

COMMENTARY

FORUM: AVIAN SUBSPECIES IN THE 1980'S

Subspecies seem always to have generated a good deal of controversy among ornithologists. Some have considered them to be sacred units of taxonomy, each reflecting a discrete category of geographical variation (and perhaps incipient speciation) within a species. Others have held them to be artifacts that have reality only in museum trays and that are useful only to those who delight in fiddling with nomenclature. With the recent upsurge of interest in ecology, behavior, physiology, and evolutionary dynamics, the importance of the traditional subspecies has seemingly diminished. As ornithology enters the 1980's, it seems appropriate to examine the status and utility of subspecies in this science once again.

In late 1981 I therefore invited several indi-

viduals to contribute essays expressing their personal views on avian subspecies. My charge to them was framed as a series of questions: How should subspecies be defined? Is the concept just a tool of classification that is no longer of much use? Can or should the concept be revised to make it more compatible with contemporary views in population biology? Do subspecies exist, as real biological units? Each prepared a contribution independently of the other essayists, and each essay represents an explicitly personal view. Collectively, they do not resolve the issue, or provide definitive answers to the questions I posed. If they stimulate some thought and some study, however, they will have served the purpose of this Forum well.—JOHN A. WIENS

OF WHAT USE ARE SUBSPECIES?

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The subspecies has had a long history in taxonomy. In the Linnaean period it was called "variety," and no distinction was made between individual and geographical varieties. The first authors, like Esper, who used the word *subspecies* used it to designate geographical varieties, and this has continued to be the meaning of subspecies, at least in zoology. What was at first not clearly recognized was that introducing the term and concept of subspecies was the entering wedge of the destruction of a purely essentialistically defined species. The majority of authors, right to the end of the 19th century, defined even the subspecies essentialistically as a constant, well-defined entity at a lower level than the species. Any distinct natural population that was not considered sufficiently different to be called a separate species was called a subspecies. Owing to this purely morphological definition,

many sibling species, particularly in entomology, were first described as subspecies.

After 1859 the subspecies acquired a dual biological meaning. On the one hand, it was considered the "incipient species" of Darwin, that is, as a stage in the speciation process. On the other, it was considered by certain authors like Gloger, Bergmann, and J. A. Allen to be evidence of the adaptive response of species to local climatic conditions. That the first of these two meanings was ordinarily true only for isolates while the second was particularly conspicuous for widespread continental species was not at first recognized and subsequently caused a good deal of confusion.

The subspecies concept had perhaps its greatest importance in the history of ornithological systematics during the shift from the morphological to the biological species concept, roughly from the 1880's to the 1920's. While the morphological criterion of intergradation had previously been the exclusive subspecies criterion, "geographical representation" now became the yardstick. As Stresemann

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(1975) has described so well, every isolated "species" was now scrutinized for the possibility that it was simply a "geographical representative" of some other species, in which case it was reduced to the rank of subspecies. The subspecies was now defined as a member of a polytypic species, not simply as a "slightly different" local population. The new way of looking at geographical isolates, particularly the downgrading to subspecies rank of every isolate, even when not clearly connected by intermediates, resulted in an extraordinary simplification of taxonomy at the species level. Among the 607 species of North American birds alone, 315 taxa that had originally been described as full species were subsequently reduced to subspecies status. The newly recognized polytypic species were much more distinct, real entities of nature than the purely morphologically defined "species" of the 1880's. Morphological difference was replaced as species criterion by reproductive isolation.

After the naming of subspecies had been, so to speak, legitimized and had, at least in principle, been given a biological meaning, a veritable orgy of subspecies describing began, reaching a climax in the work of such authors as Mathews and Oberholser. But even more conservative authors, like Stresemann, Hartert, Joe Grinnell, and myself, thought that they made an important contribution to systematics by the naming of rather minutely differing populations.

In retrospect, it has become clear not only that many of the so-called subspecies described from the 1920's to the 1940's did not differ in the slightest, but also that the recognition of minutely differing populations served, in most cases, no good purpose. Ornithologists like Lack, Whistler, and Voous played a leading role in criticizing indiscriminate subspecies describing (Mayr 1954). As a result, a rather elaborate methodology was proposed (Mayr 1969) to determine what criteria should be used to justify description of a new subspecies.

The criticism went even further, however, and the question was raised whether one should not dispense with the subspecies category altogether. One began to realize that subspecies are not types, even though they had been thus treated by the essentialist taxonomists. They are populations or groups of populations, and maybe a purely populational ap-

proach to geographic variation would be superior, it was said. Also, it was realized that the designation of "incipient species" was true only of isolates but not of contiguously distributed continental subspecies. Hence, it became clear that the subspecies was not a concept of evolutionary biology but simply a handle of convenience for the clerical work of the museum curator. The subspecies was likewise found deficient when studied as the adaptive response to local environmental conditions. During the study of clines, workers found the more-or-less arbitrarily determined subspecies borders to be often more of a hindrance than a help, and those who studied geographic variation with biometric and multifactorial methods usually paid no attention to subspecies designations in their analyses of populations.

The question can now be asked whether this downgrading of two major biological meanings of subspecies has not deprived the subspecies of any value at all. This is a legitimate question, but anyone who has administered large museum collections realizes what an important sorting device the subspecies still is. It remains the lowest recognized taxon. As such it does call attention to differences between geographically separated populations. It is perhaps most useful in island regions, because it directs attention to differences among the inhabitants of different islands. Furthermore, it turns out that the describing of subspecies is a useful heuristic procedure. Those who scrutinize new collections for possible new subspecies have often called attention to trends in geographic variation that might have been overlooked otherwise.

Aside from such more-or-less clerical uses of subspecies, what can be suggested as continuing scientific challenges posed by subspecies? There are a number of such challenges. In continental areas very often characters within a species do not change gradually but in definite steps, which form the subspecies borders. This raises two types of questions. First, is the step a zone of primary intergradation owing to a definite "step" in the selective factors of an environment, or is it an indication of secondary intergradation, that is of a hybrid belt between two previously isolated populations? This leads to a whole series of additional questions. What does the genetic analysis indicate about the nature of the zone of transition? Is

the morphological transition correlated with a changeover in ecological or behavioral characters? Indeed, how concordant is the geographic variation of several attributes of subspecies?

At the present time the study of nonmorphological characters is perhaps the most important aspect of the study of subspecies. It is sometimes found, particularly in isolated or semi-isolated subspecies, that the morphological change is correlated with a shift in niche occupation or such behavioral aspects as prevailing song type. Those ornithologists who are not taxonomists by background but were raised as ecologists or students of behavior often find the subspecies designations of the taxonomist useful as clues to problems that might be studied profitably.

In the early 1940's an argument developed as to whether or not there was a difference between geographic and ecological races. I agreed with those who emphasized that there are no ecological races that are not at the same time geographical races (Mayr 1942: 193). David Lack, who in an earlier publication, had proposed a process of sympatric speciation by the formation of sympatric ecotypes, abandoned these views after 1942. More important, by applying the principle later designated as "competitive exclusion," Lack postulated that subspecies that were incipient species had to acquire ecological differences before they could invade each other's geographic ranges. That different subspecies differ in their ecological requirements had been known to perceptive naturalists since Darwin's time. I am sure one will find it described in some of Joe Grinnell's writings. After all, he was familiar with the subspecies of Song Sparrows (*Melospiza melodia*) on San Francisco Bay, with the Pileolated Warbler (*Wilsonia pusilla*), and other species

with pronounced geographic variation of ecology.

I might summarize my findings by saying that the subspecies fulfilled a most important historical role by undermining the essentialistic species concept and also by contributing to a far better understanding of the geographic variation of species taxa in nature. The so-called climatic rules of Gloger, Bergmann, and Allen were at first studied through an analysis of subspecies. Today, however, the primary use of subspecies is as a sorting device in collections, that is as an index to populations that differ from each other "taxonomically." To have an inventory of such taxa is often of considerable use to the student of the geographic variation of behavior and of changes in niche occupation. The study of subspecies thus has become populational, with a greater emphasis on ecology and behavior than on morphological "taxonomic" characters. On the whole I agree with Inger (1961: 278) that "the subspecies, despite its limitations and despite our occasional faulty applications, is a concept that has proved useful and I think we will continue to use it."

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