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# SECTION III

## SPECIALISTS VERSUS GENERALISTS

*Overview*

# SPECIALIST OR GENERALIST: AVIAN RESPONSE TO SPATIAL AND TEMPORAL CHANGES IN RESOURCES

HARRY F. RECHER

Under what conditions should a species specialize on a particular set of resources and when is being a generalist the most successful strategy? These questions have been central to the development of community ecology as a science since MacArthur and Levins developed theories of resource allocation and limiting similarity (Levins 1968; MacArthur 1970; MacArthur and Levins 1964, 1967). These early models assumed that species competed for resources that were presented as a continuum along which species segregated. The degree of specialization or the extent of segregation depended upon the similarity of resources and their abundances. Specialization was favored if resources were abundant or very different. If resources were similar or scarce, being a generalist or a jack-of-all-trades was deemed the best strategy.

The models predicted other responses to a changing resource spectrum. For example, as species specialized on particular resources, more species could co-exist and community diversity would increase. If a generalist dominated the available resources, there would be fewer opportunities for co-existence and diversity would decrease. Models were not mutually exclusive and arguments were raised for a range of alternatives. Thus, in a community of generalists, species diversity could increase if overlap in the use of resources was possible. This might occur if resources were superabundant relative to the demands of the species using them, or if other factors (e.g., predation, chance climatic events) prevented competition from going to completion, with one species excluding another.

These mathematically elegant, albeit simple, models provided a conceptual framework on which a generation of ecologists based their studies of avian foraging ecology and community structure. This was true for those who rejected the assumption that species necessarily competed for resources (e.g., Wiens 1977, Simberloff and Boecklen 1981) and for those who accepted competition as the driving force in the evolution of differences among species (e.g., Cody 1974, Diamond 1978).

There is no doubt that the models of MacArthur and Levins launched an extremely valuable period of scientific enquiry. There is now a considerable literature on the foraging ecology of terrestrial birds and a number of these studies present valuable empirical descriptions of community structure. Nonetheless, gaps remain in our knowledge of terrestrial birds. If I wanted to be glib, I would say that most studies of the foraging ecology of terrestrial birds have focused on the breeding season; most have compared a few species of birds in one or at most a few places; most have treated the individuals of populations as the same; most have combined data collected through the day or over a season or over a year. Few studies have attempted to measure the kinds and abundances of resources available to birds or to directly measure their use by birds. When resources have been measured, emphasis has been on the abundance of prey and has generally failed to distinguish between abundance (the total amount of the resource) and availability (the amount of the resource that birds can use). There have been few attempts to measure either the abundance or availability of different foraging substrates (e.g., amount of different kinds of bark available to bark foraging birds). A consequence of this narrow data base is that questions of temporal and spatial changes in the use of resources by birds have never been satisfactorily answered. Nor, apart from a small number of studies, such as those of Darwin's finches by Peter Grant and his colleagues (see Grant 1986), are there adequate data that describe individual variation in foraging habits in a way that allows the separation of the effects of learned behavior and environmental factors from genetic differences.

Although ornithologists have often described the ways that co-existing species apportion resources, questions of when to be a specialist and when to be a jack-of-all-trades remain a challenge. There are not only interesting ecological

questions of when, where, and why species specialize (or generalize) on particular resources, but there are practical considerations. The conservation and management of terrestrial avifaunas requires more detailed information on temporal and spatial differences in the use of resources by species than is available for the majority of species.

I am not the first to recognize these omissions in foraging ecology. Papers in this section of the symposium focused on questions of "Specialist or generalist? Avian response to spatial and temporal changes in resources." Harry Bell and Hugh Ford presented data on the changes in the diets of Australian warblers (Acanthizidae) as the abundance of food decreased during a long drought. Thomas Martin and James Karr studied the foraging behavior of North American wood warblers (Parulinae) during migration and contrasted this with the behavior of the same species during the breeding season and on their wintering grounds. Kenneth Rosenberg described the foraging ecology of specialized dead-leaf foragers in Amazonian forest understory in relation to resource (food and substrate) abundance and the presence-absence of potential competitors. The papers by Stephen et al. and Kellner et al. investigated the response of birds to a superabundant food resource (periodical cicadas) in Ozark forests and the effects that changes in the abundance of a major food item might have on patterns of avian predation on other prey organisms. Thomas Sherry presented an overview of the importance of distinguishing ecological and evolutionary processes in studies of avian foraging ecology. Many of his ideas were derived from studies of the Cocos Finch (*Pinarolaxias inornata*), a species that exists in the absence of competitors (Grant 1986). Each paper in this section represents the kinds of studies that are required for the continued development of our understanding of the foraging ecology of terrestrial birds. By focusing on the behavior of individuals within a population (Sherry), following changes in the behavior of birds over long periods (Bell and Ford) and between seasons (Bell and Ford, Martin and Karr), and studying the behavior of birds in response to known abundances of prey (Kellner et al., Stephen et al., Rosenberg) each of the major areas of avian foraging ecology where more information is required was identified.

## SPECIALIST OR GENERALIST?

What is a specialist and what is a generalist? The answer depends on the design of the research, the hypotheses tested, and the system studied. In simple terms a specialist is a species that uses a narrow range of resources and a generalist is one that uses a wide range of resources. Whether any particular species qualifies as a specialist or generalist depends on the species to which it is compared (do they use more or fewer kinds of resources?) and the resources in question (are they diverse or restricted?).

Whether or not particular resources are used depends on morphological and behavioral limitations, learned patterns of behavior, and physiological requirements. For example, the different conclusions reached by Martin and Karr (this volume) and Greenberg (1984a, c) in describing the behavioral plasticity of wood warblers appear to result from the different foraging behaviors investigated. Martin and Karr studied the behaviors used by warblers in taking prey, whereas Greenberg investigated their response to different substrates. Species that had a diverse foraging repertoire were conservative in their use of substrates.

The response of a bird to its environment and the resources it uses depends on the availability of particular resources, the individual's needs (e.g., its physiological requirements), and the presence or absence of other individuals and species. Responses to any variable are graded. Not only do species differ in their use of resources through time and in different places, but the extent to which they specialize or generalize in their use of resources may change. A pattern of change in resource use is as significant a part of the ecology of a species as its use of resources at any particular time or place. Equally important are individual differences within a population in the use of resources.

## TEMPORAL PATTERNS

An individual studied intensively for 24 hours may use a narrower range of resources than the same individual studied over a season or from year to year. Similarly, there will be changes in behavior and in the use of resources between seasons and from year to year. These changes will occur in response to weather, to changes in resource abundance and availability, to the differing physiological requirements of birds as they proceed through their molt and reproductive cycles, to the different demands of migration and breeding, and to changes in the species composition of avian communities. In part these changes will be shown by increased or decreased specialization on particular resources.

As resources become more abundant, many species use a broader range of resources and niche overlap increases (e.g., Bell 1985b, Recher 1989b). Often these changes are associated with seasonal patterns of prey abundance: with increased food abundance during spring and summer, niche overlap increases; with decreased food abundance during autumn and winter, niche overlap

decreases (e.g., Bell and Ford, this volume; Recher 1989b).

Early work on the ecology of terrestrial birds focused on species relationships during the breeding season with emphasis on the use of food resources. The argument was that, with the need to obtain large amounts of food for egg production and feeding young, breeding placed the greatest demands on birds (e.g., Lack 1968b). It was therefore assumed that competition for resources would be greatest during the breeding season and that species would be most different at this time. Food was assumed to be the critical resource (Martin 1987).

The emphasis on breeding, food resources, and competitive interactions between co-existing species restricted the diversity of studies undertaken. Perhaps because of the practical difficulties in working with mobile populations, little work has been done on terrestrial birds during migration. However, as demonstrated by Martin and Karr (this volume), migration places considerable demands on birds and may be a significant factor in the evolution of specific behavioral and morphological traits. Migration often occurs when food resources are restricted and weather (particularly low temperatures) limits foraging opportunities or requires increased energy for survival. Species interactions at this time may be more significant than those on breeding or wintering areas where food may be abundant, individuals occupy familiar territory, and the energy requirements of individuals are less demanding (e.g., Fretwell 1972, Martin 1987).

Changes in resource abundance not only occur between seasons, but may vary significantly between years. Severe drought conditions in southeastern Australia during 1982–1983 led to almost total reproductive failure of forest and woodland birds and to increased mortality (Ford et al. 1985, Recher and Holmes 1985). Bell and Ford (this volume) showed how birds first specialized on particular resources with decreased niche overlap and then used a wider range of resources with increased overlap as food abundance decreased during prolonged drought.

## SPATIAL PATTERNS

The distribution and abundance of resources not only changes with time, but varies significantly between habitats and regions. Kellner et al. (this volume) and Stephen et al. (this volume) used the presence or absence of periodical cicadas to study the response of birds to an abundant food resource. Cicadas were an important food where they occurred. However, it was difficult to demonstrate either a significant shift in avian foraging behavior or to find a response in other prey organisms that may have been released from high levels of avian predation as birds obtained more of their requirements from cicadas.

Demonstrating a response to spatial patterns in resource abundance is difficult. Martin and Karr (this volume) suggested that birds have a characteristic foraging signature, which they define as the ranked abundance of different kinds of foraging maneuvers (e.g., relative proportions of hawks, snatches, and gleans). The signature remains unchanged, although the proportions of particular behaviors may vary, despite changes in resource abundance and physiological requirements. A problem with demonstrating a response to changing patterns of resource abundance is the difficulty in measuring resource availability. Rosenberg (this volume) emphasized the importance of studying resources that can be accurately and precisely measured. He demonstrated that birds selected the most profitable foraging substrates and shifted between substrates as resource abundance changed between habitats. Competition for resources may also have affected the kinds of substrates birds used.

The presence or absence of potential competitors is often assumed to affect spatial variation in the use of resources by terrestrial birds. Keast (1976) drew attention to changes in the foraging behavior of some Australian birds in Tasmania and southwestern Australia and suggested this was in response to the absence of certain competitors. For instance, Brown Thornbills (*Acanthiza pusilla*) appeared to forage higher in the forest canopy in places where the canopy foraging Striated (*A. lineata*) and Little (*A. nana*) thornbills were absent (Keast 1976). Studies that I have recently completed suggest that changes in the foraging behavior of Brown Thornbills in the absence of other acanthizids result from differences in the spatial and temporal patterns of resource abundance, including kinds of prey and foraging substrates, rather than a release from competitive pressures (Recher et al. 1987, Recher unpubl. data).

## CONCLUDING REMARKS

Papers in this section addressed questions of spatial and temporal variability. They demonstrated that it was potentially misleading to characterize a species as either a foraging specialist or generalist without defining the resources being used, describing the temporal and spatial scale of the measurements made, and presenting some measure of the degree of individual variation within the population studied. Evolutionary and phylogenetic relationships also need to be considered, along with resource abundances, the physiological requirements of individuals, reproductive condition, and possible interactions with other individuals or species.

Greater understanding of foraging ecology requires a redirection of research. There is a need for long-term studies on temporal changes of foraging patterns in response to changes in resource abundance and the numbers and kinds of birds occurring together. Resources should be defined more broadly than food alone and a distinction made between abundance and availability (see Hutto, this volume), and the availability of various foraging substrates needs to be related to avian foraging patterns and community organization. More work on the ecology of birds during migration or away from their breeding and wintering areas is required. This is particularly important for a balanced approach to the conservation and management of species.

Manipulative studies that change the abundance and distribution of resources will be increasingly important in defining factors affecting avian foraging ecology. However, comparative studies that use natural experiments and contrast behaviors of the same species at different places or times will continue to make a significant contribution in describing patterns of variation in foraging ecology. Regardless of the approach taken, it is necessary to document the existence of individual variation. To what extent do patterns result from genotypic differences, response to differences in resource distribution, learning, or social interactions?

The ways birds respond to changes in the kinds or abundances of prey and their own physiological needs require more attention. Immediate and often short-term adjustments in foraging behavior are probably of greater significance to the survival of individuals and their reproductive success than the possibility of competition for resources between individuals of different species. As such there is a need to re-evaluate the reasons co-existing species differ in their use of resources. Selection is at least as likely to be for efficient foraging with the necessary flexibility to adjust to short-term changes in resources as it is to avoid competition.