

tation testing in the Virtual Genetics Lab. As the name implies, this provides interactive material to replace the use of real practicals in microbial genetics.

Would the material arouse a student's interest in genetics and deepen his or her understanding of the subject? The Virtual Genetics Lab starts off as fun, and this must encourage interest. Quite soon however, one gets down to very repetitive mouse movements in order to generate some data. For example, the complementation test involves using a syringe icon to produce all pairwise combinations of 10 mutants. This is all very sensible, but one's mind does wander away from genetics to thoughts of how can one speed up the mouse movements. I suppose this does make the point to students (possibly subliminally) that research involves perspiration as well as inspiration, but less committed students' minds may stray. However, when one gets down to analysing data, things improve markedly. Only the first 17 out of 1000 segregants have to be classified in the three point cross and only 8 out of 160 tetrads in the tetrad analysis before the rest of the data is provided, and then the student is into thinking about the results. Direct monitoring of each step by computer must be a better learning method than using pencil and paper, with checking by the lecturer at the end of the class.

The teaching section on complementation was disappointing. The basic material on the theory and practice of complementation was clearly set out just as in any standard textbook, but now the computer seemed a distraction which would not be found if the same material was on the written page. The programme advances automatically every few seconds. The student can, and should, pause as required, but the pausing distracts in a more intrusive way than moving ones eye down a printed textbook page would. Also, the graphics are inevitably not as good as the very high standard of illustrations routinely achieved by publishers of textbooks. However, the use of movement definitely is a great advantage in the description of chromosome behaviour and must help students' understanding in ways that are not achievable in textbooks.

The self-assessment multiple-choice questions are the simplest part of the program, but in some ways, the most useful. Their interactive nature must be of value in the student's learning process. They were well prepared and covered a good range of standards.

Overall, this is not going to be a panacea for the problems of too many students and too few resources, but then it is naive to hope for a panacea anyhow. This package is a brave attempt to solve a very difficult problem and contains some useful material which could, with judicious planning and adaptation, fit into many undergraduate courses.

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**Narrow Roads of Gene Land, Vol. 1, Evolution of Social Behaviour.** W.D. Hamilton. W.H. Freeman Spektrum, New York. 1995. Pp 552. Price £20.00, paperback. ISBN 0 7167 4530 5.

W.D. Hamilton has made enormous contributions to modern evolutionary biology and the publication of his collected papers is long overdue. This is volume one, beginning with his first paper in the *American Naturalist* (1963) sketching his ideas of kin selection that were fleshed out the following year in *Journal of Theoretical Biology* and ending in 1980 with a paper on evolutionary dispersal strategies. Inbetween we get senescence, biased sex ratios, the selfish herd and insect altruism, along with a large dose of evolutionary entomology. It is sometimes forgotten that Hamilton is an exceptional entomologist with an encyclopaedic knowledge of the class, and extensive experience in the field, from the North Downs to Amazonia. The break in 1980 is natural because since then Hamilton has been occupied chiefly, although not exclusively, with the evolution of sex and in particular the role that parasites and pathogens may play. Hamilton's work lends itself well to collection in a single volume because unlike most contemporary scientists he has worked largely alone, developing a series of intertwining themes, rather than heading a laboratory of students and collaborators. Indeed only three of the fifteen papers reprinted here are co-authored (with Bob May and Hugh Comins on evolutionary dispersal strategies, and with Nancy Moran on the evolution of plant defences to herbivores).

But the current volume is more than a collection of papers as each of the fifteen publications is preceded by an essay describing its genesis and incorporating a large chunk of autobiography. Hamilton read genetics at Cambridge but moved to London in 1960 to begin a PhD at University College (UCL) and the London School of Economics (LSE). Already, he had had the critical insight into the evolution of social behaviour and he spent his PhD collecting relevant data and formulating a quantitative theory. Neither UCL nor LSE took him to its bosom, both frightened of the spectre of genetic determinism he appeared to represent, and Hamilton movingly describes a rather lonely life spent in library and digs, plagued by self doubt and worried that he may be wrong, or just stating the obvious. But he persevered and the acceptance of the preliminary note in the *American Naturalist* spurred him to write the definitive account in *JTB* (though I have to say that on re-reading these papers I still find the mathematical formalism completely counterintuitive). Having completed his PhD, in 1964 he became a lecturer in the Biology Department at Imperial College, an appointment I had always considered a masterpiece of my Department's prescience and judgement, although Hamilton's more prosaic explanation is that there were two candidates and the other one declined the job. Based at Imperial's Silwood campus, he developed theories of the selfish herd, the evolution of ageing, and the effect of local mate competition on the

sex ratio. The germs of all these ideas appeared to have been formed in postgraduate or even undergraduate days, and particularly interesting is Hamilton's account of the scientists who most influenced his thinking, among whom G.C. Williams is prominent. A curious aside is that the 'Geometry for the selfish herd' was originally submitted to Martin Gardner's 'Mathematical Games' section of *Scientific American*. At Silwood, and on trips to Brazil, Hamilton was able to continue studying insects, and a wealth of insect biology informs his papers on biased sex ratios and insect sociality, as well as the more explicitly entomological publications on fig wasps and insects living under bark. In 1979 Hamilton moved from Imperial College to Michigan; he had not enjoyed English undergraduate teaching and has some harsh things to say about Imperial undergraduates (though not as harsh as their reports to the teaching committee). In contrast he much enjoyed American graduate school teaching and the penultimate paper in this volume on the evolution of plant defences against herbivores is a collaboration with Nancy Moran, then a PhD student at Michigan.

The most extraordinary of the essays in this book describes Hamilton's friendship with George Price. Originally a physicist and a chemist, he had worked in the States as a scientific journalist but had moved to London after his divorce and a serious illness. He had developed an interest in population genetics but instead of reading the literature had worked out his own equations for changes in gene frequency under hierarchical selection. Hamilton recognized the importance of Price's covariance formula, and published its first application, a much more elegant mathematical description of altruism (and spite) than in the original 1964 paper. But Price never saw the paper. In London he had undergone a profound religious experience that had converted a militant atheist into a devout and biblically literal Christian. He sold his possessions and engaged in frequently dangerous charitable work with the poor and destitute in London. Now impoverished himself, and suffering from the after effects of his

serious illness, he lived in a series of progressively more run-down apartments, in one of which he committed suicide. His funeral was sparsely attended, chiefly by his religious friends, but also by Hamilton and by John Maynard Smith with whom Price had pioneered the use of game theory in analysing animal conflict. George Price's life calls out for a full scale biography, but until then Hamilton's affectionate reminiscences, and Steven Frank's excellent essay on 'George Price's contribution to evolutionary genetics' (*Journal of Theoretical Biology*, 175, 373, 1995), are a lasting tribute to a brilliant and complicated man.

This book serves several important functions. The well-known papers are brought together and the book will replace many collections of dog-eared photocopies. The book should lead to some of the other papers becoming better known. The full impact of the two papers in this volume on evolutionary dispersal strategies (a third in the series was written by Hugh Comins alone) is only recently becoming apparent and the papers deserve a wider audience. The entomological papers should also be more widely read, especially by entomologists. Finally, the book will be read for the fifteen essays which are written in a unique and engaging style: part Darwin, part Proust, with a dash of Pooter. They provide a vivid insight into Hamilton's intellectual development as one of our leading evolutionary theorists, as well as a fund of anecdotes and vignettes of his friends and acquaintances. Yet the story is incomplete, with very little about his early life and his formative years at Cambridge. Once Hamilton has finished the second volume of the collected papers, I hope his publishers persuade him to write a full autobiography.

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