

SUBSPECIFIC TAXONOMY: UNFASHIONABLE DOES NOT MEAN IRRELEVANT

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For a number of years following World War II, systematic biology received very little support from universities and granting agencies. The pendulum of fashion has begun, slowly, to reverse itself, and there is now somewhat more awareness of the fundamental importance of systematics to all aspects of biology. This small renaissance is due in large part to the discovery or development of new methodologies but also to the worthwhile lobbying of the Association of Systematic Collections and its component organizations. As is usually the case, however, students have been attracted overwhelmingly to the newly fashionable methods of studying systematics. These are mostly expensive and attract large grants. Institutions housing the collections appropriate to the more traditional methods of studying systematics are finding it almost impossible to hire staff trained in the exploitation of these irreplaceable resources; some have not even tried to. Students interested in a subject as basic as avian anatomy in relation to systematics, for example, have an appallingly short list of potential major professors.

Given the trend away from the teaching of systematics at all levels, it is not surprising that few ornithologists currently concern themselves with studies of infraspecific variation and the definition and naming of subspecies. Much of the renaissance of avian systematics, such as it is, concentrates on higher classification. This is quite proper, as all agree that past and current higher classifications of birds are, as I put it in 1978, "based in very large part on decisions between conflicting bodies of evidence, interwoven with a large measure of guesswork." But any student who is genuinely interested in the phenomenon of geographic variation in birds, systematics at the specific and subspecific level, and the several aspects of ornithology into which this can lead is hard put in the 1980's to find an institution

whose faculty would encourage him or her in such studies.

Interest in infraspecific variation in birds has been waning in North America for decades. As a crude index of this, I find that trinomials were used in *The Auk* in 42% of 99 papers and notes in 1951 but in only 23% of 95 in 1981. Most of the 1981 usages were casual rather than critical (such as the use of *Icterus galbula bullockii* to indicate which "kind" of Northern Oriole was censused, in a paper otherwise confining itself to binomials). In 1951, however, a substantial number of the papers included subspecific analyses.

Those of us who are stimulated by research at the specific/subspecific levels have suffered more than just a pervasive lack of interest among our colleagues. The very concept of named and described subspecies has come under attack, occasionally savagely and with a deplorable *ad hominem* approach. Much of the criticism, when analyzed, turns out to be based on the work of a handful of authors whose lack of acceptable minimal standards (or downright carelessness) would be admitted by all of us. One can point to bad papers in every field of science.

The critics of subspecific studies should try to give their colleagues in this field credit for a little common sense and for the ability, basic to all human experience, to learn from the mistakes of their predecessors. To the best of my knowledge, most of the taxonomists who described new subspecies based on the comparison of worn and fresh-plumaged or of faded and newly collected series of specimens are now either dead or retired. And those who criticize us for using statistically inadequate series for comparison are sometimes the same persons who declare that there are enough specimens in museums and that there is no need for further collecting. Again, give us credit for our experience. Of the 77 subspecies that I have described (with or without coauthors), two were based (O horror!) on single specimens. Both of these represented significant range extensions and were well outside

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the range of variation of all other specimens of the species. We can, of course, be misled. I have retracted, in print, two of my subspecies of Philippine birds, but in both instances I had utilized *all existing material*, and it was not until newly collected series became available that it was evident to me that the differences described were bridged by individual variation. A very few of my subspecies have been "synonymized" in post-Peters volumes of the "Peters" Check-list, but only by authors that I know did so without having examined specimens.

A frequent statement about the subspecies concept is that it is acceptable for insular or otherwise discontinuously distributed species but useless or misleading for continuously distributed continental species. This is a criticism with some merit, but, again, it is based largely on the work of older taxonomists with a very typological concept, working with samples from an inadequate number of localities. There is no excuse for not using the material that is available, even if it does take time to assemble a good series through borrowing. It was only the examination of a composite series far larger than ever before gathered together that enabled Eaton (1957) to show that the characters used to define the supposed races of Northern Waterthrush (*Seiurus noveboracensis*) were *not* geographically correlated. But many continental species are surprisingly consistent over large portions of their range and differ consistently from other widely distributed adjacent populations. One cannot ban the application of the subspecies concept to continental species—trying to trace the origin of their differentiation and their subsequent history is part of the fascination of studies in geographic variation. We *do* try not to designate named subspecies when the "zones of intergradation" occupy larger areas than those attributed to the subspecies themselves!

As mentioned earlier, bad papers can of course be found to "justify" these and other criticisms of the subspecies concept. I like to think that most of us still working in this field are doing somewhat more enlightened research. But this is not to say that some naive beginners may not fall into the same traps as did earlier workers. The chances are that, if this happens, it is because the novice was not able to find anybody to work with who could demonstrate how to do it right, and, if the pa-

per gets published, it will probably be because the editor, guaranteed to be a specialist in some other field, didn't find a knowledgeable referee. This takes us full circle, to the lack of available training in these kinds of studies.

Is the practice of describing and naming subspecies biologically irrelevant, as some critics continue to claim? I, of course, think not. Can it be shown that familiarity with the traditional subspecies concept and its application may be a useful background for any of the newer approaches to avian systematics? The answer is certainly yes. I am gratified to see that some of the younger (to me) workers are bucking the trend by testing these modern approaches against the subspecies concept as manifested in traditional museum studies. An outstanding example is the recent paper by Corbin (1981) on genetic heterozygosity in Pacific coast White-crowned Sparrows (*Zonotrichia leucophrys*). As Robert Zink, who has been doing similar work with the dramatically polytypic Fox Sparrow (*Passerella iliaca*) has admitted to me, the heterozygosity being studied involves loci that may have nothing whatsoever to do with the species' responses to selection that have resulted in the traditionally invoked subspecific characters. Unless one is prepared to reject all our long held assumptions about natural selection, one must accept the concept that most, if not all, of the visible variation within a species is correlated in some way with selection and hence with survival. Eventually, we will probably find ways to study the *invisible* (i.e. genetic) bases for these very characters. Thus, the existing and continuing inventory of named subspecies, reflecting observed morphological and pigmental responses to varying environmental conditions, can and will serve as a framework for new studies in geographic variation using hitherto inaccessible characters.

Meanwhile there remain all of the traditional arguments for the usefulness of the subspecies concept within studies of zoogeography, speciation, migration, comparative ecology, etc., most of which will probably have been addressed by other participants in this forum. I must fervently hope that there will be enough recruits to this historically honorable field of ornithology to be able to staff the major museum collections, with their unique resources for fundamental research in systematics at all levels.

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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