

LITERATURE CITED

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MIGHT THERE BE A RESURRECTION OF THE SUBSPECIES?

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My thoughts about the future of the subspecies concept in ornithology acknowledge its historical importance and its current ill repute. But they also anticipate its resurrection, because, for better or for worse and despite all the evils of jargon and inappropriate nuance, communication requires labels. When properly used as legal labels for meaningful geographical entities, subspecies can make our work as ornithologists more efficient and effective.

The classical subspecies concept has fostered our knowledge of distribution, movements, and variations of birds, despite the annoyances of various excesses and disparate individual standards. The discovery of new "forms" has catalyzed and sustained research interest in basic patterns of geographic variation. Inevitably, decisions must also be made about whether distinct "populations" are good species or not. As a result, formal description and pigeon-holing of variants has played a role in the development and acceptance of the biological species concept.

We now must face the disturbing question of whether or not subspecies are meaningful biological entities. If not, the concept must be redefined in new and meaningful ways or else abandoned altogether. Powerful new multivariate statistical analyses of large, excellent samples often reveal discordant patterns of character variation. Many "subspecies," therefore, will prove to be artificial entities based on inadequate samples or perspective. To the degree that other subspecies correctly reflect

concordant character variation with distributional shifts (step clines) or breaks (isolation), the possibility of real or incipient species becomes paramount. Thomas Uzzell once suggested to me that most cases of geographic variation in birds, as in reptiles, will prove to belong to either the discordant character variation problem or the incipient species problem, in which case the subspecies concept will have little future value to systematics.

One of the weaknesses of the subspecies concept is that taxonomic decisions too often become ends in themselves and distract our thoughts from underlying biological problems. I would draw briefly on my own limited experience with subspecies as a parable in this context.

I have actually described three new subspecies, perhaps my only credentials for writing this essay. Robert W. Storer and I discovered an extraordinary amount of geographical variation in a small bird on a small island. Doubting that we would ever have a chance to study it further, we decided to name four subspecies, in hopes that someone would be disturbed enough to look at the situation more closely. We used the formal labels of subspecies to call attention to a problem and to encourage further research.

Unexpectedly, I ended up returning to Reunion Island in the Indian Ocean myself and ultimately recommended scrapping the subspecies we had described. Extensive collections revealed the inadequacies of our initial, limited samples. My fieldwork revealed complex patterns of concordant and discordant character variations as well as overlapping clines in color morph frequencies. I viewed the

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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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