

SECTION II

FORAGING BEHAVIOR: DESIGN AND ANALYSIS

Overview

BIOLOGICAL CONSIDERATIONS FOR STUDY DESIGN

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AD HOC AND A PRIORI HYPOTHESIS TESTING

Research on avian foraging is still mostly in the descriptive, empirical stage of development. Most of us, despite intentions to the contrary, simply follow birds and record what they do. Our study designs focus on where we plan to make observations, when we will make them (e.g., time of day, season), how many observations we hope to collect and, perhaps, how we will stratify our observations among groupings of interest (e.g., species, sex, age class, habitat type). We then toss the data into a statistical computing package to test the hypothesis that our dependent variables do not differ among the groupings we defined. Often we reject the null hypothesis, and then we are left searching for biological explanations for the differences we observed. How interesting are conclusions derived from such a process?

Any clever biologist can explain any observation by envisioning a perfectly reasonable series of events that could have led to that observation. One particularly striking example is that of a well-known ornithologist who analyzed bird abundance at a number of sites in relation to the characteristics of vegetation. Based on a multivariate statistical analysis, he developed a very reasonable explanation connecting the patterns of bird abundance to the specific vegetation features; but he then discovered that a keypunching error had caused the data to be shifted by a column. The result was that none of the vegetation data corresponded to the variable names he was using in the analysis. The data were essentially unrelated to the variables he used to explain his results.

The lesson is that retrospective explanations of observed phenomena are not very insightful nor do they lead to strong inferences. Considering all of the sources of error that authors in these proceedings have discussed, we may often be guilty of making biological mountains out of statistical molehills composed of variation attributable to both sampling and measurement error.

There is certainly a place for descriptive studies. After all, strictly empirical observations are the stuff of knowledge, and we are not advocating their abandonment. Rather, we are cautioning that researchers avoid the temptation of going too far in developing ad hoc explanations of descriptive data.

The power of a priori hypotheses, derived from basic biological principles or theory, is much greater than that of ad hoc hypotheses. Real, not illusory, progress is made when such hypotheses are accepted or rejected after analysis of results of a carefully designed and executed study. Such hypotheses are predictions of future outcomes as opposed to explanations of past outcomes. The confirmation of these predictions (which often involve directional or one-tailed hypotheses) is much more difficult to achieve than the usual null hypothesis of no differences. As a result, we are more confident of conclusions derived from results of such hypothesis testing.

OTHER CONSIDERATIONS

STUDY OBJECTIVES

The design of any foraging study must, obviously, be dictated by the objectives of the investigation. Less obvious are the limitations that the design imposes on the legitimate conclusions drawn from the results. It is foolhardy, for the reasons cited above, to draw conclusions about evolutionary fitness from a study designed to gather descriptive data. One can certainly derive evolutionary hypotheses for further testing from such data, but not conclusions. Thus, the objectives of a foraging study should be carefully thought out and explicitly stated.

A wide variety of inferences can be drawn from foraging data if researchers design appropriate studies and collect appropriate data. The objectives of a study are then determined by the level of biological inference that the researcher wishes to achieve. These levels of inference can be ranked based on the amount of information necessary to make specific conclusions (Table 1). Few studies have gone beyond the second level of infer-

TABLE 1. LEVELS OF BIOLOGICAL INFERENCE FOR FORAGING DATA AND THE KINDS OF RELEVANT DATA AND HYPOTHESES NEEDED TO DRAW MEANINGFUL CONCLUSIONS

Level of inference	Relevant data and hypotheses
1. Use	Descriptive statistics for relevant foraging categories. Null hypotheses of "no differences"
2. Selection	Data from level 1, plus data on availability of substrates or food. Null hypotheses of no relationship between use and availability
3. Survivorship	Data from levels 1 and 2, plus data on differences in survivorship because of differences in resource levels. Null hypotheses of no relationship between survivorship and selective resource use
4. Reproduction	Data from levels 1-3, plus data on differences in reproductive success in relation to differences in resource levels. Null hypotheses of no relationship between reproduction and selective resource use
5. Fitness	Data from all previous levels followed over the reproductive life of the individual. Heritability analyses of foraging behaviors. Null hypotheses of no relationship between fitness and heritable components of selective resource use

ence, primarily because of the inherent difficulty in collecting data to support higher-level inferences. If we are to develop sound theories of the adaptive basis of various combinations of foraging behaviors, it is necessary to reach to higher levels. Theories regarding adaptive syndromes (Eckhardt 1979), optimal foraging, or dynamic models (Houston et al. 1988) must be taken as tentative at best, until it is possible to demonstrate their usefulness by collecting data on fitness and heritability of resource-use behaviors (level 5, Table 1). All of the challenges associated with the demonstration of natural selection for morphological characters apply here (Endler 1986). We expect that even greater difficulties will be encountered in attempting to develop theories regarding the adaptive basis of culturally-transmitted foraging behaviors (McKean, this volume).

SAMPLING SCALE

A study design must also recognize the spatial and temporal scales of results. Will the study be

focused on variation of behavior for a single bird at, say, different times of day; on males versus females; on one population versus another; one species versus another; one community versus another; or on some combination of these hierarchical levels? A related question is the geographic applicability of results. Is it better to conduct an intensive study over a small geographic area (more precise but less general) or to do a less intensive study over a broad area (less precise but more general)?

For any level of analysis, the variance will probably be large. The basic goal of the study design is to partition the total variance in order to minimize error (unaccounted-for variance) while maximizing the proportion of variance explained by the factor (or factors) of interest. Achieving this goal will usually require prior information (e.g., literature review, pilot study) to estimate relative magnitudes and sources of error. For example, if study objectives dictate an analysis of foraging habitat selection at the population level, a researcher would benefit from knowledge of variation among individuals comprising the population. The overall frequency distribution of resource use for the population may range from completely overlapping, congruent distributions of individual birds, to completely nonoverlapping distributions. In the former case, variance among individuals is low and individual behavior could be sampled at random with respect to individual birds. In the latter case, variance among individuals would be high and sampling should be tightly controlled to accurately estimate the true population variance. Individuals might then be "blocks" in the analysis so that interindividual variance could be partitioned out of the total, thus clarifying comparisons of interest.

RESOURCE AVAILABILITY

Quantifying availability

A critical problem in studies of food exploitation is how to quantify available resources. A researcher studying competition, for example, must know something about availability of resources (particularly that resources are limiting) to evoke competition theory. From a study design perspective, the fundamental question to address is: "What is the resource?" Here, the distinction might be made between ultimate and proximate factors, as described by Hildén (1965). Proximate factors are features or characteristics of habitat that serve as direct or key stimuli to habitat selection. In this context, is the resource a particular food item or the substrate from which the item is gathered? If the latter, how finely should the substrate be described? For example,

a cerambycid larva, preyed upon by a Hairy Woodpecker (*Picooides villosus*), was found 2 cm deep in the sapwood of 4-m tall, broken-topped, ponderosa pine (*Pinus ponderosa*) snag in a mixed conifer, mid-elevation forest. What is the resource?

The answer to the question posed above is probably found in the way a bird perceives its environment. If one could think like a bird, one could define the resource. But herein lies another problem. One can measure availability by forcing the world into a preconceived set of categories: the procedure is to sample each category, usually through some randomized design covering the study area, and compare frequencies of use and availability to estimate selectivity of resource units. But how should one estimate availability of resource units as perceived by the bird? In nearly all studies, it is assumed that a random sample from the study area is a suitable estimate of the choices available to the bird, but this is only true when resource units are homogeneously distributed and properly defined. Thus one is forced to assume that the choices available at any point in time or space are essentially constant as seen from the perspective of the foraging bird (Hutto, this volume). We contend that this is an unrealistic view and that conclusions about selectivity derived from such analyses are suspect.

To better account for patchy distributions of resource units, study designs will probably need a focus at a finer level of resolution, most likely at the level of individual birds. If a bird is pictured as moving through the environment, availability of resources should change at each bird location. The appropriate sampling universe may be perceived as lying within an area that could be defined, say, by the average distance the bird moves between foraging locations. The sampling universe should include only those resources that the bird is morphologically and behaviorally equipped to exploit. To estimate use versus availability, a researcher could record the location of each foraging attempt, then go back to each location and sample available resources within the appropriate universe for comparison with the resource used at each location (e.g., Seidel and Whitmore 1982). Although more cumbersome than random samples of the study area, such an approach would provide a more realistic view of selectivity in patchy environments.

The researcher's decision as to whether to sample actual prey or the substrate with which the prey is associated is also important, especially in studies of insectivorous birds. Unfortunately,

none of the current techniques for sampling insect availability offer sufficient accuracy for any but the most general inferences. For this reason, most researchers have opted for sampling substrates in the hope that substrate conditions are correlated with prey numbers or biomass. Much more work is needed to validate this critical assumption.

Temporal variation

Another major issue in studies of food exploitation is the need to relate changes in bird behavior to changes in resources. Within-season variation in resource availability may account for much of the variation in samples of foraging behavior. If adequate methods are developed for a static assessment of resource availability, the next challenge is to design the study so that temporal variation (in both resources and behavior of birds) can be measured and analyzed. A number of contributors to these proceedings recognize this problem and have demonstrated significant seasonal, within-season, intersexual, interage, and variation in foraging behavior. What is still lacking are definitive data testing whether such variation results from changing resource abundance or whether it is more related to changing preferences of the birds themselves (e.g., Sakai and Noon, this volume).

CONCLUSION

We suggest that studies of foraging behavior and resource use must now expand upon the descriptive stage to include more intensive studies of underlying biological mechanisms. The types of data that we envision as being most important are partial or complete data on fitness, resource availability (accounting for morphological capabilities of the foraging bird), and the spatial and temporal scales at which these phenomena occur. As empirical data become available from well-designed studies of the biological mechanisms underlying the ecology and evolution of avian foraging, we expect that new theoretical advances will be stimulated and the study of avian foraging behavior will progress to a new level of scientific rigor. Perhaps researchers will begin to understand the factors that determine how individual birds track resources.

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