
Book Reviews

Genetics and analysis of quantitative traits. By MICHAEL LYNCH and BRUCE WALSH. Sinauer Press, 1998, 980 pages. Price \$64.95. ISBN 0 87893 481 2.

Quantitative genetics traces back to Fisher's (1918) synthesis of mendelian genetics with the biometric analysis of continuous traits. It provides an elegant statistical framework for understanding the relation between phenotype and genotype, and the response of populations to natural and artificial selection. Until recently, this body of theory was confined largely to plant and animal breeding, and even there, only the most elementary aspects were in common use. In the past decade, the availability of fast computers and abundant molecular markers has stimulated sophisticated applications over a wider field, and has again brought together discrete Mendelian genetics with the continuous variety of whole organisms.

Lynch and Walsh set out to combine in a single definitive text the diverse applications of quantitative genetics to plant and animal breeding, human genetics, and evolutionary biology. *Genetics and analysis of quantitative traits* is the first of what will now be two volumes; the second will cover *Evolution and selection of quantitative traits*. Despite its broad scope and long gestation, this volume is much lighter than one might expect. In less than 1.5 kg and 1000 pages, it covers the whole field, and succeeds remarkably well in bringing together methods that have been developed in diverse contexts. The explanations of difficult concepts are admirably clear, and should be accessible to those without a strong mathematical background. Methods are derived from first principles, and illustrated by well-chosen worked examples; there are also helpful appendices on basic statistics, matrix algebra, and likelihood. The references are comprehensive, covering both the early literature in which most of the theory was outlined, and the papers of the last few years in which it is elaborated and applied.

The sophisticated and precise theory of quantitative genetics rests on uncertain biological foundations: we have only the barest outline of the genetic basis of continuous variation, and of the evolutionary pro-

cesses by which it is maintained. Lynch and Walsh give thoughtful summaries of several key issues: for example, mutation; regulatory vs. structural variation; developmental stability; correlations between characters; and phenotypic plasticity. Particularly intriguing is a survey of 52 attempts to detect quantitative trait loci (QTL) using inbred lines, they find for half of all traits, one locus accounts for at least 20% of the phenotypic variance (Ch. 15). However, they also caution that there is a serious statistical bias which leads to overestimation of the effects of detected QTL, and point out that the rapid generation of variation by mutation, and prolonged selection response, are strong evidence for polygenic variation. Overall, this volume will be an indispensable reference for all in the field, and an excellent basis for graduate courses.

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Melanism. Evolution in action. By M. E. N. MAJERUS. Oxford University Press, Oxford 1998. 338 + xiii pages. Price £23.95 (paperback). ISBN 0 19 854982 2

Melanism in organisms is the condition of being black. More precisely, it refers to darkness conferred by eumelanin and pheomelanin pigments, some of them reddish or brown; subfusc would be a more inclusive term. There are a myriad reasons why dark pigments should occur, sometimes simply as by-products of other more significant metabolites. Usually, the term promises adaptive colouration, and hence the study of evolution, natural selection and, no doubt, polymorphism. These issues are addressed here in general and with reference to specific cases. The first three chapters cover the definition of melanism, its

manifestation and distribution in nature, and some principles of genetics. Population genetics and evolution are then discussed, emphasis being given to selection and how it may maintain polymorphism. This is done, as it may be, without use of a single equation. The book is written for biologists, both professionals and amateurs with a special interest in entomology, and the presentation is very clear and straightforward.

Cases such as mimetic polymorphism in edible swallowtail butterflies are included. In these, the blackness is not really the central issue, since it arises from the need to resemble a model. In the model species the black colour may be aposematic but no more or less significant than red, white or yellow which would make a conspicuous and easily recognised pattern. For the most part, however, Majerus concentrates on the topics most readers will associate with the term, namely industrial melanism and the study of species on which he is an authority, moths and ladybird beetles. The last book on the subject was Bernard Kettlewell's *The Evolution of Melanism* (1973), large, chaotic but full of useful information and centrally concerned with the peppered moth story. The black form *carbonaria* and several forms with darkness intermediate between it and the typical phenotype, increased in frequency in industrialized and urbanized parts of Britain, starting in northwest England, then spreading elsewhere. The resulting pattern was one of very high frequencies of melanics in the urban regions, low ones in the rural west but quite high in eastern rural areas, notably East Anglia. Majerus recounts this story and brings it up to date in a much more lucid account. Atmospheric pollution has declined and changed in pattern, while the frequency of melanics has declined dramatically. More information is available on behaviour and ecology, and population genetic models are now more realistic. All this helps us to understand the changes and put them into a modern evolutionary context.

There are one or two things in Majerus' account which I think are arguable. Thus, although migration was certainly thought to have resulted in the spread of the *carbonaria* form in the 19th century, the explanation of the change in industrial areas was not really based on a selection, migration balance. Modelling by Haldane and later by Sheppard which suggested the existence of heterozygote advantage tacitly assumed that migration had an insignificant effect. If it is included the evidence for heterozygote advantage disappears, and I would probably rate migration more highly than Majerus in forming the patterns seen. With respect to resting background, Majerus makes considerable play of the fact that earlier workers carried out experiments on selective predation in locations on trees much lower than the usual resting positions of the moths. However, it can be argued that

differences between parts of the same tree are insignificant compared with the difference between epiphyte-rich rural trees and urban ones, so that the inter-habitat comparison is unlikely to have been compromised. Such minor differences may be settled by experimentation and discussion, but the peppered moth example is widely quoted, and disagreement sometimes taken to render the whole fabric of the story suspect (e.g. Lambert *et al.*, 1986). Those who have worked on the peppered moth think that selective predation related to camouflage is of paramount importance in any explanation, but that other types of selection may be at work as well. Majerus points out that the comparative study of British peppered moths and the American subspecies *B. b. cognataria* provides a natural experimental replicate. The scalloped hazel moth *Odontoptera bidentata* provides another useful comparison. Its size and season of flight are not dissimilar to those of *B. betularia*, yet in north west England it shows a much stricter relation between high melanic frequency and actual urbanization. This pattern appears to associate not only with lower migration levels, but also with a tendency to rest in cracks, instead of on surfaces as *B. betularia* does (Bishop & Cook, 1980). If it removes itself from the risk of predation, then the search for other causative agents becomes more pressing.

That is certainly the case with respect to melanism in ladybirds, of which Majerus has made a special study. Melanism is associated with industrialization in some species, not in others. Many species are polymorphic and some have a large number of morphs. Majerus provides a fascinating review of the situation. He discusses sexual selection in the 2-spot ladybird *Adalia bipunctata*, which is genetically determined but in different ways in different places. This species has numerous melanic morphs, controlled by an allelic series or supergene, two of them common but most present at frequencies of 1 per cent or less. He reviews the evidence that some species may be Batesian or Müllerian mimics. In the light of all the evidence he produces a model which assumes a very featureless adaptive landscape, with numerous similar fitness modes. This sounds a little like a neutral model, since neutrality implies equivalence of selection rather than its absence. It may be interesting to compare allele (or supergene) frequency distributions with those expected if the alleles were neutral.

The book is attractively presented with plenty of useful illustrations, including a section in colour. Some editorial points still need attention; e.g., *Philaenus spumarius* has become shuffled as *Philaneus spunarius* and work by D. A. West is credited to another author, B. K. West. An up-to-date review of melanic polymorphism is provided, set in a context which is sufficiently jargon-free to appeal to the amateur entomologists, whose work is so important,

and authoritative enough for the professional geneticist. The clarity and coverage resemble not so much Kettlewell's book as E. B. Ford's *Butterflies* (1945) and *Moths* (1955). This should be the major work in the field for many years to come.

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