

## RETAIN SUBSPECIES—AT LEAST FOR THE TIME BEING

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The thousands of formally named subspecies of birds range in distinctiveness from groups of populations barely discernible on the basis of weak divergence in a single character to geographic forms that illustrate trenchant differences in morphology, coloration, and voice. With such a breadth of variation covered by one taxonomic umbrella, small wonder that biologists continue to question the meaning and usefulness of this category. The heart of the problem lies in the fact that the complexity of natural variation below the species level defies easy organization; it is a mixed bag. Furthermore, each species seems to show a unique pattern. Indeed, the patterns of geographic variation already known in birds are so complicated that systematists could be faced with a bewildering future in which the number of patterns ultimately to be discovered will equal the number of species examined. But it is much too early to entertain this possibility. Instead, what we must face in the 1980's is the unhappy fact that the number of adequate studies of intraspecific variation is still so small that no sensible generalizations about patterns are yet possible. And, until many additional detailed studies of variation have been conducted, we cannot fairly judge the subspecies concept.

But this dilemma is hardly grounds for despair. Despite significant weaknesses, the subspecies concept has some distinctly positive elements. For example, subspecies tell us about the migratory routes and wintering areas of populations of birds that represent distinct portions of the breeding range of that species. Some subspecies also provide indisputable evidence for the early stages of allopatric speciation in relation to environmental barriers. These are issues of undeniable importance and for years they have been raised in defense of subspecies. I would like to comment briefly on two other related attributes, each of significance to the growth of ornithology and associated disciplines in the 1980's.

The first useful feature concerns the heuristic role that subspecies can play. Subspecies names alert researchers of whatever stripe to geographic forms with potential differences in features additional to those by which they were initially characterized. Thus, ecologists searching for possible examples of geographically differing foraging behavior, or comparative physiologists seeking allopatric populations that might differ in their energetics, should start by examination of representatives of distinctive subspecies within polytypic species. Systematists, as well, can profit by looking closely at subspecies named on the basis of particular kinds of characters. After all, some of these "subspecies" will turn out after careful study to be full species. This possibility pertains especially to a significant number of geographic forms of tropical birds whose natural zones of interaction remain unstudied. Many of these "subspecies" differ obviously in color, facial pattern, or voice—features of potential service as ethologic isolating mechanisms. Subspecies names, therefore, function importantly as signposts calling attention to populations of significance for their general research potential.

Another attribute of subspecies relates to information retrieval. A great body of information of many kinds is filed in the literature under subspecies names. For example, consider the voluminous data that exist on geographic distribution and variation in size and color. These facts will be of increasing interest and value for their potential application to a major unsolved problem in evolutionary biology, namely, the mode of integration of diverse kinds of characters during the formation of the definitive genotype and phenotype of the biological species. One of the most promising approaches to this difficult problem is through a detailed genetic-phenetic analysis of character differentiation at intermediate stages in the speciation process. Close examination of patterns in taxa exemplifying a graded series of these stages should provide valuable insight into how the discordant variation often seen in *subspecies* is coordinated as the species-level of genetic and phenetic organization is ap-

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proached. Although it is true that such analyses could be accomplished without consideration of subspecies, the fact that extensive data on character variation are already cast in a framework of subspecies names makes information retrieval for such tasks vastly easier than it would be otherwise. Thus, in voting to retain subspecies for the time being, I emphasize the present *usefulness* of the category.

But, despite the utility of the subspecies concept for the aforementioned reasons, the time for serious house cleaning is long overdue. Like those ecologists who are still clearing the detritus strewn through their discipline over the last two decades by the excesses of the theoreticians, avian systematists must sweep away the long accumulation of subspecific names based on trivial variation and/or faulty taxonomic procedure. To be worthy of formal names, subspecies should be objectively demonstrable through repeatable techniques that prove the existence of geographic differences in any of several character suites, whether of morphology, coloration, behavior, or allozymes. New, refined, and broad-scale studies must incorporate and integrate modern approaches from statistics, colorimetry, audio-spectrography, and biochemistry if they are to provide convincing results. Only then can we determine the real patterns of variation present in each group and decide which modes of variation, if any, are worthy of formal names.

Alas, not many new studies of this scope are likely to be undertaken in our present climate of shrinking support for collection-related ornithology. And it is not only financial help that

is needed. The studies I recommend would require extensive collecting of specimens for skeletons and tissues. Even modest collecting of birds often unjustifiably meets with increasingly formidable resistance, opposition based largely on ignorance and emotionalism rather than on sound reasons for protection. Education could help overcome the serious problems related to specimen acquisition. To start with, permit-granting personnel, and the public that influences them, must be informed of the basic laws of productivity and of density-dependent population regulation. These facts should convince anyone of the trivial impact of collecting on wild populations of birds. Furthermore, the fundamental importance of collections to effective management and conservation practices, and to both recreational and professional ornithology, needs much more widespread appreciation. Thus, the significance of collection-related ornithology to fields other than systematics must be recognized. Avian systematics and the many branches of ornithology dependent upon it simply cannot remain as viable disciplines without a steady flow of new specimen material, which can be subjected to novel analytical procedures as they are developed. It is to be hoped that we will see greater support in the future for scientific collecting from the diverse community of persons who ultimately enjoy the benefits of this activity. Such support definitely will be necessary if a truly comprehensive examination of geographic variation in birds, and of subspecies, is ever to be undertaken.

## INFRASPECIFIC GEOGRAPHIC VARIATION AND THE SUBSPECIES CONCEPT

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There are numerous problems for the 1980's to which studies of infraspecific populations might be applied. How does structural differ-

entiation evolve? What is the significance of geographic variation for speciation? How do adaptations evolve? How does variation in behavior or environment influence speciation or evolutionary differentiation? How do rates of infraspecific differentiation relate to rates of

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