proached. Although it is true that such analyses could be accomplished without consideration of subspecies, the fact that extensive data on character variation are already cast in a framework of subspecies names makes information retrieval for such tasks vastly easier than it would be otherwise. Thus, in voting to retain subspecies for the time being, I emphasize the present *usefulness* of the category.

But, despite the utility of the subspecies concept for the aforementioned reasons, the time for serious house cleaning is long overdue. Like those ecologists who are still clearing the detritus strewn through their discipline over the last two decades by the excesses of the theoreticians, avian systematists must sweep away the long accumulation of subspecific names based on trivial variation and/or faulty taxonomic procedure. To be worthy of formal names, subspecies should be objectively demonstrable through repeatable techniques that prove the existence of geographic differences in any of several character suites, whether of morphology, coloration, behavior, or allozymes. New, refined, and broad-scale studies must incorporate and integrate modern approaches from statistics, colorimetry, audiospectrography, and biochemistry if they are to provide convincing results. Only then can we determine the real patterns of variation present in each group and decide which modes of variation, if any, are worthy of formal names.

Alas, not many new studies of this scope are likely to be undertaken in our present climate of shrinking support for collection-related ornithology. And it is not only financial help that is needed. The studies I recommend would require extensive collecting of specimens for skeletons and tissues. Even modest collecting of birds often unjustifiably meets with increasingly formidable resistance, opposition based largely on ignorance and emotionalism rather than on sound reasons for protection. Education could help overcome the serious problems related to specimen acquisition. To start with, permit-granting personnel, and the public that influences them, must be informed of the basic laws of productivity and of density-dependent population regulation. These facts should convince anyone of the trivial impact of collecting on wild populations of birds. Furthermore, the fundamental importance of collections to effective management and conservation practices, and to both recreational and professional ornithology, needs much more widespread appreciation. Thus, the significance of collection-related ornithology to fields other than systematics must be recognized. Avian systematics and the many branches of ornithology dependent upon it simply cannot remain as viable disciplines without a steady flow of new specimen material, which can be subjected to novel analytical procedures as they are developed. It is to be hoped that we will see greater support in the future for scientific collecting from the diverse community of persons who ultimately enjoy the benefits of this activity. Such support definitely will be necessary if a truly comprehensive examination of geographic variation in birds, and of subspecies, is ever to be undertaken.

INFRASPECIFIC GEOGRAPHIC VARIATION AND THE SUBSPECIES CONCEPT

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There are numerous problems for the 1980's to which studies of infraspecific populations might be applied. How does structural differentiation evolve? What is the significance of geographic variation for speciation? How do adaptations evolve? How does variation in behavior or environment influence speciation or evolutionary differentiation? How do rates of infraspecific differentiation relate to rates of

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speciation? To what extent are all kinds of geographic variation under genetic control? Problems like these have been addressed by only a few ornithologists. Existing museum specimens are not likely to provide the necessary diversity of data or critical samples. Additional specimens, years of fieldwork, other kinds of data (comparative anatomy, physiology, biochemistry, cytology, DNA hybridization, behavior), and perhaps experimentation may be required. In short, these problems are extraordinarily difficult to solve.

How does the subspecies relate to these problems? Before offering an answer, I must make a clear distinction between the discovery, analysis, and explanation of geographic variation on the one hand and the describing of subspecies on the other. An author engaged in the first pursuit may or may not engage in the second, but the description of subspecies implies a prior knowledge of geographic variation. In this essay I will address the utility of the subspecies description as a way of presenting geographic variation and the value of the existing literature on subspecies as a source of data.

Regrettably, the scientific name itself assumes an undue importance in the ritual of the subspecies description. In subtle ways, emphasis on the name directs the formal description toward minimal usefulness. The proper proposal of a scientific name requires little more than a diagnosis based on but one or a few characters. A new form may be compared to only one or a few adjacent subspecies rather than to all variants of the species. Any attempt to analyse data from the many existing subspecies diagnoses would be thwarted by gaps in the data and inconsistency of the characters described. A conscious or subconscious desire to find a difference may lead to biased or meaningless presentation of data; for example, means and ranges of measurements of two predetermined "populations" based on color or pattern may be quite different (and falsely supportive) even if the variation is smoothly clinal. A reductional approach to the description of geographic variation serves the proposal of new names particularly well, but indepth studies of variation throughout a species often reveal multidirectional clinal trends and other complications that are antipathetic to the naming of subspecies. In such studies subspecies may be discussed, but they are often fitted uncomfortably to the patterns of variation and are ancillary to them. Even assuming a thorough approach to subspecies description, I believe that a review of subspecies is not the most informative way to present the variation within a species, because it makes variation compartmental in an artifical way and obscures the synoptic comparison and interaction of character variations.

I would guess that the acceptance and respectability of subspecies over the years is partly based on a widespread notion that they represent tangible biological entities that are in some way the forerunners of species and thus an important part of the evolutionary content of classification. Some named populations may be incipient species, but many surely are not, and there is no way to judge which is which from the literature. Thus, the lack of a consistent biological definition of the subspecies as well as the reductional approach to its description make it difficult to use. In addition, there are often problems with identification that are not solved by writing subspecific names on labels. A specimen can only be assigned a subspecies name on a probability level that is unknown and that differs from one subspecies to another.

What functions have subspecies descriptions served, and are these functions still viable? Despite certain shortcomings of the trinomial, it is still the most efficient way of referring to geographic subsets of the species population. The literature on subspecies contains many interesting facts and interpretations relating to bird distributions, and it provides a basis for new studies of infraspecific geographic variation. Well-defined subspecies may serve to track the movements (using museum specimens or even sight records) of members of the population away from their breeding range. This contributes, often in fascinating ways, to our understanding of migration, dispersal, wandering, and wintering. In addition, the geographic origins of introduced populations can sometimes be traced. In the fields of conservation and wildlife management and in the experimental sciences the identification of infraspecific populations may also be an important consideration. These functions are not much affected by the lack of a biological subspecies definition or the tendency for reduc-

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 SUBSPECIES[1]

BURT L. MONROE, JR.[2]

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 inhabiting 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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