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# Avian Subspecies: Summary and Prospectus

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# CHAPTER 14

# AVIAN SUBSPECIES: SUMMARY AND PROSPECTUS

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Abstract.—The 14 papers in this monograph represent the first broad-based evaluation of avian subspecies in decades and one of few, if any, multifaceted treatments of subspecies for any taxon. As such, there are multiple points of agreement and disagreement. Most authors consider the concept of subspecies a valid taxonomic category for units below the species level. All authors point to the need to reexamine taxa with modern methods to confirm their identity as subspecies. All authors also agree that the best approach to recognizing a subspecies is to include multiple characters (e.g., an mtDNA study alone will not suffice). However, issues regarding the reconciliation of data sets in which we expect evolutionary rates to differ, how various methods are implemented and compared, and the statistical analyses used have not been resolved. We conclude by calling for renewed interest in examining avian subspecies that have not had modern approaches applied to their classification. Each species evaluated will add to an improved understanding of avian diversity and its generation and will be a significant contribution to conservation.

Key words: biodiversity, conservation, debates, taxonomy, techniques.

**Subespecies de Aves: Síntesis y Perspectivas**

Resumen.—Los 14 artículos que conforman esta monografía representan la primera evaluación general de las subespecies de aves en décadas y uno de los pocos, si no el único, tratamiento multifacético de las subespecies para cualquier taxón. Como tal, existen muchos puntos de acuerdo y desacuerdo. La mayoría de los autores consideran el concepto de subespecie como una categoría taxonómica válida para unidades bajo el nivel de especie. Todos los autores señalan la necesidad de reexaminar los taxones con métodos modernos para confirmar su identidad como subespecies. Todos los autores también concuerdan en que la mejor aproximación para reconocer una subespecie es incluir múltiples caracteres (e.g., un estudio con sólo ADNmt no sería suficiente). Sin embargo, no se han resuelto asuntos relacionados con la unificación de conjuntos de datos para los cuales esperamos que las tasas evolutivas sean diferentes, con la forma en que diferentes métodos son implementados y comparados, y con los diferentes análisis estadísticos que son usados. Concluimos haciendo un llamado a renovar el interés en estudiar las subespecies de aves para las cuales aún no se han aplicado aproximaciones modernas de clasificación. Cada especie evaluada adicionará conocimiento importante para el entendimiento de la diversidad de las aves y los procesos que la generaron, y será una contribución significativa para la conservación.

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During the past two decades, the annual number of publications in organismal biology that include the topic of subspecies has approximately doubled (Fig. 1), a trend likely to continue given our increasing knowledge of biodiversity, technological advances, and efforts to successfully manage and conserve species at risk. Thus, it seems clear that the concept of subspecies and the biological variation that it encompasses will retain importance for a long time to come.

Our motivation for addressing subspecies was to provide a counter-perspective to ongoing criticisms of the concept by proponents of the phylogenetic species concept. We felt that subspecies needed to be constructively addressed within the framework of the biological species concept, which, despite debate, remains the dominant species paradigm from both legal and research perspectives. Further, in organizing the original American Ornithologists' Union symposium on this subject in 2008, we found an overwhelmingly enthusiastic response for constructively addressing subspecies and less interest in debating species concepts and whether subspecies should be done away with entirely. Insofar as we are discussing biological variation, putting aside labels, we trust that most will have found something of interest herein.

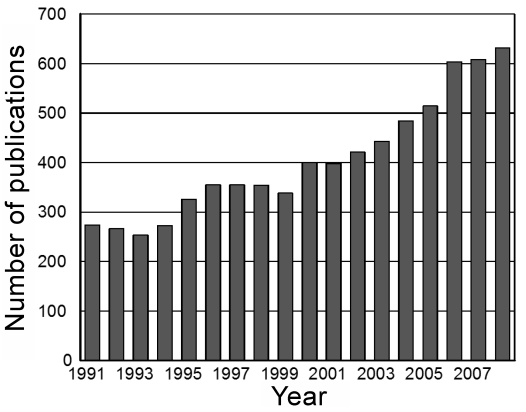


Fig. 1. The annual number of publications including subspecies as a topic found on the Web of Science (1991–2008; http://thomsonreuters.com/products_services/science/science_products/a-z/web_of_science) in the disciplines zoology, plant sciences, ecology, evolutionary biology, genetics and heredity, veterinary sciences, entomology, ornithology, biodiversity, conservation, marine and freshwater biology, and agronomy. This same pattern also occurred when only ornithology was considered (not shown).

Among the 13 preceding chapters, readers will find that authors generally agree that subspecies are a useful, albeit difficult, taxonomic category. Although subspecies are problematic almost by definition, a confounding issue that these authors acknowledged is that many, if not most, avian subspecies need a modern reconsideration of their classification. So many subspecies were described before the advent of modern statistics, sampling, molecular methods, and the quantification of phenotypic traits that they need to be revisited to determine whether the patterns described earlier actually hold true. Thus, the criticism that many avian subspecies do not represent significant geographic variation needs to be tempered with the realization that we have a great deal of updating to carry out before accepting such claims as valid. A modern treatment will most likely result in many avian subspecies being determined invalid and either lumped or perhaps downgraded to categories such as grades or distinct population segments. Furthermore, we will probably find that many avian subspecies are actually full biological species. Use of more representative data sets and modern methodology to determine species limits among allopatric populations will accelerate recognition of these taxa.

We do not advocate discarding historical work just because it was not done to current standards. Consider, for example, that Darwin (1859) provided a solid foundation for evolutionary biology without using modern genetics or statistical tests, and that Linnaeus's simple original description of *Corvus corax* in 1758 remains valid. We also do not wish to imply that the descriptive science of biodiversity can only go forward using sophisticated analyses; any volume of *Zootaxa* or the *Proceedings of the Biological Society of Washington* demonstrates that classic descriptive taxonomy retains an important place in modern biology. Nevertheless, such descriptions represent the beginning of the process of biodiversity science, and it is just that, a process—the erection and testing of hypotheses using a series of approaches and more data (and more specimens) until the true situation has been robustly inferred. The history of taxonomy and systematics shows that this process is usually neither short nor easy for most lineages. Most named subspecies are stalled somewhere along this lengthy process, and some even remain to be named. So we are not likely to arrive quickly at a stable subspecies-level taxonomy even if legions of taxonomists take up the

charge. Specimen shortages alone preclude this, even in the comparatively well-studied class Aves (e.g., Stoeckle and Winker 2009). Nor are there any shortcuts evident among the tools of statistics or genetics, even though statistical and genetic analyses are integral parts of subspecific research, as examples in this volume show.

Continued improvements in the development and implementation of new and robust statistical analyses are needed to evaluate subspecies. For example, the 75% rule used by many today is simply a guideline, not a formal statistical test, and it does not adequately address the issue of clines, which requires new statistical approaches. In this volume, James, Patten, Phillimore, and others provide new approaches (or ideas) to address the need for improved statistics, but each will need follow-up. We do not expect a silver bullet to appear; the challenge remains in evaluating both the biological and statistical significance of results in the light of guidelines for categorizing populations. More work is needed on the latter, as well.

For example, new approaches are needed to determine the lower limits of valid subspecies. Authors in this volume agree that multiple characters are important to consider in subspecific diagnosis, yet reconciling the differences we expect to find among our measurements of different characters can make overall interpretations challenging. For example, how do we reconcile the discord between mtDNA and phenotypic evolutionary rates discussed by Oyler-McCance, Pérez-Emán et al., Pruett and Winker, and others? And how do we reconcile plumage and morphological differentiation when both have a genetic component that current (putatively) neutral molecular tools are almost certainly not sampling? The difficulty stems from comparing results in population or subspecific divisions found using one approach with results from another approach when the factors being compared change on totally different time scales (because of the different rates of evolutionary phenomena such as selection and genetic drift). Thus, any strict subspecific diagnosis will have to have a subjective element, as does diagnosis of most taxa.

Although several of the chapters show why multiple data sets are important in assessing taxonomic designations, use of molecular methods alone to improve our understanding of variation among populations is increasing. Reconciling such approaches, often done without phenotypic data, with a taxonomy based on phenotype will continue to be challenging. Scientists dealing with this issue for marine mammals have proposed the concept of demographically independent populations (B. Taylor, National Oceanic and Atmospheric Administration, pers. comm.). Demographically independent populations correspond to ecological time and are defined as a unit in which internal population dynamics are far more important for maintaining unit integrity than external dynamics. Although there is no broadly accepted amount of dispersal to define a demographically independent population, marine mammalogists have decided that dispersal on the order of 1% or so per year is important for demographic differentiation in marine mammals. At this level of interchange, there is no expectation for development of a recognizable phylogeographic signal, but instead frequency differences in haplotypes or a small number of private microsatellite alleles would suffice as evidence for defining demographically independent populations. They consider subspecies to be in the gray area between demographically independent populations and species.

One growing challenge to updating subspecies descriptions is to consider the situation that occurs when what was historically a smooth cline of variation among populations has been anthropogenically broken up into allopatric segments that now possess all the attributes of diagnosable subspecies (because of the loss of intermediate populations). Do we modify taxonomy accordingly? How might this affect management, if at all? This pattern promises to become more prominent as the effects of habitat fragmentation and climate change become more pronounced throughout the world.

Even if all agree that we need to revisit subspecific classifications, how will this be undertaken? Professional societies responsible for maintaining lists of biodiversity need to catch up to (and keep up with) the management and conservation needs of agencies, countries, and societies. Because this work is often done on a volunteer basis and is rarely considered cutting-edge science at universities and museums, the priorities of taxonomists and of professional biodiversity managers often differ—this is one of the reasons why this gap has developed. Bridging it again will require some creativity from both sides. Recognition of the problem, as illustrated here, is a promising first step.

We treat subspecies as discrete taxonomic categories, although we recognize that the real situation is too complex to be fully captured in this simple way. Subspecies address the geographic component of

variation and differentiation, and although definitions and diagnoses may have to vary among cases, they will be scientific and repeatable if the criteria in each case are made explicit. As scientists, professional societies, agencies, universities, and museums renew their commitment to this topic and readdress subspecies using modern approaches and make revisions accordingly, we are certain that the outcome will be renewed acceptance of the concept of taxonomic units below the species level. We acknowledge that this acceptance will be gradual, and it will proceed largely on a species-by-species basis, as the case studies in this volume illustrate.

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