Book Reviews

Plant–animal interactions: an evolutionary approach

Herrera, C. M. and Pellmyr, O. (Editors) 2002. *Plant-animal interactions: an evolutionary approach*. Blackwell Science, Oxford, U.K. 313 pp. Cloth, ISBN 0-632-05267-8, £39.99.

Amongst ecologists there is a growing awareness that many plant traits and plant assemblages are shaped by animals that share their habitats, and it is these interactions that provide an essential dynamic to contemporary evolutionary and ecological studies. However, the multidimensional character of plant–animal interactions challenges experimental and quantitative ecologists, as we seek to develop generalisations that apply beyond the community or plant species of interest. *Plant–animal interactions: an evolutionary approach* is a multi-authored book that attempts to provide a modern synthesis of the topic, while identifying worthwhile approaches for future research. Part 1 outlines the role plant–animal interactions have in maintaining biodiversity (Price) and includes a section on adaptive radiations relevant to New Zealand. A chapter giving a paleontological perspective (Labandeira) on the origin of plant–animal interactions provides a worthwhile corrective for neo-ecologists interested in explaining present-day interactions in isolation from their history. Part 2 focuses on different forms of herbivory and devotes a chapter each to insects (Strauss, Zangeri), mammals (Danell, Bergström), and birds (Hulme, Benkman). I appreciated the authors' attempts to examine both the animal and plant aspects of herbivory at all levels of biodiversity, from the individual to the ecosystem. Part 3 focuses on well-known mutualisms, namely animal pollination (Pellmyr) and seed dispersal (Herrera), and it is here that the subtlety and complexity of the evolutionary dynamics of plant–animal interactions is perhaps most clearly seen. Recognising the structural diversification amongst flowers and fruits coupled with profound variation in animal feeding and behavioural traits, and the contrasting population dynamics and mobility of the plant and animal participants, the authors provide a well thought out examination of the evidence for relative fitness-related benefits and the level of coevolution. Part 4 is a synthesis of the field, with a somewhat misplaced chapter on ant–plant (largely mutualistic) interactions (Beattie, Hughes), and a consideration of future directions (Thompson).

The volume is a rich source of ideas and information, and many of the major issues identified for future research (e.g. role of plant polyploidy in shaping the evolution of plant–animal interactions) are well suited for exploring in New Zealand. The chapters are clearly and constructively written, mainly by Northern Hemisphere ecologists from both Europe and the USA, which tends to limit the examples, but does reflect the geographical intensity of studies to date. Depth of coverage of different aspects is often uneven, but key references are provided for further information. In my view, the aim "to provide a manageable synthesis of recent developments in the field of terrestrial plant–animal interactions" has been well achieved. I have already used the book to understand unfamiliar areas, and suspect that others will find it equally helpful.

William G. Lee
Landcare Research
Private Bag 1930
Dunedin, New Zealand

A new approach to modelling large herbivores and their food supplies

Owen-Smith, R.N. 2002. *Adaptive herbivore ecology: from resources to populations in variable environments.* Cambridge University Press, Cambridge, U.K. xvi + 374 pp. Hardback, ISBN: 0-521-81061-2, £65.00.

Norman Owen-Smith has published extensively on the behaviour, diet selection, demography, and population dynamics of wild herbivores in southern Africa. Disenchanted with the proliferation of numerical population models that have 'become largely decoupled from environmental influences', Owen-Smith's aim in this book is to model the interaction between large herbivores and their food supplies in a mechanistic framework.

The thesis of this book is what Owen-Smith terms the GMM model. The GMM model simply states that herbivore biomass is governed by the rate of biomass gain (G), the rate of metabolic loss (M), and losses through mortality (M). (GMM is also an acronym for the Getz Metaphysiological Model, named after Wayne

Getz, who introduced Owen-Smith to this approach.) By reviewing the literature, Owen-Smith provides sound evidence that biomass gain depends on resource availability, metabolic costs on environmental conditions and resource supply, and mortality on senescence plus predation risk interacting with resources.

This book contains many innovations in two broad areas. First, the equations derived for the three components of the GMM model in multiple scenarios. Second, the estimation of the parameters for these models from both published and unpublished data. Owen-Smith's empirical sense shines brightly; he almost always cites published studies to support his model building. The result is a series of up-to-date reviews of foraging behaviour, physiological processes, diet selection, growth, reproduction, metabolism, and mortality. Most equations are drawn and populated with published data, sometimes reanalysed.

Having justified the GMM model, Owen-Smith then applies it to the questions of habitat suitability, competition and facilitation among large herbivores, and the instability of populations. For all these questions the modelling leads to new hypotheses and ways of seeing. For example, it is suggested that 'population instability [of Soay sheep] depends upon whether resource gains fall below the critical starvation threshold during the course of the dormant season when resources are non-renewing': the conventional wisdom is that the instability is due to the population's high intrinsic rate of increase.

Owen-Smith does not provide a recipe book for modelling, but a mechanistic philosophy justified both by theory (e.g. allometric relationships) and data. This book is thus a major advance in our understanding of large herbivore-plant interactions. It is more complex than the interacting functional and numerical responses derived for kangaroos in pasture [Caughley, G.; Shepherd, N.; Short, J. (Editors) 1987. *Kangaroos: their ecology and management in the sheep rangelands of Australia.* Cambridge University Press, Cambridge, U.K.], and more general than the model proposed for Soay sheep [Illius, A.W.; Gordon, I.J. 1999. Scaling up from functional response to numerical response in vertebrate herbivores. *In:* Olff, H.; Brown, V.K.; Drent, R.H. (Editors), *Herbivores: between plants and predators*, pp. 397–425, Blackwell Science, Oxford, U.K.].

In such a wide-ranging book it is almost inevitable that there will be errors. One irritating error, at least to a New Zealander, is the citation of Caughley's work on irruptive oscillations followed by a statement that the 'archetypal example is the mule deer inhabiting the Kaibab region': Caughley's paper discredited the Kaibab example! I was surprised that Caughley's work on kangaroo-pasture dynamics (see above) was not cited, but it was pleasing to see Caughley's earlier modification of the Lotka-Volterra equations to the plant-herbivore system is recognised.

Several problems become apparent; The biomass conversion coefficient (*c*), an important parameter in the GMM, is estimated from dry matter digestibility, thus ignoring the potentially large effects of secondary compounds. Another problem is the estimation of parameters from data. Although Owen-Smith often has sound *a priori* justifications for models, on multiple occasions the model seems to fit the data poorly: caveats are needed. On other occasions data could be explained by several alternative models, but only one is considered.

Some Australasian rangeland ecologists have developed interactive models using functional and numerical responses, *a la* Caughley for kangaroos and pasture. Owen-Smith criticises functional responses, believing that 'more attention should be given to the resource dependence of mortality, in interaction with predation and other influences'. Owen-Smith advocates the use of the Michaelis-Menten equation (rather than the Ivlev), and suggests that the parameters should be estimated as an asymptotic limit.

The herbivore side of the interaction is greatly advanced in this book, whereas the food supply side is far less developed. Owen-Smith recognises that a major limitation of his book is the use of a modified logistic model to describe the biomass dynamics of vegetation, noting that 'a more elaborate model… is beyond the scope of this book'. Indeed, he suggests that 'much of the instability of herbivore populations may be a consequence of their long-term impacts on vegetation structure and composition'. However, Owen-Smith's modified logistic models, different for grass and browse, are themselves useful advances.

Does the author achieve his aim? Yes. This is a book of great scope that deserves to be widely read. However, readers should bear in mind that any modelling seeks to answer a question. Owen-Smith has addressed the questions that interest him, and in doing so has provided a framework for others to elaborate. For example, researchers interested in the impacts of large herbivorous pests on native vegetation will need to develop appropriate models of the latter to link with the herbivore-centric framework developed in this book.

Dave Forsyth
Arthur Rylah Institute for Environmental Research
123 Brown Street
Heidelberg
Victoria 3084
Australia