that we can measure that might be relevant to the system we are investigating. We then make predictions about these measurable quantities. Each prediction should be testable, unknown, and as surprising as possible. Finally, we test our predictions or have someone else test them. The results put us back to step one.

If I may borrow an analogy from C. S. Lewis, the scientific method in general and theory, hypotheses, or ideas in particular have the same relationship to the experience or data of science as garden tools have to a garden. Neglect the tools and the work goes very slowly, with a great lack of order and beauty. With the tools in hand, and properly used, weeds are eliminated, every plant grows in its place, and the whole garden accomplishes its purpose of being something that builds up all who visit there. The tools are therefore invaluable. But if we lay a hoe down next to the rankest weed, we see at once that the weed is far more beautiful, and amazing, than the hoe. So the most tedious list of measurements of an ornithological phenomenon is far more amazing and beautiful, when compared to the most elegant theory or model. Only the gardener who is thoroughly frustrated with a weedy garden rejoices at the sight of a hoe, and then not because the hoe is beautiful, but because he sees it as a means to a more beautiful garden.

The scientific method is drawn from the experiences of the best or most effective scientists in history. It is in part a method of imitation, but is also proven to be effective by application of Bayesian statistics (see R. A. R. Tricker 1965, The Assessment of Scientific Speculation, New York, Elsevier Publ. Co.). In the context of the scientific method, the value of models is apparent. Mathematical models clarify explanations by listing assumptions and explicating logical steps. They also allow one to make more precise and unlikely predictions from hypotheses. To see models as more than they are, either positively or negatively, is to be avoided, as such a view provokes resistance from those who are in a place to test the predictions generated by the model. Like all sciences, ornithology progresses when those who are efficient in gathering data employ their efforts in testing predictions proposed by theoreticians and when theoreticians employ their efforts explaining the data gathered by field workers or modeling the explanations offered by others. This requires humility on the parts of both kinds of workers, as well as a deep concern to see the field generate as many interesting results as possible. The most cursory inspection of the state of mind of the contemporary American citizen, coupled with some reflection on the effect of good ornithology on that state of mind, raises the whole issue to urgent status.

MATHEMATICS, ECOLOGY, AND ORNITHOLOGY

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Ornithologists and other field biologists, being accustomed to a science based on the solid cornerstones of fact and observation, often look with suspicion upon theory and mathematics and bristle at the invasion of their territory by a new breed of investigator with no formal credentials in the discipline. To some extent, these reactions are justified: much of mathematical ecology is simply mathematics dressed up as biology, and is dismissed by field biologists as being of no relevance to their

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interests. The pages of ecological journals have experienced a glut of mathematical publications, often neither good mathematics nor good biology; an unfortunate consequence is that these camouflage those few pieces of work that do address questions of interest to biologists and the novel perspectives that may be exposed by a mathematical approach.

Most mathematical ecologists, indeed most mathematical biologists, trace their heritage from the great Italian mathematician Vito Volterra, whose contributions to pure mathematics were as profound and insightful as his revolutionary work on ecological systems. Volterra was attracted to a consideration of possible causes of fluctuations in the Adriatic fisheries by his son-in-law, the prominent zoologist Umberto D'Ancona. Volterra's work was a *tour de force,* in which he demonstrated with relatively simple mathematical models how the predator-prey interaction itself could lead to cyclical behavior. His usage of mathematics was in the best sense: as a deductive tool to explore the consequences of particular assumptions. Unfortunately, most successors of Volterra, lacking his imagination, have restricted themselves to ever more arcane mathematical investigations of special versions or extensions of Volterra's particular models, often unknowingly retracing paths Volterra trod years before; but the true legacy of Volterra is in the innovative use of mathematics to crystalize biological ideas and to allow insights otherwise impossible.

The construction and elaboration of theories involves two stages: postulation of axioms or premises and deduction of consequences. The chasm between naturalist and mathematician exists to a large extent because they view theory in different ways: the naturalist is interested in the premises *per se,* and in what they say about the biological system; the mathematician is accustomed to being presented with a set of axioms, and to working entirely within the world thereby defined. The mathematician must learn that the biologist's fundamental interest is in the truth or falsity of the axioms; the biologist must appreciate the power of the deductive phase. That the conclusions the mathematician derives are implicit in the assumptions is a trivial remark: even exceedingly simple postulates may carry implications that the finest human mind cannot grasp without the aid of mathematical formalism. The mathematician draws on experience, analogy, and a rich literature of methods and results derived in other contexts to explore the abstract world of the model. In this pursuit he is of a kindred spirit to the natural historian, exploring his world with a sense of discovery rather than invention.

Who is the mathematician who comes to biology, and why does he do so? There is, of course, the classic portrait: the problem solver, the servant who wishes to place his tools at the disposal of the biologist to solve the biologist's problems. Largely because of the central position of statistics in biology, this is the most familiar role and the easiest for the biologist to accept. But one must also recognize two other modes. First, mathematics, both pure and applied, has always depended upon external sources to provide inspiration for new developments and directions, and biology has in recent years provided a rich harvest of new ideas. In mining biology for such ideas, mathematicians are in a great historical tradition, developing mathematics for others to apply, whether now or in the indeterminate future. The biologist need not be interested in such efforts, but should recognize their pursuit as legitimate activity. However, the fruits of these labors must not be confused with biology; esoteric mathematical concepts are often too glibly applied to biology, pretentiously and arrogantly assigned importance beyond their true merits. There is no question that much of mathematical ecology has suffered from this oversell, in part because the guilty mathematicians have no feeling for the biological problems, in part because their biological accomplices do not really understand the limitations of the mathematics involved. There is a tendency to forget that the statements the mathematician can make are only statements about his model, not about reality; the premises that form the axioms in the mathematician's logico-deductive system are not established or self-evident truths, but are hypotheses. Such excesses have led to justifiable skepticism among biologists.

There is, however, another kind of scientist, part mathematician and part biologist, schooled in the lore of biology and trained in the methods of mathematics. As in theoretical physics, where, as others have pointed out, the mathematician made major contributions only after he essentially became a physicist, these individuals are driven by their own questions about ecological systems and are not interested in simply solving the problems of others. Sometimes the theories they construct shed light on the questions others have posed; sometimes they do not. The mathematical ecologist brings a different perspective to the biological system, and may be interested in totally different kinds of questions than his nonmathematical colleagues. These questions are intrinsically no more and no less valid than classical ones, but add a new dimension to our veiw of ecological systems. Ultimately one may hope that the various approaches will blend and that a comprehensive subject of ecology will result, but it is premature to expect this for some time. Much of ecology is still in a descriptive phase, and the subject is much more diffuse than other disciplines. There do not exist, as in physics or molecular biology, questions that everybody recognizes as the central ones, and perhaps there never will. One of the goals of mathematical ecology is to contribute to a synthesis by simplifying to isolate concepts, by abstracting common ingredients from disparate situations, and by drawing analogies; to this task, mathematics is ideally suited. The economy of mathematical description facilitates the detection of hidden symmetries and patterns. However, in using such descriptions one must be on guard against the tendency to oversimplify and to proceed without sufficient caution from the specific to the general.

Mathematics has great potential as a tool for biology, and this role is enhanced if mathematical papers include clear statements of assumptions and objectives; mathematics allows one to focus ideas and make them precise, and to do preliminary testing of hypotheses without actual new experiments. This objective is very different from the employment of mathematical models for predictive purposes or management, and this distinction is not well understood even by modellers. Mathematical ecology as a predictive "science" is in a much weaker position than mathematical ecology as an explanatory or suggestive vehicle, and for the purist the predictive role is at best an uncomfortable one. Prediction requires substantiated axioms, but because ecological principles are usually empirical generalizations, they sit uneasily as axioms.

Theoretical ecology, concerned primarily with explanation and suggestion rather than prediction, begins from the premise that it is not possible to understand our world without embedding it in a larger set of possible worlds and then asking why things are the way they are. This involves the deliberate construction of imaginary species, of hypotheses not known to have been satisfied in any real situation. Such "axioms" need not be defended; the mathematician wishes to explore their consequences to try to understand either why they are not true, or alternatively under what circumstances they would be applicable. "What if there were no gravity?" is a sensible question whether or not such a condition could ever be realized. Moreover, as in physics where such ideal concepts as zero gravity, absolute zero, and the frictionless pendulum provide useful standards against which to measure and compare, consideration of simplified models that isolate the effects of a single or a few factors may be a useful first step toward the understanding of more complicated systems in which many factors interact. Thus the classical theory of single-locus Mendelian population genetics is indispensable as a foundation for describing the more complex genetic systems that underlie most evolutionary change; and even the oversimplified Hardy-Weinberg, the frictionless pendulum of population genetics, has been of inestimable importance. Beyond these beginnings, still simplistic two-locus extensions of the classical models have helped to clarify the roles of linkage, recombination, and epistasis. Although one must always be aware that the whole is more than the sum of its parts and that systems possess properties different in nature from those of their individual elements, it is still immensely valuable to understand the behavior of the basic units.

To the ornithologist, the mathematician may seem a strange bird, with very different rearing and priorities. His standards of mathematical elegance and conciseness and desire for generalization, abstraction, and simplification may seem poorly suited to the complexities of the real world. But if ecology is to become a science, it must be more than a collection of anecdotes. We all seek principles that are general in applicability, and common language in which to describe distinct systems. These needs have led ecologists to seek mathematical formalization of their ideas and to liaisons with mathematicians. Although the classical mathematical methods appropriate to physics may not be the right ones for biology, the fundamental goal of the mathematical approach remains the detection of emergent patterns of order out of what seems chaos; this is the common quest of all ecologists as we develop our science.