

tional diagnosis. Admittedly, only a small percentage of subspecies can be used for some of these purposes.

The subspecies description and diagnosis are certainly not the best format for the presentation and explanation of geographic variation within species, and inclusion of the trinomial within scientific nomenclature has created some problems. Yet, without this formal recognition and simple format, I doubt that the published record of infraspecific variation and distribution would be even half as complete as it is, and world lists of birds probably would not include infraspecific categories. The inclusion of subspecies and their distributions in Peters' "Check-list of birds of the world," however, could make it uniquely useful in coming years to those who are concerned with the sorts of problems that were mentioned at the outset. For their solution these problems will often require the proper choice

of subjects—those that present the appropriate natural "experiment." For example, one approach to the problem of the evolution of adaptations might be an analysis of the kinds of structural differences that occur between a reference species and others related to it at different taxonomic levels. The specific and subspecific levels might each include several examples that show different geographic relations with the reference species (sympatry, allopatry, intergradation, etc.). By browsing in Peters' Check-list, one could locate such subjects and determine the most efficient locations for fieldwork. To test the generality of the findings, one could also locate comparable subjects within an ecological counterpart on another continent. In this way, and perhaps in others, I believe that the subspecies will find new applications to the explanation of infraspecific geographic variation.

A MODERN CONCEPT OF THE SUBSPECIES¹

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The matter of geographic variation and subspecies has been the subject of considerable discussion and controversy in recent years. I don't think there is any question about the importance of geographic variation in ornithological study; such information is critical to the development of evolutionary models for avian speciation events. The controversy centers primarily around the manner in which it is expressed nomenclaturally (i.e. what is or should be called a "subspecies," and whether or not the *nomenclatural* concept is a necessary one).

At the moment, one problem seems to stem from the definition of a "subspecies": an aggregate of local populations of a species inhab-

iting a subdivision of the range of the species and differing taxonomically from other populations of the species. There are many forms of geographic variation, from primary variation of a relatively minor and clinal type (such as in size or degree of pigmentation, or in characters that are not expressed morphologically) to instances of secondary contact between very morphologically distinct forms that, nevertheless, still interbreed freely (the "megasubspecies" of Lester Short). Thus, the "subspecies" category loses a great deal of its potential usefulness if applied to all these situations. The more liberal usage of the "superspecies" concept in recent years to include conditions of secondary contact where isolating mechanisms have developed partially or locally has helped restrict the subspecies category at this end of the evolutionary spectrum; these "semispecies" situations are now often treated as "allospecies" of a superspecies complex.

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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

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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-

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