Heredity **82** (1999) 343–345

Book reviews

Foundations of Social Evolution. Steven A. Frank. Princeton University Press, Princeton, N.J. 1998. Pp. 268. Price £13.95, paperback. ISBN 0 691 05934 9.

How could natural selection, based on the relative rates of reproduction of different individuals, favour genes that cause their bearers to expend resources to benefit their genetic competitors? The answers we can give to this question provide the true test of the maturity of our understanding of the logical process of natural selection, for it has been precisely this topic that has caused even some of the best biologists of earlier generations to stumble.

With *Foundations of Social Evolution*, Steven Frank makes a substantial and enthusiastic contribution to our understanding of the levels of selection, altruism, and social adaptation. In particular, as the title suggests, he provides a solid theoretical foundation upon which models of natural selection may be based. He does this by investigating in a very general way the concepts of kin selection, marginal fitness, and reproductive value, a task which takes a full two thirds of the book. The final third illustrates the principles and modelling philosophy that have been developed in a comprehensive tour of the theory of sex allocation. This describes the large-scale structure of the book, but in no way does justice to the breadth of topics into which Frank provides insight. Along the way he applies the theory he develops to analyse, *inter alia*, parasite virulence, 'the tragedy of the commons', Wright's shifting balance theory, conditional behaviour, and childhood mortality.

However, the reason that every evolutionary theorist should read this book is Frank's discussion and use of Price's (1970) Covariance Equation:

$$\bar{w}\Delta\bar{z} = Cov(w,z) + E(w\Delta z),$$

where w is fitness and z some quantitative character. In population genetics, z is generally thought of as a genetic trait, but Price's Equation is a mathematical tautology which is applicable to any selective system and any character, without any assumptions about the specifics of heredity. In particular we may substitute fitness w for z, and once it is realized that z can be partitioned into components or predictors Price's Equation becomes a powerful tool for analysing the levels and components of selection. Using this method, the author illustrates and develops Hamilton's (1970, 1975) inclusive fitness theory, and provides a deep understanding of what the coefficient of relatedness and Hamilton's Rule really means — it has little to do with geneaology. Price's Equation is also used to provide an enlightening derivation and analysis of Fisher's Fundamental Theorem, as well as to illustrate that there are two distinct processes in social evolution, both governed by what look *prima facie* to be the same form of Hamilton's Rule. Sadly, the numerous insights that Frank provides cannot all be described adequately in a short review.

As mentioned previously, this book is about the theoretical foundations of social evolution. There are few actual biological examples contained in what is a technically very dense book. There is also little discussion of the evolutionary fine-tuning of altruistic behaviour, no discussion of the literature on repeated games (Trivers' classic 1971 paper on reciprocal altruism is not even mentioned), and no discussion of Zahavi's (1977) handicap theory of altruism. These are not weaknesses of the book, it is a research monograph with a particular aim and should be judged as such. However, it is a great pity that the book does not contain a summary of its core ideas in a language soothing to those terrified by regression models, path diagrams, matrix algebra, and partial differentiation. The ideas contained in it are important, and of wide interest, not just to mathematically minded evolutionary biologists and geneticists.

Even given that the audience for this book will be limited to the mathematically inclined, it does have a number of serious failings. First, the choice of notation, although in line with standard practice in the field, is atrocious. It is almost impossible to read the book in anything but a close linear fashion. This is deeply ironic given that the author quotes Bertrand Russell on the pedagogical value of a good notation. Secondly, the book suffers from poor organization – it tends to flip backwards and forwards between topics, there are two introductions, and Hamilton's Rule is derived at least five times in the first two substantive chapters. Frank seems to do this to give a historical perspective and credit to the originators of particular ideas, but it would have been better if he had simply presented his vision and then discussed the previous literature within its framework. Thirdly, the book is not self-contained: Frank repeatedly refers the reader to four or five of his own journal articles and a similar number by other authors, which contain more detail and clearer explanations. A brief explanation of the regression models and path diagrams would also have been helpful and made the book more immediately accessible.

In summary, *Foundations of Social Evolution* is an important work that demands to be read. Every evolutionary biologist should have a copy within arms reach. Moreover, due to the fact that its central arguments are independent of the selection system and mode of heredity, its ideas should also be of interest to a wide range of readers, economists in particular. On the down side, the book would have had the potential to reach an even wider audience had it contained an extended outline of its core insights with as little mathematics as possible. It is also unfortunate that its impact on the theoretical community is likely to be diminished by poor organization and notation. I've read it thrice and am still unearthing buried treasure.

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Phenotypic Evolution — A Reaction Norm Perspective. Carl D. Schlichting and Massimo Pigiucci. Sinauer Associates Inc, Sunderland, Massachusetts. 1998. Pp. 387. Price £29.95, paperback. ISBN 0 87893 799 4.

Every biologist interested in evolutionary biology should read this book. In a highly readable manner Schlichting and Pigliucci outline the present status of thinking on the importance of reaction norms in phenotypic evolution. The book has one central purpose, to propose and defend the proposition that to understand phenotypic evolution we must take into account phenotypic plasticity, not simply as an interesting peripheral phenomenon but as an integral part of the evolutionary process. Although I am already strongly biassed in this direction, I think that the authors produce an extremely strong case which should encourage more research in this fast-developing area. One of the great strengths of this book is that it presents an historical perspective, an assessment of the present state of thinking, and, the authors' own opinions on where future research should be directed.

The first two chapters present an overview of approaches and an historical review of the development of ideas. These two chapters are a particular delight to read and show how some evolutionary biologists, such as Waddington, tended to be marginalized during the neo-Darwinian synthesis, but have lately become rehabilitated. Thus these chapters not only present the historical view but give insight into the sociology of science. Chapter 3 outlines the basic concepts of reaction norms and phenotypic plasticity. Schlichting and Pigliucci divide the study of reaction norms into two avenues, the statistical description via quantitative genetics and the mechanistic analysis through manipulative experiments. Chapters 3 to 9 present the analysis of phenotypic evolution using the reaction norm perspective as judged from these two methods of study. Chapter 10 presents an overall summary and 14 potential research projects, which should be of particular value for graduate students in this field.

In their attempt to encompass the entire field of phenotypic evolution Schlichting and Pigliucci have on occasion included areas that I did not find fitted well into their perspective. A particular example is their chapter on allometry: as a discussion of allometry the chapter is interesting and informative but in their last section entitled 'Plasticity of character correlations' they assert that correlation coefficients are themselves allometric coefficients, which to me seems to be stretching the definition of allometry. This said, the section is interesting but should be viewed simply as the evolution of suites of correlations.

This book is provocative and will likely promote debate, which is a sign of success. To give an example of where the book provoked me: Schlichting and Pigliucci seem to view quantitative genetic analysis as a temporary necessary evil that will be eliminated once we have a better set of mechanistic models. To illustrate the inadequacy of the quantitative genetic approach they present a model that purportedly demonstrates that different phenotypic outcomes are possible even with identical correlations and phenotypic optima (p. 81). The model is a single locus, two-allele one, which is hardly representative of quantitative genetics. To give an analogy; it is like using an ostrich as a model for the analysis of flight in birds. Certainly ostriches are birds, and have wings, but they are not truly representative of the majority of birds. Pigliucci's model does demonstrate that it is possible to construct models that have aberrant behaviour, but it does not demonstrate that this behaviour is typical of quantitative genetic models. Because of the limited character states available in a single-locus model it is not surprising to find that it is limited in its evolutionary trajectories.

There are a number of other assertions with which I disagree but this does not detract from the enormous value of this book. It has brought together very disparate sets of data under a common umbrella and thus provides a unifying theme in evolutionary biology, surely one of our major goals.

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Sperm Competition and Sexual Selection. T. R. Birkhead and A. P. Møller (eds). Academic Press, London. 1998. Pp. 826. Price £39.95, paperback. ISBN 0 12 100543 7.

Significant advances in evolutionary biology are often associated with simple but elegant ideas. Parker's (1970) suggestion that competition for fertilizations between the sperm of different males could be a powerful evolutionary selection pressure is a clear illustration of this point. Nearly 30 years on, the study of sperm competition and its evolutionary consequences is an extraordinarily diverse and still rapidly expanding field. A major success of Birkhead & Møller's book *Sperm Competition and*