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Author(s) :Frances C. James

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AVIAN SUBSPECIES: INTRODUCTION

FRANCES C. JAMES¹

Department of Biological Science, Florida State University, Tallahassee, Florida 32306-4295, USA

MOST OF THE 13 papers in this monograph were delivered at the meeting of the American Ornithologists' Union, the Cooper Ornithological Society, and the Society of Canadian Ornithologists in Portland, Oregon, during 4–9 August 2008, in a symposium session organized and chaired by Susan M. Haig and Kevin Winker. The purpose of the symposium was to review the history of subspecies in ornithology, the relevance of subspecies to studies of biodiversity and to conservation policy under the Endangered Species Act, and examples of recent research that involves subspecies of birds. The papers added after the symposium complement the others. As organized here, the first seven papers are general in nature and the last six are examples of recently analyzed case histories. The authors present various interpretations of the concept of subspecies and of methods for assigning individuals to subspecies, but they all favor the retention of subspecies as a taxonomic category. Arguments to the contrary are presented to provide perspective.

The term "subspecies" applies to either a taxonomic category in the International Code of Zoological Nomenclature (ICZN; Ride 1999) or to a particular trinomial example (e.g., *Turdus migratorius migratorius*, which was listed in the first AOU Check-list in 1886). In the classic summaries for North American birds (Peters et al. 1934–1987, Ridgway and Friedmann 1901–1950), subspecific designations were based on variation in measurements and plumage among specimens prepared as museum study skins. The most comprehensive recent list of birds of the world (Clements 2007) reports that ~57% of the more than 2,000 bird species from Canada to Panama have subspecies. The validity of such lists is questionable, however, because many continental subspecies

were described from small or geographically isolated samples and may therefore reflect arbitrary breaks in clines (continuous patterns of character variation). I prefer to think of the early studies of subspecies as based on admittedly inadequate samples from major patterns of intraspecific variation. When the clinal variation is examined more closely, it is often found to be concordant across species and is itself of substantial evolutionary interest (James 1991). Nevertheless, the designation of subspecies on the basis of arbitrary divisions of clinal character variation is not warranted by today's standards. As our understanding of the patterns and processes of intraspecific differentiation has expanded, the impossibility of readily assigning complex patterns of variation to discrete categories has become ever clearer.

In modern ornithology, a subspecies is usually defined as a breeding population that occupies a distinct segment of the geographic range of its species and that is measurably distinct in phenotype, genotype, or both (for various definitions, see Mayr 1969; Avise 2004; Patten, this volume; Remsen, this volume). Although such designations have always been controversial, criticism of the subspecies concept intensified when researchers began to apply genetic tools such as haplotypes of mtDNA to studies of intraspecific variation (Ball and Avise 1992, Zink et al. 2000, Zink 2004). Others (e.g., Edwards and Beerli 2000) noted the wide confidence limits of such estimates and implored that any such conclusions be based on multilocus data. The extent to which gene trees are reliable predictors of population history, even when they are based on multiple loci, is actively debated in molecular evolutionary circles (Barrowclough and Zink 2009, Edwards 2009). Advocates of subspecies are interested in

¹E-mail: james@bio.fsu.edu

both the phenotypic variation, which is interpreted as mostly genetically based and adaptive, and the phylogeographic patterns as revealed by neutral genetic variation in markers such as that in mtDNA and microsatellites (Winker 2009). The three-way choice seems to be whether to admit defeat and abandon subspecies as a taxonomic category, to restrict the diagnosis of subspecies to molecular criteria, or to devise criteria that combine molecular and morphological variation.

The official nomenclature of the ICZN, which includes subspecies as its lowest rank, is consistent with the "biological species concept" of Mayr (1942b, 1963), in which taxa below the species level are recognized as relevant to the process of speciation. Distinctive parapatric (adjacent) and allopatric (isolated) populations that are considered not reproductively isolated from other populations of the same species are judged to be subspecies. Note, however, that not all subspecies should be viewed as incipient species (Mayr and Ashlock 1991). Adherents to alternative views, such as the "phylogenetic species concept" (Cracraft 1983), consider that assessment of reproductive isolation should not enter into taxonomic decisions and that the designation of taxa should be based only on evolutionary history. The "evolutionary species concept" (Wiley 1981), which focuses on the establishment of lineage independence, incorporates elements of reproductive isolation, monophyly, and fixation of diagnostic characters. In a recent review of species concepts, Coyne and Orr (2004) concluded by supporting the biological species concept as a paradigm but with important caveats about hybridization. For examples of some of these alternative views, see Cracraft (1983, 1997, 2000), Zink (2004, 2006), Navarro-Sigüenza and Peterson (2004), and Peterson et al. (2006). Not surprisingly, members of each of various camps think that their paradigm is the better one for serving conservation (biological species concept: O'Brien and Mayr 1991, Haig et al. 2006; others: Peterson and Navarro-Sigüenza 1999, Cracraft 2000). Advocates of the phylogenetic species concept would elevate all diagnosable populations to full species status (thereby possibly doubling the number of species of birds).

Among the most recent and most stinging criticisms of subspecies of birds are those of Zink (2004, 2006), who claimed that the mismatch between subspecies of continentally distributed North American and Eurasian birds and their geographic patterns of mitochondrial haplotypes

is so great that the category of subspecies is actually misleading studies of biodiversity and should perhaps be abandoned. The symposium in Portland was organized partly as a response to such challenges. Haig and Winker agree with advocates of the phylogenetic species concept that many current subspecies may be based on arbitrary divisions of phenotypic clines and that others should probably be elevated to full species status. They think, however, that the deficiencies of subspecies can be accommodated by (1) more attention to definition, (2) more explicit methods of diagnosis, and (3) a modern examination of each case. Please see their summary and prospectus.

Molecular methods have become a powerful way to reveal intraspecific differentiation and even cryptic species (Bickford et al. 2007). One conservation-related example is the recommendation based on mtDNA and microsatellite data that the geographic ranges of the three morphologically defined subspecies of the Snowy Plover (*Charadrius alexandrinus*) be changed (Funk et al. 2007). Another conservation-related recommendation is that because the endangered Ivory-billed Woodpecker (*Campephilus principalis bardii*) in Cuba is as genetically distinct in mtDNA from the U.S. population as it is from the Imperial Woodpecker (*C. imperialis*) in Mexico, the Cuban population merits a species name of its own (Fleischer et al. 2006).

If finding the upper limit of the subspecies category is partly a conceptual issue (what model to use for species), delimitation at the other end of the spectrum, finding the lower limit, involves an even grayer area. At this end, the position of Zink (2004, 2006) that sequences of portions of a single gene like mtDNA are a sufficient index for defining biodiversity and evolutionary differentiation below the species level seems to be an extremely conservative one (Greenberg et al. 1998, Bulgin et al. 2003, Phillimore and Owens 2006). Winker (2009, this volume) emphasizes that intraspecific phenotypic variation has a genetic basis (even though it may also have a nongenetic component). This variation, properly analyzed, is what most clearly reveals patterns of genetically based local adaptation and regional differentiation in the face of gene flow. This adaptive variation has not been well detected by studies of neutral elements of the genome, yet this aspect of genetically based variation can develop in a few generations and is essential to understanding evolution (Badyaev and Hill 2000, Badyaev 2005).

The difficulties of statistically characterizing subspecies once they have been defined by morphological criteria have not yet been fully confronted by adherents of the biological species concept. An important step was made by Amadon (1949), who proposed an admittedly arbitrary guideline, that 75% of a sample of specimens should be distinguishable from 99% of a sample from a reference population. Recently this idea has been extended by Patten and Unitt (2002), who developed their D statistic to test differences between localities determined *a priori*. Unfortunately, any such comparisons between two populations will be flawed unless their spatial relationship is considered (see Fig. 1). Skalski et al. (2008) contend that, unless the populations are allopatric, the proper null hypothesis is actually that no valid subspecies exist. Even when sample-size problems with t -tests are accommodated, *a posteriori* tests risk Type 1 error, the designation of subspecies when the geographic variation, at least in the character under consideration, is clinal. According to Skalski et al. (2008), neither

univariate nor multivariate tests are appropriate for testing the presence of a cline, because the locations of the samples are decided *a priori*. The important question is whether an abrupt change, or a change in the rate of change, occurs with linear clines or with isopleth maps in two dimensions. The paper on diagnosis by Patten (this volume) suggests appropriate methods of analysis (step regression, spline regression, kriging) and some available software.

The tough statistical problem of distinguishing subspecies in the presence of clinal variation is partly illustrated in Figure 1, which plots the average value of a hypothetical quantitative character against its location on a geographic cline. The line with filled squares could be a subspecies distinction at location 5 on the cline because of the sharp discontinuity in the value of the character, and the line with filled circles is just clinal variation, but if the populations at location 1 on the cline and location 10 on the cline are compared, they are equally distinct. Any comparison between locations 1 and 10 based on population

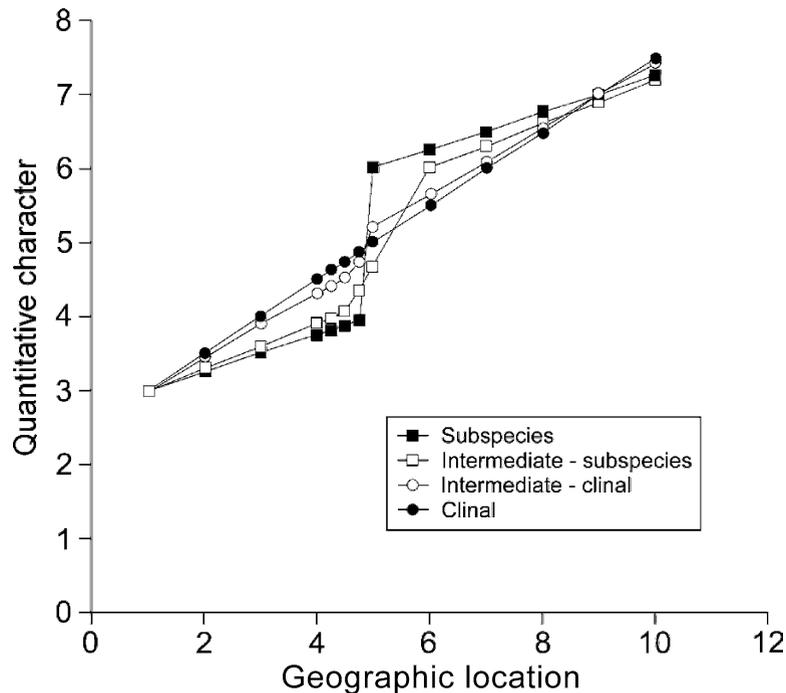


FIG. 1. Along a linear transect within the geographic range of a species, a morphometric character like size could change in a stepwise fashion as expected with a subspecies (closed squares) at location 5 or continuously as expected with a cline (closed circles), or the variation could be intermediate (open squares, open circles). Given the same pattern of variation, the scale of the analysis (locations 4–5) affects the interpretation.

distinctness (like the 75% rule) would not be able to distinguish the difference. And what about the intermediate cases, open squares and open circles? Those could be considered either smooth variation (clinal) or a distinct jump (subspecies), depending on how fine a scale was applied. At a fine scale, the changes around location 5 look like smooth changes (albeit faster than those on either side). At a coarser scale, they might look like abrupt changes, so even approaches that look for distinct changes will run into subjective issues in the choice of scale. This problem can be solved only by greater explicitness about the description and diagnosis of a subspecies than has been used in the past, and this case is just one character and one dimension. Covariation in multiple characters is reassuring (Barrowclough 1982), but despite birds' exceptionally determinate growth, various characters of their size, shape, and plumage often show different patterns of clinal variation across the two-dimensional map.

In Chapter 2 of this monograph and elsewhere (Haig et al. 2006), Haig and colleagues summarize the complexities of the administration of the Endangered Species Act by the U.S. Fish and Wildlife Service (USFWS). Acknowledging that protection should apply below the species level, at least for vertebrates, the act applies not only to full species but also to subspecies and distinct population segments (DPS) that are deemed to be at risk. Included among the criteria for a DPS are that it be a somewhat discrete unit and that it have some unique characteristics, traits that we expect would apply to subspecies by definition. Haig et al. (2006) proposed that the AOU take the USFWS criteria into account when considering the formulation of more explicit criteria for subspecies.

Because many hundreds of subspecies have not had recent review, we should not be surprised that the USFWS is asking professional societies like the AOU for an updated definition of subspecies and for clearly defined criteria for their diagnosis. Without this guidance, decisions about whether a subspecies is the unit for protection can fall to nonbiologists. For example, major lawsuits involving development rights have been brought in which final decisions were made by juries or judges. One well-publicized case concerned the endangered subspecies of the California Gnatcatcher (*Polioptila californica*; Atwood 1988) in the coastal sage scrub. It was deemed to be neither genetically nor phenotypically distinct (Zink et al. 2000, Skalski et al. 2008). The population

would have lost its protection except for its subsequent designation as a DPS, on the basis of its endangered status.

In Chapter 1 of this monograph, Winker reviews the history of avian subspecies in detail and emphasizes that even though all species probably go through a subspecies stage, not all subspecies are incipient species. He and several authors in this volume are optimistic that statistical diagnosis of allopatric populations will be possible, so that reliable subspecies can be defined. In Chapter 2, Haig and D'Elia explain that the onus of finding a reliable definition of subspecies is on the scientific societies and that the request from the USFWS for such a definition is reasonable. In Chapter 3, Patten insists that subspecies should be phenotypically diagnosable, and he points out that even the "75% rule" of Amadon (1949), which emphasizes effect size rather than simply statistically significant mean differences between populations, is not fully satisfactory. He has developed a new statistic, *D* (for diagnosability), that distinguishes among locations (presumably for allopatric populations), and he also gives several statistical approaches for estimation in cases with continuous distributions and in which no locations are hypothesized *a priori*. Patten contends that testing subspecies for monophyly is misdirected, because subspecies should not be expected to be monophyletic.

In Chapter 4, Phillimore explores the idea that subspecies nomenclature as a whole may capture the early stages of the speciation process, and he applies a birth–death model to species-age and subspecies-richness data from avian subspecies worldwide. In Chapter 5, Fitzpatrick acknowledges the lack of consensus on the value of subspecies and what they mean. He argues that subspecies status is given to a heterogeneous mix of evolutionary phenomena and that genuine standardization is probably impossible. He considers subspecies a useful tool of convenience but does not consider them capable of resolving policy issues such as endangered species listings without additional criteria. Remsen's contribution in Chapter 6, like Patten's, views subspecies as minimum diagnosable units and adheres to Patten's modification of Amadon's 75% rule. By excluding fringe localities and preferring 95% diagnosability, he seems to equate subspecies with some versions of phylogenetic species. In Chapter 7, Pratt summarizes his views about what he considers to have been overlumping of related

populations on different Pacific islands. He advocates elevating many of these populations—many of those in Hawaii, in particular—to full species status while retaining the framework of the biological species concept. Neither Pratt nor any of the authors here recommends that decisions about species and subspecies status be made on the basis of conservation, but of course elevating taxa to the species level raises their visibility.

The remaining papers, Chapters 8–13, are case studies. Chapter 8, by Pérez-Emán, Mumme, and Jabłonski, examines phylogenetic structure and variation in plumage in the Slate-throated Redstart (*Myioborus miniatus*), which occurs from northern Mexico south to Argentina. A Central American clade includes four named subspecies that are well differentiated in plumage but homogeneous in mtDNA. The authors report past field experiments that show that subspecific variation in the extent of the white in the tail reflects evolutionary adaptation to regional prey or habitat characteristics that maximizes flush-pursuit foraging. This adaptive evolutionary divergence was not revealed by the mtDNA data. Cicero, in Chapter 9, reviews research on three subspecies of the Sage Sparrow (*Amphispiza belli*), a particularly interesting case because initially Grinnell (1898a) had considered two of the subspecies, which coexist after the breeding season, to be separate species. Chapter 10, by Oyler-McCance, St. John, and Quinn, reports that, solely on the basis of the criterion of reciprocal monophyly, they would have failed to recognize five species of lek-breeding grouse. They warn against making taxonomic revisions even at the species level based solely on mtDNA data. In Chapter 11, Marantz and Patten analyze morphometric variation in the woodcreeper genus *Dendrocolaptes*. They examined more than 3,000 specimens and found that the differentiation based on plumage was not concordant with differentiation in measurements. In Chapter 12, Wilson, Valqui, and McCracken discuss geographic variation in the

Cinnamon Teal (*Anas cyanoptera*), which occurs broadly throughout the Western Hemisphere in five discrete populations. In this case, their application of the 75% rule, based on assignment of individuals to the five populations by a discriminant analysis, seems justified. Rounding out the set of papers with Chapter 13, Pruett and Winker describe geographic variation in Alaskan Song Sparrows (*Melospiza melodia*). They include data for body mass, mtDNA sequences, and microsatellite loci. The mtDNA did not show reciprocal monophyly among subspecies, but subspecies differed in body mass and microsatellite allele frequencies. The authors emphasize that multiple lines of evidence, genetic and morphological, should be used in assessing subspecific status.

Overall, this set of papers is an important update to the literature on intraspecific geographic variation in birds. Without solving the problem of diagnosing (as contrasted with defining) species or subspecies, the collection airs the philosophical position of advocates of the biological species concept. Each contribution emphasizes the importance of subspecies to our recognition of intraspecific genetically based geographic variation in the phenotypes of birds. This variation should be studied simultaneously with the neutral or nearly neutral genetic variation being detected by today's molecular methods. Ideally, these multiple characters covary, but that is not always the case. These papers do not resolve the problems discussed above, but they do present the case for continuing research within the paradigm of our current nomenclatural system.

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