

SECTION IV

ENERGETICS AND FORAGING THEORY

Overview

STUDIES OF FORAGING BEHAVIOR: CENTRAL TO UNDERSTANDING THE ECOLOGICAL CONSEQUENCES OF VARIATION IN FOOD ABUNDANCE

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Patterns at all levels of biological organization can originate as consequences of differences in survival or reproductive success among individuals. Therefore, foraging behavior takes on a special significance in explaining patterns in nature because survival and reproduction depend, ultimately, on an individual's success at acquiring and using energy from food resources. One could choose any of a number of research questions to make the points that I shall raise, but let me focus on the specific problem of understanding whether food abundance is an important determinant of breeding bird community structure.

Are the abundances and kinds of species within a specified area determined primarily by current resource conditions, or by conditions that individuals experienced at some time in the past? Historically, we have viewed communities as being composed of interacting species that somehow adjust themselves in space so that their combined abundances provide the most complete use of current resource production (to paraphrase MacArthur [1969]). The biological reality of such a proposition began to be questioned seriously by Wiens (1977, 1983), who felt that breeding-season food levels are unlikely to play a significant role in determining the local population sizes of most breeding bird species because (1) food is abundant during summer, (2) bird populations are far below food-based carrying capacities, and (3) time lags in the response of populations to changes in the environment are pronounced. Wiens argued that the structure of breeding bird communities may, instead, be determined largely by infrequent events, or ecological "crunches" (as they have come to be known), during which populations *are* limited by food.

Under this view, much of the variability in community structure from one place to another, or one time to another in a given location, is probably due to stochastic processes acting during the more frequent periods of relaxed selective

pressure (Wiens 1983). In fact, Rotenberry and Wiens (1980a) and Wiens (1981) found that the population sizes and territory positions (community composition) of shrubsteppe birds changed independently of annual changes in probable food resource levels. This led them to develop their "checkerboard" model, where changes in the distribution of individual birds on a study plot from one year to the next were suggested to be about as predictable as changes in the distribution of checkers on a checkerboard after it has been given a vigorous shake. They reasoned that in order for food levels to affect the density or distribution of birds, bird populations must be at or near their food-based carrying capacities.

The pendulum has swung back again toward MacArthur's original view with the suggestion that, while food may be abundant overall during the breeding season, there will still be spatial variation in levels of food abundance. Moreover, because a bird's use of time should be strongly influenced by the availability of food (Hutto 1985a, Martin 1986), its breeding success may depend heavily upon whether it has settled in a relatively food-rich or food-poor location. This view has its roots in optimal foraging theory, and emphasizes the fact that food limitation is not an all-or-none phenomenon. Rather, there is a continuum of possible levels of food availability and, therefore, a continuum of amounts of time that must be devoted to feeding activities. Thus, for food abundance to affect bird density or distribution, bird populations do not have to be at or near their food-based carrying capacities (Martin 1986). Even though food may not limit numbers of adults surviving the breeding season, it could still affect the reproductive success of those birds. Moreover, natural selection could lead to a close match between bird population sizes and food abundance if it were to favor those individuals that were flexible enough to settle

and forage in a manner that maximized their foraging efficiency and, consequently, their breeding success.

Before we can begin to reconcile these seemingly opposing views and understand the factors that affect community structure, we will need to understand the factors that determine smaller-scale patterns, because the processes ultimately responsible for ecological patterns at the community level may actually go on at a more local level (Rotenberry and Wiens 1980b, Wiens and Rotenberry 1981). Specifically, "future studies of community organization could be strongly benefited by more detailed studies of foraging behavior and reproductive success of individuals, and less preoccupation with populations" (Martin 1986). Individuals are, after all, the units of natural selection that survive or reproduce differentially.

With this new emphasis on the foraging ecology of individuals, several long-standing questions are being addressed with renewed vigor. Take, for example, the classic question of why no two species occupy the same niche. For 30 years the dogma has been that if species are too similar ecologically, they will compete heavily for food resources and be unable to coexist. In recent years, the importance of such competition has been challenged on the grounds that differences among species could be due to past history or to chance alone, and have nothing at all to do with interactions among species (Connor and Simberloff 1979, 1984, 1986; Strong et al. 1979; Simberloff and Boecklen 1981). While these are viable alternative explanations, the approach that has been used to distinguish between chance and competition has proven unsuccessful because of a failure to focus on the biology of individuals. Rather than look for predicted mechanisms, researchers have tested hypotheses by looking for predicted community-level consequences. Unfortunately, the latter predictions are not inferences that necessarily follow from any of the hypotheses (Diamond and Gilpin 1982; Gilpin and Diamond 1982, 1984; Wright and Biehl 1982; Case and Sidell 1983). A focus on individual organisms may lead us in a more promising direction. Specifically, if competition between two species is powerful enough to cause their divergence along some resource dimension, then individuals that lie inside the zone of ecological overlap along that dimension should do less well than those that lie outside that zone. The "past history" and "chance" models make no such prediction.

Although Wiens' view of competition was perhaps overly skeptical, a valuable consequence of his skepticism has been the present shift toward studies of the behavioral limits on individuals. For example, we are now asking whether individuals have the flexibility to be able to track changes in food resources through space and time. If so, then MacArthur's early view that population sizes of species closely match resource production might be correct after all.

The development of optimal foraging theory has also brought considerable attention to the foraging behavior of individuals. The earliest attempts to model optimal solutions to foraging behavior rarely incorporated realistic physiological, morphological, or behavioral constraints on individuals. Individuals were predicted to use those behaviors that netted the greatest amount of energy per unit time, even if the behaviors were impossible to perform. Nonetheless, these early models led us toward the realization that we need to know more about the range of behaviors that individual organisms can achieve.

The following series of papers provides a splendid example of the new understanding we are gaining through the discovery and incorporation of constraints on the foraging behavior of individuals. For example, Karasov notes that digestive rates may constrain foraging behavior by placing an upper limit on foraging rates. In addition, the presence of significant differences in digestive efficiencies among food types makes it clear that simple tallies of prey density cannot be used as estimates of energy availability. That birds are morphologically and psychologically constrained in their capacity to forage optimally is illustrated exceptionally well in the papers by Moermond and Greenberg. Finally, the papers by Dunning, Maurer, and Stephens give us a preview of the way biologists are beginning to incorporate some of these constraints into a new generation of foraging models.

This is an exciting phase in the study of foraging ecology because foraging constraints may influence everything from habitat use, through mating systems, to community structure. Researchers are beginning to take a more reductionistic approach to the study of ecological patterns by paying close attention to the foraging behavior of individuals. At the same time, they are framing questions in the context of higher levels of biological organization, which gives their studies broader significance relative to earlier studies of foraging behavior.