Heredity **80**(1998) 393–396

Book reviews

Adaptation. Michael R. Rose and George V. Lauder (eds). Academic Press, San Diego. 1996. Pp. 511. Price £24.95, paperback. ISBN 0 12 596421 8.

Adaptation harks back 18 years to Gould and Lewontin's 1979 paper 'The spandrels of San Marco and the Panglossian paradigm', a citation classic which tore at the heart of adaptive story-telling in evolution. According to Gould and Lewontin, many adaptive explanations had been devised *post hoc* and depended on the tautological assumption that adaptation was the only explanation possible. 'Spandrels' are attractive architectural features in San Marco Church, Venice, which were by-products of placing a round dome onto a square building, equivalent in evolutionary terms to a structural necessity, rather than having been designed especially for decoration. Pangloss was Voltaire's caricature of a philosopher for whom 'all is for the best in this best possible of all worlds'; the implication being that the adaptationist programme was equally illogical.

By its publication, this lengthy book (511 pages of 9 pt type) shows just how successful the 18-year-old 'spandrels' critique has been. The introduction is even called 'post-spandrel adaptationism' (Rose & Lauder). The adaptationist and gene selectionist 'right wing' (so-to-speak) of evolutionary biology has conceded ground to the 'left's' non-adaptive alternatives. Sadly, after a debate such as this, all that remains of a battle between provocative extremes is the bourgeois middle ground. And that is what this book is: very solid, and very balanced, with each point of view treated carefully. There are a few omissions. 'Gene selectionism' in sociobiology is not treated, perhaps because the editors think the subject is dead. Maybe this is as well. There is plenty of philosophy in the book already: each author, in a careful, balanced way, defines exactly what he (no 'she's here, except one co-author) means by 'adaptation'. I would like to have read a discussion of whether speciation is adaptive, another omission. Perhaps, we know too little about the subject for its inclusion, even though the topic dates from the days of Darwin.

Although the even, careful tone can sometimes make for boring reading, this is a very useful book with some excellent high points. Amundson, writing history of science from the unlikely location of Hilo, Hawaii, produces a beautifully fresh history of adaptative explanation. I liked Kirkpatrick's population genetic caveats about adaptation, and I intend to use them in teaching undergraduates. But Kirkpatrick's final statement 'Perhaps it is serendipity that allows adaptation to flourish in our world' is extraordinary, and atypically unbalanced for this book. It's not at all surprising that optimization will be achieved in particular fitness dimensions, while at the same time, organisms will rarely approach a global fitness optimum (Seger & Stubblefield).

Reznick & Travis summarize their own elegant work on quantitative genetics of adaptation, though I was dissatisfied with their attempts to generalize to other areas. Their discussion of mimicry, my speciality, is particularly flawed. Reznick & Travis state that warning colour was discovered before mimicry, as seems, in retrospect, logical. However, the idea of warning colour was actually suggested by Wallace eight years AFTER publication of the theory of mimicry by Bates in 1862. Reznick and Travis also ignore the fact that recent experts like J.R.G. Turner and H.F. Nijhout have returned close to the Punnett and Goldschmidt view that major gene mutation does a lot (though not all) of the work involved in mimetic adaptation; this was not mentioned, and indeed does not sit easily with the multi-locus generalization of adaptive evolution espoused by Reznick & Travis. Nor do the authors discuss recent mapping studies of quantitative trait loci, which show that many quantitative adaptations may actually involve relatively few genes of major effect.

The chapters by Novacek and Vermeij provide well-written, insightful (to this neontologist) summaries of controversies in macro-evolution, particularly on whether clade- and species-level adaptation is possible. Hudson reviews the impressive evidence for adaptation at the molecular level, mostly undreamed of 18 years ago, but many features of which are still unclear. Summaries of phenotypic manipulations (Sinervo & Basolo), comparative methods based on phylogenies (Larson & Losos) and genomic parasites (Hurst) were also very useful. Other useful, careful, balanced, etc, chapters had traits that mildly annoyed me: Lauder (too much on Dennett), Rose (too many 'Alice in Wonderland' metaphors), Wade (interdemic selection too narrowly defined, and too many own papers cited — 32!).

In the end, perhaps, the only test of all this soul-searching will be in the application of theories of adaptation to alternative, non-biological systems like computer programs, economics, and robots (Frank). While it is tempting to sneer at catch-all complexity theory, if ideas about adaptation cannot be generalized to such systems, they fail an important test of their right to be called science. Besides, general adaptation theory may be much more useful than its biological subsidiary. Recently, the organizing committee of the major UK population genetics group e-mailed computer 'virus'-infested documents to its entire membership. These crude computer viruses are quite bad enough; we should be thankful they do not (yet) evolve, but are merely designed by pranksters. When self-adjusting, reproducing computer programs become common, we are going to have real problems! I look forward with interest to the day when biologists who have

worked in muddy ponds or obscure branches of population genetic theory are invited by governments and corporations to help design defences against generalized evolutionary threats.

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Shapes of Time — The Evolution of Growth and Development. Kenneth J. McNamara. The Johns Hopkins University Press, Baltimore. 1997. Pp. 342. Price £29.00, hardback. ISBN 0 8018 5571 3.

I began this book with keen anticipation, having long been interested in the links between development and evolution, and knowing that McNamara has discussed this extensively from a palaeontological perspective. But I soon began to worry, and finished alarmed that a book so full of dubious assertions, errors and speculations had been published by a reputable press.

Let's cut straight to the main problem. Chapter 12 concludes: 'Evolution is not only about genetics and natural selection. Just as crucial are the changes in timing and rate of development, with the three, genetics, heterochrony, and natural selection, forming an interdependent evolutionary triumvirate'. Earlier we read: 'Evolution of new structure is not a function of profound genetic mutations — we are dealing here with changes in the time that particular structures start to grow/under the influence of changes in the timing of expression of certain proteins'.

It is widely accepted that the developmental basis of many evolutionary changes has been heterochrony (Haeckel coined this term to denote alterations in developmental timing that could distort the recapitulatory sequence he regarded as a key feature of embryonic sequences. Since then, the term has come to mean any timing changes in development, starting, stopping or rate, that lead to changes in the end result). How does heterochrony occur? Most researchers would see heterochrony as the result of changes in the timing of genetically regulated processes. Indeed, if these changes are to be evolutionary, they must be heritable, and therefore based on genetic differences. Yet McNamara continually plays down the role of genes. The best documented example of heterochrony in action is the 'heterochronic genes' that have produced the variable vulval morphologies in nematodes: we see here how an extra set of cell divisions can form a larger structure, or delay in an inductive event a different structure.

McNamara, despite an otherwise amazingly eclectic range of examples, fails to discuss this one, and generally gives the impression that heterochrony is a process separate from what genes do.

Since the days of Goldschmidt's 'hopeful monster', few have thought that large, sudden mutations are important in evolution. When McNamara writes of 'profound genetic mutations', he is decrying a view of evolution held by no-one, if by this phrase he means Goldschmidt-style mutations. However, he fails to point out that 'changes in the timing of expression of certain proteins' involve genetic changes, their 'profundity' being somewhat dependant on their results.

Further, he seems to regard heterochrony as the only way in which new morphologies (and behaviours) can appear. In chapter after chapter, he recklessly interprets every imaginable evolutionary development heterochronically. Haeckel, however, had another term, 'heterotopy' – the change in position of a structure over evolutionary time, and modern writers have described a wide range of ways in which developmental changes other than timing can lead to new forms.

The book is not all bad. It is written in a lively, personal style (aimed, possibly, at the general readers who learn their biology from Gould or Dawkins) and is best when McNamara is enthusing over fossils. The chapter heading quotations are nice: I enjoyed being reminded of Aldous Huxley's neoteny novel *After Many a Summer* although my copy keeps the title at that, rather than completing the Tennyson quotation. The illustrations are workmanlike, but too few; many of McNamara's descriptions cry out for a helpful illustration. There are numerous fascinating examples: did you know of the *Drosophila* species with 4 cm long sperm? But then there are the errors: W.S. Haldane? Shea's anti-human-neoteny paper 'The case for human neoteny re-considered' has the 're-considered' omitted; plethodontid' is used to mean 'urodele'; von Baer could hardly have used embryological concepts in the quest for ancestral relationships, since he was an anti-evolutionist; a poor section on vertebrate development (Chapter 8) has the skeleton developing from endoderm and ectoderm; the Irish elk is said to have horns.

It is unfortunate that this book has appeared at the same time (and at a similar price) as Gerhart and Kirschner's beautifully produced *Cells, embryos and evolution*. Buy it, not this.

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Selection Indices and Prediction of Genetic Merit in Animal Breeding. N.D. Cameron. CAB International, Wallingford. 1997. Pp.208. Price £22.50, paperback. ISBN 0 85199 169.

Selection theory, on which all organized animal breeding programs are now securely based, has its roots in the work of J.L. Lush, his colleagues and graduate students at Iowa State University in the late 1940s and early 50s. In essence, the theory is a wholly statistical one. The fundamental effects it deals with are all the results of individual