

COMMENTARY

THEORY AND OBSERVATION IN MODERN ORNITHOLOGY: A FORUM

ALL sciences pass through phases in their development or maturation, from initial efforts to describe and catalog the diversity of phenomena they deal with, through attempts to synthesize some patterns from this maze of observations, to the final, ongoing stage of deducing theories of bold predictive powers from simple, general premises. At the present time, some feel that there is a widening gulf between the "old" and the "new" in ornithology, and indeed in biology in general. Historically, the foundations of ornithology are in classical natural history, but studies of birds have also contributed substantially to the development of theory in a variety of areas, perhaps most conspicuously ecology and behavior. Now, as theory has become more popular, more mathematical, and more abstract, some feel that the realities of nature have been largely ignored in the rush to develop fashionable theory, while others express the belief that only through the development and testing of theories or hypotheses can science progress, and natural history is too descriptive to contribute much any longer. At the extremes, I have heard theoretical work denounced as armchair, pie-in-the-sky storytelling, and careful descriptive fieldwork distained as an activity for pseudo-scientists and amateurs, which can only provide fodder for the real scientists, the theoreticians.

To me it seems obvious that each of these extremes is untenable. Theorizing with no knowledge of the real world is as sterile and empty as endless gathering of natural history observations with no guiding questions or concepts. But the divergence in viewpoints and allegiances is nonetheless widespread.

I thought that this issue should be addressed, and I asked several individuals to contribute personal essays considering it in whatever manner they felt appropriate. Each essayist participated independently, without knowledge of who was contributing or what they said. Their comments are presented here with minimal editorial change, in order to preserve the true spirit and flavor of each contribution. The individuals who have contributed these essays represent a wide array of disciplines, backgrounds, and approaches. I hope that their comments will stimulate thinking and perhaps further discourse about this issue, which I regard as central in the future development of ornithology.—JOHN A. WIENS.

ORNITHOLOGISTS AS UNCONSCIOUS THEORISTS¹

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There is no such thing as a pristine, unbiased observation. Every ornithologist carries with him into the field an armory of preconceived notions, expectations, and hypotheses about the nature of Nature. Observations can never be untrammelled by theoretical constraints, because the mind of the observer is imbued with current (or

¹ I thank Mark Ridley for his helpful comments and the S.R.C. for financial support.

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not so current) theories. Most scientists generally accept this view. It can easily be illustrated with reference to ornithological examples, perhaps the most striking of which are "facts" that were well known to ornithologists but assumed little significance until later theoretical innovations forced observers to look again at their birds or their data.

Ostriches, as has been known for many years, have peculiar nesting habits (Sauer and Sauer 1959). Several females share a communal nest, one does most or all of the incubating, and the eggs (there may be as many as 40) are rolled around in the nest by the incubating bird, a behavior that was originally interpreted as a thermoregulatory adaptation. These facts are certainly curious, but it was not until the theoretical climate of the 1970's had prepared the way, that B. C. R. Bertram (1979) began to unravel their true significance. The theories to which I refer might loosely be called "selfish genery" (Dawkins 1976) and are attributable largely to W. D. Hamilton, R. L. Trivers, and J. Maynard Smith. Selfish gene theory warns the field ornithologist to look out for apparently cooperative behavior and treat it with the utmost scepticism. [It is perhaps no coincidence that one of the most common garden birds (*Prunella modularis*) in the most ornithologically studied country in the world (Britain) has recently been found to have an extraordinary system of helpers at the nest by two workers independently (M. K. Warui, M. Birkhead pers. comm.).] Bertram's study of Ostrich communal nesting from the selfish gene point of view has shown that individual females contributing to the same clutch can recognize their own eggs, possibly by means of weight or subtle surface texture cues. Further, the incubating female, far from moving eggs around as a thermoregulatory device, shifts the eggs of other birds away from the center of the nest to the edge, where they form a protective ring insulating her own eggs against predator attack. Although there still remain many unanswered problems, it is already apparent that the questions asked about ostriches in the light of selfish gene theory are going to reveal a rich and fascinating story.

Shell dropping by gulls and crows provides a second example of how new theories can alter the interpretation of old facts. It has been very well known to ornithologists for many years that gulls and crows in coastal habitats drop mollusc shells onto hard surfaces to break them open and get at the otherwise inaccessible contents. Until recently, this behavior would have been viewed rather as a possible example of proto-tool-using than as an illustration of a general theory about foraging. But recently, R. Zach (1979) showed how shell dropping by Northwestern Crows (*Corvus caurinus*) can be treated as a test of optimal foraging theory. Zach measured the energy content of different-sized whelks (*Thais lamellosa*) available to the crows and estimated the height from which they have to be dropped in order to break the shell. He was then able to predict successfully the most profitable size of whelk for a crow and the height to which the bird should fly in order to break it open with the minimum expenditure of effort. A simple theoretical analysis provided new insight into an apparently simple behavior pattern.

But theory, in particular mathematical theory, can do more than provide a window through which to view Nature. We can assess our understanding of a particular phenomenon by trying to make predictions and testing them. If the predictions fail, then we have to modify our hypothesis about how the system works. Not all predictions are equally valuable, however, some are so general or qualitative as to be virtually useless as a test of the hypothesis from which they arise. The best predictions are those that are unique and easily refutable, because they are the ones that

are capable of revealing whether an idea is right or wrong. One way to make predictions easily refutable is to make them quantitative: the statement that a woodpecker will move from one tree to another at some stage in its life is neither interesting nor likely to be refuted, but to propose that a woodpecker will switch between trees A and B after 15.36 min is to make a very powerful prediction indeed. In general, this kind of prediction arises from mathematical modelling. R. Dawkins and M. Dawkins (1974) have developed this point further in their concept of Predictive Information Value (PIV). They argue that a good hypothesis is one with high PIV: it is one that sticks its neck out by making predictions that are, among other things, precise and unexpected. The hypothesis that Vee-flight formations of geese produce an aerodynamic advantage for the birds can be used as an example. It is an appealing hypothesis, but, as stated so far, it does not make easily testable predictions. When the hypothesis is developed in the precise mathematical terms of aerodynamic theory, however, a test can be done by measuring the angle of the Vee and the distances between birds in the flight formation. The hypothesis makes precise predictions about the Vee angle and interbird distances, and Gould and Heppner (1974) were able to show that, at least for a simple model, these predictions are not consistent with field measurements.

For some people, the key word in the last sentence will be "simple." The accusation is often levelled at theoreticians that their models are too simple to explain the complexity of the natural world. This criticism misses the point. A model is not meant to represent the complexity of Nature but to capture the essence of a phenomenon. Even if it is known that some of the assumptions of a model are wrong [for example, the assumption that air is completely incompressible was used in designing aircraft at the time of the second world war (Maynard Smith 1976)], an oversimplified model may contain most of the essential features of a system. Only by building a simple model and testing whether or not it works can we assess whether the oversimplification involved is too great.

In case I have given the impression that I see no difficulties with theories encountered by field ornithologists, let me end with two critical comments. Theorizing can obviously go too far. A possible example is the MacArthur-inspired fashion among community ecologists for building models of resource partitioning based on niche theory and the Lotka-Volterra equations. In these exercises, a few basic starting assumptions are used to build an elaborate edifice of theory, which in the end produces rather qualitative (low PIV) predictions. One can test an hypothesis by examining either its predictions or its premises. Ayala (1972) has demonstrated that, in at least one case, the premise of linear effects of competition in the Lotka-Volterra equations is violated, but as I have discussed earlier, oversimplifications may be permissible if the model is robust enough to capture the essence of a problem. A more stringent criticism is that predictions of species-packing theory are not easily refutable. An oft-quoted prediction is that $d/w > 1$ for stable coexistence (d = niche spacing, w = niche width). This is a weak prediction: it says little more than "species have to be somewhat different to coexist" and is therefore not easily refutable. Testing is even harder when one discovers that d and w are very difficult to measure.

Making measurements in the field may sometimes present a major difficulty with tests of a theory. I can illustrate this from personal experience. Twelve years ago I was working on the breeding success of Great Tits (*Parus major*) in two habitats: mixed oak woodland (which was generally considered to be an optimal habitat) and farmland (suboptimal). At first I found no difference in clutch size and fledging

success, but, with a much larger sample, a small but significant effect emerged: farmland birds did less well and lived at a lower density than those in the wood. A year later, S. D. Fretwell and H. L. Lucas, Jr. (1970) published their theoretical work on habitat selection in which they introduced the idea of an "Ideal Free Distribution." Had I been testing their ideas, I would have been pleased to stop after collecting my first small sample of data, which showed that the birds in the two habitats were doing equally well. To collect a small amount of data and stop is not the best way to test an ideal free distribution. A more stringent test might be to look for frequency-dependent responses to perturbations from the supposed equilibrium.

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WELCOME MATHEMATICIANS

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Most ornithologists are naturalists and, like other naturalists, have for centuries been pursuing their studies in the field, the stage on which the drama of the living world takes place. Their primary aim from the start has been to record faithfully the events that they observed, and for each event the setting and the circumstances as best they could read them; they have, thus, first sought to answer the what, when, and where questions posed by the world of nature. But naturalists have by no means ignored the how and why questions that the human intellect incessantly raises; it is to them, in fact, that the modern world owes many of its greatest unifying concepts, including the theory of evolution by natural selection.

Meanwhile, at their desks in our institutions of higher learning, mathematicians have been combining and manipulating figures and abstractions in search of the nature of systems underlying the order we see in the universe. To most naturalists the objectives and methods of these closeted intellectuals have seemed remote and only vaguely relevant. Then, suddenly, mainly in the past two decades, mathematicians searching for applications of their art descended on the naturalist's domain

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