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Evolutionary ecology of marsupials

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Introduction

Evolutionary ecology is concerned with the ways in which organisms living in different environments enhance their survival and reproduction. In this text we consider the evolutionary ecology of the marsupials, a group of mammals which have fascinated biologists since the discovery of their unique mode of reproduction. In doing this we do not offer an exhaustive review of all aspects of ecology. Rather, we focus on instances where marsupials elucidate problems in evolutionary ecology and vice versa. Most of our endeavour must be viewed as an attempt to place descriptive data in a standard theoretical framework which we hope leads naturally to the generation of hypotheses which examine the resilience of the framework and provide new directions in marsupial research.

Origins of theoretical ecology

Ernest Haeckel (1866) coined the term 'Oekologie' to embrace animal/environment relationships while discussing animal morphology in the light of Charles Darwin's new theory of evolution by natural selection. Despite the early importance of evolutionary theory in distinguishing ecology as a science, a theoretical basis for much of ecological research has been lacking. McIntosh (1980) points out that there were only two references to theory and one to hypothesis in the pre-1950 cumulative indices of the major American ecological journals *Ecology* and *Ecological Monographs*, but that since that time a theoretical literature has burgeoned.

Recent historians of science have commented that this literature gives two distinct views of the organisation of ecosystems, with different historical bases (Ghiselin, 1974; MacFayden, 1975; F. E. Smith, 1975; Harper, 1977; McIntosh, 1980; Simberloff, 1980). These are:

1 *Systems ecology*, which sees ecosystems as developing evolutionary entities which guide the evolution of species but which are to some extent independent of their constituent species. This view has a recent antecedent in F. E. Clements' (1905) now-discredited 'organismic' view of the community, and some authors have traced its origins to Platonic idealism and Aristotelian essentialism, which formed the predominant western pre-Darwinian view of nature (e.g. Ghiselin, 1974; Simberloff, 1980).

2 *Evolutionary ecology*, which treats the ecosystem as the sum of its parts (species), with understanding of the whole system deriving from studies of species populations and their characteristics as products of natural selection. This philosophy is clearly post-Darwinian, and much of its history is eloquently reviewed by Hutchinson (1978).

While we agree with Levins & Lewontin (1980) that properties of ecosystems and communities are objects of interest in their own right, the ability to synthesise these two views of ecosystems has remained elusive (see e.g. Wilson, 1980). In this book we adopt the second view above, and argue that evolutionary theory represents the chief unifying perspective through which natural history data can be usefully interpreted, and around which predictive hypotheses can be formulated (see also Southwood, 1980).

Although Darwin's ideas were widely understood by the end of the nineteenth century, the reinterpretation of the different subdisciplines of biology in an evolutionary framework has proceeded at different rates in different fields. Historians of science attribute particular importance to the synthesis of the concepts of natural selection and Mendelian genetics in the 1920s and 1930s by authors such as R. A. Fisher, S. Wright and J. B. S. Haldane (see Mayr & Provine, 1980, for a full discussion). It was not immediately obvious how population processes and species interactions related to an evolutionary theory that was based on the reproductive success and survival of individuals, despite explicit considerations of ecological questions by Darwin and Fisher. This led to the persistence of a theoretical vacuum for the interpretation of life histories and behaviour, and to the occasional misapplication of evolutionary theory, especially through an undue emphasis on group selection (e.g. Wynne-Edwards, 1962). New ways of resolving these difficulties were provided by, among others, D. Lack (1947, 1954, 1968), G. E. Hutchinson (1957, 1959) and R. H. MacArthur (1972), who examined the causes and consequences of variation in the life history of organisms and the responses of individuals to competition and other species interactions, and by G. C. Williams (1966), who critically reviewed the conditions for group and individual selection.

Much of the work after this time was couched in simple mathematical terms (for a synopsis see Roughgarden, 1979) and provided a theoretical framework which has led to an expansion of the application of mathematical solutions to ecological problems. It also contributed to the intense interest now shown in evolutionary ecology. Unfortunately, the mathematical content of this later work either discouraged the natural historians who had generated the descriptive data which the theories attempt to place within a coherent framework, or occasionally led to uncritical acceptance of mathematical predictions of dubious ecological relevance. This has led to an increasing gap between theorists and empiricists. As one of the founders of evolutionary ecology, G. E. Hutchinson (1975, p. 516) has commented:

> Many ecologists of the modern generation have great ability to handle the mathematical basis of the subject. Modern biological education, however, may let us down as ecologists if it does not insist...that a wide and quite deep understanding of organisms, past and present, is as basic a requirement as anything else in ecological education. It may be best self-taught, but how often is this difficult process made harder by a misplaced emphasis on a quite specious modernity.

The ecology of marsupials

Only a few ecological studies of marsupials have had some theoretical content. Main, Shields & Waring (1959) were able to identify three motivations for early ecological research: economic pressure for control of pest species (including grazing kangaroos and feral marsupials in New Zealand), conservation of well-known but endangered species and some academic questions, particularly those related to how populations behave. The most influential academic study of this sort had its genesis during the 1950s, and began as an investigation of population 'crashes' in the quokka (*Setonix brachyurus*) on Rottnest Island (see Main *et al.*, 1959). This research laid the foundations for a number of investigations of the ecological strategies exhibited by macropods (e.g. by Newsome, 1965; Main, 1971; Main & Bakker, 1981), and the Macropodidae continues to be the best understood of the various families of marsupial.

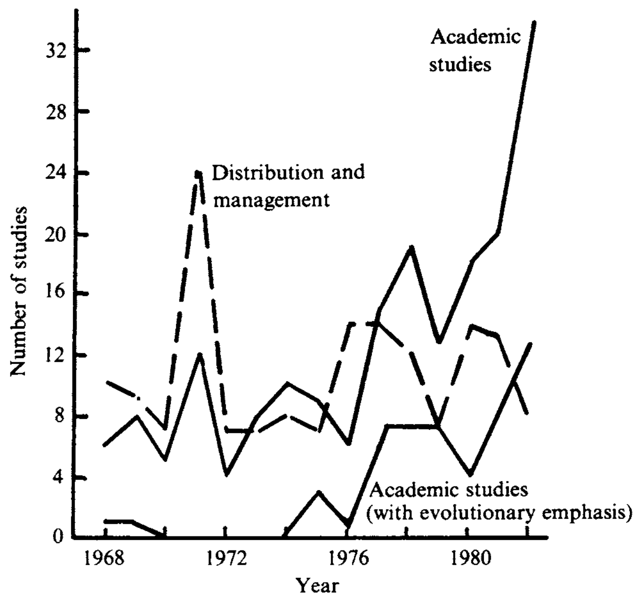
A convenient starting-point from which to examine the impact of evolutionary theory on more recent studies is the year 1968, following the publication of the classic texts *Adaptation and Natural Selection*, by G. C. Williams (1966), and *The Theory of Island Biogeography*, by R. H. MacArthur & E. O. Wilson (1967), which heralded a new maturity in the application of evolutionary theory to ecological questions. It is clear from Fig. 1.1 that the amount of research which focused on management and the clarification of distribution fluctuated irregularly during the period 1968–82. By contrast, there was a proliferation of studies with a more purely academic orientation in the latter years, though only a few of these discuss data in an evolutionary context. Where this is the case, however, most invoke evolutionary explanations *a posteriori*, rather than seek to test hypotheses pertinent to evolutionary theory.

Synopsis of argument

The explosion of interest in evolutionary ecology has very recently influenced the course of marsupial research. This book consists of six loosely-connected essays which attempt to integrate these fields. The arguments we put forward are summarised below.

Throughout the text we stress the importance of the quality of food and

Fig. 1.1. Trends in Australian research on marsupial ecology during the period 1968–82. Data obtained from Calaby, J. H., Current Literature on Marsupials, an occasional series in *Australian Mammalogy* and *Bulletin of the Australian Mammal Society*.



of its dispersion in space and time for the evolution of marsupial life histories and social behaviour. In Chapter 2 we summarise the range of foods exploited by marsupials and the problems associated with the procurement and processing of different foodstuffs. The influence which body size has on the efficiency of procurement and processing is stressed, and the range of body sizes of marsupials with different feeding strategies is identified.

Because fitness will ultimately be expressed in terms of changes in survival and/or reproduction, variations in these parameters (life history traits) have attracted considerable attention in evolutionary theory. The chief difference between eutherians and marsupials is the timing of reproduction and development, with marsupials investing comparatively little in gestation. We promote the view that organisms must be viewed as a combination of recent adaptation and old constraints, and that constraints may restrict diversification of higher taxa.

In Chapter 3 we contrast the eutherian and marsupial radiations, and conclude that the marsupials may be distinguished by a slower 'pace of life' and conservative morphological and behavioural variation. Although causes for marsupial conservatism have been suggested, none are strongly supported by available data. We develop a case which suggests that specialisation for early extrauterine life may have restricted the capacity of marsupials for paedomorphic change. Marsupials should thus be viewed as specialised, rather than primitive.

In Chapters 4 and 5 we examine the adaptation of life history traits within the constraints identified in Chapter 3. In Chapter 4 we examine the predominantly carnivorous and omnivorous polyprotodont marsupials. Data are available for three families, the Peramelidae, the Dasyuridae and the Didelphidae. All three occupy many habitats across a broad geographic range. The Peramelidae show little variation in life history traits, but can be distinguished from other marsupials by their rapid reproductive rates. By contrast, the Dasyuridae exhibit a variety of life history strategies, and these appear to be explicable in terms of the effect of body size on reproductive rate and the predictability and seasonal availability of food. The bandicoots (peramelids) mainly show facultative changes, while the life histories of dasyurids are more rigidly controlled. Studies of the Didelphidae have been restricted to tropical species, and so we are unable to place them within this perspective. However, recent data suggest that quality of food determines their reproductive rate.

The herbivorous, nectarivorous and plant exudate-feeding diprotodont marsupials are considered in Chapter 5. They show considerable diversity in both habitats occupied and life history traits but are less fecund than most polyprotodont marsupials. Once again the variety of life history strategies is largely explicable in terms of the constraints of body size, differences in the quality of food and the seasonal availability of food. There is less variation in litter size than in the Dasyuridae and litters are generally smaller. Instead variation in the interval between litters assumes greater importance in determining fecundity. In the Tarsipedidae, Burramyidae and Macropodidae, this interval may be reduced by overlapping consecutive litters. This overlap is considered to be one of the ecological values of embryonic diapause, which is found only in these taxa among marsupials. Social organisation is documented for a number of these diprotodont marsupials and is shown to be more diverse than previously recognised. Variation in social organisation is related to the quality and dispersion of food.

Marsupials may be suitable for further investigation of variation in life history and social organisation as the young can be marked and sexed during the period of obligatory attachment to the teat. This means that genetic relationships and the natal site of weaned young can be established with unusual confidence. In Chapter 6 we illustrate and expand upon the nature of this advantage by discussing our ongoing research on *Antechinus*. Australian species of this genus have the simplest life history known among higher vertebrates, as synchronous, seasonal breeding and complete post-mating male mortality mean that there is never more than one cohort of males and generally not more than three cohorts of females (often less) at any one time. This simplicity and synchrony, coupled with the ability to mark and sex young, has provided the opportunity for investigating topics not normally tractable in empirical studies of mammals. We discuss the relationship between reproductive effort and mortality, the evolution of geographic variation in brood size and the evolution of extraordinary sex ratios.

In Chapter 7 we go on to consider the impact of coevolution on the structure of communities of species. Mutualisms involving marsupials which require further investigation include plant/pollinator, fruit/frugivore, grass/grazer and fungus/fungivore interactions. The evidence for coevolution in these categories is reviewed, and the need for quantitative studies of the impact of marsupials on plant reproductive success is stressed. Recent attempts to invoke competition between species as a determinant of the structure of marsupial communities and the morphology and behaviour of constituent species are reviewed, and placed in the perspective of the ongoing controversy about the role competition plays in structuring communities. The need for experimental studies is stressed.

We conclude by suggesting a number of profitable avenues of inquiry which would fill in gaps in the knowledge discussed in this book or test hypotheses that we feel are worth further investigation.