

this enthusiasm, although there are large areas where the data are too poor and/or the character variation too small for such methods to be applied with success. However, Poulin has made an important contribution if the book can persuade just a few evolutionary biologists to study parasites instead of great tits, and make a parasitologist or two aware of the fact that their subject is science – not just data.

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The marginal value of relations

A review by Michael Doebeli

Foundations of Social Evolution. By Steven A. Frank. Princeton University Press, Princeton. 1998. xii + 268 pages. ISBN 0-691-05934-9. 16.95/£13.95 paper, 49.50/£35.00 cloth.

Evolutionary dynamics is determined by heritable variation between individuals, by variation in reproductive success and by the correlation between these two types of variation. If there is no heritable or no reproductive variation, there is no evolutionary change. If the correlation between heritable trait variation and reproductive variation is zero, evolution is neutral. If this correlation is nonzero, evolution is adaptive. This book is about adaptive evolution when the correlation between trait values and reproductive success is influenced by social interactions and kinship.

Steven Frank starts out by introducing the Price equation as the formal tool for keeping track of the correlations between heritable changes in trait values and fitness (Chapter 2). For these correlations, relatedness plays an important role, and using the Price equation Frank presents a natural derivation of Hamilton's rule (Chapter 3). This illustrates his contention that Hamilton's rule is a result rather than a starting point for analysis, because this famous rule hides too many details of the interactions determining evolutionary change. After having read the book, I tend to agree: Hamilton's rule is often very handy for interpreting results, but it is too simple to provide a detailed causal understanding of evolutionary change. Instead, such understanding is provided by Frank's approach, which is more basal and more explicit (Chapter 4). In essence, this approach consists of identifying fitness components, attaching reproductive value as weights to these components, and then investigating the marginal changes in total fitness that are due to changes in breeding value resulting in correlated responses of the various

components. At the fitness maximum, this marginal change is zero, that is, a marginal increase in some fitness components is exactly balanced by a corresponding decrease in the others, and evolution comes to a halt. How to apply these techniques to social evolution, how to determine correlated responses that are caused by social interactions and kinship, is the content of Frank's book.

And room there is for new perspectives on old problems: the book is a gold-mine for anybody who is interested in the theory of social evolution. Among many other topics, Frank discusses the dynamics of correlated traits in connection with peak shifts on adaptive landscapes (Chapter 5), the significance of conditional behaviour and kin recognition (Chapter 6), and the influence of demography and spatial population structure on kin selection (Chapter 7). After going into some details about how and why reproductive value must be incorporated into models of social evolution (Chapter 8), he finally embarks on a detailed treatment of the problem of sex allocation (Chapters 9–11), which exemplifies the usefulness of his approach. As a nonspecialist, I was fascinated by how many different angles of this problem can be examined using Frank's framework. There is no doubt that his approach yields many new insights, because it makes explicit fitness components which traditionally only appear implicitly in models of social evolution. This allows us to identify selective mechanisms, and to disentangle their impact on the evolutionary process.

The book is written in a very terse style, which makes for a rather gripping read, but it is often hard to follow the author's thoughts because of the lack of details given. The book does not have the virtue of a gentle beginning and instead starts out with what for many readers will be the most difficult part: formulating kin selection in the context of the Price equation (Chapters 2–4). That's not only bad tactics, but also unnecessary and mainly due to the author's personal affinity for a particular formalism. I think that the important message of the book – the analysis of correlated traits and reproductive value in fitness maximization models of social evolution – could have been introduced in a more pragmatic and understandable manner. After Chapter 4, the Price equation never reappears, and all the material in later chapters could have been developed using a more intuitive and less formal (but no less correct) language. For example, in Chapter 4, Frank puts much emphasis on 'direct' fitness being a more general concept than 'inclusive' fitness in Price's framework, but no example is worked out in which the difference really matters. In fact, when the issue arises in the applications in later chapters, direct fitness is invariably replaced by its more familiar inclusive relative. There is another thing that put me off course repeatedly: references to 'later sections' where things will be made 'more clear' abound; such references make readers think that they are missing something, and almost all of these references are too imprecise to be of any practical use. For example, a

statement like: 'This is particularly useful for kin selection, in which one often assigns a fitness component of a neighbour to an actor whose phenotype controls the neighbour's fitness component. This will be made clear later.' (p. 61) is hard to digest.

But enough of petty criticism, there is another very important point that Frank makes repeatedly, involving the concept of comparative statics. Frank maintains that his maximization models are not designed to make predictions about particular systems, but rather to establish correlations between changes in parameter values and differences in expected evolutionary outcomes. Thus, Frank argues very convincingly that the main goal of evolutionary optimization models is to make comparative predictions. True to its title, his book lays down the theoretical foundations for making such predictions in social evolution.

At the very end, when discussing the benefits and limitations of the fitness maximization approach, Frank mentions that dynamic evolutionary models may be necessary to study antagonistic interactions such as host-parasite arms races. However, there is another general approach to evolutionary theory which does not rely on 'conflict and power' but is dynamic nevertheless. This is the theory of adaptive dynamics developed by Hans Metz and his colleagues (Dieckmann & Law, 1996; Metz *et al.*, 1996; Geritz *et al.*, 1998). This theory is based on evolutionary invasion analysis and contains maximization as a special case. Because this theory incorporates

ecological interactions as evolutionary driving forces it also entails many other phenomena, most notably perhaps the phenomenon of evolutionary branching (Geritz *et al.*, 1998). It remains a challenge to define invasion fitness in the context of kin selection, and it would be extremely interesting to see the results emerging from a combination of Frank's theory of social evolution with the theory of adaptive dynamics.

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