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Book reviews

Human Gene Evolution. David N. Cooper. BIOS Scientific Publishers, Oxford. 1999. Pp. 490. Price £75.00, hardback. ISBN 1 859961 51 7.

This is a wonderful book, but it made me wonder about books. What are they *for* nowadays? It would be very straightforward to argue that all the information collected in this book might just as well be put on a website, with the great advantage that updates could be made without posting any paper to anyone. I suspect that the pragmatic answer is that books are still a lot easier to sell, and for this kind of book many people will still prefer a physical book with an index rather than a searchable website. What kind of book is it? Essentially it is a work of reference, but with the facts accompanied by lucid and critical explanation. It is especially timely in providing a comprehensive and scholarly review of the state of knowledge on human gene evolution at the end of the 'pregenomic era'. It distils a huge amount of dispersed primary literature into an accessible reference source, and for me (and probably many others) it will be most valuable as a source of examples of all the rich and strange inhabitants of the genome: overlapping genes, semiprocessed pseudogenes, genes with 4 bp exons, genes with 3′ UTRs of −2 bp, and genes involved in fusion splicing and exon scrambling.

As one would want from such a source, the text is well integrated by cross-referencing and the index is excellent — and the depth of resource it represents can be illustrated by the fact that of the 490 pages you get for £75, more than 150 are occupied by references or index. This book is not, however, simply a catalogue, and at all points care is taken to integrate the examples with explanation of the principles at stake. If I have to find minor imperfections, there are one or two references appended to the wrong chapters, and a figure curiously distant from the text describing it, but there is little to compromise the impact of the whole.

Overall, I simply have to admire the thorough and scholarly approach to the subject. It must have involved a huge amount of work, and the author can rest assured that the product will not simply be rendered redundant by the production of the genome sequence. On the contrary, this book will serve as a starting point for making sense of the avalanche of 'information' that venture will produce.

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Migration and Colonization in Human Microevolution. Alan G. Fix. Cambridge University Press, Cambridge. 1999. Pp. 236. Price £40.00, hardback. ISBN 0 521 59206 2.

During the twentieth century various biological disciplines tried to reconstruct and understand the origin and past history of modern humans. For anthropologists and human geneticists the study of microevolution, i.e. the factors affecting the variation of gene frequency patterns, has been the major field of investigation. In the early thirties, Fisher developed a systematic theory of evolution by natural selection and predicted that in a large population even slight selective differentials could replace a less advantageous twentieth with a more favoured one. At the same time Wright also developed a general theory of evolution and his argument was based on the fact that a species is composed of many small and nearly isolated subpopulations and within most there exist some boundaries to breeding. The size of these isolates is very important in the evolutionary process and assuming the population is randomly mating and there is no selection or mutation, such subdivisions will show genetic differentiation as a result of chance processes. When the isolation is partial the rate of divergence will depend on the amount of migration or gene flow. Gene flow between subpopulations retards the process of genetic differentiation. It is obvious therefore that in addition to conventional genetic factors, an understanding of demography, ecology, environment of the natural habitat, social behaviours and all other factors which promote migration and colonization are very important for understanding present day population structure. Since extensive information was available from historical records of the social and demographic structure of the human population, this led to the development of many classical models of population structure. More recently computer-intensive simulation methods have been developed which allow the study of migration and its effects through time, during the microevolution of humans.

The other vital achievement of the late 1900s was a revolution in the development of methodologies for genome analysis. There was a sudden explosion of new molecular markers, which helped in the reconstruction of the history of human migration and in testing explanations for demic diffusion. The spread of *Homo sapiens sapiens* to occupy the New World, colonization of Oceania and expansion through Europe *via* demic diffusion of agriculture were initially investigated using classical markers (blood groups, enzymes and proteins, human leucocyte antigens and immunoglobulin allotypes), but later confirmed by the study of autosomal (STRs) and sex-related mitochondrial and Y chromosome markers. With all these new inventions and the sequential expansion of population genetics in mind, Alan Fix has attempted to trace the role of migration in human populations by taking examples of well investigated populations which vary extensively in population density, land occupied and social integration.

The book includes six chapters. In the first migration is examined through causal models based on the overlapping interest in migration among different biological disciplines. As

the book uses detailed data on human migration from anthropological and historical sources this chapter defines the basic terminology used in later ones. Chapter 2 is very interestingly designed. It selects populations from different parts of the world, representing diverse social and environmental conditions, with very variable densities. For low population density, extensive land use and family groups it includes the populations of Yolgnu (Australia), Kung-San (South Africa) and Aka pygmies (Central Africa), while for low to moderate density, extensive agriculture and local kin groups it selects the populations Vaupes and Yanomama (Lowland Amazonia), Semai-Senoi (Malaysia) and Gainj-Kalam (New Guinea). For high density, intensive agriculturist and local groups and castes, the populations covered are the Basques (Spain), Oxfordshire populations (England) and Uttar Pradesh (India). No perfect correlation was observed between migration pattern and the continuum of increasing population density, intensity of land use and socio-cultural integration; however, all these factors have been shown to affect mobility and marriage patterns or gene flow.

The next two chapters deal with highly computer-intensive methods for analysis of human migration. Chapter 3 includes classic population genetic models (the island, isolation by distance, stepping-stone, migration matrix and neighbourhood-knowledge models) of migration and population structure. The merits of these models are examined by using basic variables (life-cycle timing, unit of migration, kin structure, population size, geography and distance) identified from populations studied in the previous chapter. In Chapter 4 more complex computer simulation models explore further the consequences of these variables. Chapter 5 focuses attention on the large-scale migrations within continental boundaries and colonization of the vast territories of the New World and Oceania. Several controversies are addressed concerning the origin and spread of *Homo sapiens* and the variation in genetic diversity observed for different types of classical and molecular markers among different continental populations. It is suggested that migration may explain some existing controversial issues. Chapter 6 draws concluding epilogues from various sections dealt with in the foregoing chapters. There is also a detailed list of references and a satisfactory subject index.

This book has several interesting features. It is written in simple language and avoids extensive mathematical equations. As a result, is likely to be popular among readers from a large number of biological disciplines. For those working with the analysis of human diversity it provides an important introduction to the use of extensive datasets on classical and molecular haplotype markers in the resolution of the micro-evolutionary debate concerning our species. In addition to the anthropogeneticist this book is highly recommended for all biological research workers who are interested in understanding the role of migration in evolution.

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Foundations of Mathematical Genetics (2nd edn). Anthony W. F. Edwards. Cambridge University Press, Cambridge. 2000. Pp. 121. Price £12.95, paperback. ISBN 0 521 77544 2.

This book is essentially a reprint of the first edition (published 1977) but with the important addition of a final chapter on 'Fisher's Fundamental Theorem of natural selection'. The book's scope is much narrower than its title implies. It gives a detailed mathematical analysis of selection models with discrete generations of random mating and constant genotypic viabilities. Successive chapters are devoted to analysing models for the following genetic systems: two alleles at a single locus; multiple alleles; sex-linkage; and two diallelic loci. The treatment is entirely mathematical: theorems are stated and rigorously proved. Apart from the final chapter on the recent interpretation of Fisher's Fundamental Theorem, the rest of the book concerns material most of which had been published before 1970. There is little discussion of the biological justification for the models or how they may be used to estimate selection parameters from observational data.

In spite of its purely mathematical approach, the book carries an important message, still widely ignored, for all evolutionary biologists. Great emphasis is placed on conditions for equilibrium and changes in mean viability. The chapter on many alleles at a single locus gives results all evolutionary biologists should be familiar with, even if the proofs, set out in an elegant matrix algebra, are passed by. Edwards gives rigorous proof that mean viability always increases at a multiallelic locus with constant viabilities. Provided this represents an 'internal' equilibrium (where a number of different alleles remain in the population), it will be a point of globally stable equilibrium. This is the most general model for which proof has been obtained that a population 'climbs an adaptive peak' to a point of maximum fitness. Even for the simplest two-locus, two-allele model with constant viability, Moran (1964) proved that mean viability does not maximize: counter examples can easily be constructed showing decreasing mean viability. Yet still, the textbooks — for example, in the Open University textbook *Evolution* (Skelton, 1993) — show populations climbing adaptive peaks. But it is precisely when there is more than one peak, implying strong interaction, that fitness does maximize. Edwards shows that if the viabilities at the two loci are additive, viability does then maximize in this model. From an evolutionary biologists' point of view, this is a trivial and uninteresting result: the loci are essentially independent. The existence of two adaptive peaks would imply strong interaction between the loci: alleles at one locus must determine the viabilities of alleles at the other. However, in no case have I been able to construct a diagram like that in Skelton (1993) with two *internal* peaks: if two peaks exist, they are always at the corners of the two-dimensional diagram of gene frequencies. I conjecture there is never more than one internal peak. Formal proof that populations do climb adaptive peaks has never, at least so far, dissuaded evolutionary biologists from taking the ascent for granted. Refutation of this seductive but erroneous metaphor of the evolutionary process could usefully have been given a far greater emphasis in Edwards' book.