GENETICS & EVOLUTION

THE EVOLUTION OF INDIVIDUALITY.
By Leo W. Buss. Princeton University Press, Princeton (New Jersey). $40.00 (hardcover); $12.95 (paper). xv + 203 p.; ill.; author and taxonomic indexes. ISBN: 0-691-08468-8 (hc); 0-691-08469-6 (pb). 1987.

Metazoans seldom reproduce vegetatively; they often die of cancer; and they almost always sequester their germ lines. Plants often reproduce vegetatively, seldom die of cancer, and almost never sequester a germ line. Buss argues that these and many other patterns can all be understood in a unified way as the evolutionary outcomes of conflicts that occur during development among genetically variant cell lines. On this view there is literally an ecology of cell types, a natural history of development. The individual as we know it has not always existed; it evolved in stages, as certain variant cell lines attempted to force others into terminal differentiation and thus away from reproduction. Patterns of development may seem smooth and efficient today, but they should be viewed in part as ritualized reenactments of ancient struggles.

The argument is a very interesting one, and it persuaded me that I should stop taking "the individual" for granted and should instead think of it as an important problem. But I am not yet convinced that an embryo can plausibly be viewed as a jungle composed of warring cell lines, red in tooth and claw. Selfish genes, such as segregation distorters, do indeed evolve in higher plants and animals, and they can be thought of as perpetrators of conflict within an individual; many are presumably neutralized or held at low frequencies by resistance genes that evolved in response to them. But this process does *not* require genetic variation *within* individuals. Buss's scenario, in contrast, *does* require genetic variation that arises during development. How much variation of this kind might there be, given plausible mutation rates? Could it really drive the process that Buss envisions? These kinds of questions cannot be answered without the aid of explicit mathematical models.

One line of evidence Buss uses to argue for the existence of selfish variant cell lines comes from slime molds, but I think this case may be somewhat misleading. Slime molds live their vegetative phases as swarms of independent amebas that must reaggregate to form the slug that then develops into a fruiting body. Cheaters that insist on being spore cells and refuse to serve in the stalk can easily arise because they can parasitize strains other than their own. (One would predict that as amebas, they tend to migrate farther than other strains do.) The embryo of a higher plant or animal would not seem to face this problem, being derived from a single cell, without any intervening dissociation.

Buss's approach is selectionist, with a vengeance, but it differs significantly from the familiar Williams-Hamilton-Dawkins style of thought with its strong emphasis on the individual as a gene-machine. Buss's approach is pluralistic and hierarchical:

> The history of life is a history of transitions between different units of selection. The transition focused on here—that between the cell and the individual—is but one such transition. Others must have preceded it. Numbered among those preceding must be the origin of self-replicating molecules, the association of autonomously replicating molecules into self-replicating complexes, the incorporation of such complexes into cells, the establishment of a multigenomic cell via incorporation of autonomously replicating organelles, and, with the evolution of sexuality, the origin of species. Just as transitions preceded the transition which established the multicellular individual, transitions establishing new units of selection have followed. Among these must be the association of individuals into kin groups and the association of neuronal activities into ideas capable of replication and variation (p. 171).

In other words, the hierarchy of levels of *organization* is also a hierarchy of levels of *selection*. The lower levels may be less active than they once were (individuality being firmly established in most multicellular taxa), but selection still acts on every level at which there is replication and the inheritance of variation. In this respect Buss's views seem something like an inverted form of current thinking about group selection and species selection.

In organization and in spirit, *The Evolution of Individuality* is a series of discursive essays, not a rigorous analysis. The argument flows almost like a dream; it is qualitative and nonlinear; various themes reappear again and again in different guises; there are many footnotes, some of which are essays unto themselves. Along the way we meet an astonishing diversity of biological facts, a nearly equal diversity of hypotheses, and many comments on the history of thought about development and evolution. (A major contention is that Weismann's theory of the germ plasm has wrongly overshadowed his theory of hierarchical levels of selection.) There are many beautiful line drawings illustrating obscure organisms, embryologies, and life cycles. Because the argument contains so many strands woven together in a complex way, some readers may find it helpful to begin with the *last* chapter (The Evolution of Hierarchical Organization), which gives a

fairly concise and unadorned summary of Buss's views on the issues that recur in different contexts throughout the book.

The Evolution of Individuality seems likely to inspire many interesting models, experiments, and analyses of comparative data. Even if many of its particular claims turn out to be wrong, it could permanently change the way we think about life histories.

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THE LATEST ON THE BEST. *Essays on Evolution and Optimality. Based on a conference held at Stanford University, California, April 1985. A Bradford Book.*

Edited by John Dupré. The MIT Press, Cambridge (Massachusetts). $27.50. xiii + 359 p.; ill.; name and subject indexes. ISBN: 0-262-04090-5. 1987.

The use of optimality theory in evolutionary biology is the subject of this collection of essays by philosophers, psychologists, and biologists, and reviewed here by an evolutionary biologist who uses optimality theory in his own work. It consists of 16 chapters organized into four parts: Methodological Questions, Evolution and Optimality, Applications, and Applications to Human Behavior.

The level of argument is generally very high, with a resulting clarification of the issues that can only lead to better understanding of evolutionary theory. The vulgar application of optimality arguments, simple-minded pan-adaptationism, is not under discussion here, but rather the foundational issues of explanation, causation, model-building, and hypothesis-testing in the face of complexities that arise across a range of hierarchical levels. Optimization emerges as one of several justifiable approaches to evolution but certainly it is inadequate as an exclusive method. I found the contributions of Beatty, Kitcher, Sober, Maynard Smith, Lewontin, Emlen, Staddon, and Hirshleifer especially stimulating. Shepard's chapter on the evolution of mind impressed me as being less well grounded.

For an evolutionary biologist, the book amounts to a critique of what one is doing while one is doing it. To a certain kind of mind, the challenge inherent in fine-tuning the engine of a car while it is driving down a freeway at high speed provides an existential thrill not available in normal scientific activity. (Here evolutionary biology is the car, the freeway is the scientific approach to understanding the world, the engine is the collection of theoretical approaches to evolutionary understanding currently in play, and the fine-tuning consists of the philosophical critique of optimality models represented in this book.) To such minds, this book will be a delight to read, for its various chapters lay bare the implicit assumptions that practicing scientists and philosophers make in constructing explanations.

For others, the deep exploration of a single approach requires a willed suspension of disbelief. They want to see how much optimality can bring, and they can't continually worry about its drawbacks. Instead, they concentrate on exploring its strengths, which yields insights into the method that are essential for comparing it with other approaches. To such minds, this book will be interesting, but a distraction. (To the book's credit, even this issue is explored, albeit rather superficially, under the heading of how much attention biologists should pay to philosophers.)

To me this book was a pleasure, the best-balanced discussion of the application of optimality theory to the problem of adaptation that I have read. Critics of optimality should read it before engaging in discussion those of their colleagues who use optimality theory in their work. Their conversations might then concern deeper and more substantive issues than are often discussed. Biologists who use optimality theory should also read this book because of the light that it sheds on what they are doing and to prepare themselves for conversation with the above-mentioned critics—but if you react as I do, you won't take the comments of the philosophers more seriously than the interplay between your own ideas and data.

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DIE NEUTRALITÄTSTHEORIE DER MOLEKULAREN EVOLUTION.

By Motoo Kimura. Verlag Paul Parey, Berlin. DM 49.80. 303 p.; ill.; author and subject indexes. ISBN: 3-489-62543-X. 1987.

EVOLUTIONARY BIOLOGY, VOLUME 22.

Edited by Max K. Hecht, Bruce Wallace, and Ghillean T. Prance. Plenum Press, New York. $45.00. xiii + 291 p.; ill.; index. ISBN: 0-306-42742-7. 1988.

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