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[1]

George F. Barrowclough[2]

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 differing 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 intraspecific nomenclature? In spite of the wide-

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spread and continuing abuse, I see some utility to the formalism, but only if standards become much more rigorous. First, we need to acknowledge that a useful subspecies concept will have to have as a goal the same objective as other taxonomic categories—*predictiveness.* The point of classification is to provide a hierarchical framework to be used for the retrieval of information. For example, all members of the class Aves share some characteristics; all galliforms share additional ones, and so forth. Finally, all individuals of the Helmeted Guineafowl (*Numida meleagris*) share more attributes with each other than they do with other members of the family. The biological relevance of the classification lies in the fact that, if it accurately reflects the hierarchical relationships of some taxa, then in knowing this classification we can make predictions concerning the states of characters without examining them and have a fair degree of confidence in the prediction. For example, although guineafowl originally were linked on the basis of external morphological characters, subsequent sociobiological research suggests they all have monogamous mating systems. Therefore, I would predict that if someone discovered a new species of guineafowl, it would have a monogamous mating system, unlike that of many other gallinaceous birds. Hence, the usefulness of the classification for nontaxonomists lies in this power to predict the extent to which new generalizations may hold based on inexhaustive sampling of the taxonomic hierarchy. A classification informative only for the characters used to formulate it has little or no relevance to most biologists.

Can subspecific taxa yield predictions about characters that are not true at the species level? That is, are there circumstances under which unique predictions might be made given knowledge of intraspecific nomenclature that could not be made if we merely knew that two populations were members of the same species? The answer appears to be yes. If portions of a single species share a substantial evolutionary history that is distinct from that of the rest of the same species, then some predictions might well obtain. That is, if a fragment of a species has been isolated sufficiently long to acquire a number of unique character states (and this may require tens of thousands of years or more), but not sufficiently long for speciation to occur, then a trinomial reflecting such information might be relevant to physiologists, behaviorists, ecologists, etc.

How might such intraspecific taxa, with their own evolutionary history and continuity, be recognized? There is no absolutely certain way, although a single character would clearly not be sufficient. Rather, we need to look for a concordance of geographically varying characters that do not simply form clines. More realistically, we must look for a pattern of contiguous geographical samples occupying regions of multivariate character space distinct from the regions occupied by other geographical samples [e.g. Johnson (1980)]. A few intermediate points representing populations in secondary contact shouldn't bother us, but any suggestion of a continuous distribution without a sharp break or step suggests primary differentiation. Better, however, and strongly desirable would be identical patterns of discrete clusters of points in multivariate space for multiple suites of characters. For instance, if separate analyses of electrophoretic, plumage, and morphometric variation all delimit the same "discrete structures" in multivariate space, then there is reason to assume there is something special about these entities, and intraspecific taxa are probably warranted. Nevertheless, it should be clear that it is only the minority of detailed studies of geographic variation that are going to find such patterns. Thus, with such a new standard for the recognition of intraspecific taxa, one would never set about looking for subspecies to describe; rather, they would be the occasional by-product of studies of geographic variation.

Thus, I feel that most currently described subspecies are not useful in the sense that higher taxa are useful; the methodologies and standards used to create them (a posteriori probability of separating some percentage of one from the same percentage of the other, on the basis of a single character) do not ensure any predictiveness of other characters. This renders the trinomial useless to all biologists except a few taxonomists. A plausible method does exist, however, for identifying populations for which a trinomial would have biological relevance, but it would require intensive studies of geographic variation of many characters to delimit the taxa, and for most species no trinomials would be justified. Thus, the search for subspecies must not be an end in itself. Their description ought to be the occasional result of studies aimed at understanding the patterns and processes associated with geographic variation.

LITERATURE CITED

JOHNSON, N. K. 1980. Character variation and evolution of sibling species in the *Empidonax difficilis-flavescens* complex (Aves: Tyrannidae). Univ. Calif. Publ. Zool. 112: 1–151.

WILSON, E. O., & W. L. BROWN, JR. 1953. The subspecies concept and its taxonomic application. Syst. Zool. 2: 97–111.

THE SUBSPECIES CONCEPT: THEN, NOW, AND ALWAYS

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While President of the A.O.U., I encouraged the Chairman of the Check-list Committee seriously to consider restricting the next edition of the Check-list to the species level, and I was relieved when the Committee voted to do just that. My action was not prompted by disaffection with the subspecies concept, but rather by the conviction that a meaningful revision with subspecies could not be produced for at least another decade and that it was imperative that a revised check-list of species appear with reasonable dispatch. Those who have read the early volumes of *Systematic Zoology* realize that a debate over the concept of subspecies is not a novel idea. Nonetheless, the Editor of *The Auk* has suggested that many of his readers may not be aware of the arguments. He may be right. There certainly is the possibility that his readership has not accepted the arguments, for colleagues' responses to my position on the A.O.U. Check-list varied from delight to chagrin with what they initially perceived as my "abandonment" of subspecies.

One useful attribute of subspecies, sometimes overlooked in the heat of such debates, is the fact that they *can* be omitted from a check-list, field guide, atlas, or whatever. Subspecific names are not essential, and can be regarded as optional if deemed burdensome.

Subspecies have a more positive utility for those interested in geographical variation within species, as I hope to demonstrate with examples from my own research. Though my primary objective in revising the genus *Myiarchus* was to define species limits within this difficult group, some of the more interesting findings were those relating to differences in the biology of infraspecific units, including morphology, vocalizations, breeding and molt chronology, and migratory behavior. The trinomial system was indispensable as a means of describing this variability.

Swainson's Flycatcher (*Myiarchus swainsoni*) is a widespread South American species found east of the Andes and southward into the subtropical zone of Uruguay and central Argentina. The two southernmost subspecies are nominate *swainsoni*, which breeds in southern Brazil, Uruguay, and northeastern Argentina, and *ferocior*, which breeds over much of the remainder of Argentina, western Paraguay, and southeastern Bolivia. Because they differ substantially in morphology and vocalizations, it is not surprising that they were formerly considered specifically distinct, and I was able to demonstrate experimentally that *ferocior* in Argentina and Bolivia and nominate *swainsoni* in Brazil do not respond to the playback of one another's vocalizations. Under these conditions of "sympatry" created by experimental playback, the two forms show the same indifference to each other that they show to other species of *Myiarchus*. Had an ecological barrier developed to prevent secondary contact of these forms, it is probable that they would have continued to be treated as allopatric species. But we know now that there is a relatively narrow zone of secondary intergradation extending from central Paraguay south

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