annectent field of ecological genetics is still in a primitive stage, largely, I suspect, because of the chance circumstance that *Drosophila* studies have dominated population genetics for so long. *Drosophila*, being sparsely distributed and elusive in the field, is one of the worst animals with which to study ecology. But the ecologists have begun to produce predictive theories on their own that are of great interest to the rest of evolutionary biology. R. H. MacArthur, after dismissing critics of his highly abstract method of theorizing with an impatient wave of his hand ("Think how physics would be without its frictionless pulleys, conservative fields, ideal gases, and the like"), reviews some of his well-known ideas on competition and species diversity. Time and again he produces intriguing predictions, some of them susceptible to testing by direct measurements, which contribute new insights concerning the foraging behavior of animals, properties of the niche, and competition among species. J. L. Harper, who has the distinction of being the first botanist to speak to animal ecologists in their own language, reviews progress in experimental plant ecology. The puzzling phenomena he describes in competition and synergism among plants, together with the lack of any visible laws relating competitive ability to biomass, growth rate, and seed production, make a unifying theory in botany impossible at this time. And there are too many differences between higher plants and animals to permit botany to borrow freely from zoology. Nevertheless, Harper and his co-workers have now demonstrated that plants are very superior material for such studies, and future progress should be rapid.

C. H. Waddington stresses the shortcomings of classical selection theory and outlines a method for the study of selection of simple allelic systems in heterogeneous environments. The same subject is taken up by Richard Levins, who uses his powerful fitness-set method to predict the consequences for genetic variation of varying such parameters as developmental flexibility, degree of inbreeding, and amount of environmental heterogeneity. Levins' exposition is as hurried, brilliant, and hypercondensed as in earlier papers; one gets the feeling he is receiving secrets of the universe from a space visitor anxious to be on his way. Th. Dobzhansky provides a thoughtful essay on the intuitive meaning and the methods of measuring adaptedness, Darwinian or reproductive fitness, and persistence (fitness in the Thoday sense), three of the general properties of populations. Bruce Wallace, in his meticulous manner, develops an original method of graphical analysis in which the complex interactions of population size, density-dependent mortality, and frequency-dependent fitness are visualized. The method promises to predict not only the equilibrial frequencies in a two-allele case but also the equilibrial population size.

Speciation theory is still the least analytic branch of evolutionary biology. In the book the multiple consequences of episodes of rapid population growth on species-level evolution are considered in detail by H. L. Carson, but still largely in terms of verbal imagery. Speciation is also pondered from a novel viewpoint by G. E. Hutchinson, who suggests that the phenotypic limits of "good species," in other words, species that taxonomists find easy to distinguish, are set by discontinuities in the environment, regardless of whether the organisms are bisexual metazoans or such parthenogenetic groups as the bdelloid rotifers. The means are discussed, in a still tenuous fashion, by which taxonomic characters and niche dimensions might be mapped onto one another. Finally, in the closing chapter, L. B. Slobodkin remains, as in his earlier writings, sternly cautionary about the prospects of a predictive evolutionary theory. He allows that one is possible in principle, provided a way is found to relate homeostatic ability, which Slobodkin regards as the single most important quality of organisms and populations, to the persistence times of species.

It is clear from these contributions that the grip of the neo-Darwinist savants on evolutionary biology is at last loosening, and that the subject is being turned into a creative, chancy, young man's game. There is a refreshing quality in Lewontin's frank protest:

> It is unhappily true that there are population biologists who reject the analytic method and insist that the problems of ecology and evolution are so complex that they cannot be treated except by holistic statements. The influence of these people has held up progress in population biology for many years and, in addition, has tended to degrade population biology as a science. They are the stamp collectors of biology who, because they themselves are unable to analyze the complex problems of ecology and evolution, try to convince the rest of us that nothing but "objective description" of nature is possible.

Even so, I hope that the revolt will proceed at the right pace and not get out of hand. The analytic cutting edge is not all of evolutionary biology. I fear (and think I even see in some departments of biology in this country) the beginnings of an unholy alliance between the population model builders and molecular biologists to exclude systematists and descriptive ecologists. In their understandable desire to press on down the mainstream of biology together, let them not forget that evolutionary biology cannot exist without the substantive knowledge being carefully built by descriptive biologists. More than anywhere else in science, their expertise takes long periods of time and concentration to acquire, and once lost it is not easily retrieved. If they go, post-Darwinism will eventually become as sterile as neo-Darwinism did in its most antitheoretic moments.

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The Evolution of Reproductive Rates

Ecological Adaptations for Breeding in Birds. DAVID LACK. Methuen, London, 1968 (U.S. distributor, Barnes and Noble, New York). xii + 409 pp., illus. $15.

As there have been few breakthroughs in population ecology only a few ecologists stand above the others in eminence. David Lack is one of these few; his approach and ideas collected in *The Natural Regulation of Animal Numbers* (Oxford University Press, 1954; reprinted 1967) have been, and for many continue to be, an immensely profitable source of inspiration and frame of reference. Since the publication of this first major work, two more large volumes, *Population Studies of Birds* in 1966 and that under review, have appeared. These deal, respectively, with the two most general and important aspects discussed in the earlier book, population regulation and the evolution of reproductive rates. Both books, as a primary concern, attempt to uphold earlier hypotheses with the help of and in some instances in spite of more recent evidence.

All students of the subject will doubtless find *Ecological Adaptations for Breeding in Birds* useful. Its two stated aims, to provide a handbook of data on breeding birds and to interpret and interrelate these data, are sufficiently

realized for this to be so. It provides a presentation of Lack's views (together with whatever supportive evidence exists) plus a fairly complete collection of facts and references, and these are worthwhile assets. Some of its limitations, with respect first to methodology and then to the clutch size theory, are discussed below.

Lack's general procedure is to take quantitative data on a large number of variables, to express (qualitatively) a supposed correlation between two of the variables, and then to interpret the correlations and examine their general applicability to other bird groups. The process has some deficiencies. Statistical estimates of confidence are omitted "because these might impute too great value to [the data]" (p. 12). Yet the whole book is essentially a discussion of these data, and whether the discussion is qualitative or quantitative in tenor some objective evaluation of trends and relations should have been provided. Variables are numerous (a few are egg size, egg size relative to size of bird, clutch size, number of clutches per year, duration of parental care, survival, and age at first reproduction), but most are taken in pairs in the quest for correlations, even though each is closely related to others and all are to some extent interdependent. The establishment of a correlation is often treated as an end in itself, with little regard for additional complex questions that present themselves once the correlation has been established. For instance, seed-eaters tend to feed in flocks, and certainly coloniality may be causally linked with this, but why flocking harvests seeds more effectively, if it does, is not known. Perhaps for these reasons (and also because some important variables are not quantified—coloniality is not even adequately defined) the correlations have a bewildering will-o'-the-wisp quality and wax and wane ephemerally as different groups of birds, even supposed ecological counterparts, are tested. Also disturbing is a tendency for possible connections to become, later in the text, accepted relations. Thus the information in table 1 that 1⅔ out of 6⅔ subfamilies of seed-eaters are polygynous becomes by page 32 "the link between a seed diet and polygyny."

Part 1 relates nesting dispersion and pair bond to food and habitat. J. H. Crook has successfully demonstrated a relationship in the case of weaverbird species (Lack's chapter 4), but extension of the technique to other birds does not elicit similar generalizations. In part this may be due to Lack's use of subfamilies as units of resolution. He convincingly defends this technique by stressing that at the subfamily level correlations will be due to convergent evolution rather than to taxonomic proliferation within a group, but it remains difficult to see why a consistent relation between, for example, coloniality and seed-eating in ten species of a genus is not more impressive than the same relation in an unrelated monotypic genus. The author might alternatively have restricted his treatment to the better-known species, but we would have then been denied many interesting tidbits of information. Throughout the book the most insights appear when the subfamily is abandoned for a higher resolution at the species level (chapters 4, 5, 21, 22).

Wynne-Edwards' ideas, in the absence of a demonstrated mechanism for group selection, are taken lightly by most ecologists. Not so by Lack, who is at such pains to state the case against Wynne-Edwards that many of his book's contentions or even hypotheses are merely truisms if one believes in natural selection, as surely the overwhelming majority of the intended audience does. The occurrence of sentences that are quite information-free is not uncommon: "the main advantage of monogamy is that both male and female leave, on average, most offspring if both help to raise the brood" (p. 4); that is, monogamy is advantageous because birds practice it and the only birds around are those with practices favored by natural selection. And ". . . it is advantageous for young to grow as fast as possible, but they must not grow too fast for the available food" (p. 5). In part 2 *ex hypothesi* statements on food availability also contribute little: "clutch size tends to be larger . . . presumably due to differences in the availability of food for the young" (p. 182), a presumption which is stated repeatedly (pp. 167, 170, 190, 229, 243, 263, and elsewhere).

For a book concerned intimately with reproductive rate factors it is unfortunate that such variables as age at first reproduction, clutch size, and generation time are not related in a demographic or even a qualitative way. Had this been done, it might seem less "remarkable that any species of bird can survive in which, at most, each bird raises one chick in two years" (p. 276). Lack pioneered investigations of survival from broods of different sizes, concluding that average clutch sizes are adjusted to the average food supply. We note, however, that had clutch size evolved for reasons other than adaptation to the amount of available food, we would expect a coevolution of behavior (foraging rate, ability to locate food) such that this same relation between clutch size and food would hold. R. Carrick's example (p. 8) of a bird which, when its brood size was artificially doubled, expired before the food supply did is particularly illuminating; it died apparently of exhaustion after "greatly increasing its feeding rate." In a way the theory concerns a proximate answer reflecting economy in behavioral plasticity; there is probably no strict chicken-and-egg relationship between foraging rate and clutch size, so what ultimately determines the latter is a slightly different question.

The familiar clutch size theory in its original form was attractive and simple (but statements such as "birds raise as many young as they can" [*1*] do justice neither to the theory nor to its adherents). It could not, however, easily account for certain clutch size variations such as the lack of proportional increase in clutch size as latitude, and hence day length, increases (why are data on the daily amounts of time birds spend feeding young at different latitudes never published?). Nor could it account for longitudinal or habitat trends, or clutch size variations in birds which do not feed their young or are nocturnal or crepuscular in feeding activity. With the help of recent ideas and information from Ashmole, Frith, and Marcström these insufficiencies have been largely overcome, and at the expense of simplicity more precision has been obtained. But, unfortunately, the wide applicability of the theory depends on the existence of largely undemonstrated food variations which must *ex hypothesi* follow observed clutch size trends. This can, at times, stretch our credulity: There is more food in England than in Scandinavia (p. 5) for titmice, but less for other birds (pp. 166, 167). Some food is suitable for small young but not for adults if they are to form eggs (p. 190). Fruit must be a poor food for young (pp. 191, 174 ff.). Food is scarcer on islands (pp. 170, 228–89), even though total bird density can be greater (*2*). Prey is harder to obtain for larger than for smaller raptors (p. 181). Clearly food has in this discussion assumed an overriding importance, to the detriment of more careful consideration of other factors. To give a simple example, food is

presumed to be sparser offshore than inshore for marine birds (p. 247, although terns are apparently an exception—p. 263), and above the forest canopy than within it for swifts (p. 195), but little attention is paid to the fact that for each of the areas in which food is supposedly less abundant birds also have to travel much farther for it.

The coevolution of such factors as food availability, number and growth rate of the young, predation, and others that affect the survival rates of parents and young in my view receives inadequate treatment, yet is the essence of the problem. Perhaps only a really cohesive and simultaneous handling of variables, preceded by some a priori structuring and grouping on which individual subrelations can be hung, will avoid the rather confusing mass of cross-relations through which *Ecological Adaptations* takes us. The book pushes its approach as far as it can go, but in fact little further insight into its difficult subject has been gained since Cole's 1954 paper (*3*). Perhaps the problems will prove more amenable in the hands of the "strategists," by whom several tentative starts have been made (*4*).

A concluding word should mention the delightful drawings by Robert Gillmor, which do much to make progress through the book more enjoyable.

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Physiological Optics

Light, Colour and Vision. YVES LE GRAND. Second English edition, translated from the French by R. W. G. Hunt, J. W. T. Walsh, and F. R. W. Hunt. Chapman and Hall, London, 1968 (U.S. distributor, Barnes and Noble, New York). xiv + 566 pp., illus. $11.25.

Optique Physiologique was originally published as three volumes in 1946, 1948, and 1956. Volume 1, *La Dioptrique de l'Oeil et Sa Correction*, has twice been revised, but has not yet been translated into English (it should be). Volume 3 has recently been translated as *Form and Space Vision* by Millodot and Heath (Indiana University Press, 1968). The first English edition of the second volume, considerably updated, appeared as *Light, Colour and Vision* in 1957. Superbly translated by a distinguished trio of British specialists, it achieved rapid acclaim and has become one of the most widely cited modern sources of fundamental information about vision. The appearance of this second English edition will be greeted with particular interest by those who have made extensive use of the first.

Robert Cunningham and Sons have once again done the printing: binding, paper, type, plates, and format are so similar that the new edition might easily be mistaken for the old. And a careful examination reveals many more similarities. The same 20 chapters are again distributed within two major groupings. Section A, containing the first 15, includes "Experimental Facts," while "Theories of Vision" are presented in section B. All of an original 210 subheadings are retained in section A, where only five new ones ("absorption in the lens," "standard daylights," "the colorimetry of large fields," "colour contrast," "the problem of flash blindness") are listed.

But there are also many changes. An examination of the bibliography reveals that an extensive amount of new literature has been cited. The first edition contained a numbered list of 190 specially selected books and fully referenced journal articles of "wide scope." To this list 81 new items have been added. The original 13½ pages of additional journal references, cited without titles, have been expanded to 21 pages.

Although the updating of section A is a patchwork affair, it reveals that physicist Le Grand has been keeping a sophisticated eye on recent developments. Most readers are likely to find many references that they have overlooked during the productive decade that elapsed between editions.

With the help of two of the original translators, section B has been extensively revised. More than 20 new subsections have been written, and six of the old ones have been deleted. These changes reflect contributions to visual theory resulting from new advances in electrophysiology, psychophysics, retinal densitometry, microspectrophotometry, and photochemistry. To the physiologist, these sections will again seem superficial; Le Grand admits that this material is "less familiar to me" than what is covered in section A.

Few changes have been made in the extensive tables and formulas which comprise valuable features of the book. All original figures except one have been retained: only five new ones have been added. Regrettably, ten pages of exercises and their solutions (this was originally a textbook) have been eliminated, probably to keep the volume—now ten percent thicker—within bounds. The index is again excellent.

Le Grand's opinions are sprinkled throughout the book, particularly in section B. The reader will probably wish to quarrel with some of them. But they make for lively reading and are not too rigidly held. As Le Grand puts it: "even if this Section B contains a little science-fiction, it is of great importance for men of science to try to understand the human machine." Those who study this book will be rewarded by an enhanced understanding of the physics of human vision.

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Gamete Fusion

Ultrastructure of Fertilization. C. R. AUSTIN. Holt, Rinehart and Winston, New York, 1968. x + 198 pp., illus. $5.95.

Electron microscopy has been brought to bear on fertilization only in the past decade. Not all stages known histologically have yet been seen at the higher magnifications. The author of *Ultrastructure of Fertilization* briefly mentions what has not been studied and why, then summarizes what has been. The acrosome reaction, the cortical granule response, and relations between gamete cell membranes have been studied in most detail, in sequential stages, and in various species. Sperm penetration through egg investments is sufficiently understood to permit a very systematic presentation with subsections on sperm structure, egg investments, and sperm penetration for each of nine invertebrate groups and mammals (chiefly rabbit). Conjugating protozoa as well as gametes have been considered with respect to nuclear migration, nuclear union, and especially those cell membrane interactions that lead to cell fusion. In such matters of how cell membranes merge and where and what they come from and disappear to, research is moving beyond high-magnification comparative anatomy through