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PART I

The foundation of avian community ecology

A scientific discipline operates on a foundation composed of three factors: its history, its logical and theoretical structure, and its methodology. These factors indicate what is known in the discipline and how that knowledge was gained, how practitioners of the science think, and what procedures are available and acceptable. They determine what sorts of questions are interesting or appropriate, how the questions should be framed, whether or not answers can be obtained, and how much confidence should be placed in those answers. The three factors are interrelated: history exerts a powerful influence on the theory and thinking that are current in a discipline at any time, and these in turn often dictate what sort of research is likely to produce findings that will contribute to further progress. The research traditions that develop in this way both determine and are constrained by the methods that may be used to gather observations or conduct experiments. Developments in methodology and thinking and the accumulation of facts comprise the history on which subsequent activities in the discipline build.

In order to understand and evaluate how science is done in avian community ecology and what is known or thought about bird communities, we must consider these elements of its foundation. In the three chapters that follow I develop this background.

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The development of avian community ecology

Community ecology is concerned with identifying the patterns that characterize natural assemblages of species, understanding what has caused these patterns, and determining how general they are. Birds have been especially popular with ecologists investigating communities, perhaps because birds are diurnal and often conspicuous, their behavior can be documented with relative ease, and their distribution, natural history, and systematics are generally well known. As a consequence, a tremendous amount of information has been published on bird communities, and studies of such communities have contributed in major ways to the conceptual and theoretical framework of community ecology as a whole (Wiens 1983, Karr 1983). We know a lot about bird communities, or at least we think we do.

One of the themes of this book, however, is that we may not know as much as we think about bird communities. Knowledge and thinking in any science should be subjected to periodic re-examination. In this chapter I begin such an evaluation by considering how communities are defined, how recent views of communities developed, and how controversy has emerged about these views.

What is community ecology about?

The best way to determine the scope of operation of a discipline is to ask how it is formally defined. Dictionaries or introductory ecology textbooks provide an array of such definitions, and they cover a broad range of meanings. Whittaker (1975), for example, considered a community to be 'an assemblage of populations of plants, animals, bacteria, and fungi that live in an environment and interact with one another, forming together a distinctive living system with its own composition, structure, environmental relations, development, and function'. At the other extreme, MacArthur (1971: 190) advocated a more relaxed definition: 'any set of organisms currently living near each other and about which it is interesting to talk'.

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If one surveys the spectrum of community definitions, several features consistently emerge (Table 1.1). The co-occurrence of individuals of several species in time and space is central to all definitions. Most also stress the importance of interactions (indeed, interdependencies) among these populations. Communities are often viewed as possessing a dynamic stability that tends toward an equilibrium composition. Moreover, this composition may be repeatable or constant under similar environmental conditions, allowing the recognition of community 'types'. Some authors stress the emergent properties of communities, attributes of structure (e.g. species diversity) or functioning (e.g. energy flows) that are found only at this level of organization.

To some extent, the different definitions of communities are consequences of different objectives. Plant ecologists, dealing with spatially fixed assemblages, often emphasize the description of such associations and their changes over successional time; animal ecologists, confronted with mobile, behaviorally active organisms, often stress the importance of interactions and functional relationships among species. Some workers define communities in terms of habitat units (e.g. rocky intertidal communities; Menge 1976), others by life-form categories (e.g. tree or herbaceous understory communities), others by taxonomy (e.g. bird or lizard communities). Any of these approaches can be rationalized by persuasive arguments. MacArthur, for example, justified his restriction of attention to co-occurring birds rather than, say, birds and butterflies by emphasizing the importance of finding general patterns and noting that 'there are many of these if we confine our attention to birds or butterflies, but no one has ever claimed to find a diversity pattern in which birds plus butterflies made more sense than either one alone' (1972: 176).

MacArthur's emphasis was on the operational value of a community definition rather than its abstract soundness. The difficulty of dealing operationally with the apparently enormous and complex web of interactions among populations, however, led Andrewartha and Birch (1954, 1984) to conclude that community ecology 'is not likely to give rise to a satisfactory, or even to any, general theory about the "distribution and numbers of animals in nature"' (1954: 4). It is nonetheless clear that the notion of the community must have some operational value, for it has provided a framework for a tremendous number of studies. As Schoener (1986a) has observed, community ecology is one of the most alluring (but also among the most tumultuous) of ecology's subdisciplines. For the remainder of this book I will accept the operational utility of talking about bird communities as assemblages of individuals of several species that occur together.

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Table 1.1. *Common elements of definitions of ecological communities, and some problem areas related to them*

Element	Problem
1. Contain several species	Degree of inclusiveness
2. Species co-occur in time and space	Scale of study
3. Populations interact	Nature of interactions; non-interactive sets of species
4. Assemblage is stable; properties self-regulating	Definition of equilibrium; nonequilibrium conditions
5. Composition repeatable in similar environments	Determination of boundaries
6. Possesses emergent properties in structure and functioning	Are emergent properties statistical consequences of individual components?

The historical roots of contemporary avian community ecology

Initial development

In the early part of this century, previous thinking about ecological communities crystalized into two sharply differing views, which, with different dressings, continue to dominate our thinking today (McIntosh 1985, Underwood 1986a). On the one hand, Clements (1916) argued that communities were discrete, repeatable assemblages of species that were so closely integrated in their functioning that the community as a whole possessed properties paralleling those of individual organisms. At the other extreme, Gleason (1917, 1926) held that communities lacked internal organization or integration, being no more than fortuitous coincidences of the ranges of species that responded to environmental conditions quite independently of one another. The opposing views were strongly held and sharply argued, but the Clementsian view took hold and dominated community ecology for several decades (McIntosh 1967, 1970, 1975, 1982; Richardson 1980, Worster 1977). A major ecology textbook of the period (Allee *et al.* 1949) aggressively promoted Clements' view while scarcely mentioning Gleason.

For various reasons, the conceptual edifice of Clementsian communities began to crumble during the later 1940s and early 1950s (McIntosh 1975, 1985). Disillusioned with the rigid inflexibility of community classification, the strained analogies with 'supraorganisms', and the exaggerated emphasis on climate as the determinant of community patterns, many ecologists studying plant communities began to consider Gleasonian alternative. This trend was bolstered by the development of mathematical techniques such as

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ordination and gradient analysis, which often demonstrated quantitatively the lack of interdependence in species' distributions (Whittaker 1953, Curtis 1959). Some elements of the Clementsian view, however, were transformed into principles of ecosystems (Odum 1969) and continue to play a dominant role in research in that discipline (Simberloff 1982).

How did all of this affect studies of bird communities? Not very much, really. Rather few such studies were conducted prior to the 1950s. Some studies (e.g. Kendeigh 1934, 1945, Twomey 1945, Fawver 1947) were conducted within the general Clementsian framework, but most often the associations of various bird species with life zones, vegetation formations, or biotic communities (biomes) were simply described (e.g. Palmgren 1930, Lack 1933, Pitelka 1941, Odum 1950). Birds were not considered to form communities in their own right but rather were superimposed on communities that were climatically or vegetationally defined. The studies of Bond (1957) and Beals (1960) of assemblages of breeding birds in Wisconsin woodlands, however, were conducted in the context of a Gleasonian view, and both clearly documented that the bird species were distributed on gradients of forest vegetational composition largely independently of one another.

The transformation of avian community ecology

During the late 1950s and early 1960s, however, animal community ecology underwent a transformation and revitalization, largely as a result of the work on birds by David Lack and, especially, Robert MacArthur. Lack's views on bird communities took form during the early 1940s and were expressed most clearly in his studies of shags and cormorants (1945b), raptors (1946), and Galápagos finches (1945a, 1947). He emphasized the importance of interspecific competition in structuring communities through its effects on the evolutionary development of ecological and morphological differences among co-existing species. The hypotheses that he derived from his observations were intuitive and qualitative rather than mathematical, and were not designed to be especially testable (Ratcliffe and Boag 1983). Lack apparently was influenced little by either the Clementsian or Gleasonian view, but instead drew his inspiration from the theory of competition that emerged from Gause's (1934) laboratory experiments and Mayr's (1942) views on speciation (Ratcliffe and Boag 1983, Kingsland 1985). Lack turned his attention to the mechanisms of population regulation in the late 1940s and did not return to considerations of community ecology until two decades later (Lack 1971, 1976).

The proximate impetus for the transformation of avian community

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ecology came from the work of MacArthur and his colleagues. Drawing on themes developed by Hutchinson (1951, 1957) and influenced by Lack's studies, MacArthur looked at bird communities in new and different ways. MacArthur visualized community patterns in neat and simple theories, usually accompanied by mathematical formulations. As had Lack, he derived his concepts more often from population ecology than from Clementsian or Gleasonian community ecology. He shared with Clementsians, however, a firm belief that communities were organized, integrated assemblages, not simply independent collections of species that happened to co-occur because of ecological similarities. Both MacArthur and Lack, then, emphasized the importance of interactions and interdependents among species in producing structured community patterns.

The effect of this work on community ecology was profound. From a somewhat biased perspective, Cody and Diamond (1975: vii) observed that

> when this era began in the 1950's, ecology was still mainly a descriptive science. It consisted of qualitative, situation-bound statements that had low predictive value, plus empirical facts and numbers that often seemed to defy generalization. Within two decades new paradigms had transformed large areas of ecology into a structured, predictive science that combined powerful quantitive theories with the recognition of widespread patterns in nature.

Kingsland (1985: 176) suggested that, together with Hutchinson, MacArthur brought mathematical methods that 'had been lingering on the fringes of ecology squarely into the mainstream of the science'.

Characteristics of the MacArthur approach

What was so powerful about the MacArthur approach to community studies? To some degree, it became popular because it filled a void. Animal community ecology in the 1950s was stagnating, and the MacArthur approach posed a large number of new and interesting questions and provided a model for answering them. MacArthur's studies were a special impetus to investigations of bird communities. With the benefit of hindsight, we can discern from MacArthur's own writings (e.g. MacArthur and Connell 1966, MacArthur 1971, 1972) and those of his students and colleagues (e.g. Cody 1974a, Cody and Diamond 1975, Fretwell 1975, Diamond 1978, Pianka 1981, Hutchinson 1978; see also Ricklefs 1975, Wiens 1976a, 1977a) some of the basic features of this approach (modified from Wiens 1983):

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1. There was an emphasis on the importance of detecting and explaining patterns in nature. 'To do science,' MacArthur wrote, 'is to search for repeated patterns, not simply to accumulate facts' (1972: 1). Observations that failed to form clear and repeated patterns were not interesting.
2. The most interesting and important patterns and theories were those that possessed *generality*: 'science should be general in its principles' (1972: 1). General patterns were most likely to have a general explanation, whereas little progress could be expected if scientists became excessively preoccupied with the details of patterns that characterized only specific situations and that, therefore, were likely to have a specific explanation of limited generality. As MacArthur (1968: 159) noted, 'these kinds of general events are only seen by ecologists with rather blurred vision. The very sharp-sighted always find discrepancies and are able to say that there is no generality, only a spectrum of special cases.'
3. The patterns of communities were usually held to be consequences of *deterministic* processes. Although chance did enter into some of MacArthur's formulations (e.g. island colonization, MacArthur and Wilson 1967; the occupancy of patchy habitats, Horn and MacArthur 1972), the primary emphasis was upon a strictly deterministic relationship between cause and effect.
4. Most community patterns were a result of *competition* between species in the face of limited resources. Such interactions lead to the exclusion of marginally adapted species from communities, leaving the assemblages optimally structured by the ecological spacing among their members. As Cody and Diamond (1975: 5) put it, 'it is natural selection, operating through competition, that makes the strategic decisions on how sets of species allocate their time and energy; the outcome of this process is the segregation of species along resource–utilization axes.'
5. Communities, and therefore the patterns they expressed, were presumed to be at or close to an *equilibrium* determined by resource limitations. Environments might vary in time or space, but population changes, driven by competition, would rapidly adjust the structure of the community to the changed conditions, preserving the general patterns. A corollary of this assumption was that suitable habitat was fully occupied by individuals and that the community as a whole was 'saturated', containing the optimal number and kinds of species for the resource conditions.

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Kingsland (1985) suggested that, in deliberately selecting problems so as to minimize the complicating effects of past history, MacArthur emphasized populations and communities in apparent equilibrium.

6. *Optimality thinking* was prevalent. The patterns of populations and communities were considered to be products of natural selection, acting primarily through competition, and as a consequence were optimal. Thus, Cody (1974b: 1156) observed that 'all important processes and patterns in biology are products of natural selection', which is 'a mechanism that maximizes fitness . . .; it leaves only the best-adapted or optimal phenotypes for our inspection'.
7. Investigations were guided by *theory*, which provided predictions about the patterns of communities that could be tested with observations. Theory thus determined which measures or observations were appropriate and pointed field or laboratory work in specific directions. MacArthur (1972) observed that it is not only important to distrust theory until it is confirmed by facts but also that one should not put too much faith in facts until they have been confirmed by theory, and May (1976) lamented that the wide variation among observations 'tended to discourage theoretical activity'.
8. The most appropriate and efficient way to discern patterns and test theories was through *comparisons* of different situations in nature. Such 'natural experiments' capitalized on the variation that occurs naturally in the environment: differences or similarities between islands and mainland, between different elevational zones on a mountainside, between habitats at different latitudes, and so on. Active experimental manipulation of species or their resources was considered unnecessary and possibly confusing (Diamond 1978, 1983, Cody 1974b).
9. Often, theories were tested or patterns explained by the use of *selected examples*. Observations that agreed with theoretical expectations especially well were used to confirm the theory, while contradictory or less confirmatory observations received little attention or were simply not mentioned. Attempts to define patterns or test the match of observations to predictions through rigorous statistical procedures were infrequent.
10. The *methodology* of documenting patterns or testing the predictions of theory generally received little attention and often lacked

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> rigor. Although much of the theory was expressed in mathematical terms, field data were frequently gathered following no particular design or sampling protocol, and resource conditions were often simply inferred rather than measured. Moreover, observation was usually restricted to a few variables of interest, those that were 'already identified with environmental variables for which competition takes place, as indicated by resultant displacement patterns' (Cody 1974a). MacArthur (1971: 190) expressed a similar view when he wrote that 'there is no such thing as a "correct" or "incorrect" measure of diversity or stability or anything else. The virtue of a measure resides solely in the neatness of the relations constructed from it.'

Perhaps the most evident manifestation of the importance of the transformation in ecology precipitated by MacArthur's work is in the questions that community ecologists began to ask in the 1960s. When Beals (1960) analyzed the bird communities of the Apostle Islands in Lake Superior, for example, he focused on ordinating the species and only noted in passing that the number of species present decreased as island size became smaller. A few years later, the species–area relationships among these islands and their relations to colonization and species–turnover patterns would more likely have been the targets of such an investigation. Community ecologists increasingly asked questions such as: What factors determine the limits to the similarity of coexisting species? How does the diversity of bird communities relate to the structural diversity of their habitats? What happens when a species competes with several other species? What determines the number of species in a habitat? On an island? In a continent? Are there regularities in the size distributions of species in communities? Do communities in similar environments converge in structure? Are there 'rules' that describe the process of community assembly? Such questions were new and interesting and generated considerable enthusiasm. They formed the framework for new kinds of community studies, and the characteristics of the 'MacArthur approach' noted above prescribed a protocol for this research.

The MacArthur approach as a paradigm

Elsewhere (Wiens 1983) I have argued that this approach displayed many of the attributes of a Kuhnian paradigm (Kuhn 1970a). It presented a coherent, unified tradition of scientific research that defined which problems were interesting and merited study and which were not. It formed the intellectual and conceptual foundation for the education and training of students in the discipline. And it discouraged alternative expla-

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