions and intensities of selection, Endler's greatest problem is coping with phenotypic and genetic correlations. Is a character spreading because it is advantageous, or is it "riding the coattails" of an advantageous trait with which it happens to be associated? Endler relies on a formalism of Lande and Arnold (1983) to solve this problem. Their method involves finding the multiple regression of fitness on the phenotypic characters under study. This involves solving systems of simultaneous equations whose coefficients are the estimated phenotypic variances and covariances of these characters. Estimates of these coefficient variances and covariances are usually imprecise: the solutions to these equations are necessarily at least as imprecise. This procedure may be almost as prone to error as extracting the eigenvalues of a "community matrix" of competitive or predator-prey relationships of all pairs of species in an ecological community (cf. Levins 1968). Nevertheless, this often unreliable method is the best we have: it will be useful only where one understands the organisms well enough to choose the "right" quantities to measure, quantities which allow us to escape the pitfalls of the method.

Endler's tabulations of selective intensities lead him to believe that selective differentials are often quite strong, say 20% or more. Since the techniques he trusts only detect strong selection, he may overstate his case: Simmons and Crow's (1977) study of mutations affecting fitness in *Drosophila* populations suggest that, although some mutations are lethal, most selective differentials are no more than a few percent. Nonetheless, these studies make one wonder why many species change so little during their stay in the fossil record (Cheetham 1986). What can the studies tabulated by Endler tell us about the workings of macroevolution? We will not know until we can set these studies in the context of the ecology of the species concerned, and learn more about the relevant new variation. Endler remarks that progress in these areas will depend on students showing greater interest in how selection works, what it works on, and why (see below).

Where do Endler's observations lead? In his final chapter, Endler discusses various views of the role of selection in evolution. Are most genetic polymorphisms selectively neutral, or are they maintained by natural selection? Have most characteristics attained their selective optima, or have genetic correlations and developmental constraints prevented this? Endler considers these and other questions in terms of the joint role in evolution of selection and variation.

Since selection can only "choose" from the variants available, constraints on variation receive much attention, some of which, as Endler points out, is rather rhetorical. This rhetoric can be seductive. The evolution of any one species seems hedged about by constraints. Endler himself remarks that a species which has lost its capacity for sexual reproduction will never regain it; a species with exoskeletons is most unlikely to have descendants with vertebrate-style internal skeletons, etc. Looked at this way, evolution seems a matter of chance. If, however, one compares independently

evolved biotas with an eye to the nature and completeness of evolutionary convergence, the picture changes radically. Comparison of Australia, Madagascar, and South America shows how effectively, and how predictably, the descendants of a few small mammalian migrants radiate to fill a variety of niches. Such comparisons show that, although variation and natural selection may be equally essential in evolution, natural selection is the *formative* principle, the agency that imparts to living things their astonishing organization and purposiveness. The central unanswered question, for Endler and for the rest of us, is, what features of genetic systems, and of the variation they generate, allow natural selection to do this?

This book seems far hastier and less precisely written than its predecessor (Endler 1977). It nonetheless represents the interesting reactions of a thoughtful man to important problems. Its civil, balanced tone lives up to the quotations from Samuel Johnson which appear at the beginning of each chapter. In this book, Endler necessarily confronts the inevitable tension which arises from the fact that scientific conclusions are public property, which must be objective enough for others to evaluate, use and trust, yet their origins are very private affairs, in which intuition, aesthetics, and the chance associations arising from a lifetime's experience all play a role. In the attempt to prevent private wishes from biasing public conclusions, scientific method has often been presented in overly dogmatic form and has usurped the center of attention. As a result, questions are often asked too narrowly. A recurrent theme of Endler's is perhaps best expressed on pages 162 and 163:

"Most studies of natural selection contain three major faults: (1) no estimate of lifetime fitness; (2) consideration of only a few traits; and (3) unknown or poorly known trait function. These are frequent symptoms of a fundamental and widespread lack of interest in the organisms, an overenthusiasm for testing one's favorite theories, and little interest in why natural selection can occur."

These flaws simply reflect lack of curiosity. Endler insists these flaws must be overcome if further studies of natural selection are to improve our understanding of evolution. Curiosity is also the first step in developing a sufficiently experienced intuition to apply scientific method intelligently and usefully. Endler is not only restoring natural selection to the realm of science, he is trying to return science to the human race.—
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LITERATURE CITED

- ALEXANDER, R. D., AND G. BORGIA. 1978. Group selection, evolution, and the levels of organization of life. *Annu. Rev. Ecol. Syst.* 9:449-474.
CHARNOV, E. L. 1982. *The theory of sex allocation*. Princeton Univ. Press, Princeton, NJ.
CHEETHAM, A. H. 1986. Tempo of evolution in a Neogene bryozoan: rates of morphologic change within and across species boundaries. *Paleobiology* 12:190-202.

- DARWIN, C. R. 1871. The descent of man, and selection in relation to sex. John Murray, London.
- ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, NJ.
- HALDANE, J.B.S. 1932. The causes of evolution. Longmans Green and Co., London.
- LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- LEIGH, E. G., JR. 1986. Ronald Fisher and the development of evolutionary theory. I. The role of selection. *Oxford Surveys in Evol. Biol.* 3:187–223.
- LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, NJ.
- LEWONTIN, R. C. 1970. The units of selection. *Annu. Rev. Ecol. Syst.* 1:1–16.
- SIMMONS, M. J., AND J. F. CROW. 1977. Mutations affecting fitness in *Drosophila* populations. *Annu. Rev. Genet.* 11:49–78.
- THOMPSON, D. W. 1942. On growth and form. Cambridge Univ. Press, Cambridge.

Viable populations for conservation.—Michael E. Soulé [ed.]. 1987. Cambridge University Press, Cambridge. xii + 189 p.

Conservationists, scientists, managers, even politicians have converged on one question as key to systematic conservation efforts and emblematic of the ability of science to help prevent extinctions: What is the minimum viable population (MVP) of a threatened species? This convergence is a consequence of economic exigencies. Wishing to conserve as many species as possible, with insufficient resources, we are faced with a minimization problem, expressed in extreme form by Lahti and Ranta (1986): "Each nature reserve should be as small as possible to allow sustained preservation of the target species of the reserve, and all remaining resources should be allocated to establishing other reserves important to other target species." But what size, exactly, will allow sustained preservation? The problem is frequently restated in local terms when someone wants to harvest a particular piece of habitat and someone else sees a threat to a species. The Northern Spotted Owl requires old growth forest. Timber interests and the U.S.D.A. Forest Service want old growth to be harvested but do not want to threaten the owl, and they ask just how many birds are required (and how much forest for each) to place the bird beyond danger of extinction.

Earlier research was summarized and focussed by Shaffer (1981), who classified threats to small populations as (1) demographic stochasticity (chance variation among members of a population in survival and reproduction), (2) environmental stochasticity (temporal variation in habitat and populations of interacting species such as predators), (3) natural catastrophes such as fires, and (4) genetic stochasticity (changes wrought by drift and inbreeding). Shaffer also proposed specific time and probability frameworks: "sustained preservation" for how long and with what probability?

Models have proliferated for all four threats, and management schemes for threatened species are coming to be routinely based on MVP analysis (e.g., Northern Spotted Owl [Dawson et al. 1987]). Entire workshops are devoted to MVP analysis. However, conservation biology has evolved so quickly that there is confusion about the assumptions and predictions of models, some models are inconsistent with others, and managers tend to turn to ad hoc simulation models that have not been carefully studied. All within one decade, the notion first became widely accepted that genetic stochasticity is the biggest threat, then that demographic stochasticity is most important, and then, very recently, that environmental stochasticity is the big problem. The field moved so rapidly that these ideas spread primarily by in-press manuscripts and word of mouth. *Viable Populations for Conservation* is the first book wholly devoted to the topic and contains several excellent papers that clarify the existing muddle, point to limitations in current theory, advance new theory, and suggest future directions.

The book focusses primarily on long-term viability—at least a few centuries—of vertebrates. Key among the 10 papers are several theoretical advances. Goodman shows that much previous literature confounds demographic and environmental stochasticity, and argues convincingly that environmental stochasticity is likely to be far more important than demographic stochasticity for all but the most minuscule populations. Earlier models based on demographic stochasticity showed persistence times proportional to a power of the carrying capacity, so rather modest increases in the size of a refuge could lead to vastly increased expected persistence times. Goodman's model of environmental stochasticity leads to the depressing conclusion that the expected persistence time of a population is proportional to the square of the log of the carrying capacity. Thus refuges to assure long-term survival might be impossibly large; extensive management intervention might be required instead. Belovsky uses literature data to make Goodman's model operational, but he concatenates so many estimates and relationships with so much variation that the resulting patterns are not compelling.

Ewens and co-authors model the force that has been modelled least—catastrophes. They examine two catastrophic effects, one genetic and the other demographic. The genetic model has subpopulations extinguished by catastrophes and replaced by colonists from surviving subpopulations. They conclude that, if it is impossible to transport individuals from one subpopulation to another, the appropriate MVP on genetic grounds is one large enough to allow an acceptable rate of loss of alleles from drift within the subpopulations. If human-mediated gene flow is possible, one should instead focus on the rate of loss of alleles in the entire metapopulation. Equations are provided for each circumstance. They add the well-known fact that a small amount of natural migration suffices to stem much of the loss of alleles in the metapopulation and, to some extent, the subpopulations.

Ewens et al. model the effect of catastrophes acting through demography in a way that accords with Goodman's definition of environmental stochasticity. Oc-

asionally an event occurs such that each member of the population has heightened probability of death, independently of the other members. They explore the distribution of persistence times for combinations of N = population size and p = probability of death during the catastrophe. Their main result is depressing and in line with Goodman's: Increases in N have very little effect on median persistence time. It is $\log N$, which changes much more slowly, that is important.

The third major contribution is by Lande and Barrowclough on genetic determinants of MVP. They thoroughly review classical and recent results on interactions of drift, mutation, and selection and draw several important conclusions. First, single-locus variation and quantitative variation are affected very differently by small population size. The latter may be preserved by effective population sizes (N_e) in the hundreds, while the former may require millions for neutral variation (but many fewer for deleterious alleles that may, in the future, provide necessary variation for evolution). Lande and Barrowclough clarify the widely cited argument of Franklin (1980) that N_e of about 500 will preserve genetic variation for long-term evolution. This result is in the absence of selection and applies to traits with heritability ≈ 0.5 .

Furthermore, after a bottleneck, quantitative variation and deleterious single-locus variation may recover in hundreds of generations, while neutral single-locus variation may require millions of generations. Given the thoroughness of their review and their attempt to clear up misunderstandings, it is surprising that the authors do not precisely state the major previous result in this area. Nei et al. (1975) showed that, for single locus traits, average heterozygosity need not be greatly reduced by a small bottleneck so long as recovery is rapid. However, the average number of alleles per locus can be greatly decreased by a bottleneck no matter how quickly population size increases. Previous conservation literature states the first result but omits the second; Lande and Barrowclough apparently state the second ("it will take a very long time . . . for mutation to restore the high levels of heterozygosity") while neglecting the first.

The three main contributions just described, plus those of Shaffer and Gilpin, all treat the metapopulation concept and emphasize that geographic structuring of a large metapopulation into a group of semi-independent subpopulations protects against various forces likely to endanger small populations. This principle of "spreading the risk" seems obvious and, indeed, there is an older literature on it (Andrewartha and Birch 1954, Den Boer 1968, Roff 1974) that is ignored in *Viable Populations for Conservation*. However, as Shaffer points out, the metapopulation is an emerging area of MVP research and is already included in such management plans as that for the Spotted Owl. He adds that the trade-offs between number, size, and arrangement of reserves are not yet clear. These trade-offs have engendered heated debate but only Goodman attempts to confront this issue. He concludes cautiously that, with respect to environmental and demographic stochasticity, a group of small refuges is preferable to a single large one, so long as there is some immigration and the environmental variation of the small reserves

is at least partially independent. Most authors in the conservation literature have argued the opposite. Groups of small populations might also be expected to maintain more genetic variation than single large ones, according to Lande and Barrowclough, so long as inbreeding depression does not lead to extinction. However, even one or two breeding individuals shifted into each population would stem inbreeding depression, and several authors discuss routinely moving animals as a viable management procedure.

A continuing theme is that no current model treats all four forces together—conservationists seem engaged in an analog to the physicists' search for a unified theory of the four types of elementary-particle interaction. Ewens et al. and Soulé suggest some promising leads.

Another continuing theme among all the theorists is the need for caution in interpreting theoretical results. Soulé: "How 'good' are the models presented in this volume? Anyone knowing the history of mathematical population biology and community ecology has to be a sceptic. The ground of these disciplines is littered with broken stick models, with discarded alpha matrices, and other strange and wonderful debris. Mathematical models serve as useful vehicles for thought, but it is foolish to hitch a bandwagon to any particular one." Soulé's concern is doubtless due to the desperation with which managers, faced with immediate conservation problems, have latched on to dubious models that happen to state clear results. Wilcox (1986) heralds $N_e = 500$ as a "magic number" that will maintain genetic variation. Lande and Barrowclough show just how shaky this argument is. Ewens et al. and Soulé argue explicitly against the current practice of invoking "magic numbers" and standard numerical rules in MVP analysis, while Soulé and Lande and Barrowclough describe the advances in this volume as narrowing estimates perhaps to within order-of-magnitude range. Soulé correctly contends that such a narrowing is a big improvement over the methods of 10 years ago, even though managers cannot yet get precise and specific advice from these general treatments. Nevertheless, if one wishes to remain current in conservation biology and to see clear, incisive thinking on its major issue, *Viable Populations for Conservation* is must reading.—DANIEL SIMBERLOFF, Department of Biological Science, Florida State University, Tallahassee, FL 32306.

LITERATURE CITED

- ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. Chicago.
- DAWSON, W. R., J. D. LIGON, J. R. MURPHY, J. P. MYERS, D. SIMBERLOFF, AND J. VERNER. 1987. Report of the Scientific Advisory Panel on the Spotted Owl. *Condor* 89:205–229.
- DEN BOER, P. J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18: 165–194.
- FRANKLIN, I. R. 1980. Evolutionary change in small populations, p. 135–149. In M. E. Soulé, and B. A. Wilcox [eds.], *Conservation biology: an evolutionary-ecological perspective*. Sinauer, Sunderland, MA.

- LAHTI, T., AND E. RANTA. 1986. Island biogeography and conservation: a reply to Murphy and Wilcox. *Oikos* 47:388–389.
- NEI, M., T. MARUYAMA, AND R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1–10.
- ROFF, D. A. 1974. Spatial heterogeneity and the persistence of populations. *Oecologia* 15:245–258.
- SHAFFER, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131–134.
- WILCOX, B. A. 1986. Extinction models and conservation. *Trends Ecol. Evol.* 1:46–48.

Gulls and plovers. The ecology and behavior of mixed species foraging groups.—Christopher J. Barnard and Desmond B. A. Thompson. 1985. Columbia University Press, New York. xii + 302 p. \$30.00.

The last two decades have seen important advances made towards our understanding of the decision-making processes used by foraging animals. Similarly, numerous studies have identified many of the costs and benefits associated with single- and mixed-species flock formation. Whereas most optimal foraging studies have attempted to identify how foraging decisions are made by animals, few have tried to determine how the social environment might affect those decisions. Likewise, studies on the flocking and assembling behavior of animals have focused on identifying the costs and benefits of grouping but have not determined how foraging success might influence group structure or cohesion. Only recently have studies begun to focus on the interplay between the decisions foraging animals make and the social environment within which those decisions are made.

Christopher Barnard and Desmond Thompson do just this in a meticulously detailed study involving three charadriiform species: the Lapwing (*Vanellus vanellus*), Greater Golden Plover (*Pluvialis apricaria*), and Black-headed Gull (*Larus ridibundus*). These species form mixed-species foraging assemblages on the pastures of Great Britain in winter. Barnard and Thompson's study successfully integrates modern foraging theory into a socioecological framework. The resulting story reveals that the decisions animals make while foraging depend heavily on the social context within which decisions are made and that group structure/composition may vary depending on the foraging success of group members.

The first chapter of this book summarizes current thinking with respect to the costs and benefits accrued to individuals by foraging in flocks. Barnard and Thompson contrast the costs and benefits of flocking in single- vs. mixed-species flocks and argue convincingly that the consequences of foraging in mixed-species flocks may differ quantitatively from those of single-species flocks. In Chapter 2, brief introductions to each species and the study areas are provided. Barnard and Thompson provide an interesting discussion of the evolution of pasture use by plovers, although their suggestion that plovers first began using pastures about

4,000 years ago when man switched from nomadism to a pastoral lifestyle seems doubtful. The remaining 7 chapters, excluding an overview chapter, attempt to provide answers to the following questions about the foraging behavior of these species. (1) How are fields chosen? (2) How are foraging locations within fields chosen? (3) How are foods chosen? (4) How does flock composition, food abundance, and climate (e.g., temperature) influence the foraging efficiency and time budgeting of individuals? (5) What factors determine the patterns of arrival and departure of birds from the flock? (6) How do pirating gulls decide what to steal and from whom to steal it? (7) How does flock composition affect the vigilance behavior and responsiveness of individuals to alarms? Repeatedly, tests of hypotheses reveal that the behavior of members of one species depends heavily or is altered by the behavior or the presence/absence of heterospecifics. Below is a sample of such results.

Golden Plovers and gulls depend primarily on the presence of Lapwings to identify the best fields in which to forage. Likewise, plovers use local densities of birds as indicators of the best locations in which to forage within a field. The presence of pirating gulls causes plovers to alter the size of prey they take by reducing the amount of time they spend crouched looking for larger but more concealed worms. The temporal patterns of arrival and departure to and from pastures by each species are influenced by the species composition of the flock currently foraging on a field and also by environmental conditions. Arrival and departure patterns are not the same for each species. Plovers in flocks respond more quickly to alarms and responses of gulls than they do to alarms of other species in flocks without gulls. Plovers therefore, appear to take advantage of the early warning provided by the presence of gulls within a flock, thereby off-setting some of the costs associated with piracy by gulls.

At times this book becomes difficult to read because the presentation of results often are overwhelmingly detailed. Figures and tables placed several pages from their first reference in the text sometimes contribute to difficulty in interpreting results. For the most part, the organization of material within chapters proceeds in logical fashion, but occasionally, results in earlier chapters are logical only after the presentation of results later in the book. These are minor flaws for a book full of hypothesis testing in which results from each chapter are so tightly interwoven.

Fortunately, the authors provide concise résumés and highlighted summaries of significant points from each chapter. The take-home message of this book is clear: foraging decisions by members of mixed-species foraging groups are made using information about environmental conditions (i.e., food resources) as well as information provided by the social environment, and neither should be ignored in studies of mixed-species foraging groups. *Gulls and Plovers* will be an invaluable reference to all investigators working on the ecology and behavior of mixed species foraging groups.—STEPHEN R. PATTON, Department of Biology, University of South Florida, Tampa, FL 33620.