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SECTION I

ROLE OF BIRDS IN NATURAL ECOSYSTEMS AND THE QUANTIFICATION OF RESOURCES

Overview

QUANTIFYING FOOD RESOURCES IN AVIAN STUDIES: PRESENT PROBLEMS AND FUTURE NEEDS

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A major goal of avian ecological research is to determine both the role of birds in determining structure and functioning of ecological communities (*sensu* MacMahon et al. 1981), and how distribution and abundance of resources provided in those communities influence dynamics of populations and interactions among species (Wiens 1984b). Thus, with renewed interest in ways in which bird populations influence and react to changes in food availability, many avian ecologists are now attempting to quantify available food resources. Sampling food resources may seem like a simple problem involving only techniques borrowed from other disciplines. However, as papers in this section show, the problem is complex, and pitfalls associated with some sampling techniques make them of little use to ornithologists. Indeed, in some cases, avian ecologists now are asking questions for which standard sampling techniques do not exist.

PRESENT PROBLEMS

The basic problem associated with quantifying food resources in the context of their exploitation by birds is that two different distributions are being sampled simultaneously, each of which (Fig. 1) may be affected by independent processes. Thus, within a given habitat, one finds both a pattern of food availability that is likely controlled by a battery of environmental factors (e.g., Stephen et al., this volume) and a pattern of food exploitation that is likely a result of biological interactions (e.g., Torgersen et al., this volume). Investigators have often assumed that relatively simple processes link those two patterns, such that food exploitation is more or less directly related to food availability (and vice versa), and that this relationship directly reflects fitness of individual consumers. However, a variety of ecological and behavioral "filters" may be interposed between distributions of potential food resources in the environment and the ultimate fitness of birds, and the mapping between the two may often be complex and difficult to describe accurately (Wiens 1984b). Indeed, elucidation of that mapping is the goal of this symposium.

Even without the complication of considering dynamic feedbacks between foraging behaviors of birds and distribution of their prey, the papers in this section point out the variety of problems that confound accurate quantification of food resources. Although compendia of detailed arthropod sampling techniques exist (e.g., Southwood 1978), avian ecologists have difficulty applying those methods, because they often need to characterize entire arthropod communities, whereas most techniques efficiently sample only certain arthropod taxa (Cooper and Whitmore, this volume). Arthropod sampling is further complicated due to patchy distributions that vary substantially in time and space (Majer et al., this volume). Also, different conclusions may be reached concerning relative importance of taxa depending on level of taxonomic identification of arthropod prey items (Cooper et al., this volume), a problem that may be common to many studies where prey items are not identified to species (Green and Jaksić 1983).

Although much of the emphasis of the symposium is on arthropods, sampling plant resources also may present problems. For example, plant ecologists have been relatively uninterested in quantifying fruit abundance, leaving avian researchers to develop their own methods. Blake et al. (this volume) discussed sampling fruits in tropical communities where diversity of both fruits and fruiteaters is high, and where defining a fruit (or at least what part of a plant a particular bird consumes) can be a problem. Standard methods for sampling nectar resources have been established with the help of avian researchers interested in pollination ecology (e.g., Collins et al., this volume).

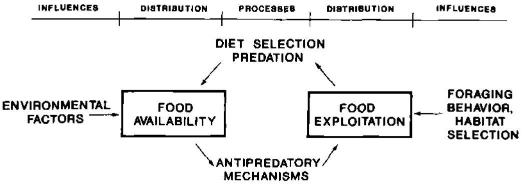

FIGURE 1. A diagrammatic view of the basic problem associated with quantifying food resources when two distributions are being sampled simultaneously. Researchers assume that those two distributions are linked such that food exploitation influences food availability through such processes as diet selection and predation, and that food availability influences food exploitation through antipredatory mechanisms such as crypsis and unpalatability. However, food availability also is influenced by environmental factors and food exploitation is influenced by biological interactions, affecting such things as foraging behavior and habitat selection.

Future Needs

Papers in this section present many suggestions for future studies. Some offer general comments concerning ecological studies, while others are directed at specific problems associated with resource sampling. We suggest that the most profitable avenue is one that operates at what we perceive to be the level of the basic problem, that of the dynamic interface between distribution of arthropods and distribution of avian foraging behavior. We recognize, however, that most researchers, either by inclination or training, will tend to emphasize one distribution over the other. For avian ecologists, how exploitation of food resources ultimately affects fitness is a question that all researchers should be interested in, but one that rarely is addressed explicitly.

Several authors pointed out the need for detailed study of bird behavior in relation to specific arthropod prey. In particular, Holmes (this volume) proposed that the two "goals" of a caterpillar are to accumulate biomass and to avoid predation. It accomplishes the first by interacting with a plant and the second by not interacting with a predator. He suggested that predation by birds on canopy arthropods, by numerically reducing prey abundance, has acted as a strong evolutionary selective force, influencing caterpillar foraging behavior, crypsis, and life history patterns. Future studies considering bird-insect interactions also should consider ecological constraints and benefits (e.g., incorporation of secondary substances from plants as a defense mechanism) arthropod prey obtain from insect-plant interactions. Wolda (this volume) identified a need for avian researchers to consider more closely behavior and microhabitat selection of arthropod prey.

Hutto's (this volume) suggestion that changes in foraging behaviors of birds may indicate changes in arthropod abundance is refreshing in its originality, but remains to be confirmed. He also raised old questions that must still be considered: How does one know whether food availability has been adequately measured? How can existing techniques be verified when independent data sets do not exist? How does one know the proper scale of measurement to assess accurately a bird's perception of a food resource? Nonetheless, Hutto's approach explicitly incorporates an examination of the dynamic feedback between avian foraging behavior and distribution of arthropods.

Future studies need to focus on the relative importance of different predator guilds or functional groups (*sensu* MacMahon et al. 1981) on prey populations, and competitive effects of predators on each other. Changes in foraging behavior and habitat distribution of birds in the absence of an avian competitor have been reported (e.g., Sherry 1979, Williams and Batzli 1979b), suggesting that interactions between avian predators might alter patterns of prey exploitation. Researchers working with sessile organisms, such as plants and marine invertebrates, appear to be making progress in delineating fundamental (i.e., preinteractive) and realized (i.e., postinteractive) niches (e.g., Grace and Wetzel 1981). It now remains for clever ecologists to devise experimental methods for teasing apart fundamental and realized food niches of birds in terrestrial communities.

More emphasis must also be placed on experimental approaches. Recent studies that demonstrate the relative importance of different predator groups on an arthropod food resource (Torgersen et al., this volume; Pacala and Roughgarden 1984; Steward et al. 1988b) are especially persuasive because of the experimental designs that were used.

We strongly agree with Dahlsten et al. (this volume) that ornithologists should consult with entomologists about arthropod sampling, as new techniques are continually being developed. It seems as presumptuous for avian researchers to devise arthropod sampling techniques as for entomologists to invent techniques for censusing birds.

A problem common to many arthropod sampling techniques is that they only measure standing crop (Hutto, this volume; Cooper and Whitmore, this volume; Wolda, this volume), which may reveal very little about arthropods that are important to birds (see Martin 1986). Another problem seldom discussed is that researchers and arthropod predators are simultaneously sampling the same distribution, so that what is really sampled is the residue of predation. Both problems seem to lend themselves to experimental manipulation, as demonstrated in the exclosure study by Mariani and Manuwal (this volume).

Future studies must address components of variation found in food resource populations. As shown by Majer et al. (this volume), statistical analyses can be designed to handle variations within and between intraspecific and interspecific distributions. Geographic variation in arthropod communities or patterns of exploitation by bird communities is another topic that is rarely addressed (Wolda, this volume). The study of spatial and temporal variation in fruit abundance in relation to exploitation patterns of birds also has just begun to receive the attention that it deserves (Loiselle and Blake, this volume).

Deciding how to analyze arthropod samples can be a sticky problem (Cooper et al., this volume), particularly because most ornithologists cannot identify arthropods to species. Although one might like to have that level of precision, it is often only necessary to know how many different species are present (Wolda; Stephen et al.; Cooper et al.; this volume). In those cases, we suggest that researchers consider the use of operational taxonomic units (Vandermeer 1972), since arthropod species can just as easily be given numbers as names. We have found that seemingly difficult arthropod groups such as spiders can usually be identified on the spot (e.g., Smith et al. 1988). In cases where it is necessary to identify individual species, ornithologists must rely on their entomologist colleagues, with whom collaboration can be stimulating and productive (e.g., Stephen et al., this volume; Steward et al. 1988a, 1988b).

A general conclusion from this section is that sampling avian food resources in a meaningful manner is a difficult problem that, in some cases, seems nearly impossible and intractable, particularly in complex communities. However, there appear to be steps that researchers can take to alleviate some of those problems. In some cases, examining relatively simple communities may lead to greater insights concerning interactions between predators and their exploitation patterns of a food resource (e.g., Pacala and Roughgarden 1984). Studies can be designed that have a broad geographical scope, yet examine only a few species on a local basis (e.g., Wiens and Rotenberry 1979). Initially focussing on a single bird species (e.g., Mariani and Manuwal, this volume) or a few bird species may be another way to gain information concerning avian exploitation patterns in complex communities. Finally, situations where many species of birds are exploiting the same food resource may hold some promise for gaining insights into ways in which food availability can influence exploitation patterns (e.g., Collins et al., this volume; Hutto, this volume; Kellner et al., this volume; Loiselle and Blake, this volume).

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