How important is natural selection?

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Natural Selection in the Wild. By John A. Endler. *Princeton University Press:1986. Pp.336. Hbk $40, £26.65; pbk $13.95, £9.30.*

THE most influential evolutionary book of the past ten years is, without doubt, Motoo Kimura's *Neutral Theory of Molecular Evolution*, and of the decade before that R.C. Lewontin's *The Genetic Basis of Evolutionary Change*. Lewontin pointed out the difficulties of explaining molecular polymorphism using traditional models of natural selection acting at single loci, while Kimura argued cogently that the most important force in controlling the evolutionary fate of most newly arising mutations is not selection but random genetic drift. This relegation of natural selection to the role of evolution's policeman, who acts mainly to remove alleles deviating from an acceptable norm and ignores the vast majority of genes in populations, is now central to large parts of theoretical population genetics, to molecular evolution and to the reconstruction of phylogenies. John Endler's impressive book attempts to restore natural selection to its traditional place as the driving force of evolution. It may become an evolutionary classic of the next decade.

As Endler points out, the term "natural selection" has meant very different things to different people. After wandering briefly in the philosophical fog which is thicker in evolutionary biology than in any science apart from psychology, he produces a definition of selection close to the Darwinian one — variation, inheritance and genetic differences in the chances of reproduction — or even to that of Oscar Wilde, that "nothing succeeds like excess". Natural selection does not necessarily lead to evolution, and it includes many biological processes apart from differential mortality. Indeed, a survey of experiments on selection in nature suggests that inherited differences in survival are less important than are those associated with mating ability, fertility or fecundity.

There have been numerous attempts to measure selection in the wild. Many of these have failed because of poor experimental design, and Endler suggests a number of ways in which selection might acceptably be demonstrated in natural populations. He discusses ten kinds of information that can identify selection, from simple correlations of gene frequency with environment, to comparisons of the same genes in related species, and to demographic studies and experimental perturbation of populations in nature. The road to detecting selection has many pitfalls. Endler finds 25 reasons why we might fail to detect it when it does exist but, comfortingly, only 21 ways in which selection might be identified when in fact it is not operating. His extensive analysis of work on natural selection in the wild suggests that strong selection on morphological characters and polymorphic alleles — selection of the intensity used by animal and plant breeders — is commonplace in nature, and that the general assumption that differences in fitness of more than about 10 per cent are rare is simply incorrect. It is nevertheless rather depressing to learn that there is as yet no case in which natural selection acting over an organism's whole lifetime has been measured. It is also true that if size and shape are controlled by many genes of individually small effect, then strong selection on morphological characters may still allow genetic drift to determine the evolutionary fate of most mutations at such loci. This distinction between natural selection on the phenotype and the genotype may yet bridge the gap between those who emphasize the importance of random change in evolution and those who hold the views so eloquently put forward in this book.

Endler himself is sanguine that "as our knowledge . . . increases, perhaps natural selection will become easily detectable at the biochemical and even the molecular level". Although ecological genetics has a long way to go before this hope will be fulfilled, it is nevertheless true that a hypothesis that selection acts on a particular system is, like the search for the North West Passage, intrinsically productive even if it is wrong. All too often great pyramids of theory have been balanced on a mere assumption that selection is unimportant: the neutral theory has been much more of a stimulus to theoretical than to experimental studies of evolution. Theory frequently asks us to measure the unmeasurable, and experiments on the genetics of populations in nature are often designed in such a way as to produce results which cannot be interpreted. What is needed is a joint approach to the problem of the importance of selection in evolution: to use one of the quotations from Dr Johnson which preface each chapter, there is nothing

> more pleasant, or more instructive, than to compare experience with expectation, or to register from time to time the difference between idea and reality. It is by this kind of observation that we grow daily less liable to be disappointed.

Natural Selection in the Wild is a unique blend of ideas about evolution set against the reality of studying it in nature. All evolutionists should read the book: it will disappoint none of them, whatever their preconceptions about the importance of natural selection. □

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THE INVAGINATE GASTRULA AND THE PLANULA

A giddy little *Gastrula*, gyrating round and round,
Was thought to show the way we got our enteron profound:
A little whirlpool in its wake maintained a tasty store,
A pocket sank to lodge it all, and left a blastopore.

As a larval epigram this description earns a prize,
But as sketching adult ancestry can only win surprise,
And when you note all early orders fixed upon the rocks,
You feel a slight embarrassment, the first of many shocks.

The foremost inconsistency is the simple, solid fact
That the Hydrozoan larva, the mouthless *Planula*, is packed
With a jumbled mass of gastric cells that drop in, slow or fast,
And show no slightest cavity till the larval stage has passed.

The larva then becomes attached, and shortly stands erect,
Nourished by the yolky stores the inner cells eject:
Their shrinkage leaves a growing space, the early enteron,
Round which a layer of cells remains, and lines the outer one.

Some tentacles are sprouted then, say 2, then 4 and 8,
And not till all is ready does the mouth break through quite late.
If mouth and gut arose at first from one invagination,
What roundabout procedure's here! What needless complication!

Invagination surely is a thing of later date—
Procedure speeded up to suit the embryonic state:
The cells as loose irregulars build up the lower grades,
And yield but slowly, step by step, to organised brigades.

Reason in rhyme — this poem is an attack by Walter Garstang on Haeckel and his followers, who, in support of their "biogenetic law", invented an ancestor for all metazoans (the Gastrea theory) and claimed to be able to trace the evolution of the gut from a dimple in the surface of the primordial metazoan. It is reproduced from a new paperback reprint of Garstang's Larval Forms and Other Zoological Verses, *published by University of Chicago Press. Price is $5.95, £4.95.*

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