

From a nomenclatural standpoint, the subspecies name is in every way equivalent to a name applied at the species level (i.e. any "species-group name" has equal standing, regardless of whether it was applied as a species or a subspecies, or changed back and forth). It seems an abuse of the naming process to create a name for a population that may differ in but one slight character (and even then, subspecies may be named where only about two-thirds of the individuals can be distinguished, based on the most liberal interpretation of the "75% rule"); in addition, such characters are usually the result not of significant genetic differences but of expressions of different allelic frequencies in the various local populations, and thus they are not yet of any importance in the speciation process.

In my opinion, subspecific names should *not* be used to describe populations differing only through smooth clines reflecting general primary intergradation; such geographic variation can be expressed in other ways, most effectively through the use of computer mapping. Subspecies (a trinomial scientific name) should be used in two situations: (1) allopatric populations where definition of the populations is clear, distinct, and total (or very nearly so); and (2) situations where secondary contact between distinct populations has occurred and the zone of intergradation is relatively narrow. In this

manner, use of the "subspecies" provides a useful tool in a discussion of the evolutionary speciation process (model) involved.

It is understood, of course, that such an application of the nomenclatural process would still lead to subjective decisions about what should and what should not be named; it would certainly narrow the presently broad scope of the "subspecies," however, as well as provide a better defined and more practical usage of the concept. Some problems would naturally arise concerning insular situations, where adjacent (but allopatric) populations might differ in some trifling manner. Much as with categories above the species level, some judgment must be exercised based on the type of variation and the range of the species: if the situation is such that a whole long series of insular populations are each slightly different from the adjoining ones, use of the trinomial might not be warranted; on the other hand, for a series of uniform populations in which there is a sudden change between two adjacent ones, it would be useful to assign subspecific names.

In summary, I feel strongly that the subspecies remains a highly significant taxonomic category, essential to discussion of evolutionary processes and models, but that it must be redefined to reflect this more restrictive concept.

THE SUBSPECIES CONCEPT IN THE 1980's

JOHN P. O'NEILL¹

Twenty-one years ago, a chance invitation to visit Peru set the stage for my lifelong interest in the avifauna of South America. Even a 3-month visit was enough to make me realize that the knowledge of Peruvian birds at that time was, to say the least, meager. Since then, my efforts, and those of the students and colleagues of the LSU Museum of Zoology, have,

in connection with a wide variety of studies, resulted in a rather thorough inventory of the country's avifauna. A natural outcome of such studies has been the accumulation of a tremendous amount of knowledge of the effect of an extremely complex geological and climatic past on the evolution of birds and other organisms there.

Until recently in the United States it was assumed that most descriptive ornithology had been fairly well finished by the middle of the present century. Ornithologists with little for-

¹ Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana 70893-3216 USA.

eign experience began to think of the areas of systematics and taxonomy as being the fields in which a few "old-time" museum people still dabbled. Most North American researchers began to think of subspecies as entities that were described on the basis of slight, local population differences that could be shown to exist by assembling a small series of specimens from a given locality. This work began to take on a "game" aspect rather than one that could be helpful to people interested in geographic variation in a particular species. Had I never visited Peru, I might still believe such to be true, and, had people like Jürgen Haffer not had the good fortune to work in Colombia, I might not have started to look at bird populations as I do now nor have realized that there does seem to be a definite place in ornithology for the subspecies concept.

Mayr (1963) defines a subspecies as "an aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species." The subspecies is not supposed to be an evolutionary unit, but only a taxonomic one. This technical distinction is a pitfall that many people, including myself, are guilty of ignoring. The idea of being able to talk about different populations of a species by simply giving them a name is extremely useful and valuable, but it is very easy to think about many of these, especially when they are geographically isolated, as also being evolutionary units.

Variation is basic to evolution, and, when that variation is stabilized in a population through natural selection, it may represent the first major step in species formation. This variation can be seen in two main forms, continuous, or clinal, variation and discontinuous, or allopatric, variation. The former can also be smooth or it can occur in a series of isolated "steps." It is unfortunate that many early ornithologists, especially people like H. C. Oberholser, chose to look at very few specimens from any one of a wide variety of areas and to describe minute, often meaningless differences that embraced the most micropopulational distinctions rather than characterizing the "aggregate" referred to in Mayr's definition. The description of subspecies often became an obsession of such people, who sometimes knew little about the birds they were working on or the areas from which the birds came. All

too often the "subspecies" that were described were nothing more than micropoints in a cline, and this cline was not recognized because so little material was available.

My work, and that of my colleagues in South America, has convinced me that the subspecies concept is an extremely useful tool that does have a place in the ornithology of the 1980's. Understanding both the geographical and morphological limits of these described entities depends upon having an adequate series of specimens with which to work and a good knowledge of the geography and ecology of the area from which they came. My comments in this discussion reflect my ideas as developed by studying birds and are not an attempt to discuss the subspecies concept in vertebrates in general, even though I believe that what I am saying has application to terrestrial vertebrates other than birds.

Advances in technology and relative ease of travel have greatly aided studies of speciation, systematics, and taxonomy. These areas used to be thought of mostly as museum science, but today's ornithologists are able to study living birds and to collect data previously unavailable. The days of the nonbiologist, professional collector are essentially gone. Now, the people who are describing populations of birds are the same ones who are collecting the specimens. A specimen collected today is often accompanied by tape recordings for vocal analysis, frozen tissue for protein or DNA analysis, detailed notes on foraging activities, exact locality data, extensive notes on the ecology of the area where it was collected, careful documentation of its reproductive condition, and a whole host of other valuable data.

Although variation can be characterized and described, if two closely related populations are allopatric, then a wide variety of information must be used to make a decision as to their status. In-depth field studies may show that the two forms have diverged sufficiently to be regarded as species comprising a superspecies rather than subspecies. On the other hand, two forms that exhibit obvious morphological differences may have no detectable behavioral, ecological, or vocal differences and thus are best regarded as members of a polytypic species. The establishment of the rank of two populations in allopatry is, by necessity, a subjective matter. The availability of a wide variety of information about the populations al-

lows the ornithologist to make the best decision as to their status.

In the mostly forested eastern Andes there are many different patterns of geographic variation. One of the most obvious is that exhibited by nonforest species that are isolated in the grassland islands atop these mountains. One of the best examples of such a distribution is the populations of the furnariid genus *Schizoeaca*. Essentially, every sizeable mountain-top grassland has a representative of the genus, and these forms have been treated both as full species and as subspecies of a single polytypic species. Until recently most populations were represented by only a few specimens, and little or nothing was known about them as living birds. A comparison of the call notes and songs coupled with a detailed review of external morphology suggests that more than one species may be involved and perhaps more than one species group. On the other hand, if we look at populations of the Slate-throated Redstart (*Myioborus miniatus*) from México south into the Andes, we find that the belly color changes from deep red to orange and on into bright yellow. All available information shows little difference in behavior, vocalizations, or ecological requirements, and thus they are best treated as subspecies of a single species. During cooler climatic times montane forests were probably connected throughout Middle America, and there was probably a continuous cline from yellow-bellied populations in the Andes to red-bellied ones in the mountains at the northern end of the range. Today, these forests are not continuous and the redstart populations are no longer in contact with each other, but the geographic variation is obvious and should be recognized. Because most of the "belly-color groups" are allopatric, they are best recognized by being given names, and our manner of classification has a provision for that in the trinomial system.

There are three basic conditions of geographic variation that merit recognition—variation in a smooth cline, variation in a step cline, and variation in isolation that is not clinal. Variation that is known to be clinal and occurs smoothly (i.e. with all characters grading into each other along the cline) warrants being discussed, but the various intergrading populations should all be included in a single taxon. Local populations can be talked about by geographic names such as the "central Texas

birds," etc. When the parts of a cline are broken up by climatic or geological changes into isolated units, such as probably happened with the *Myioborus* redstarts, each "aggregate of populations" that makes up a unit that is morphologically separable from other such units should be named. The decision to call these units subspecies of a species or species within a superspecies must be made subjectively using all available knowledge as to their relationships and to what would happen if the two units were to come into contact. The same situation occurs when variation in populations occurs in isolation but when such variation is not expressed in a series of orderly "steps."

Although the subspecies by definition is not supposed to be an evolutionary unit, the populations that are named, especially when they are isolated, may be on the way toward a differentiation that may eventually reproductively isolate them from other such groups of conspecifics. To me the subspecies concept should be connected to an evolutionary unit if it is to be useful. The subspecific name should be applied to groups of populations in which variation between the groups is clinal. When there is a break in this cline and thus a break in gene flow and a corresponding break in character gradients, then another subspecific designation is warranted.

The basis for the description of a subspecies is character differences, as seen in representatives (usually specimens) of that population, and thus adequate material in the form of a good series of specimens is mandatory. To make the subspecies concept more valuable, I think at least 95%, rather than 75%, of the specimens of the population should exhibit characters that make them referable to that population. There are very few populations of birds of which adequate series of specimens exist, and thus understanding the variation in a population is often difficult, if not impossible. Ornithologists also have problems in getting adequate samples, because birds are "pretty" and "popular" and thus governments are not often willing to permit the collection of enough material. A permit to collect a series of 30–40 mice or frogs is usually issued without hesitation, but a request to collect 30 birds of a common species is usually considered excessive!

Geographic variation is the product of the earth's past, both geologically and climatically.

By studying and defining this variation, ornithologists are able to add to the knowledge of the earth's history. Obviously, not all variation among closely related bird populations has progressed to the point at which those populations merit species status. To recognize these populations by naming them as subspecies is to acknowledge their existence and to demonstrate how the earth's history has affected them. This idea is nowhere better illustrated than in the Andes, where geographic variation is obvious and populations are often isolated from each other. I think that the subspecies concept is a valid one but that it should be connected to an evolutionary unit. If subspecies are evolutionary units, then the usefulness of the concept is greatly enhanced. If there is no break in gene flow (i.e. a smooth cline), then all populations in that "aggregate of populations" should be considered to belong to one form. When there is a break in the gene flow by any type of separation (geographic, ecological, etc.) then recognition of a second unit or subspecies would be warranted. Variation within a cline can be discussed and described, but only a single name need be applied. Two subspecies that seem to be morphologically alike but are separated by a form that is different would be separate evolutionary units and thus would not be referable to the same subspecies.

Graves (1980) re-examined the Colombian population of *Diglossa (carbonaria) brunneiventris* and found that the population was separable from the Peruvian birds. I feel that his action was correct in that the Colombian and Peruvian brown-bellied birds, which are separated by all-black populations, are separate evolutionary units and should not be placed together under one name.

To make the subspecies concept embrace an evolutionary unit would not affect its convenience, would make it more useful, and would get rid of the need to differentiate between the "evolutionary" and the "taxonomic" implications that seem to be so often misused. I have obviously oversimplified many of the problems and have left out a great amount of information that warrants discussion, but this is necessary because of space constraints. I do, however, find the concept to be very valuable and very useful in the 1980's.

LITERATURE CITED

- GRAVES, G. R. 1980. A new subspecies of *Diglossa (carbonaria) brunneiventris*. Bull. Brit. Ornithol. Club 100: 230-232.
- MAYR, E. 1963. Animal species and evolution. Cambridge, Massachusetts, Harvard Univ. Press.

SUBSPECIES AND SPECIES: FUNDAMENTALS, NEEDS, AND OBSTACLES

ALLAN R. PHILLIPS¹

Populations are nature's building blocks. When they do not differ consistently from other (usually more or less adjacent) populations, the whole series forms a single subspecies—or species if essentially isolated reproductively. Character complexes commonly varying, at these levels, are measurements, details of colors, or more rarely facial patterns or colors of soft parts. In most widespread species (especially if not strongly migratory or nomadic),

one or more of these complexes does vary geographically, forming more-or-less well-defined subspecies. There may also be areas where the variations are inconstant; such variable populations should not be arbitrarily squeezed into one or another of the truly distinct subspecies. Common patterns of racial or subspecific variation are clinal or convergent, open-ring, broken-ring or divergent, parallel, and nonclinal or random (which should normally not be named) (Phillips 1959).

Treatment of species and subspecies has varied widely. Most Europeans before Hartert rejected the subspecies concept, calling every

¹ Apartado Postal 370, San Nicolás de los Garza, Nuevo León, México 66400.