1 · *An introduction to ecological versatility*

All scientific disciplines tenaciously seek a unified view of their subject. For example, the quest in particle physics and cosmology is to integrate the disparate physical forces in nature into a single, united framework, with as little or no dependence on empirically derived values for the model parameters (Green *et al*. 1987, Rees 1987). Although the objective is not quite so grand in community ecology, it is just as, or in some respects, more challenging because we have to deal not only with the contemporary dynamics of communities but also with the evolution of organisms. We seek a comprehensive picture of how and why resources are distributed among individuals and populations in the ways that they are, and the effects on population and community dynamics that stem from these distributions (J. Roughgarden cited in Lewin 1986, Hall and Raffaelli 1993). The immense diversity of living organisms and the wide range of physical and climatic variation on Earth, when coupled with organic evolution, have provided a seemingly endless supply of novel circumstances and outcomes. This variety has impeded the progress of the science of community ecology, which many judge to have been almost excruciatingly slow (Oksanen 1991a). Nevertheless, a rich and dynamic variety of new ideas aiming to unify community ecology continues to emerge, such as the 'macroecology' (Brown and Maurer 1989) and 'metapopulation' (Gilpin and Hanski 1991) concepts of relatively recent vintage.

In any event, one of the most obvious features of ecological communities is that species display manifestly different levels of ecological specialization (McNaughton and Wolf 1970, Futuyma and Moreno 1988). But why should specialists and generalists exist at all? Why don't all species show the same level of expertise in using resources? Generalists often are thought to hold advantages over specialists in having access to greater amounts of resources, which permits potentially higher densities and increased opportunities to satisfy or optimize nutritional requirements, if the resources are foods (McNaughton and Wolf 1970, Emlen

1973, Westoby 1978, Bernays and Graham 1988). No single food resource will be nutritionally optimal for a consumer, so that 'extreme' specialists have few options in balancing use between resources to achieve an optimal nutrition. Thus, a specialist may have to rely on resources that are either predictable or stable in availability and that entirely satisfy the specialist's requirements. On the other hand, specialists may be able to use resources more efficiently than generalists. In some cases, specializations leading to a use of resources (especially foods) with limited variation in 'quality' may have a distinct and demonstrable selective advantage (e.g., Stockoff 1993).

It is worth keeping in mind that the concepts of 'specialist' and 'generalist' are idealizations and that both are extreme cases in a continuum of patterns of resource use (Fox and Morrow 1981). In addition, few organisms show a rigid level of specialization or generalization – most seem to exhibit some degree of plasticity as circumstances change (Glasser 1982, Greenberg 1990a).

Most explanations for the patterns of specialization and generalization in natural communities can be regarded as belonging to one of two main classes. The first are interaction-based explanations that attempt to link the effects of interactions between organisms to patterns of resource use. Herbivory, parasitism, predation, omnivory, symbiosis (including mutualism) and interspecific competition comprise this set. Competition between species has been regarded as a major structuring force in natural communities, particularly by theorists (e.g., MacArthur 1969, 1970, 1972, May 1973, 1981). The other interactions have attracted varying degrees of theoretical attention and, like competition, are reviewed here in the context of their effects on patterns of resource use.

The second class of explanations consists of mechanisms within populations that affect the span of resources used. The degree of phenotypic differentiation within a population affects our perception of the diversity of resources used by that population. One obvious example is the ontogenetic, ecological differences in species displaying complex life cycles (Wilbur 1980). For example, in anuran amphibians and fishes, juvenile stages may be exclusively herbivorous while adults are exclusively carnivorous (Wilbur and Collins 1973, Werner and Gilliam 1984). Gender-based differences in resource use also are common (e.g., Selander 1966, Freeman et al. 1976, Cox 1981, Hedrick 1993). Like ontogenetic differentiation and gender-specific patterns, polymorphism, polyphenism (Moran 1992), and ecological plasticity each can influence the

degree of diversity of resource use within populations. Each of these mechanisms is considered in this book.

The first class of explanations for patterns of resource use that are based on interspecific interactions has an extensive theoretical basis. This is especially true for interspecific competition (Law and Watkinson 1989). Much of this work uses community *stability* to derive the expected patterns of resource use in natural populations. For example, in competition theory, the stability criterion is equivalent to asking either: (1) which patterns of resource use allow competitor populations to coexist at stable densities (*asymptotic stability*)? or (2) which patterns of resource use make sets of coevolved species invulnerable to invasion by immigrant populations (*invasibility*)?

The coevolutionary method had its heyday in the 1960s and 1970s, but there has been an increasing tide against it over the past decade or so (e.g., Levins 1979, Speith 1979, Hastings 1988, Getz and Kaitala 1989). Workers now are more reluctant to accept that coevolution between populations is the most profitable way of thinking about how interspecific interactions might affect resource use. As Bock (1987) noted: 'assemblages are dominated numerically by widespread species, whose past histories and present population dynamics cannot have anything specific to do with communities as we have tended to delimit them'. This means that the numerically dominant elements of many local assemblages display patterns of resource use that are characteristic of the species at large, and that are hardly affected by the local milieu (see also Gleason 1926, Brown 1984).

But if the stability approach is no longer as fashionable as it once was, what alternatives are there? Connell and Sousa (1983) considered 'persistence within stochastically defined bounds' to be more applicable than stability based on a survey of published material on natural systems. A related concept is that of *permanence* (Jansen 1987), which involves looking for community dynamics in which the population densities of all species remain positive and finite. Under the permanence criterion, the densities of populations in natural communities should be 'bounded away from zero', even though these dynamics may be chaotic or cyclical (i.e., non-equilibrial, Law and Blackford 1992). In other words, as populations become rare, there should be mechanisms encouraging their recovery (e.g., density–dependent switching by predators). Another method was presented in an interesting series of papers by J. W. Glasser and his colleagues, who turned the problem around by effectively

asking: what are the dynamic consequences and implications of specify-ing patterns of resource use first (Glasser 1982, 1983, 1984, Glasser and Price 1982)? Rather than deriving patterns of resource use by looking for stable configurations, what happens if specialists, generalists, and facul-tative strategists interact with one another in model communities? Does this approach offer insights that coevolutionary theory has missed? The vagaries of natural environments (climate, resource fluctuations), community composition (particular sets of competitors, mutualists and natural enemies; migratory fluxes) and a host of other factors make the Glasser approach a more reasonable one than a reliance on the coevolu-tion of syntopic populations. Modelling the dynamics of alternative strategies of resource use and the interactions between rival strategies requires much more work and refinement, and for this reason, forms a substantial part of this book.

Niche breadth (or niche *width*) is the usual term for describing the variety of resources used by species. There has been some confusion about the precise meaning of specialization and generalization, as evidenced by the landmark review of Fox and Morrow (1981). They noted that some species display extremely restricted use of resources at any one place (*local specialists*) while others are able to use most resources (*local generalists*). However, by substituting similar though distinct resources from place to place, and thereby retaining local specialization, some species nevertheless can occupy many types of habitat (e.g., Nitao *et al.* 1991). Some local specialists are so specialized that they can subsist on only one resource, leading to habitat specificity if that resource is restricted to one form of habitat. Local generalists may or may not show the capacity to occupy many different habitats. These observations lead one to distinguish between specialization and generalization in a local sense, that is, in populations within single habitats, and specialization and generalization in the ability of *the populations of a species* to occupy a variety of habitats.

The issues associated with the extent of the geographic distributions of species – *range* – have been covered in great detail elsewhere because range forms an interface between many disciplines, including biogeo-graphy (e.g., Cain 1944, Darlington 1957, Brown and Gibson 1983, Myers and Giller 1988, Hengeveld 1990), evolution and genetics (e.g., Simpson 1965, Endler 1977), animal behaviour (e.g., habitat selection, Rosenzweig 1991, and territoriality, Cody 1978, Murray 1981), land-scape ecology (Forman and Godron 1986), and areography (Rapoport

1982). However, range and specialization and generalization of habitat use need not be directly related, depending upon the geographic distribution of habitats. Thus, some species might occur over vast areas but only in specific habitats (e.g., rocky outcrops), while others might be geographically localized, but within that small area, occupy all available habitat types (see Hesse *et al*. 1951).

So, there really are three levels to consider in terms of ecological specialization and generalization: (1) the diversity of resource use at the local scale; (2) the diversity of habitats occupied; and (3) the extent of geographic range. The latter has been covered at length in comparatively recent reviews (e.g., Brown and Gibson 1983, Hengeveld 1990), so there seems to be no need to study the determinants of range in much detail here. The niche, so to speak, of the current book is resource use at the local scale, plus a consideration of the relationships between local- and habitat-based specialization and generalization. To further clarify the distinction between these scales, a short overview of some of the issues involved is presented next. Species are viewed as consisting of sets of populations communicating (by migration and/or dispersal) to a greater or lesser extent depending upon their vagility and the barriers to interchange (Hesse *et al*. 1951, Briggs 1974, Opdam 1991). Populations usually are thought of as sets of potentially interbreeding or interacting conspecific individuals.

The local scale

The use of a wide range of resources implies a high niche breadth (generalization), while using few resources, or a reliance on a single resource, connotes a low breadth (specialization). Populations can be regarded as being located along a conceptual continuum from specialized through to generalized. It is clumsy to have to refer continually to the specialized–generalized continuum, so I adopt the simpler term *ecological versatility*. Ecological versatility can be defined formally as *the degree to which organisms can fully exploit the available resources in their local environment*.

I use the term *exploit* to mean the acquisition, handling and/or processing, and conversion of resources into gains in fitness, where the latter comprises all aspects related to fitness, including maintenance, reproduction, and survival. Resource *utilization* is used in this book to refer to just the acquisition of resources, with no explicit reference to

how the resource use is converted into a gain in fitness. There has been no formal distinction between these terms in the literature, so these definitions of exploitation and utilization are specific to this book.

Ecological versatility explicitly depends upon both the fitness returns from utilizing resources and the relative availability of resources. How fully a set of resources is exploited is gauged by how closely the fitness gained from exploiting a resource corresponds to its relative availability. An idealized generalist matches the fitness gains precisely with the relative availabilities of a suite of resources. It is worthwhile expanding on the fitness and resource availability aspects to explain their significance in greater detail.

Why is fitness so important, which amounts to why focus on the exploitation of resources rather than on their utilization? By way of illustration, consider food resources. It turns out that the nutritional aspects of food use and the fitness gains associated with their use need not be related in a straightforward way (Real 1975). This has led to a contention between models of foraging strategies in large herbivores (e.g., ungulates) and carnivores because of the much wider range of nutritional values of plants compared with animal prey (Owen-Smith 1988, du Toit and Owen-Smith 1989, Verlinden and Wiley 1989). When one tries to predict the optimal diet for a predator, one can largely ignore the nutritional content and relative digestibility of alternative prey types, which are more or less the same for all prey types. The solution depends much more on the distributions and handling times of alternative prey types (Pyke 1984, Stephens and Krebs 1986). On the other hand, herbivores use food types that may differ markedly from one-another in nutrient content and the concentrations and kinds of chemical deterrents and inhibitors (digestibility). Thus, although acquisition rate is thought to dominate the returns for most predators, digestion rate probably controls diet selection in herbivores (Belovsky 1986, Verlinden and Wiley 1989). The actual fitness returns from the components of the diets of predators therefore depend upon things like how alternative prey are distributed in space and how long it takes to handle them. Either of these factors may be affected by differential exposure to natural enemies in using alternative prey, which can modify the fitness returns. In large herbivores, fitness gains often are more closely associated with the sheer bulk of fodder that has to be digested than with finding it, leading to complicated expressions linking together nutritional content, food bulk, digestion rates, and gut volume (see Belovsky 1986).
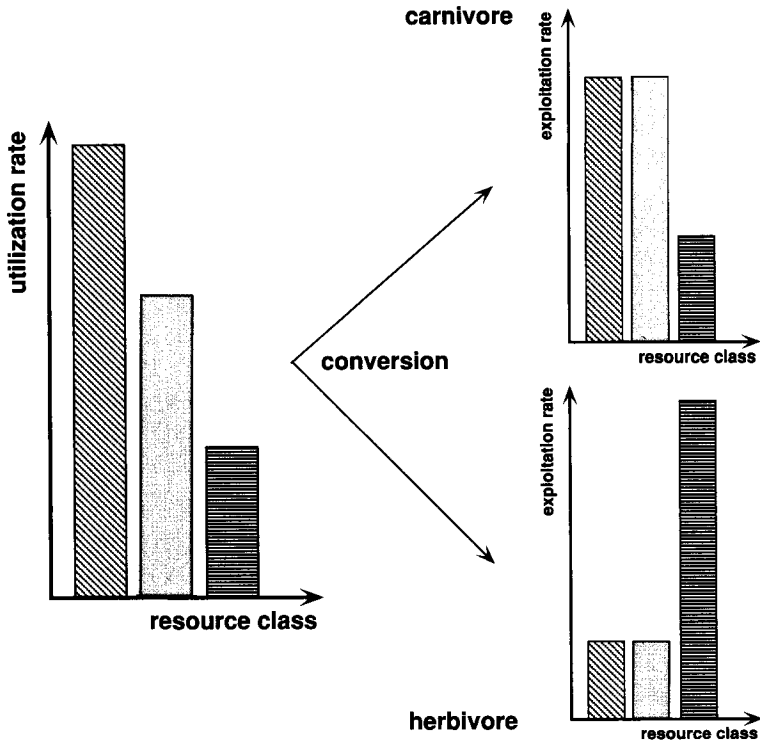
Fig. 1.1 Hypothetical example illustrating the difference between utilization and exploitation rates. The relative value of three dietary constituents remains much the same after conversion in a carnivore but, due to nutrient content or digestibility perhaps, the respective values for a herbivore differ markedly from the relative utilization rates.

To make this contrast more concrete, consider a predator and a herbivore each having diets consisting of three components, in the proportions 3 : 2 : 1 (i.e., utilization rates; Fig. 1.1). The fitness returns to the predator may be much the same set of ratios, 2.5 : 2.5 : 1, say, but the distribution for the herbivore may be much more biased because of nutritional imbalances and digestibilities, 1 : 1 : 4, say. In this example, the predator depends more evenly on the fitness returns from all three resources than does the herbivore, and can be considered to be more generalized (ignoring relative availabilities for this argument). This clearly is a contrived example between very different organisms and related to a single part of the resource spectrum (i.e., food), but the principle is generally valid.

The relative availability of alternative resources is the other key issue in determining versatility. How does availability influence versatility? Let several resources provide more-or-less similar returns in fitness per unit utilized. Then, a generalized consumer appears to be indiscriminant because it exploits resources in the proportions in which the resources occur in its environment (Petraitis 1979, Fox and Morrow 1981). In contrast, a specialist exploits resources differentially, so that some resources are used in higher proportions than their availability, and hence, other resources are underutilized (hence a low versatility).

Although ecological versatility may appear to be synonymous with niche breadth or niche width, there are important distinctions. The most crucial of these is that versatility explicitly depends upon the correspondence between resource exploitation and resource availability. Estimates of the breadth of resource use that do not refer to the relative availability of the resources are not of much use for the reasons discussed by Petraitis (1979) and others. In particular, differences in breadth may merely reflect biased resource availabilities rather than indicating the selectivity of, or suitability for, consumers. Versatility also hinges on resource exploitation, which involves the derived fitness increments from using resources rather than the relative use of resources themselves. Niche breadth is based on utilization, which can cause problems for deciding the units on which to gauge breadth (e.g., numbers or volumes of prey? Case 1984). Niche breadth also suffers from being a general term encompassing not only the diversity of resources used at the local scale, but also other aspects of the ecological flexibility of a species, including the variety of habitats used (e.g., McNaughton and Wolf 1970). Fox and Morrow (1981) have drawn attention to the problems associated with such a broad definition. In summary then, ecological versatility, strictly set at the local level of the population, is a more constrained, better-defined concept than its counterpart niche breadth.

Habitat use

The preceding definitions refer to the strictest meaning of the term ecological versatility – the degree of correspondence between the exploitation and availability of resources at the local or population scale. But the capacity of the populations of a species to occupy many distinct habitats also is an inherently important ecological characteristic (Bock 1987). Indeed, the versatility of habitat use historically has attracted more

interest than local versatility, perhaps because of the evolutionary and biogeographic implications (e.g., Jackson 1974).

It is important to re-emphasize that versatility in habitat use is a quite-distinct concept from that of range. Hesse *et al.* (1951: Chapter 8) established this distinction well. They used the term *ubiquity* to denote the diversity of habitat types that the populations of a species occupy. Thus, a *ubiquitous* species has populations occupying many distinct types of habitat while a *restricted* species is confined to a limited number of habitat types. Note that some workers seem to be unaware of this priority for the term ubiquity (e.g., Burgman 1989, Rahel 1990), so one must be wary about the precise meaning of ubiquity in this book. For the extent of geographic range, Hesse *et al.* (1951) used the term *cosmopolitanism*. Thus, a *cosmopolitan* or widespread species has a large geographic range, while a *localized* species occurs in only a small geographic area. 'Large' and 'small' geographic ranges are somewhat arbitrary terms of course, but Hesse *et al.* (1951) used the area of geographic extent compared with the vagility of members of a species as a heuristic to clarify the point. I follow the terminological conventions of Hesse *et al.* (1951) throughout this book.

Several authors have recognized that ubiquity amounts to the evenness of densities of populations of a species among alternative habitat types (e.g., McNaughton and Wolf 1970, Rice *et al.* 1980). A completely ubiquitous species would exhibit the same density irrespective of habitat type. This means that the species responds weakly to large-scale habitat heterogeneity. The degree of ubiquity is sensitive to the changes in the relative densities of populations in different habitats. Even though a species has populations in every habitat type that is sampled, it can be regarded as effectively restricted if the density in one habitat is much greater than in any of the others. This idea of the evenness of the spread among habitats is central to the concept of ubiquity.

These points can be demonstrated by looking at some patterns of densities among various woodland and forest habitats of year-round resident species of birds in central Victoria, Australia (Fig. 1.2). The densities of the grey shrike-thrush (*Colluricincla harmonica*), for example, were not significantly different among the five habitats, thereby fulfilling the definition of a ubiquitous species. The eastern rosella (*Platycercus eximius*), a parrot, occupied all habitat types, but in significantly higher densities in the more open riparian (dominated by river red gum, *Eucalyptus camaldulensis*, and grey box, *E. microcarpa*) and lowland
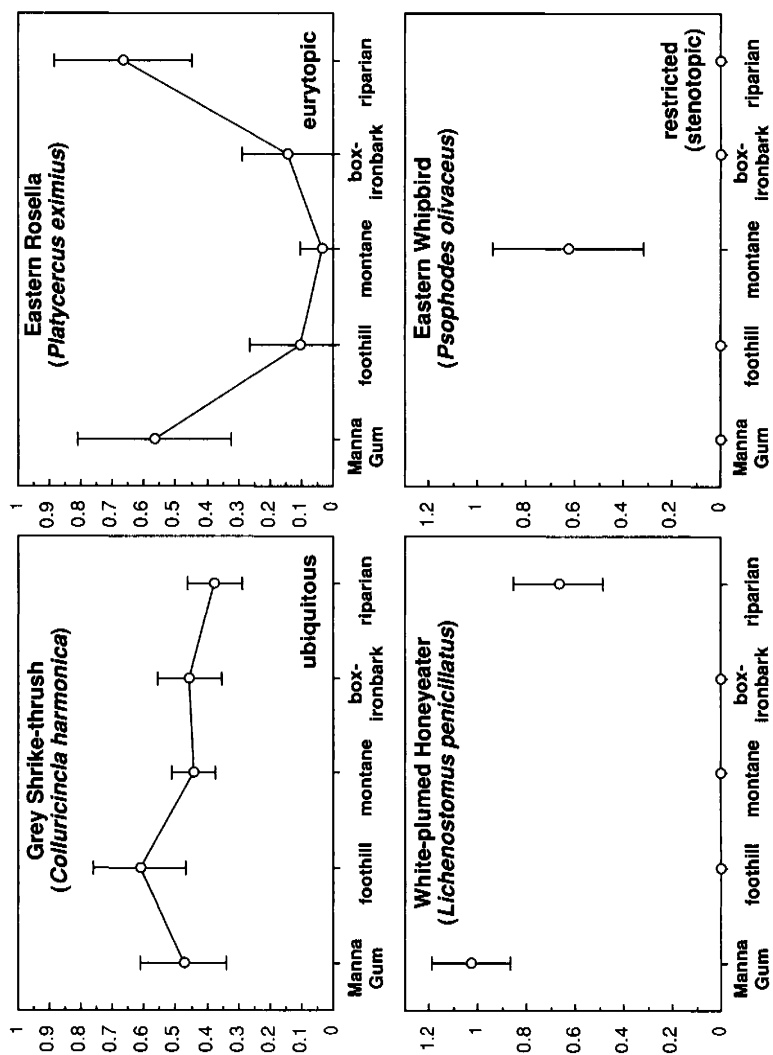
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Fig. 1.2 Various degrees of ubiquity exhibited by four species of birds in woodland and forest habitats of central Victoria, Australia. Data are means and 95% confidence intervals for four 'replicates' of each of five kinds of habitat. Data were first standardized relative to the maximum recorded density at any replicate site (hence maximum of 1.0), then transformed by using arcsin–square roots (data collected by the author).