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Source: Ornithological Monographs No. 67

Published By: American Ornithological Society

URL: https://doi.org/10.1525/om.2010.67.1.6

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Ornithological Monographs
Volume (2010), No. 67, 6–23
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Printed in USA.

CHAPTER 1

SUBSPECIES REPRESENT GEOGRAPHICALLY PARTITIONED VARIATION, A GOLD MINE OF EVOLUTIONARY BIOLOGY, AND A CHALLENGE FOR CONSERVATION

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Abstract.—In this review I summarize the history of the subspecies concept and the major debates and issues surrounding its use, with an emphasis on ornithology, in which the concept originated. The study of subspecific variation in birds has been an important driving force in the development of evolutionary biology. Subspecific study has also been essential in the description and preservation of biodiversity. Although controversy has surrounded the concept of subspecies since its inception, it continues to play an important role in both basic and applied science. I cover 10 relevant issues that have been largely resolved during this 150-year controversy, although not all are widely appreciated or universally accepted. These include nomenclature, sampling theory, evolutionary biology, and the heterogeneity of named subspecies. I also address three big unresolved questions and some of the philosophy of science related to them: What are subspecies, how do we diagnose them, and what does subspecific variation mean? Discordance between genotypic and phenotypic data at these shallow evolutionary levels should be expected. The process of diagnosing states that exist along a continuum of differentiation can be difficult and contentious and necessarily has some arbitrariness; professional standards can be developed so that such diagnoses are objective. Taxonomies will change as standards do and as more data accrue. Given present evidence, our null hypothesis should be that subspecific variation probably reflects local adaptation. In looking forward, it seems assured that geographically partitioned variation—and the convenient label "subspecies"—will continue to play an integral role in zoology.

Key words: adaptation, birds, diagnoses, evolution, history, philosophy of science, sampling error, speciation, taxonomy.

Las Subespecies Representan Variación Estructurada Geográficamente, una Mina de Oro de la Biología Evolutiva y un Desafío para la Conservación

Resumen.—En esta revisión hago un resumen sobre la historia del concepto de subespecie y los principales debates y asuntos que rodean su uso con énfasis en la ornitología, en donde el concepto se originó. El estudio de la variación subespecífica en las aves ha sido una fuerza importante que ha impulsado el desarrollo de la biología evolutiva. El estudio de las subespecies también ha sido esencial en la descripción y la preservación de la biodiversidad. Aunque la controversia ha rodeado el concepto de subespecie desde que fue acuñado, éste continúa jugando un papel importante tanto en la ciencia básica como en la aplicada. Abordo 10 asuntos relevantes que han sido resueltos en buena parte a lo largo de esta controversia de 150 años, aunque no todos son apreciados ampliamente ni aceptados de manera universal. Entre éstos se incluye la nomenclatura, la teoría sobre muestreos, la biología evolutiva y la heterogeneidad de las subespecies nombradas. También abordo tres preguntas grandes no resueltas y parte de la filosofía de la ciencia relacionada con ellas: ¿qué son las subespecies, cómo establecemos su diagnosis y qué significa la variación

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subespecífica? La discordancia entre datos genotípicos y fenotípicos a estos niveles pandos de diferenciación evolutiva debería ser esperable. El proceso de establecer rasgos para diagnosis a partir de un continuo de diferenciación puede ser difícil y controvertido y necesariamente incluye algo de arbitrariedad; es posible establecer estándares profesionales para que el proceso de diagnosis se haga objetivo. Las taxonomías cambiarán conforme cambien los estándares y se acumulen más datos. Con base en la evidencia actual, nuestra hipótesis nula debería ser que la variación subespecífica probablemente refleja adaptación a nivel local. Mirando hacia el futuro, parece seguro que la variación estructurada geográficamente—y el nombre conveniente de "subespecie"—continuará jugando un papel integral en la zoología.

THE VERY FIRST volume of *The Auk* contained debates about subspecies, and it is noteworthy that 125 years later the subject still draws considerable interest. Unresolved issues in science remain so either because they are neglected or because they represent fundamentally difficult areas. Subspecies have by no means been neglected in zoological research, which leads one to conclude that this phenomenon of geographically partitioned morphological variation within species—to which we commonly apply the label "subspecies"—has some inherently interesting and difficult properties. Here, I first summarize the history of avian subspecies and consider the many relevant issues—from nomenclature, to sampling theory, to evolutionary biology—that have been largely resolved as the biological sciences have matured. I then examine several major questions that remain unresolved, including what subspecies are, how we should diagnose them, and the meaning of subspecific variation. This discussion requires consideration of the philosophy of science surrounding these issues. Finally, I consider likely aspects of the future use of subspecies.

HISTORY

The 19th century.—The concept of geographically partitioned variation below the species level was born of evidence and of need. The typological species concept of Linnaeus and taxonomists of his era did not explain geographic variation within putative species. An assortment of terms was used to label these variants: varieties, races, forms, subspecies, con-species, geographical races, incipient species, and other terms (Coues 1884, Cutright and Brodhead 1981, Mayr 1982a). Linnaeus's own term "variety" was applied to within-population variation and to variation among populations (e.g., breeds of dogs), and by the mid-1800s the term "subspecies" began to become established, taxonomically embodied by the trinomial: the addition of a third Latin name to the traditional binomial nomenclature established by Linnaeus in the previous century (Mayr 1982a). Interestingly, this practice was perhaps first formally encoded in zoological nomenclature by the American Ornithologists' Union [AOU] in the first edition of the *Check-list of North American Birds* (AOU 1886).

The recognition of geographically partitioned variation (geographical varieties) was integrally important in stimulating scientific progress away from an essentialist, typological view of biological diversity and toward an evolutionary, populational perspective (Mayr 1982a). Thus, the variation now largely encompassed by the rubric "subspecies" played an important historical role in the development of evolutionary biology. Ornithologists were among the leaders in this scientific progress (Cutright and Brodhead 1981, Mayr 1982a), producing important work on the subject before and after Darwin's (1859) *On the Origin of Species*. Darwin used this type of variation in developing the theory of evolution (Darwin 1859, 1895), and its presence there is important:

> Certainly no clear line of demarcation has as yet been drawn between species and sub-species—that is, the forms which in the opinions of some naturalists come very near to, but do not quite arrive at, the rank of species: or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other by an insensible series; and a series impresses the mind with the idea of an actual passage.
>
> Hence I look at individual differences, though of small interest to the systematist, as of the highest importance for us, as being the first steps towards such slight varieties as are barely thought worth recording in works on natural history. And I look at varieties which are in any degree more distinct and permanent, as steps towards more strongly-marked and permanent varieties; and at the latter, as leading to sub-species, and then to species. The passage from one stage of difference to another may, in many cases, be the simple result of the nature of the organism and of the different physical conditions to which it

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> has long been exposed; but with respect to the more important and adaptive characters, the passage from one stage of difference to another, may be safely attributed to the cumulative action of natural selection. . . . (Darwin 1895:38–39)

Darwin (1859:47) emphasized a focus on subspecific variation that approached full species:

> Those forms which possess in some considerable degree the character of species, but which are so closely similar to some other forms, or are so closely linked to them by intermediate gradations, that naturalists do not like to rank them as distinct species, are in several respects the most important for us.

From these passages it is clear why subspecies were important very early in the field of evolutionary biology, and indeed they address topics that are at the forefront of the discipline today.

Stejneger (1884) considered that the Swedish ornithologist Carl Sundevall was the first to use trinomialism in a modern sense in ornithology when, in 1840, he treated poorly delimited species as geographic varieties, to which he gave a third name in addition to the binomial specific name. Although Stejneger (1884) stated that Sundevall's use of trinomials was closely followed by Herman Schlegel (1844), his own copy of his bound works at the U.S. National Museum in Washington, D.C., bears numerous annotations regarding his subsequent discoveries about the use of subspecific nomenclature in the 1840s and 1850s. In these annotations, Stejneger (loc. cit.) pointed to the early use of trinomials by Keyserling and Blasius (1840) and to the importance of Sélys Longchamps (1842). Mayr (1982a) omitted detailed historical discussion and considered that Schlegel (1844) was the first to routinely use trinomials. The use of trinomials grew rapidly during the remainder of the 19th century.

As Cutright and Brodhead (1981) summarized, the development and use of subspecies in the New World was particularly strong, likely for two reasons. First, North American ornithologists had a larger continent to understand, with more geographic and ecological variation than Europe, producing greater phenotypic variation in widespread taxa. Second, as Darwin (1859, quoted above) made clear, understanding this geographic variation provided insight into the process of natural selection and the origin of species. Developing an understanding of geographic variation was indeed rich ground, and a panoply of the North American ornithologists of the day have been highlighted as practitioners, including Cassin (1856), Baird (1858), Lawrence (1864), Coues (1866, 1871, 1872, 1884), Allen (1871), and Ridgway (1881; Stejneger 1884, Cutright and Brodhead 1981).

Although subspecies were less accepted in Europe than in North America, important ornithologists there were also using trinomialism during this period; Bonaparte (Parzudaki 1856, Stejneger loc. cit.), Blasius (Newton 1862), Dubois (1871; Stejneger 1884), and Seebohm (1881) were among them. Curiously, although it may have been his irritation with the credit that Coues had been given for winning widespread acceptance of the use of subspecies that caused Stejneger to write his brief history (Cutright and Brodhead 1981; cf. Stresemann 1975), his 1884 paper (especially with his own annotations) remains one of the most important foundations for a detailed history of the development of the concept and use of subspecies in ornithology. The North American precedence in the widespread use of subspecies was largely one of promotion and acceptance only, however, for as Haffer (2001) observed, there were continental European workers who covered vast areas of Eurasia and adopted similar views; however, they were not associated with museums and thus were not leaders in taxonomy. The conservatism of the latter prolonged the practice of "essentialistic microtaxonomy" in Europe until well into the 20th century (Haffer 2001).

Elliott Coues's visit to Europe in 1884, where he was well received for his prominence in scientific ornithology (Cutright and Brodhead 1981), was an important event in the spread of the use of subspecies and trinomial nomenclature (Stresemann 1975). But Coues's visit alone was not unique in promoting subspecies in Europe; see, for example, Seebohm's (1881) introduction and his treatment of *Hypolais* [sic]. Nor was Coues's visit sufficient to overcome staunch opposition (Haffer 2001). Much of the debate over subspecies was related not to their existence, but to the adoption of trinomial nomenclature to denote these often minor variants. As R. Bowdler Sharpe wrote near the end of his life, "That races or subspecies of birds exist in nature, no one can deny, but, to my mind, a binomial title answers every purpose . . ." (Sharpe 1909:v; cf. Seebohm's [1881] treatment of subspecies as binomials, which he was forced to do by the editorial dictates of that publication). Philip L. Sclater, one of the world's most important and influential ornithologists

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during the second half of the 19th century and editor or co-editor of the journal *Ibis* from 1859 to 1864 and again from 1877 to 1912 (and thus an important gatekeeper for the publication of European ornithology in English), was also a major opponent of trinomialism (Elliott 1914, Stresemann 1975). The objections of Sharpe, Sclater, and others opposed to trinomialism stemmed largely from conservatism (the Linnaean binomial system was accepted tradition and sufficient) and from concern over "the danger of an outbreak of frivolous names given by scribblers who were only eager to publish and had no critical judgement . . ." (Stresemann 1975:252). Coues (1884:246) himself recognized this potential drawback, considering that trinomialism

> is so sharp a tool that without great care in handling, one is apt to cut his fingers with it. It is of such pliability and elasticity, and lends itself so readily to little things, that in naming forms one is tempted to push discrimination beyond reasonable and due bounds. . . . This is the real difficulty . . . its abuse in the hands of immature specialists.

The recognition and use of subspecies in the New World was standard by the late 1800s, and, despite such prominent opponents as Sclater and Sharpe, in Europe the use of subspecies by such careful and important workers as Ernst Hartert, Karl Jordan, Walter Rothschild, and others eventually prevailed (Stresemann 1975, Mayr 1982a, Rothschild 1983, Mallet 2007). But an important change was implemented in the process. Under the morphological species concept of the late 19th century, evidence of intergradation was key to the recognition of subspecies, whereas morphologically distinct isolates were usually treated as full species (Mayr 1982a).

In 1891, Hartert wrote

> I believe it is right to regard as subspecies forms that differ only in a small variation in size, lighter or darker coloring, or small variations in pattern, even though one does not have the intermediate forms at hand. This type of nomenclature shows the closeness of the relationship, whereas the simple specific name gives no indication whether the species are poles apart or very nearly related. (Stresemann 1975:259)

In 1892, Hartert met Walter Rothschild and was soon thereafter hired as a curator at the Tring Museum (Rothschild 1983). At Tring, the ornithologists and entomologists Rothschild, Hartert, and Jordan produced a body of work that effectively expanded the definition of subspecies to include geographically isolated, closely related populations (Rothschild 1983, Mallet 2007). Mayr (1982a) considered this development to be based on the biological species concept, which had yet to be defined, but which decades later came to dominate taxonomy and systematics.

The 20th century.—The recognition of closely related but geographically isolated populations as subspecies was an important turning point in how the concept of subspecies was applied; it now encompassed both distinct but intergrading populations and distinct geographic isolates not sufficiently differentiated to warrant recognition as full species. Several more decades were required (until the 1940s) for modern terminology and concepts to be fully developed, but this concept of subspecies was an integral part of that process. Bernhard Rensch, Julian Huxley (who contributed, among other things, the term "polytypic species"), and Ernst Mayr were important contributors during this period (Mayr 1982a, Mallet 2007). Ultimately, the hierarchical levels of differentiation (populations, subspecies–polytypic species, superspecies) that could be seen within many taxa, among populations that were separated to greater or lesser degrees geographically, provided a framework for understanding biological diversity that contributed several key tenets to the Evolutionary Synthesis of the 1930s and 1940s (Futuyma 1998).

In taxonomy, the effects of adopting this expanded view of subspecies were also profound. Recognition of polytypic species (species that comprise two or more subspecies) and adoption of the biological species concept caused a major reduction in the number of species-level taxa, from >20,000 in the 1920s to ~9,000 in the 1980s (Mayr 1982a). But there was overlumping, with perfectly good allopatric species lumped into polytypic species and treated as subspecies. We are still rebounding from this process as an increasing number of allopatric subspecies are, with additional data, being recognized as full biological species.

Mayr (1982a) considered that birds were well suited to this new taxonomy that included polytypic species and that its application to Aves caused the group to be especially valuable for both evolutionary and ecological studies. But here he omitted mention of further disagreement over the utility of the subspecies concept, which has waxed and waned since its inception.

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Wilson and Brown (1953) wrote an important and influential critique of subspecies, their main concerns being that (1) characters varied in different and nonconcordant ways, and that, depending on which character was used, different subspecific delineations could result; (2) there was a great deal of arbitrariness in defining subspecies, especially in delimiting the lower limits; and (3) subspecific taxonomy was getting in the way of real research (e.g., on geographic variation) by demanding an artificial formality and a system that lacked sufficient flexibility.

Mayr (in Inger 1961:283) observed that when Wilson and Brown (1953)

> recognized that these subspecies of the literature were not subspecies they acted just like the little boy who knocks himself against the corner of the chair and beats the chair for being so bad: they let out against the subspecies their anger at the specialist of ants for having mistreated and misused the subspecies concept.

Wilson (1994:208) later wrote that he and Brown had overstated their case. Concordant changes in multiple characters often occur; this is the geographically partitioned variation that is the hallmark of good subspecies. Wilson and Brown (1953) were correct that subspecific taxonomy is probably most difficult and arbitrary at the lower limits of the subspecies category and that undue focus on subspecific taxonomy had, in effect, created what they termed a "subspecies mill." Indeed, the fears of Sharpe came to pass, and even Mayr (1951:94) had to admonish ornithologists to put less effort into describing minor subspecies and more into studying the trends of geographic variation.

In 1982, an invited forum on avian subspecies by 11 authors was published in *The Auk* (Wiens 1982). As might have been expected, although this forum provided a series of strong essays on the subject, together they did not provide definitive resolution of the key issues debated in relation to subspecies since Darwin (Wiens 1982); such resolution remains evasive.

In sum, the use of trinomials in the literature of the time shows that, in referring to subspecies and subspecific variation, Darwin (1859, 1895) was communicating effectively with the leading scientists of the time on a subject important to them. Ornithologists were in the vanguard in adopting the use of subspecies, both because the concept helped researchers understand biological diversity and its generation (Cutright and Brodhead 1981, Mallet 2007) and because in many other taxa describing species-level diversity remained (or remains) a dominant pursuit (Mayr 1982a). The problem of an accepted definition, however, alluded to by the passages of Darwin (1859, 1895) quoted above, has persisted within and among taxa to the present (Mayr 1982a, Haig et al. 2006). Examples of how definitions have progressed are given below in my discussion of unresolved issues.

Sharpe's and others' fears that subspecies names would be inappropriately applied to many dubiously distinct forms (Stresemann 1975) were prophetic, and many unwarranted named subspecies remain to be eliminated. However, a certain naivete is evident among many authors in the second half of the 20th century, who seemed to desire that scientists forgo describing their discoveries and observations (in describing subspecies in this case) until enough specimens and data were in hand to understand true patterns of geographic variation. Or, conversely, they felt that such studies should be restricted to hypothesis-testing approaches rather than the descriptive approach most often used in subspecies-level, discovery science. These views do not sufficiently acknowledge the important stepwise progress of science in describing and understanding biodiversity at its finest levels. In addition to changing techniques and differences in data interpretation, specimen limitations alone have long precluded a shortcut to accurately summarizing biodiversity (e.g., might an apparent discontinuity instead represent clinal variation as yet insufficiently sampled?). Not only is the job not yet done (e.g., Zink and Remsen 1986), but the decline of taxonomy as a discipline in major universities during the second half of the 20th century has caused much of the unresolved mass of dubious names, questionable species limits, and phenotypically undescribed or unexamined populations to languish. And if new generations of students are not being trained in this presently less popular aspect of biodiversity science, we postpone a full understanding of biodiversity and hobble our abilities to document and manage this diversity during a period of major global changes. This is a huge challenge for 21st-century biology. How will we meet it?

Issues That Are Largely Resolved

Numerous issues have been largely resolved in the long debate over subspecies, even if all are not widely appreciated or universally accepted.

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Nomenclature.—As Mallet (2007) pointed out, the International Code of Zoological Nomenclature (ICZN) regulates just that—nomenclature—and does not treat the difficult problem of how one determines what taxonomic rank a lineage or group of specimens represents. The subspecies concept thus comprises two important but now largely separate issues: trinomial nomenclature (that battle is over and is encoded in the Code; ICZN 1999) and the thornier question of what constitutes a subspecies—that is, in what cases do we apply trinomialism? The nomenclatural tool is here to stay; we as taxonomists and systematists simply need to do as Darwin (1859:47) suggested and come to some agreement on how and where to apply it.

Subspecies can be genuine biological units.—There are many examples of good subspecies, cases in which multiple species concepts would agree that populations that exhibit diagnosable (see below) differentiation from their nearest related population(s) in more than one phenotypic character do not achieve the threshold required of full species. Some of the best examples of subspecies occur among Song Sparrow (*Melospiza melodia*) populations in northwestern North America (Pruett and Winker, this volume). One reason I think that Song Sparrows are a good example is that there are no obvious species limits in this group under the phylogenetic species concept; probably because of the apparent recent colonization and ongoing gene flow (though frequently low), reciprocally monophyletic units (using any character) would be difficult to recover in this species when good samples (numerically and geographically) are examined. Yet the populations in Alaska recognized as legitimate subspecies exhibit increasingly concordant divergence in multiple characters as isolation increases (Pruett and Winker, this volume). Another good series of subspecies occurs in Rock Ptarmigan (*Lagopus muta*) across the Holarctic; some of the more pronounced occur among the Aleutian Islands (Fig. 1). Some of these subspecies might be considered phylogenetic species, but evidence of gene flow and the capacity for gene flow among populations in this species causes the taxonomic fit to be better with the polytypy of the biological species concept. Importantly, in both of these examples the recognized variation is discontinuous (i.e., it does not occur in a smoothly clinal way). Populations that exhibit clinal variation in one or more characters are likely to be legitimately subdivided into subspecies only when discontinuities occur (classically termed "step clines"; Mayr 1963, Mayr and Ashlock 1991).

FIG. 1. Summer adult male Rock Ptarmigan (*Lagopus muta*) from the Aleutian Islands, Alaska. From left to right are ventral and dorsal images of *L. m. evermanni* (from Attu Island), *L. m. townsendi* (from Kiska Island), and *L. m. atkhensis* (from Tanaga Island).

Sampling error.—The problem of sampling error—that summaries of diversity change with increased sampling—was recognized quite specifically by the first AOU Committee on Classification

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and Nomenclature in formally adopting trinomialism (AOU 1886:31). What has yet to be fully appreciated (though see Funk and Omland 2003, Brumfield 2005, DeSalle et al. 2005) by researchers using rather small data sets of DNA sequence in phylogeographic and barcoding studies is that this same problem of sampling error exists here, too. The parallels between the historic naming and lumping of subspecies and the recognition and subsequent (or future) loss of monophyletic mitochondrial DNA (mtDNA) clades are obvious but are nevertheless overlooked by many researchers today.

In the description of phenotypic diversity, initial specimens or data sets might indicate sufficient geographic variation to name subspecies (Fig. 2A). Increased geographic sampling might show clinal variation, necessitating the elimination of recognized subspecies (Fig. 2B), or sufficient discontinuous variation to warrant continued recognition of the subspecies initially described (Fig. 2C). Increased numeric sampling might show that individual variation within populations is too high to enable credible diagnoses of the individuals in each population and, thus, that they do not warrant subspecific labels (Fig. 2D), or that such variation is sufficiently low to enable a high degree of diagnosability between populations for which subspecies designation is appropriate (Fig. 2E).

Similarly, in the description of the distribution of genetic variation, initial data sets may indicate highly partitioned variation in the form of monophyletic clades (Fig. 3). It may be appropriate to label these clades with names (although I disagree that species or subspecies limits should be diagnosed using a locus or two of DNA sequence data alone; Winker et al. 2007). Such trees can be reconstructed from genetic or phenotypic data, but the same sampling-error issues remain. Increased geographic sampling might uncover a population that has characteristics of more than one described population (Fig. 3B) or lend further support to the initial summary by finding continued geographic partitioning of population-defining characters (Fig. 3C). Increased numeric sampling might reveal that one or more populations comprise an admixture of what were thought to be population-defining characters (Fig. 3D), or that these clade-defining characters are segregated, warranting continued recognition of these units (Fig. 3E). Power analyses addressing this problem are considered below.

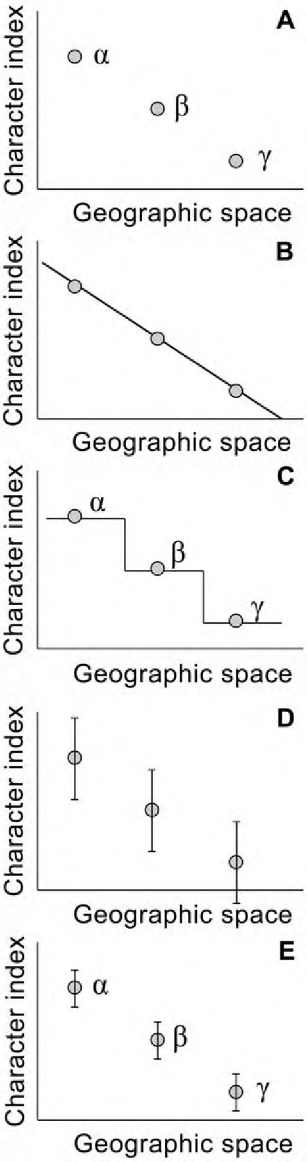

FIG. 2. A simple diagram of how initial sampling of biological diversity across geographic space might indicate (A) the existence (and cause the description) of multiple subspecies. Subsequently increased geographic sampling might show (B) that variation is clinal and the recognition of subspecies is unwarranted or (C) that variation occurs in a discontinuous (here, stepwise) manner and that continued recognition of subspecies is warranted. Similarly, increased numeric sampling might reveal (D) such degrees of intrapopulation variation that reliable diagnoses of previously described subspecies are not possible or (E) that such variation is sufficiently low to enable reliable subspecific diagnoses.

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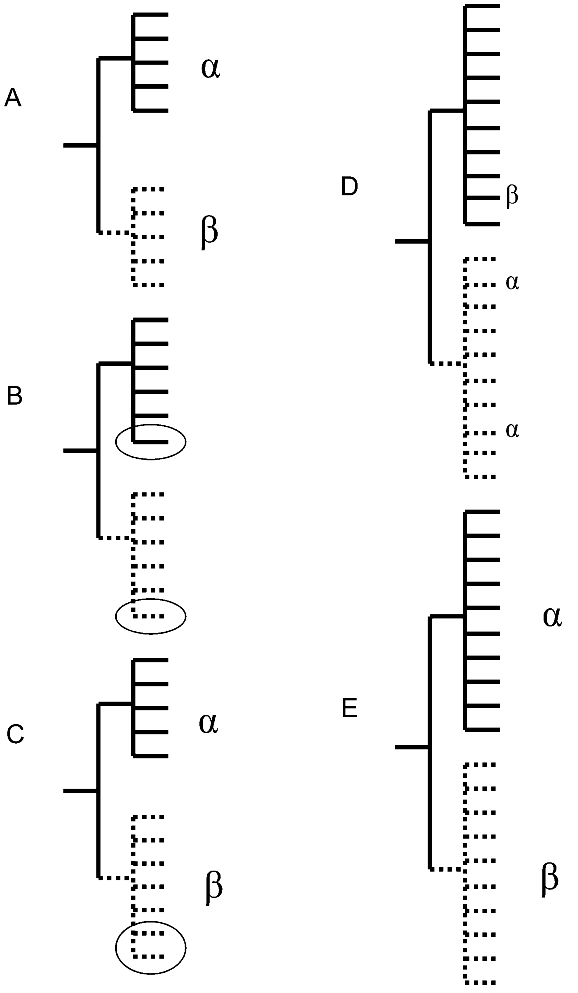

FIG. 3. A simple diagram of how initial sampling of biological diversity across geographic space might reveal two monophyletic clades, indicating (A) the existence (and possibly causing the naming) of different (sub)specific units. Subsequently increased geographic sampling might show (B) that a newly sampled population (here, $n = 2$, circled individuals) has individuals from each clade, suggesting that named units are not warranted, or (C) that this newly sampled population retains the initially described geographic partitioning of variation and that continued recognition of those units is warranted. Increased numeric sampling might reveal (D) that one or more populations comprise a mix of individuals that possess what initially seemed to be population-defining characters (e.g., wherein an individual from the β population is found with α population characters and two individuals from the α population possess β characters). Conversely, increased numeric sampling might continue to show (E) strong separation of these clade-defining characters, warranting continued recognition of these monophyletic units.

Importantly, both increased geographic and numeric sampling are usually needed to ascertain the veracity of initial diagnoses. For example, isolation-by-distance effects might cause increased numeric sampling to support unit recognition, but a lack of increased geographic sampling might cause zones of intergradation to be overlooked. Incomplete data will affect diagnoses and ensure continued modifications of taxonomies as understanding improves.

Diagnosable units.—It is important to emphasize that I use the term "diagnosable" in a probabilistic sense and not in a cladistic sense. Consider the now classic "75% rule" (Amadon 1949, Patten and

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Unitt 2002) as our probabilistic threshold in recognizing subspecies (discussed more below). This level of diagnosability falls considerably short of the 100% diagnosability criterion of cladistics. In other words, reciprocal monophyly (two groups monophyletic with respect to each other), no matter what characters one chooses to use, provides a level of unit diagnosability in cladistics that is not appropriate as a lower threshold for evaluation of subspecies. Why? Because a probabilistic framework of diagnosability is more concordant with the processes of divergence between populations: gene flow can and often does still occur between populations, leading to an evolutionarily important relationship between diverging forms (in this case a lack of independence) that must be accounted for in assessing and managing biodiversity. The working hypothesis of the biological species concept (which allows some hybridization; Johnson et al. 1999, Winker et al. 2007, Price 2008) accounts for limited gene flow between species; subspecies, by definition, must also allow some gene flow to occur.

Typological thinking has no place in defining and recognizing subspecies. Further, in recognizing the populational processes of divergence, simple statistically significant differences between populations are expected and are decidedly not sufficient grounds for the recognition of subspecies (Mayr et al. 1953, Patten and Unitt 2002).

Gene flow.—It is widely accepted that gene flow inhibits divergence between populations. What is not often remembered, however, is that to the best of our knowledge the effects of gene flow on the process of divergence are highly nonlinear (Fig. 4). Even at low rates, gene flow can prevent speciation and even local adaptation under strong selection (Rice and Hostert 1993, Hostert 1997, Postma and van Noordwijk 2005). Another consideration is that populations may evolve collectively when alleles of high selective advantage spread among them at even very low levels of gene flow (Morjan and Rieseberg 2004). Because low rates of gene flow can act as a sort of evolutionary glue that prevents populations from diverging, sampling error becomes particularly important in assessing data on the distribution of genetic variation. Using sequence data from a genetic locus such as mtDNA and the coalescent, 10 individuals from each of two populations provide a good sample size for analyses of gene lineage histories and lineage sorting (Harding 1996, Rosenberg 2007). But gene flow is not adequately surveyed with such samples, because even

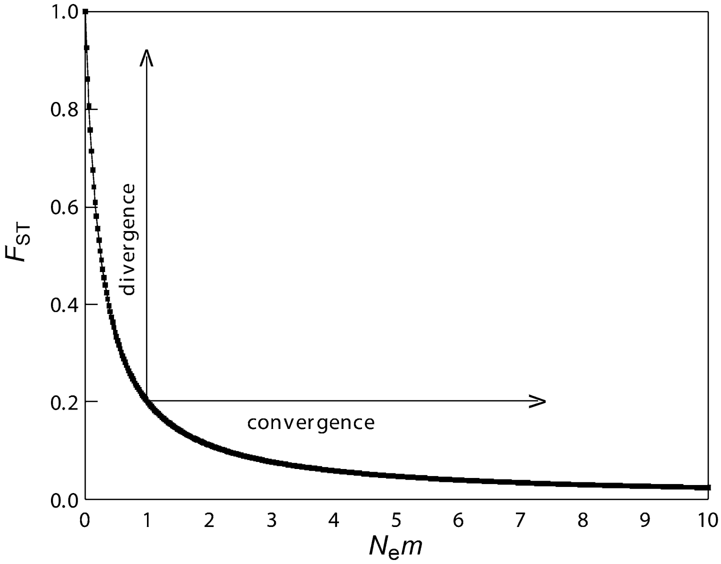

FIG. 4. The relationship of Wright's (1943) F_{ST}, an index of interpopulation genetic differentiation, to the product of effective population size (N_e) and the rate of gene flow (migration, or rate of effective gene flow), m. Note the highly nonlinear relationship and that the inflection point, at $N_em = 1.0$ (one migrant per generation), marks a transition under neutral conditions between populations that are diverging and populations that are effectively fused. After Cabe and Alstad (1994).

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moderate levels of gene flow could escape detection. Using Gregorius (1980) for power analysis, a sample size of 11 gives a 95% probability of detecting all alleles (or haplotypes) in a population that occur at ≥30% frequency. From Figure 4, it can be seen that this level of power does not come anywhere near the inflection point of divergence under neutral conditions (nor, likely, under strong divergent selection; Rice and Hostert 1993, Hostert 1997). This observation of the limited power of most phylogeographic studies is not meant to deter them, for more are urgently needed. Rather, it is to focus interpretation of these studies on the populational processes of divergence (for a good example in birds, see Brumfield 2005). Gene flow and phenomena such as clinal variation, isolation-by-distance, reticulation, and polyphyly and paraphyly are to be expected when populations are in the process of diverging (cf. Funk and Omland 2003). Knowing when these phenomena can be ruled out in explaining the distribution of genetic variation is very important.

Subspecies are interesting and have value.—Insofar as subspecific labels for geographic variation have not only been deemed necessary by historical leaders in biological research but have also been used as guides for both historic and modern research, the value of the concept has been proven despite a lack of agreement over what exactly a subspecies is. The continuing value of the concept can be seen in both applied and basic research. Two examples will demonstrate this.

Outside of game species, the classic study of museum specimens (subspecies) has provided most of our knowledge of the nonbreeding distributions of the birds of North America. Identification of population movements, especially of migratory forms during the nonbreeding season (except for game species, in which hunters effectively provide large band-recovery efforts), has been accomplished mostly on the basis of subspecific plumage characters. Classic examples are summarized throughout the fifth edition of the AOU Check-list (AOU 1957), exhibiting this practical utility of subspecies very well.

In basic research, one of the best examples of the interest and value of subspecies is a research program that ends up questioning the utility of the concept itself. In reviewing 18 species studied by R. M. Zink and colleagues (Table 1), it can be seen that the species they chose to work with had an average of 13.5 recognized subspecies each. The congeneric species not chosen for these studies averaged about 3.1 recognized subspecies (Peters et al. 1931–1987). In 10 of these 18 studies, the species with the most recognized subspecies of any in the genus was the focal taxon (Peters et al. 1934–1987). The probability of this occurring randomly is quite small ($P \approx 0.008$). Regardless of why these species were chosen as the focal taxon of their respective genera, if subspecies were not often used as a guide for this body of research (and in some studies they clearly were not), then they were at least an important component.

I am not using this analysis to condemn the approach of Zink and his colleagues (Table 1). Whether they chose to work with species that have above-average subspecific diversity (in contrast with congeners) or whether this was merely an accidental (though highly significant) correlation, their research nevertheless tells us something about avian subspecies. Where I differ with Zink's (2004) conclusion is in our perspective on what the evidence tells us, a difference that is not simply a glass-half-empty versus glass-half-full situation. Zink's (2004) message was that the vessel itself (subspecies) is faulty, a condemnation reminiscent of that of Wilson and Brown (1953; cf. Mayr in Inger 1961:283). As Zink (2004) showed, much of this body of work could be focused around the concept of subspecies, and therefore that concept had scientific interest and some merit. In the process of speciation, discordant distributions of largely neutral genetic variation and phenotypic variation (which for many if not most characters will have a substantial non-neutral, adaptive component) are to be expected, as Price (2008), Winker (2009), and others have pointed out. Phillimore and Owens (2006), using a larger and geographically more diverse data set than Zink (2004), found a greater level of mtDNA and subspecies concordance. In fact, a large body of research has used subspecific designations to better understand diversity and its distribution and to ask important questions of microevolutionary processes (e.g., Remsen 1984).

Subspecies represent a heterogeneous taxonomic category.—Since the end of the 19th century, when allopatric forms that showed relatively small differences were included with intergrading forms as subspecies, the category has been one of heterogeneous named populations (e.g., fig. 1 in Fitzpatrick, this volume). This fact remains an irritant to many of those concerned with subspecies. The basis for subspecific names is not and never has

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Table 1. Eighteen species chosen for research by R. M. Zink and colleagues, showing the study, the number of subspecies in the focal taxon, total species in the genus, average number of subspecies among species in that genus (minus the focal taxon), and whether the focal taxon had the highest number of recognized subspecies in the genus. Taxonomy is an amalgam of American Ornithologists' Union (1998) and Peters et al. (1934–1987).

Source	Species	Subspecies (*n*)	Species in genus (*n*)	Subspecies in genus[a]	Study species highest
Zink et al. 1987	*Callipepla californica*	4	5	2.25	
Karl et al. 1987	*Larus californicus*	0	35	0.91	
Zink et al. 2002a	*Dendrocopos major*	27	33	5.44	X
Zink et al. 2002b	*Picoides tridactylus*	11	2	—	X
Johnson and Zink 1985	*Vireo olivaceus (complex)*	14	25	2.58	
Zink et al. 2000	*Polioptila melanura* (or *californica*)	6	8	4.14	
Drovetski et al. 2004	*Troglodytes troglodytes*	35	5	12.75	X
Zink et al. 2001	*Campylorhynchus brunneicapillus*	7	11	3	X
Zink et al. 2003	*Luscinia svecica*	7	25	1.83	
Zink and Blackwell-Rago 2000	*Toxostoma curvirostre*	7	10	1.89	X
Pavlova et al. 2003	*Motacilla flava*	18	9	3.13	X
Zink and Klicka 1990	*Geothlypis trichas*	13	13	1.75	X
Zink 1988	*Pipilo fuscus*	18	7	5.5	
Zink and Dittmann 1993a	*Spizella passerina*	6	6	2.4	X
Zink et al. 2005	*Passerculus sandwichensis*	21	9	4.25	X
Zink 1994	*Passerella iliaca*	18	9	9.25	
Zink and Dittmann 1993b	*Melospiza melodia*	39	9	6.63	X
Zink et al. 1991	*Quiscalus quiscula*	3	8	4	

[a] Average excluding the focal taxon.

been reserved exclusively for evolutionary units (Mayr 1969:41). The existence of or potential for gene flow between subspecies precludes this exclusivity. In this, subspecies differ from higher taxonomic ranks, but as Smith and White (1956) pointed out, this is fully consistent with nomenclatural theory, which is based on denoting differences. And because most species have probably passed through some sort of subspecies stage of differentiation, Darwin's (1959, 1895) insight that this passage is important remains a stimulus for studying subspecies. As eloquently put by Smith and White (1956:190), "The gap from non-species to recognizable species is necessarily bridged by stages of major evolutionary import." Also, our recognition of a nomenclatural category in which some units may very well become full species and others will not gives us a conceptual tool of inestimable value in understanding the process of speciation (Smith and White 1956). Subspecies and their heterogeneity therefore do not represent a problem to basic science so much as they represent an opportunity.

We should not eliminate subspecies altogether.—Smith and White (1956) presented one of the best rebuttals to the condemnation of subspecies by Wilson and Brown (1953), and most of their observations remain applicable today. For those who study speciation, recognition of units only at the species level and above ignores stages of differentiation that are clearly important in the speciation process. Subspecies have a demonstrated utility if only for this research purpose alone, making their use largely unstoppable. This does not mean that they must be used by all. However, it must be recognized that the work that goes into subspecific taxonomic revision has become rather unpopular, leaving something of a mess of unresolved subspecific names, species limits, and specimens and data that remain to be critically reexamined in this context.

Subspecies are a challenge to conservation.—Subspecies represent a challenge to conservation that might be summed up in a relatively simple way: homogeneity is more easily managed than heterogeneity. Recognizing the conservation

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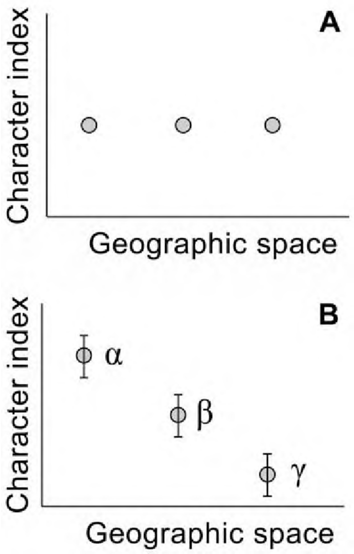

FIG. 5. Subspecies represent a challenge for conservation. The conservation implications of a taxon that (A) exhibits no structured geographic variation (the no-trinomial view) is a much simpler situation than that implied by (B) the more complex adaptive space likely occupied when trinomials are applicable.

implications of a taxon that exhibits no structured geographic variation (the no-trinomial view) is much simpler than responding effectively to the complexity that exists when different adaptive space is likely occupied by subsets of populations (Fig. 5). Use of subspecies in this context includes an important assumption: that subspecies labels are applied to populations that possess unique properties in an evolutionary, adaptive sense. Although many populations that possess very minor differences (i.e., invalidly considered diagnosable) have been named as subspecies and remain to be eliminated, this is probably a useful null hypothesis (see below).

Human imperfections play a considerable role.—Our own human tendencies have had predictable influences on the subspecies phenomenon. Sharpe's concern about the dangers posed by authors who lack critical judgment yet are eager to publish accurately anticipated what Smith and White (1956) termed the "*mihi*" itch of taxonomists to describe new taxa, and what Wilson and Brown (1953) called the "subspecies mill" generated a surfeit of names to describe, at times, even the most minor differences among museum specimens (i.e., differences that are not useful for diagnosing populations at levels even less stringent than that of the 75% rule). But the opposite side of that proverbial coin—the bracketing human condition to writing up trivial phenomena—is laziness among those not wanting to recognize subspecies because of the work necessary to accurately determine and describe geographic variation (Smith and White 1956). Detailed study and description of biological diversity at and below the level of species is fundamentally hard work, whether one is performing a pioneering study or reevaluating the work of others with new data. Knowing that we scientists have both of these tendencies might help temper action at the extremes.

UNRESOLVED ISSUES AND PHILOSOPHY OF SCIENCE

What is a subspecies?—In summarizing some of the key views on subspecies between Darwin (1859) and now, we might conclude that we have not come remarkably far from Darwin's (1859) view that in determining the taxonomic rank of a form that is near the species level we will have to be guided by scientists with judgment and experience.

The debate now is not over binomialism or trinomialism (taxonomy) but over how to diagnose and recognize geographically partitioned variation that may or may not exhibit intergradation. Allopatric populations that show comparatively minor differences but with no evidence of intergradation are common, especially among islands. Parapatric, intergrading populations (e.g., step clines) also occur. No species concept can decisively solve this problem; some subjectivity will be involved (e.g., Winker et al. 2007).

Allen (1871), in focusing on the fact that intergrading forms should not be considered full species, hastened adoption of the acceptance that "subspecies are distinguishable forms which intergrade, while species do not intergrade" (Stejneger 1884:75; cf. Coues 1871:371–372). In Allen (1871) and Coues (1871), one can see the beginning stages of what eventually would comprise the AOU's early views in adopting formal use of subspecies (Allen and Coues were members of the committee), which were summarized pithily: "In a word, *intergradation* is the touchstone of trinomialism" (AOU 1886:31). This school of subspecies was soon enhanced by including discontinuous forms that did not intergrade but that differed to a degree similar to that found among

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parapatric subspecies. As Hartert defined subspecies in 1903:

> We describe as subspecies the geographically separated forms of one and the same type, which taken together make up a species. Therefore not just a small number of differences, but differences combined with geographic separation, permit us to determine a form as a subspecies, naturally when there is general agreement of the main characters. (Stresemann 1975:262)

Amadon (1949) felt that if subspecies names were applied conservatively they would call attention to geographic variation and incipient speciation, which recalls Darwin's (1859, 1895) points quoted above. To help achieve that conservatism, he formalized the 75% rule, a popular lower limit for the delineation of subspecies. He defined this rule

> to mean that 75 per cent of a population must be separable from all (99+ per cent) of the members of overlapping populations to qualify as a subspecies. An equivalent statement is that 97 percent of one of two overlapping populations must be separable from 97 per cent of the other. (Amadon 1949:258)

Rand and Traylor (1950) recognized that subspecies were based on natural phenomena but that their delimitation was subjective, and they suggested that a less conservative quantitative rule be applied: to be recognizable, just 80–90% of one subspecies should be separable from the same amount of another. Amadon's (1949) more conservative rule seems to be the most widely adopted quantitative criterion (e.g., Mayr 1969, Patten and Unitt 2002).

Mayr (1982a:289) stated that

> A subspecies is now defined as "an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species (Mayr, 1969:41)."

He also considered subspecies to be a category of convenience for taxonomists (Mayr 1982a), reflecting precisely the views of Darwin (1895:39) on the terms applied to what he called this "insensible series" of differentiation. In Mayr's (1969, 1982) usage, "differing taxonomically" meant differing "by sufficient diagnostic morphological characters." He felt that taxonomic differences have to be observable in museum specimens (Mayr 1951:93) and that "what is taxonomically different can be determined only by agreement among taxonomists" (Mayr et al. 1953:31). Importantly, "no nonarbitrary criterion is available to define the category subspecies. Nor is the subspecies a unit of evolution, except where it happens to coincide with a geographical or other genetic isolate" (Mayr 1969:41).

Principles of Systematic Zoology (Mayr 1969, Mayr and Ashlock 1991) and its precursor, *Methods and Principles of Systematic Zoology* (Mayr et al. 1953), represented one of the most important touchstones of animal taxonomy for the second half of the 20th century, and they are still heavily used (although out of print). These works gave important common ground to the taxonomic practices among researchers working on various animal taxa. Between Mayr (1969) and Mayr and Ashlock (1991), however, there was a decrease in the detail with which subspecific diagnoses were treated, reflecting both a greater conservatism in the use and recognition of the category and the fact that standards for recognizing subspecies had become more rigorous (Mayr and Ashlock 1991:98). In ornithology (and vertebrate taxonomy in general), that rigor may be best expressed in the assertion of the 75% rule (Mayr et al. 1953, Simpson 1961, Patten and Unitt 2002); critically, however, determinations still depend on the material available and how it is used (e.g., Cicero and Johnson 2006).

Simpson (1961) corrected two misapprehensions about subspecies. First, he stated that they are not what he termed "little species" and usually are not incipient species: "They are taxa of a markedly different kind from species, and relatively few of them will ever become species although some are, to be sure, approaching that status" (Simpson 1961:175). Second, he observed that

> subspecies do not express the geographic variation of the characters of a species and are only partially descriptive of that variation. They are formal taxonomic population units, usually arbitrary, and cannot express or fully describe the variation in those populations any more than classification in general can express or fully describe phylogeny. They are not, for all that, any less useful in discussing variation. (Simpson 1961:175)

Simpson also observed that

> When there are semiarbitrary groups in a species, their designation as subspecies should

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> hardly raise a question if the data are adequate and the taxonomist finds the subspecies valuable for his purposes. It is no argument against such usage that recognizable subgroups do not occur in all species, because the subspecies is a nonobligate category and need not, even in principle, be used throughout the whole of a classification. (Simpson 1961:173)

Avise (2004:362–363) suggested a phylogenetic approach to intraspecific taxonomy that united strengths of the biological and phylogenetic species concepts, and he proposed that subspecies are

> groups of actually or potentially interbreeding populations (normally mostly allopatric) that are genealogically highly distinctive from, but reproductively compatible with, other such groups. Importantly, the empirical evidence for genealogical distinction must come, in principle, from concordant genetic partitions across multiple, independent, genetically based molecular (or phenotypic; Wilson and Brown 1953) traits.

The strongest disagreements over the taxonomic category of subspecies have tended to occur at both the lower and upper bounds of the unit: when does geographic variation become sufficiently partitioned (and in which and how many characters) to warrant a named subspecies; and when do allopatric populations (recognized as subspecies) achieve sufficient differentiation to be considered full species? The 75% rule is a widely accepted quantitative definition for the lower limits (Amadon 1949, Mayr et al. 1953, Simpson 1961, Mayr 1969, Mayr and Ashlock 1991, Patten and Unitt 2002, Haig et al. 2006). For the upper limits there are a series of now classic comparative criteria in which the phenomena that occur at contact zones (e.g., degrees of intergradation or hybridization) and/or in similar cases in closely related taxa are used to infer subspecies or species status (Stresemann 1921 [as translated by Haffer 2007:46], Mayr 1969, Mayr and Ashlock 1991). Advances in genetics and the allure of molecular taxonomy can provide insights (e.g., Petit and Excoffier 2009), but these tools still do not alleviate the difficulty of diagnosing allopatric taxa and will likely just be added to the taxonomist's toolbox and used in traditional ways. These classic comparative methods are not an exact methodology, nor are they purely objective, but they have proved highly effective in zoology for describing and categorizing diversity (e.g., Remsen 2005).

Biodiversity diagnoses.—In many respects, the diagnosis of subspecies is similar to determinations in other fields that are, of necessity, based on arbitrary thresholds. Importantly, objective criteria can be applied to diagnoses of conditions that occur on continua and bear arbitrarily determined thresholds. Hey et al. (2003), in discussing uncertainties in species determinations, made the important observation of parallels in other disciplines, but in their limited treatment emphasizing the social (or philosophical) over the scientific aspects they did not fully develop those parallels.

In biology we work daily with a hierarchical scale of differentiation: populations, subspecies, species, genera, families, and a succession of higher taxonomic categories. Parallels abound in everyday phenomena and in our language to describe them. There is always some water in the air; at what point does it become fog? Or when does a heavy fog or a drizzle become rain, or light rain become moderate or heavy? When do physical symptoms become full-blown pneumonia? When does a breeze become a wind, and when do strong winds become storms, and when do storms such as tornadoes and hurricanes reach certain force strengths? When is a celestial body a planet? In each of these examples we can point to genuine cases of rain, pneumonia, wind, and planets and recognize that there are precursors that do not qualify. As we have seen with subspecies and planets (Margot 2006), arguing over where to place the threshold (and what gets excluded) can be contentious.

These debates over how to categorize phenomena cannot effectively call into question the existence of real states that exist along a continuum (in the case of subspecies, a biological continuum of differentiation). Among cases, discontinuities usually exist that help us understand the nature of these phenomena. It is left to practitioners to work out the finer details of generally agreed-upon thresholds and diagnoses. Those who do not find these details useful are free to ignore them and simply use (or not) the products of this work (cf. Inger 1961 and the comments therein). But for those who study these phenomena, or affect (or are affected by) them, attention is warranted, and the finer details of diagnoses become important. And, because biodiversity is not an ephemeral phenomenon and is threatened by anthropogenic forces, when geographically partitioned variation is present it should be properly assessed and, if warranted, managed for retention. This latter is

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in fact legally mandated at critical levels in some countries (e.g., U.S. Department of the Interior and U.S. Department of Commerce 1996, Committee on the Status of Endangered Wildlife in Canada 2005), and subspecies designations can be objectively assessed within multiple legal and biological frameworks (e.g., Topp and Winker 2008).

Yes, there are many differences among meteorologists, astronomers, physicians, and zoologists in subject matter and in methodologies, but there are commonalities as well in our efforts to diagnose conditions that often exist between agreed-upon states. It should not be a surprise that meteorologists, physicians, and astronomers have professional criteria that they use to make their diagnoses. As zoologists we can point to clear discontinuities that might tempt us to consider that we are different from these other fields, but there are definite similarities when we come to the cases that do not fall clearly into one category or another, when thresholds and criteria are often fervently debated. Data, existing and new, and reexaminations (second opinions) effectively enable us to treat diagnoses as hypotheses. Placing thresholds at points along continuous processes will always have an arbitrary component, and we can expect difficulties when knowledge is incomplete or when there are not clear boundaries (Hey et al. 2003). But we can agree as professionals that exemplary, real states exist along such continua and that there are professional guidelines to help us determine where particular cases fall.

One of the beauties of science is the way in which we scientists contribute to determining the details of such evolving guidelines. The history of the subspecies concept exhibits utilitarian changes made through time that enhanced both the concept's usefulness and its acceptability among professionals. Interestingly, and not surprisingly, a similar process occurred in the definition and widespread adoption of the Beaufort Scale, which is used to categorize air movements when reporting the weather (Huler 2004). If the past 150 years are any indication, we can look forward to a continued spirited discussion of subspecies as a long-recognized state in the processes of adaptation and speciation and in the state of biodiversity.

What does subspecific variation mean?—There are two aspects to the question of what subspecific variation means: the conceptual tool itself and the phenomena that cause the variation that it attempts to categorize. With regard to the labels, subspecies represent a heterogeneous assemblage of units, reflecting the nomenclatural application of denoting differences; this has been true since the inception of the concept (see above). Although the application of subspecific names needs ongoing reevaluation, even an ideal taxonomy will not change this unresolvable aspect of subspecies; for example, it is not possible to make them all what Simpson (1961) termed "little species." Also, as long as data remain incomplete, the hypothetical ideal taxonomy of one moment will continue to undergo change as our data and science improve.

With respect to the variation that these labels attempt to denote, a deceptively simple answer is that such variation represents evolutionary and developmental responses to geographically heterogeneous phenomena (biotic and abiotic). The phenomena involved in creating geographically partitioned variation are the very building blocks of biological evolution, the details of which remain the basis for research programs throughout evolutionary biology. As we know, differentiation can be affected by geography (e.g., isolation-by-distance, parapatry, allopatry, and their effects on gene flow), by selection (natural and sexual), and by neutral processes (e.g., mutation and lineage sorting or drift). Added to this are uncertain influences from environmental effects and developmental plasticity. At present it is safe to say that, except perhaps in a very few well-studied instances, we cannot accurately predict how these phenomena are responsible for any specific case of partitioned phenotypic variation in wild populations. Not knowing the answer at this level of detail, however, is not particularly problematic. Although we can answer this question only in the broadest terms, the fact that we can only rarely provide a highly detailed answer is more an indication of the exciting research to be done at the subspecific level than a problem of the concept itself.

It seems that, to a considerable degree, the debate over the subspecies concept comes from not being satisfied with this broad answer and yet not having, or being able to develop, a detailed one in a particular system or organismal group. This philosophical discord has often stemmed from discord in data sets, for example among those studying some attribute of subspecific variation and finding that their focus does not accord with the named subspecies of a previous worker. This has perhaps never been as pronounced as with the advent of genetic data. However, at shallow

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levels of divergence, small genetic data sets in which variation is largely dominated by neutral or near-neutral processes (Kimura 1983, Ohta 2002) should be expected to be discordant with phenotypic data sets, in which variation is likely dominated by processes that are not selectively neutral. Thus, evidence of decoupled genotypic and phenotypic marker systems may not be particularly informative when using one data type to ask questions of the other at species and subspecies levels.

However, as genomic data sets have improved, the genetic bases (protein coding and regulatory) for local, intraspecific adaptation are being revealed in many taxa (Mitchell-Olds et al. 2007). Further, phenotypic attributes of the sort used to describe subspecies are being shown to be adaptive (Mumme et al. 2006) and genetically based (Hoekstra et al. 2006). Genomic studies suggest that changes in color intensity (often an important attribute of described subspecies) can be genetically simple, but pattern changes are likely to involve *cis*-regulatory elements and mosaically pleiotropic loci rather than coding-sequence changes (Carroll 2008). Further, interspecific morphological differences appear to involve *cis*-regulatory element changes more than intraspecific ones do, which led Stern and Orgogozo (2008) to conclude that speciation causes fixation of a certain subset of the genetic variation that causes phenotypic variation within species. This not only echoes Simpson's (1961), Mayr's (1969), and others' views that only some subspecies will become species, but it provides us with important tools and hypotheses for examining the genetic bases of partitioned geographic variation and understanding them in a better collective sense in relation to speciation. And we should not lose sight of what a rich harvest subspecies and their characteristics can continue to provide for these frontiers of research in evolutionary biology.

How frequently might neutral phenotypic variation occur among populations? We do not know. Remsen (1984) demonstrated that among subspecies of many birds in the Andes of South America, there is a pronounced stochasticity in the among-species distributions of a leapfrog pattern of subspecific variation in plumage color and pattern. This led him to conclude that phenotypic differentiation at this scale had a strongly random component (Remsen 1984). Even though leapfrog patterns of subspecific variation are rare, the stochastic component to geographic variation that Remsen's study revealed confirms that evolution within populations can proceed at different rates and in different directions; it does not tell us how (or whether) selection (natural and sexual) within the subspecies involved has affected these processes or their outcomes. If multiple characters are involved, the role for selection is likely enhanced.

The question of neutral phenotypic evolution at the population and subspecies levels remains open, but even a putatively exemplary case for neutral phenotypic evolution has proved with greater study to be driven instead by selection (Schemske and Bierzychudek 2007). We cannot blindly attribute all partitioned phenotypic variation to local adaptation (which historically occurred to excess; Gould and Lewontin 1979, Mayr 1983), because factors such as environment and developmental plasticity can cause divergence between populations. The influences of these factors are not yet well understood, but progress is being made (Price et al. 2003, West-Eberhard 2003, Suzuki and Nijhout 2007). Two things are important to realize. First, phenotypic variation caused by environmental factors and the developmental plasticity underlying it can be under selection and be adaptive (James 1991, West-Eberhard 2003). Second, the processes of divergence are dominated more by selection than by neutral changes (Coyne and Orr 2004). Partitioned phenotypic variation in multiple characters is likely to reflect partitioned genetic variation and thus extend into unmeasured attributes of populations; thus, even if the characters used to define a particular subspecies should prove not to be under local adaptive selection, they may well be concordant with such.

Looking Forward

Recognition of the reality of geographically partitioned phenotypic variation within species is so ubiquitous that biologists confront it daily, from the legal and ethical promotion of protecting and enhancing diversity (even within humans) to taxonomic nomenclature (ICZN 1999). That this phenotypic reality is not predictably variable using simple tools (e.g., mtDNA data or other single-character attributes) is the problem of the tools and the practitioners, not of the concept of partitioned intraspecific variation.

Subspecies represent a rather crude depiction of among-population patterns without regard to

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the processes underlying the geographic variation they attempt to describe. Two convenient ways to consider subspecies are as hypotheses and as taxonomic bookmarks. Both views allow one to proceed with the understanding that a presumed expert found sufficient variation that "something more should be done than merely to lock together into one heterogeneous fold forms so different" (T. Gill, in Coues 1884). As with all scientific hypotheses, such determinations are subject to further study and testing. And as with bookmarks, subspecific labels highlight items of note below the species level.

Perhaps the most useful academic purpose to which subspecific variation has been put is as a frame of reference for posing questions about animals and evolution. The most practical purpose is undoubtedly to describe biodiversity and, since the mid-20th century, to focus management and conservation efforts upon intraspecific units above the level of populations but below the level of species. In both cases, an often unspoken assumption is that the partitioned morphological variation upon which subspecies are based reflects an adaptive component—that these populations, although not fully species, possess unique attributes with local adaptive value. Whether the variation that subspecies denote reflects important local adaptation is an unresolved issue, but increasing evidence suggests that we would be safer in both basic and applied biology not to dismiss such an assumption outright. Indeed, our null hypothesis should be that subspecific differentiation is indicative of local adaptation, not the converse.

If we think of partitioned geographic variation as a species' fit to a variable environmental (and adaptive) landscape (a natural extension of the null hypothesis that such variation reflects local adaptation), then we can gain insights both into the processes of biological divergence and, from the applied perspective, into the likely retention of biodiversity during periods of global change. On a global scale, populations are currently so challenged by anthropogenically forced environmental changes that we would be foolish indeed if we failed to recognize that trying to maintain a fit to a variety of geo-environmental facets is a better approach than one-size-fits-all. It would be a grave mistake to think that subspecific variation that does not lead to speciation is not of evolutionary importance; such variation might be critical for resilience and persistence, preventing extinction of existing species during episodes of environmental change. It would also be a mistake to think that, if lost, such variation could be regenerated under similar environmental conditions.

Although for over half a century we have had wide acceptance of a quantified lower limit for subspecific recognition (the 75% rule; Amadon 1949, Mayr et al. 1953, Simpson 1961, Mayr 1969, Mayr and Ashlock 1991, Patten and Unitt 2002, Haig et al. 2006), this limit became widely accepted after most avian subspecies had been described (Remsen, this volume). Further, acceptance of this quantified approach grew during a period of waning traditional taxonomy and a decline in the collection of specimens upon which this research is based (e.g., Winker 1996). Inasmuch as the simple description of biodiversity is no longer considered cutting-edge research, some might be tempted to dismiss the entire subject as a historical fad that has little place in modern science. That would be an error. In fact, the underlying reasons for studying such subjects have never been stronger. In the past few decades, we have experienced not only a resurgence in systematics, but also robust growth in evolutionary and conservation biology and ecology as well as increased interdisciplinarity in wildlife biology. In addition, entirely new disciplines such as phylogeography (Avise 2000) and landscape genetics (Manel et al. 2003, Holdregger and Wagner 2006) continue to provide a modern cachet to the fundamental aspects of geographic variation that caused the subspecies concept to be developed in the first place. Subspecific variation in each of these areas is core material; it may only be taxonomic housekeeping that has not been kept up.

Using subspecies to help us understand fundamental aspects of biological differentiation, a longstanding tradition (Remsen 1984), continues in fields as diverse as ecology, evolutionary biology, wildlife management, and genetics, demonstrating both that subspecies retain heuristic value in research and that they are indeed often correlated with phenomena of longstanding interest. For example, Belliure et al. (2000) found that dispersal distances in birds were correlated with subspecies richness. Irwin et al. (2001, 2005), focusing on the classic case of the ring species in *Phylloscopus trochiloides* (Mayr 1942b), showed how song (a trait used in mate choice) exhibited parallel changes concordant with subspecific divergence as the ring progressed north into Siberia and that genetic evidence supported a cessation of gene flow between these most-diverged populations. Sol et al. (2005)

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found that among Holarctic passerines, species with relatively larger brains tended to have more subspecies; these authors used subspecies as an index of intraspecific phenotypic diversification and relative brain size as a correlate of a propensity for behavioral changes, and their results strongly implicate behavioral change as a driving force in evolutionary diversification. In a global survey of avian subspecies, Phillimore and Owens (2006) found that ~36% were phylogenetically distinct (monophyletic with respect to individuals of different subspecies when using mtDNA sequence data), and further study revealed that biogeographic factors such as breeding range and habitat heterogeneity explained ~30% of subspecies richness (Phillimore et al. 2007). Also using subspecies, Martin and Tewksbury (2008) found that phenotypic differentiation within bird species is greater at lower latitudes, which fits evolutionary hypotheses for the latitudinal gradient in species diversity. Darwin (1859) was right in pointing out the importance of subspecies, and these and other recent efforts (e.g., see Price 2008) continue to show this.

Martin and Tewksbury (2008) summarized three lines of evidence that support using subspecies as an index of divergence in speciation research. The first, that subspecific variation ranges from subtle character differences to that approaching allopatric species and therefore reflects intermediate stages in the process, has been a mainstay of the use of subspecies in this context since Darwin (1859). The second, that ring species show the temporal progression of speciation with subspecific differentiation accruing to the point of reproductive isolation at the tips, has been another important focus in evolutionary biology (Mayr 1942b, 1963; Irwin et al. 2001, 2005; Coyne and Orr 2004). Their third point, which they demonstrated, is that the maximum number of subspecies in a species within a genus covaries positively with the number of species in that genus, which likely indicates that a lineage's propensity to differentiate is an attribute that it holds for a substantial period of evolutionary time (well through the speciation process and observable at the subspecies level).

Because in using subspecies we are trying to label and understand something that occurs at an interval along an inherently continuous process (divergence and differentiation), incomplete data and differing views, not to mention disagreement on species concepts, combine to produce ongoing debates about what subspecies are, what they reflect, and whether a particular example is one or not. But this debate can overthrow neither the biological reality that the concept embodies nor the utility that it has demonstrated for over 150 years.

Both hypothesis testing and descriptive (discovery science) approaches to our study of biodiversity continue to make subspecies useful. Consequently, the use of subspecies in ornithology remains strong. For example, major works such as del Hoyo et al. (1992–2008), Dickinson (2003), Poole and Gill (1992–2002), Cramp et al. (1977–1994), and Marchant et al. (1990–2006) all used the biological species concept and treated polytypic species at the subspecific level. Although the AOU has not given detailed treatment to the subspecies of North American birds since 1957 (AOU 1957), its commitment to that level of diversity remains strong (AOU 1986, 1998; AOU Check-list Committee pers. comm.). Indeed, legally mandated management obligations are beginning to push back on this neglect, and not just in birds (e.g., Haig et al. 2006). Moreover, there are hundreds of papers published each year in peer-reviewed journals with subspecies as a topic (Haig and Winker, this volume).

Subspecies have enthralled and frustrated zoologists—and especially ornithologists—since the inception of the concept. To rail against this concept, however, is as ineffective as railing against the wind. Subspecies have been and remain an important conceptual tool—and a taxonomic label—that can help zoologists categorize, study, and conserve biodiversity. As eternally controversial as politics, subspecies will likely remain integral to research and management in zoology.

ACKNOWLEDGMENTS

I thank S. Haig, C. Cicero, G. Graves, D. Gibson, R. Dickerman, J. Rappole, R. Banks, R. Browning, J. Klicka, J. Cracraft, T. Peterson, M. Patten, R. Zink, and J. V. Remsen, Jr., for discussions about variation within biological species, and Remsen, Haig, F. James, and M. Morrison for comments on an earlier draft.

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