

taxonomic decisions as a trivial part of the work, but, much to my surprise and dismay, they were viewed by others as a primary goal. I have even been lightly chastised for describing subspecies only to scrap them later. Ironically, little interest was expressed in the biological riddles. Perhaps I misused the subspecies concept, and, rather than "playing games" with it, I should have developed the puzzle explicitly. In retrospect, however, I now see also that thinking at that time, including my own, clearly, was biased by the taxonomy of subspecies as an end in itself. I have little doubt that further study of many classical subspecies will promote similar recommendations for their elimination.

I began my study of white-eyes (*Zosterops* spp.) with the prevailing bias that gene flow would not permit local differentiation in mobile bird populations. I ended wondering why most populations don't have more, well-marked subspecies. The existence of species with large, widely distributed populations with no external population structure, like the Cedar Waxwing (*Bombycilla cedrorum*) or the Sanderling (*Calidris alba*) is to me still totally mysterious. I doubt that great gene flow *per se* provides the explanation. Rather, I suspect the answers lie in new understandings of the nature of phenotypic compromise and flexibility.

In concluding, I return to my opening question. Might there be a resurrection of the belief in the utility of the subspecies concept in ornithological research? Do classical subspecies somehow reflect interesting units of adaptation, and, if so, what are these units? Two kinds of information are needed to know how remote these possibilities are.

First, we must learn how morphological

breaks in population structure, or clines in color and size characters, correspond with the underlying population structure and genetics. Kendall Corbin's studies of the relative frequencies of marker alleles near subspecies boundaries of *Zonotrichia* may be a major step in the right direction. Second, we must focus more closely on environmental versus genetic control of phenotypic variation in wild birds. Thus, I eagerly await the results of Frances James' transplant experiments with Red-winged Blackbirds (*Agelaius phoeniceus*), and others that may follow.

Definition of the environmental component of subspecific variations will erode some sandcastles of evolutionary interpretation. But such discoveries will not be a disaster for ornithology. Rather, they will spark a new generation of questions about the evolution of environmental sensitivity. For too long now we have been biased by assumptions of genetic determinism. A renaissance in the appreciation of the mechanisms of morphological and physiological adaptations of birds to the environment might be before us, one that will parallel current developments in understanding the mechanisms of behavioral adaptation, which range from closed instincts through variable imprinting to open learning. The evolution of heritability differences between characters or species or even subspecies could become as exciting a topic in ornithology as it is in some other biological disciplines. If so, avian biology will have reached a new plateau.

Perhaps, then, subspecies can designate meaningful entities for future discussions, and a new round of graduate student interest in subspecies will begin.

## SUBSPECIES AND THE STUDY OF GEOGRAPHIC VARIATION

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The category of subspecies is a segment of the continuum between similar populations

and distinct species. The size of this segment and just where it lies depends upon the degree to which the definer is a "lumper" or a "splitter." It therefore has no theoretical significance. On the other hand, it does have some

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practical value in that it permits naming and identifying more-or-less distinct populations below the species level. This value is greatest in the populations that are completely distinct from neighboring ones and least in those that vary clinally or intergrade with adjacent ones over large areas. In any case, it is the knowledge of the *patterns of variation* within species, not the enumeration of subspecies, that is the significant result of studies of geographic variation. These ideas may appear obvious to many, but I believe they are not as widely understood as they should be.

The "typological" view of subspecies has blinded many workers to the possibilities of statistical methods of analysis. For example, the "traditional" way of determining the source of migrating or wintering populations of wide-spread continental species has been to identify individual specimens to subspecies and to report that such and such a subspecies has been found migrating through, or wintering in, such and such an area. A far more precise method of making such determinations, especially in species that vary in mensural characters, is the population approach.

It should be clear that, in species that vary clinally or have broadly intergrading subspecies, identifying the source of a migrating or wintering population is a matter of probability. Hence, the larger the sample size, the greater the precision and degree of certainty of identifying the source. The obvious complicating factor is the possibility that there may be multiple sources of origin for a given migrating or wintering population. Such multiple sources can usually be identified by variances that are higher than those of samples from the breeding grounds and require more complex methods of analysis.

Some years ago, I analyzed variation of the Painted Bunting (*Passerina ciris*) on the breeding and wintering grounds (1951). Two subspecies, a bright eastern race (*ciris*) and a pale western race (*pallidior*), have long been recognized, and on the basis of identification of individual specimens, both forms were said to winter in México. By dividing the former race into a population of smaller birds inhabiting the Atlantic states and one of larger birds in the Mississippi Valley and by comparing the means and standard deviations of measurements of adult males of these samples (by far the largest set of data available) with samples

from the wintering grounds, I found a remarkable agreement between the samples of breeding birds from the Atlantic states, Mississippi Valley, and the western part of the range with samples of wintering birds from southern Florida and the West Indies, the Yucatán Peninsula, and the rest of México, respectively. This is consistent with the idea that the birds from the Mississippi Valley cross the Gulf of Mexico on migration, whereas the western birds use the overland route. Birds wintering in Central America agree in size with the pale western population and most are pale, but a few are bright like the Mississippi Valley population and may represent it or intermediates from eastern Texas. If this rather simple analysis showed more about the biology of the species than a "typological" approach, how much more can be accomplished by using the more sophisticated methods now available?

In studies of geographic variation, it is often necessary to divide populations into as many as four subsamples (adult males, first-year males, adult females, and first-year females) to achieve maximum precision in the analysis. This requires large numbers of specimens—upwards of 40 per sample. There are already available in collections enough skins for the analysis of many species, but there are gaps or weaknesses in the material of many other species, especially of large birds. After measuring over 1,300 Pied-billed Grebes (*Podilymbus podiceps*), nearly all the available material in museums in the United States, Canada, and England, I had found but two adults taken during the breeding season in Iowa, where the bird is common and whence I had measured 50 taken at other times of the year. This is not an isolated example. Samples of many raptors from the breeding grounds are surprisingly small. The paucity of such material from the ranges of the Harlan's and Krider's hawks and from many other parts of the range of the Red-tailed Hawk (*Buteo jamaicensis*) has prevented a thorough study of variation in this species.

Thus, collecting is still needed, not only for investigations of geographic variation but also for other kinds of research. Yet it is clear that this must be increasingly selective and that the maximum amount of information be recorded for each specimen. Long ago, Van Tyne (1952), called attention to the value of routinely weighing specimens prior to preparing them. Data on relative amounts of fat, pectoral muscle

mass, crop and stomach contents, and condition of the gonads are but a few of the other types of information that greatly enhance the value of specimens.

The use of skeletal material in studies of geographic variation is a promising new development. After reaching adult size, bones rarely change and can be measured more precisely than most parts of a bird skin: feathers become worn, tarsal measurements may be difficult to duplicate, and the rhamphotheca is continually growing and becoming worn. Analyses of measurements of bones of Recent birds are often necessary to evaluate the status of fossil material, and comparisons of geographic variation of fossil and Recent material are useful in estimating rates of change through time.

Studies of geographic variation are basic

parts of the areas of biogeography, evolutionary theory, and ecology. They involve detailed and often tedious work, but new techniques and more sophisticated methods of analysis offer possibilities for increasingly precise results. The maximum value of these results can be achieved only if the goal is understanding of the patterns of variation and not the mere subdivision into subspecies.

#### LITERATURE CITED

- STORER, R. W. 1951. Variation in the Painted Bunting (*Passerina ciris*), with special reference to wintering populations. Occas. Pap. Mus. Zool. Univ. Michigan No. 532.
- VAN TYNE, J. 1952. Principles and practices in collection and taxonomic work. *Auk* 69: 27-33.

## GEOGRAPHIC VARIATION, PREDICTIVENESS, AND SUBSPECIES<sup>1</sup>

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Once it is recognized that variation exists in natural populations, systematists are faced with the problem of characterizing that variation. In particular, the reality of geographic variation has long been recognized, but at least since the early 1950's there has been widespread doubt about the efficacy of trinomials for its description. Wilson and Brown (1953) succinctly catalogued the problems resulting in the failure of the concept of subspecies to reflect the nature of geographic variation. A named subspecies carries at least the connotation of phenotypic uniformity over an area. In fact, however, Wilson and Brown found that a widespread pattern of actual variation consists of a lack of concordance of clines in different characters (independent geographic variation), reoccurrence of characters in several geographic areas (polytopic subspecies), and the problem of virtually every population dif-

fering in some character or other (microgeographic races). Thus, this criticism amounts to a claim that subspecies lack biological relevance; that is, they do not accurately convey the actual patterns of geographic variation. That this criticism holds for avian subspecies is clear; authors of the most thorough recent analyses of intraspecific geographic variation in birds, e.g. F. C. James, N. K. Johnson, R. F. Johnston, D. M. Power, etc., have all found much of the variation to be clinal. Many of them have refrained from describing the variation in terms of trinomials because of the inherent danger of biological distortion. Thus, it seems curious that qualitative examination of color or a few skin measurements of a few specimens, often without statistical tests for clines or without adequate sampling of intermediate geographical areas, frequently results in trinomials, while the authors of large, quantitative studies frequently avoid them. This strongly suggests to me that most subspecies are not to be taken too seriously.

What then of the very concept of an intra-specific nomenclature? In spite of the wide-

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