

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.

Edwards' final chapter contains a brief proof of Fisher's Fundamental Theorem, based on his much longer discussion in *Biological Reviews* (Edwards, 1994). As it is now understood, the theorem concerns a partial change in fitness — the change in 'the breeding value in fitness'. This is the change in that component in fitness which each allele carries to the next generation, not the total change in mean fitness. In this restricted sense, the theorem is exact. Although Hardy–Weinberg frequencies are not assumed, the proof does depend on allelic frequencies being passed unchanged through the mating system to the next generation. This would only be true if matings between genotypes do not vary in fertility, for example in random mating. It could also hold for some very restrictive cases of assortative mating in which matings are strictly monogamous and equal in fertility. But whenever matings are polygynous or vary in fertility the change in gene frequency due to natural selection will then be changed again by sexual selection. If so, the proof of the Fundamental Theorem fails.

Edwards gives a simple and clear proof of the theorem and what it asserts. Anybody — that is to say almost everybody — who has been baffled by Fisher's chapter on the Fundamental Theorem in *The Genetical Theory of Selection* should now be able to understand what Fisher was trying to say.

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