Components of Fitness

Evolution and Genetics of Life Histories. Papers from a symposium, Iowa City, Oct. 1980. HUGH DINGLE and JOSEPH P. HEGMANN, Eds. Springer-Verlag, New York, 1982. xii, 250 pp., illus. $33.80. Proceedings in Life Sciences.

One of the most rapidly growing new fields in evolutionary biology is the study of life-history traits, which include the age-specific schedules of births and deaths, reproductive efforts, the cost of reproduction, and the mode of sexuality. Life-history traits are components of fitness, for any definition of fitness will involve some expression of survival and reproduction over the short or long term. Such traits usually vary continuously and are inherited in patterns best described by quantitative genetics rather than by the single-locus models of theoretical population genetics. However, the initial attempts to construct a predictive theory of life-history evolution used optimality models that ignored genetic constraints and could predict only local equilibria, not dynamical behavior. Thus it makes good sense to ask, what are the heritabilities of life-history traits, what are their genetic correlations, can we use such information to infer past selection pressures and to predict the future course of evolution, and what are the genetic constraints on optimization?

This volume of symposium proceedings contains a clear set of answers to those questions. The production of the book is professional, with useful introductions by the editors that tie together groups of papers, a transcription of the lively comments made at a concluding panel session, and an adequate index. I found several papers particularly intriguing. Tauber and Tauber show that one speciation event in lacewings involved a shift from a multivoltine to a univoltine life history via selection on the photoperiodic and thermal induction of diapause. The process was evidently rapid and involved only a few genes. Templeton gives an insightful sketch of the origin of apomictic parthenogenesis via automixis and claims that the alleged paradox of sexuality (as expounded by Williams and Maynard Smith) is no paradox at all. King finds no trade-off between reproductive effort and longevity in a marine rotifer and suggests that we should expect longevity to be twice the generation time in iteroparous organisms. (The assumptions one must make about population structure to have his argument work seem to be restrictive.) Doyle and Myers use path analysis to decompose the structure of fitness. They emphasize the importance of phenotypic correlations as well as genetic correlations in determining the response to selection.

The basic presupposition of the symposium, reiterated in several papers, is that if one wants to understand the evolution of a quantitative trait then one has to measure its additive genetic variance and its genetic correlations with other traits. Lande, Dingle, and Hegmann, in particular, emphasize the urgent need to measure the genetic covariances of life-history traits. There is considerable merit to this point, which is, after all, a straightforward application of the Modern Synthesis, but I fear it does not go far enough.

First, there is the problem of what quantitative geneticists call genotype-environment interactions, or what evolutionary ecologists call phenotypic plasticity. Giesel, Murphy, and Manlove show that genetic correlations change from environment to environment within a single population of *Drosophila melanogaster*. Their point is general and crucial. If the genetic covariance matrix is not invariant, then we need to look for regular patterns in the way the covariances change across a graded series of environments and for concordance of those patterns with the plasticity of the traits involved. Only then could we expect to predict the response to selection in heterogeneous natural environments.

Second, quantitative genetics claims to provide a dynamical theory, as opposed to the static optima of evolutionary ecology, but in fact it remains in evolutionary terms strictly a theory of local change with an effective scope of five to ten generations. If a trickle of additive genetic variability can be introduced to a population through mutation or immigration, then a trait can continue to respond to selection even though its measured heritability in each generation might not differ significantly from zero. Similar introduction of variability could lead to gradual rearrangement of a genetic covariance matrix whose structure might have initially appeared to block the coordinated change of a set of traits in an adaptive manner. Unless one understands the mechanisms that produce the observed covariances, one can make no predictions about long-term dynamics. Those mechanisms involve not just pleiotropy, a concept that is more phenomenological than mechanistic, but such matters as gene expression in development and networks of hormonal control—the genetic, developmental, and physiological mechanisms that integrate organismal function.

If one wants to get a globally dynamic theory, capable of dealing with evolutionary change over periods of the order of the life span of a species, then one needs a more detailed picture of the structure of an organism than quantitative genetics can provide. From the point of view of quantitative genetics, an organism is a black box with a large number of genes with equal additive effects sitting on one side, a mature adult phenotype sitting on the other, and nothing but a covariance matrix in between. However, we already know that there are a relatively few regulatory genes with major, nonlinear effects and a large number of modifier and structural genes with small, more nearly additive effects. We also know that the materials out of which organisms are built contain information not carried in the genes and that the properties of such materials must be considered if we are to understand phenotypic plasticity and evolutionary change. Thus, just as it makes good sense to ask what quantitative genetics can tell us about life-history evolution, it also makes good sense to ask what developmental biology and biomechanics can tell us about both.

I raise these points not to discourage the use of quantitative genetics or to criticize this volume but because I see a bandwagon beginning to get under way and I am concerned about its direction. Precisely because there are good reasons to apply quantitative genetics to evolutionary ecology, and precisely because those reasons are effectively stated and intriguingly illustrated in these papers, I foresee a rush to measure heritabilities and genetic covariance matrices in many species. However, I think we already know what most such studies would tell us and could spend our time better on other experiments. Dingle, Hegmann, Giesel, Antonovics, and their colleagues have already established that genetic covariances differ from, and are often the opposite of, phenotypic covariances, that they differ among populations and among environments within populations, and that the structure of the genetic covariance matrix places real constraints on selection. They have convinced me. We certainly do not need simply to measure more genetic covariances. We do need to see what relation their plasticity has to phenotypic plasticity, what mechanisms lead to pleiotropy and place limits on the general structure of covariance matrices, and how covariance matrices change under the application of environmental stress. Genetics is certainly necessary and useful, but it is not sufficient, for evolutionary theory.

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Plant Metabolism

Cellular and Subcellular Localization in Plant Metabolism. Proceedings of a meeting, Ithaca, N.Y., Aug. 1981. LEROY L. CREASY and GEZA HRAZDINA, Eds. Plenum, New York, 1982. x, 278 pp., illus. $37.50. Recent Advances in Phytochemistry, vol. 16.

The eight papers in this book of symposium proceedings demonstrate that there have been substantial technical advances in the isolation of cell types and organelles from plant tissue, which has allowed parallel advances in knowledge of organelle function and interactions between cells at the biochemical level. Being the result of a symposium, the book covers selected topics in some depth rather than providing a general comprehensive view. For most subjects, the current state of knowledge is discussed and aspects needing further research are noted.

Chapters on vacuoles, peroxisomes, and chloroplasts describe functions of the organelles relative to metabolic processes in other parts of the cell. Other chapters, such as those on guard cells and C_4 leaf photosynthesis, deal with specific functions of cell types.

At the organelle level, scientists interested in vacuoles should find a paper by Wagner useful with respect to techniques of vacuole isolation, pitfalls in methodology for determining distribution of material between vacuole-extravacuolar space, and specific substances or enzymes found to be located in vacuoles from a variety of tissues. Examples are given with various plant tissues where material is found located in vacuoles or appearing exclusively in the cytoplasm. Some views are given on metabolite transport, but, considering that plant vacuoles were isolated in good yields seven years ago, there has been relatively little progress on this subject. Though it is not stressed by the author, it is the opinion of this reviewer that the low percentage of cytoplasmic space relative to vacuole space (1 percent or less in some tissue, for example in plants that utilize Crassulacean acid metabolism) makes it extremely difficult to determine whether a compound is exclusively located in the vacuole and what the relative concentrations are between the vacuole and extravacuolar space. Also, in transport studies it is not clear if all methods used in preparing vacuoles from protoplasts will result in preparations free of the plasma membrane (hence the need for specific plasma membrane and tonoplast markers).

In a paper on plant mitochondria, Siedow notes unique features of plant mitochondria, in particular the alternative (cyanide-insensitive) pathway. The review brings out an important subject for future research, since the identification of components of this pathway and its function in most instances remain uncertain.

The book contains a thorough review by Huang of higher plant, algal, and fungal peroxisomes. There appears to have been little new information on higher plant peroxisomes over the past few years, with the result that the paper treats peroxisomes from the lower plants at somewhat greater length. The author's emphasis on the need to understand transport of reductive power between peroxisomes and the cytoplasm, the permeability of peroxisomes to various metabolites, and the properties and functions of peroxisomes in C_4 and Crassulacean acid metabolism plants is well deserved.

A paper by Huber on chloroplasts reflects, in part, the progress in using different plant species to study photosynthetic carbon metabolism. Emphasis is placed on how factors outside the chloroplast, such as pH, P_i (inorganic phosphate), Mg^{2+}, and K^+, may regulate carbon metabolism in the chloroplast.

From studies of functions of various cell types made over the last decade, Outlaw analyzes carbon metabolism of guard cells, giving particular attention to evidence for malate fluctuations in guard cells and the associated metabolism. Campbell and Black review a progression of studies on carbon, nitrogen, and, most recently, sulfur metabolism in the two photosynthetic cell types of C_4 plants. In a review by Cutler and Conn of the biosynthesis of cyanogenic glycosides, a discussion of the use of "channeled enzyme complexes" to compartmentalize and confine intermediates of a pathway to a particular part of the cell is particularly interesting.

Though the book covers research developments in the last decade on selected aspects of subcellular metabolism, the reader will find some aspects (for example, peroxisomes and photosynthesis) more extensively developed and understood than others (for example, compartmentation of biosynthesis of natural products, the role of microtubules in cellulose biosynthesis, and the mechanism-function of the alternative pathway in plant mitochondria).

What is notably missing in the book is studies of specialized function of cells within the vascular tissue and their significance relative to intercellular transport. Perhaps this reflects a lag in development of techniques for isolating and studying these cells relative to development of those for studying other tissues.

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Antarctica

Antarctic Geoscience. Papers from a symposium, Madison, Wis., Aug. 1977. CAMPBELL CRADDOCK, JANET K. LOVELESS, TERRI L. VIERIMA, and KATHY A. CRAWFORD, Eds. University of Wisconsin Press, Madison, 1982. xxviii, 1174 pp., illus. $35. International Union of Geological Sciences Series B, no. 4.

Antarctic geology is fascinating not only in its own right but also for its key role in the study of Gondwanaland. Most readers of this volume, like the reviewer, will never have set foot in Antarctica and are unlikely to do so. But all students of the geology of other parts of Gondwanaland will find it a truly valuable source of information. It is a well-edited and arranged compilation of about 150 papers contributed by workers from 15 countries, and, although it has taken five years to bring the book out, the great majority of the contents does not appear in any way out of date. The geographical terms of reference are interpreted generously, and there is substantial coverage of the Scotia Arc and southern South America and oceanic islands as far north as Bouvet and Amsterdam as well as of Antarctica proper. All the major fields of geology and geophysics, including marine geology and geophysics and glaciology, are represented, as is the subject of meteorite hunting.