

then they are merely titillating allegories that reveal a suspect tolerance of anthropomorphism (again, the Idols of the Tribe).

The Pierian spring.—Time and natural selection may moderate many of the excesses and aberrations that I have just described, but what can humans do to accelerate this purge? One obvious answer is to reverse the trend toward hyperspecialization that currently tinges ecology and allied interdisciplinary fields of biology. I have examined many scores of undergraduate and graduate programs of study in ecology and sister disciplines and am perplexed by the frequency of heavy emphasis on “in-house” courses (to name but a few: terrestrial ecology, aquatic ecology, marine ecology, desert ecology, forest ecology, community ecology, population ecology, behavioral ecology, statistical ecology, ecological genetics, and so on). This seems a startling paradox in fields of inquiry that are purported to rely heavily on knowledge from the basic disciplines that, by definition, they subsume. The result is that instruction in the basic sciences is diluted by redundant “interdisciplinary” coursework. Advanced students in such curricula now, on the average, escape all but rudimentary training in chemistry, frequently escape any instruction at all in physics, and worst of all, commonly elude all but undergraduate experience in the basic biological disciplines (morphology, systematics, physiology, embryology, and so on) that are the sources of knowledge for the support of their interdisciplinary aspirations. This smacks of the inbreeding that characterizes many professional schools and can culminate by sharing their status: isolation from reality, a superabundance of True Believers, and a shortage of skeptics.

Thus, the circle closes. I began by identifying some problems in contemporary theorizing in the prominent subdisciplines of ornithology and end by suggesting that these problems are abetted by vocational hyperspecialization and the limited historical perspectives that this entrains. Of course, the criticisms that I have voiced are a double-edged blade that can lacerate not just a handful of theoretical ecologists and their allies but also anyone who ventures innocently or too enthusiastically beyond the limits of personal competence. Alexander Pope, in his *Essay on Criticism*, reminds us all to “Drink deep, or taste not the Pierian spring./ There, shallow drafts intoxicate the brain/ And drinking largely sobers us again.”

Last of all, by way of summary of what I have tried to say, I am willing to provide *gratis*, to anyone who requests a copy, a flash-card bearing Elinor Wylie’s quatrain: “Go study to disdain/ The frail, the overfine/ That tapers to a line/ Knotted about the brain.”

ON DIGESTING A THEORY

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Good theories, like gourmet meals, require a lot of time to prepare, to swallow, and to digest. Robert MacArthur was a master preparer of theories. His recipes called for a thorough blending of equal parts natural history, common sense, and simple mathematics. Some years ago, I happily swallowed MacArthur’s theory of community structure; now I am having trouble digesting it. Although I no longer

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recommend this theory to young gourmets, I also am not ready to toss the scraps to hungry dogs. Rather, I believe that we can learn from our bellyaches to prepare a more palatable theory.

MacArthur proposed that the abundance and diversity of animals in general, and birds in particular, could be predicted from a knowledge of resource abundance and species-specific resource utilization. I, for one, still accept this proposition; however, I believe that MacArthur's particular theoretical recipe had two fatal shortcomings. First, his theory did not adequately consider the behavioral flexibility of consumers like birds, and second, his theory did not adequately represent major fluctuations in resource abundance, which occur independently of consumer activity. As a consequence, MacArthur's theory did not allow for the likely possibility that birds are only infrequently resource limited.

If, as Wiens (1977) has suggested, large fluctuations in resources are common in natural communities and birds only infrequently face resource limitation, then what happens in the "average" year may be insignificant to actual population regulation and community structure. I have found, for example, that in years of low seed production, sparrows consume virtually all of the grass seeds produced in woodland habitats, and local population densities are then regulated by resource levels (Pulliam and Parker 1979). Grass seed production in these habitats, however, varies over two orders of magnitude between years in response to variation in summer rainfall (Pulliam and Brand 1975), and, in many years, sparrows consume only a small fraction (<5%) of the grass seeds produced.

Because birds change their diets and even their habitat utilizations in response to fluctuations in resource abundance, measurements of resource utilization in one year may reveal little about resource utilization in other years. Similarly, competition coefficients based on average overlap of the resources used by different species and using data from many habitats over many years, as in Pulliam (1975), may indicate little or nothing about possible competition for resources in years of shortage. If two species utilize similar foods in years of plenty but feed in different habitats or otherwise specialize on different foods in years of shortage, they may, in effect, never compete for food, even though dietary analysis reveals a lot of food overlap in most years.

To determine the importance of direct competition for food, we must determine the frequency with which food eaten by one individual affects the probability that another, of the same or another species, will suffer a decrease in fitness for lack of food. As a first step, we must instigate long-term studies of food production and utilization to determine how frequently food is in short supply and how birds respond to food shortages. Even so, because years of shortage are apt to be infrequent and because different years of shortage are likely to differ with respect to which foods are or are not available, we should not count on observation alone. We need a theory to predict how food utilization changes as a function of food abundance. Such a theory will allow us to test predictions about the effect of food removal by one individual on the food utilizations, rates of energy intake and ultimately the survival probabilities and reproductive success of other individuals.

I am arguing that we need a micro-ecological theory of resource utilization before we can hope to reconstruct a macro-ecological theory of community structure. Optimal foraging theory is a micro-ecological theory in that it predicts how food, patch, and habitat utilization change as functions of food availability. For example, optimal foraging theory postulates that predators rank prey and predictably expand and

contract their diets as prey of high rank change in abundance. In early models, prey rank was assumed to be a function of only prey energy content and handling time, but more recent models have also considered nutritive and toxic properties of prey as well as the role of learning and sampling in prey choices. It is too soon to tell how accurately prey choices can be predicted by optimal foraging theory, but, to date, the theory has met with surprising success, and some of the most notable successes have been with birds (Krebs 1978, Pulliam 1980).

If we can discover how birds rank their potential prey and, if indeed, birds expand and contract their diets in predictable ways, then we can predict dietary changes in response to environmental fluctuations. Presumably, different bird species will rank the same prey in different ways. If so, we can predict how diets of different species will converge or diverge as a function of prey abundance. If the theory can also predict changes in habitat use, then we can predict how birds of one species will affect the resources available to and the feeding behavior of other species during the important years of resource shortage. I believe that it is at this micro-ecological level that competition must be understood before we can begin to reassess the importance of competition in structuring communities at the macro-ecological level. In a more general sense, greater attention to processes and relationships at such "micro" levels may be necessary before "macro-theories" can really further our understanding of many biological phenomena.

LITERATURE CITED

- KREBS, J. R. 1978. Optimal foraging: decision rules for predators. Pp. 23–63 *in* Behavioural ecology (J. R. Krebs and N. B. Davies, Eds.). Sunderland, Massachusetts, Sinauer Press.
- PULLIAM, H. R. 1975. The coexistence of sparrows: a test of community theory. *Science* 189: 474–476.
- . 1980. Do Chipping Sparrows forage optimally? *Ardea* in press.
- , & M. R. BRAND. 1975. The production and utilization of seeds in a desert grassland. *Ecology* 56: 1158–1166.
- , & T. H. PARKER. 1979. Population regulation of sparrows. *Fortschritte der Zoologie* 25: 137–147.
- WIENS, J. A. 1977. On competition and variable environments. *Amer. Sci.* 65: 590–597.

ON THE PHILOSOPHICAL BASIS OF ORNITHOLOGY

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My first premise is that ornithology is an important activity in the affairs of men. The study of birds is no mere whim. Rather, all effective civilization is dependent on the level and nature of the character in its citizens, and the practice of ornithology can build character. People are edified by their exposure to bird study.

My second premise is that the essence of all ornithology is in its data, or more generally, in the experience that people have with birds. The more interesting the experience or data, the more effective the ornithology. Interesting experience feeds the imagination, challenges the mind, stimulates reflection, exercises the memory, and energizes the person.

My third premise is that theory exists to make data more interesting or to discover

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