Named Subspecies and Their Significance in Contemporary Ornithology

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CHAPTER 4

NAMED SUBSPECIES AND THEIR SIGNIFICANCE IN CONTEMPORARY ORNITHOLOGY

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Abstract.—Subspecies, or geographic races, are diagnosable populations that, at least during the breeding season, are largely allopatric with other subspecies of the same species. In attempts to give objectivity to the subspecies concept, arbitrary rules have been applied for the recognition of subspecies (e.g., the "75% rule," whereby 75% of the individuals should be identifiable to subspecies; there are several other rules). As a case study, I examined the usefulness of the subspecies concept in describing geographic variation of a polytypic American songbird, the Savannah Sparrow (*Passerculus sandwichensis*). About 21 subspecies of this species have been recognized in the taxonomic literature, but much of the geographic variation is clinal. I argue that there is little value in subdividing a clinal continuum into different subspecies. Rather, the use of subspecies is best restricted to distinctive, and usually geographically isolated, populations. I show that this has been done for only a few of the named subspecies of Savannah Sparrows. *Received 31 July 2006, accepted 6 March 2007.*

Resumen.—Las subespecies, o razas geográficas, son poblaciones generalmente alopátricas (al menos durante la época de reproducción) y que se pueden diferenciar claramente de otras subespecies de la misma especie. Se han propuesto diferentes reglas para asignar individuos a una determinada subespecie, e.g. "la regla del 75%" (75% de los individuos tienen que ser identificables como subespecie), en un intento de dar objetividad al concepto de subespecie. Como caso de estudio, discuto la utilidad del concepto de subespecie para describir la variación geográfica de *Passerculus sandwichensis*. Se han reconocido cerca de 21 subespecies, pero gran parte de la variación geográfica es clinal. Argumento que es de poco valor el subdividir una clina continua en subespecies diferentes. Se debe restringir el uso de subespecies para poblaciones bien diferenciadas y aisladas geográficamente. Muestro que ésto se ha hecho sólo para unas pocas de las subespecies de *Passerculus sandwichensis*.

In recent years, many biologists have used intraspecific geographic variation to test hypotheses about adaptation and evolution, and named subspecies have reflected this variation. For example, Møller and Cuervo (1998) compared feather ornamentation in birds to test the hypothesis that sexual selection promotes speciation and found that ornamented species had more subspecies than non-ornamented species—which suggests an association between subspeciation and ornamentation. Likewise, Sol et al. (2005) examined brain size relative to body size in Holarctic passerines, to test the hypothesis that behavioral changes are an important driver of evolutionary diversification, and found that species with large relative brain size have undergone more extensive subspecific diversification. It is clearly important for these studies that named subspecies more or less accurately reflect units of intraspecific diversification.

Wilson and Brown (1953) identified several problems with the subspecies concept as then applied. Among these was the arbitrary lower limit of the "distinctiveness" of subspecies (i.e., how distinctive must a population be to earn a subspecific trinominal name?). There are several arbitrary rules, the most common being the "75% rule" (Amadon 1949), though efforts have been made to apply more rigorous diagnosability rules to the classification of subspecies (e.g., Patten and Unitt 2002, Remsen 2005, Cicero and

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Johnson 2006). In 1982, John Wiens, then the editor of *The Auk*, solicited comments from several American avian systematists about the utility and contemporary application of the subspecies concept. Wiens (1982:593) wrote:

> My charge to them was framed as a series of questions: Is the concept just a tool of classification that is no longer of much use? Can or should the concept be revised to make it more compatible with contemporary views in population biology? Do subspecies exist, as real biological units?

Among the contributors to this forum were George Barrowclough, Frank Gill, Ned Johnson, Ernst Mayr, Burt Monroe, Robert Storer, and Richard Zusi. Some 25 years later, these questions are still debated and deserve revisiting.

Ned Johnson (1982:605) identified four "distinctly positive elements" about subspecies:

> [1] [S]ubspecies tell us about the migratory routes and wintering areas of populations of birds that represent distinct portions of the breeding range of that species.
>
> [2] Some subspecies also provide indisputable evidence for the early stages of allopatric speciation in relation to environmental barriers.
>
> [3] Subspecies names alert researchers of whatever stripe to geographic forms with potential differences in features additional to those by which they were initially characterized.
>
> [4] Systematists...can profit by looking closely at subspecies named on the basis of particular kinds of characters. After all, some of these "subspecies" will turn out after careful study to be full species.

Most of the ornithologists who contributed to the forum concurred with Monroe (1982:608) when he wrote:

> It seems an abuse of the naming process to create a name for a population that may differ in one slight character (and even then, subspecies may be named where only about two-thirds of the individuals can be distinguished, based on the most liberal interpretation of the "75% rule").

He went on:

> [S]ubspecific names should *not* be used to describe populations differing only through smooth clines reflecting general primary intergradation.... Subspecies...should be used in two situations: (1) allopatric populations where definition of the populations is clear, distinct, and total (or very nearly so); and (2) situations where secondary contact between distinct populations has occurred and the zone of intergradation is relatively narrow.

Barrowclough (1982:602) wrote:

> ...I see some use in the formal naming of subspecies, but only if standards become much more rigorous. First, we need to acknowledge that a useful subspecies concept will have as a goal the same objective as other taxonomic categories—*predictiveness*.

If a population is distinctive in coloration, size, or some other character, is it also distinctive in other ways? Thus, subspecies are most useful if they represent distinct gene pools that predict variation in traits not originally considered.

Subspecies versus Species

Cracraft (1983, 1997) and others have suggested that "phylogenetic species," based on cladistic analyses that ignore interbreeding among populations, should replace "biological species" defined on the basis of observed or presumed reproductive isolation—and that subspecies, generally recognized within biological species, are not useful taxonomic entities (e.g., McKitrick and Zink 1988, Zink 2004). Others (e.g., Avise and Ball 1990, Johnson et al. 1999, Remsen 2005, Winker et al. 2007) have argued against this because it ignores the importance of gene flow, which runs counter to theories of speciation and population differentiation. If we embrace biological species, some taxa at the species and subspecies levels will be paraphyletic (e.g., Funk and Omland 2003), which most advocates of phylogenetic species find unacceptable. Although the boundary between subspecies and species can be fuzzy, the advent of molecular tools has led some to elevate subspecies to species on the basis of arbitrary levels of genetic distinctiveness (e.g., Hebert et al. 2004, Kerr et al. 2007). These approaches are often based on single-locus, selectively neutral markers, which reflect gene trees but not necessarily species trees (Johnson and Cicero 2004, Moritz and Cicero 2004, Winker et al. 2007). Concordance between phenotypic data (the basis for most named subspecies) and genotypic data, combined with other indicators of reproductive isolation (e.g., behavior), serve as indicators of gene flow and thus of species status between populations (Johnson et al. 1999).

Morphological and Molecular Diagnosability of Subspecies

Patten and Unitt (2002) and Cicero and Johnson (2006) emphasized the need for objective criteria and increased rigor in delimiting subspecies morphologically. Furthermore, Cicero and Johnson (2006), among others, emphasized the importance of using only breeding birds in describing geographic variation. With migratory birds, this raises a significant technical problem because often the breeding plumage is worn, thus obscuring or changing their appearance. Traditionally, taxonomists have preferred to describe species and subspecies in "fresh" plumage, although in practice few descriptions have been based on such material. In many cases, most individuals molt before leaving their breeding grounds, so there is a narrow window of time when specimens in fresh plumage can be collected from their breeding grounds. Furthermore, molt sequences of many species are poorly known, and at least some molting may take place during migration or on the wintering grounds (Rohwer and Johnson 1992, Rising and Beadle 1996, Pyle 1997). Also, gonadal changes precede molt, so it is not possible to know whether a recently molted specimen represents a local breeder or a migrant. Lastly, if the subspecies' names can be applied only to freshly molted individuals, their utility is greatly reduced. For example, if the plumage of individuals that have completed their migration is worn, how can it be matched with breeding material to clarify migration routes?

Zink (2004) argued that subspecies (or phylogenetic species) should be the units to be considered when making conservation decisions, which would be wise if named subspecies represent distinctive gene pools. However, in a mitochrondrial DNA (mtDNA) analysis of subspecies, Zink (2004) found that only ~3% of the named subspecies of birds coincided with distinct, monophyletic gene lineages. He based this result on a meta-analysis of 41 species, with a distinct bias toward Nearctic and Palearctic taxa (220 out of 230 of the subspecies examined). Because mtDNA loci within lineages are believed to evolve mostly by drift and float among populations through matrilineal inheritance, mtDNA loci give, at best, limited insight into phylogenetic and phylogeographic history (Edwards and Beerli 2000, Arbogast et al. 2002, Funk and Omland 2003). Furthermore, measures of mtDNA diversity likely do not reflect quantitative genetic variation for adaptive traits (Reed and Frankham 2001). Therefore, there is no *a priori* reason to expect mtDNA gene trees to precisely reflect either population histories or population boundaries delimited by genes that affect color, size, or shape—the traits upon which most named subspecies have been described. Despite these caveats, Phillimore and Owens (2006) repeated Zink's analysis using taxa from a broader global region and found that 36% of the subspecies represented distinct phylogenetic lineages. Not surprisingly, more island-dwelling subspecies than subspecies with a continental distribution were monophyletic. This is consistent with what I postulate about allopatric speciation: in patchy environments, populations are often smaller and gene flow and its blending effects among patches reduced, allowing local differentiation to evolve more quickly.

The Savannah Sparrow as a Case Study

Here, I assess both the historical application and the usefulness of the subspecies concept by using the Savannah Sparrow (*Passerculus sandwichensis*) as a case study. The Savannah Sparrow is a widespread North American species that has been divided into at least 17 to 21 subspecies (American Ornithologists' Union [AOU] 1957, Paynter 1970), and has been the subject of numerous studies (Wheelwright and Rising 1993). As with many avian species, most currently named subspecies were described in the first half of the 20th century, at a time when rigorous statistical analyses (e.g., *t*-tests and analyses of variance [ANOVA]) were just being developed. Specifically, my objective is to illustrate many of the problems with current subspecific taxonomy, while addressing what to do with these named subspecies: (1) Should we accept them as named? (2) Should we revisit these with an eye to making their descriptions more consistent and rigorous?

Or (3) should we do away with intraspecific groups and nomenclature?

Peters and Griscom (1938) is the only monographic study of the geographic variation and intraspecific taxonomy of the Savannah Sparrow that deals with specimens taken from most parts of the species' range. Their treatment of Mexican populations, however, was based on few specimens (and still fewer breeding specimens) and therefore was necessarily preliminary. Later, Aldrich (1940) discussed variation among eastern North American Savannah Sparrows; van Rossem (1947) published a study of geographic variation of the saltmarsh-dwelling coastal Belding's and Large-billed sparrows of southern California, Baja California, Sonora, and Sinaloa; and Hubbard (1974) analyzed variation among the Savannah Sparrows of the southwestern United States, inland Mexico, and Guatemala. More recently, I published information on geographic variation in size and shape of Savannah Sparrows (Rising 2001), and Zink et al. (1991, 2005) reported on molecular differences among populations of Savannah Sparrows. Finally, I have quantified variation among populations of Savannah Sparrows on the basis of pattern and coloration of plumage (J. D. Rising unpubl. data). All these studies contain quantitative data that support the statements made here.

Peters and Griscom (1938) based their subspecies on qualitative descriptions of size, bill shape, and morphology. Thus, *P. s. labradorius* was diagnosed as "a dark Savannah Sparrow with relatively stout bill; its depth more than half the length of the culmen" (p. 452), and *P. s. sandwichensis* as the "largest (average) of the races… with a long and proportionately slender bill" (p. 448). Even new subspecies described in that monograph were not characterized in a quantitative way. For example, *P. s. oblitus* was described as "a medium sized gray Savannah Sparrow with relatively stout bill, its depth more than half the length of the culmen" (p. 455). It was "similar to *P. s. savanna*…but grayer throughout," (p. 455) and it "intergrades with [*P. s.*] *nevadensis* where the forms meet" (p. 457). Likewise, van Rossem (1947) gave only qualitative descriptions of the saltmarsh Savannah Sparrows of Mexico, even when describing a new subspecies, *P. s. magdalenae.* He wrote (van Rossem 1947:103):

> This race is the culmination of the strongly yellow-browed, peninsular Savannah Sparrows with relatively slender bills which average less…than 7.0 millimeters in depth at base. It forms a good connecting link between the smaller-billed, more northern *guttatus* and the larger-billed *rostratus* group of the continental mainland and the San Benito Islands….

I found that differences in bill proportions among populations of non-saltmarsh ("typical") Savannah Sparrows were slight and that bill size varied clinally (Rising 2001); my analyses were based on large samples (generally >40 birds from each) of breeding birds from 55 localities from virtually throughout the species' range. From these analyses, it is unlikely that any discrete populations of Savannah Sparrows exist solely on the basis of bill size or shape.

Although some of the 21 or so named subspecies of Savannah Sparrows have been described or at least characterized by average differences—a criterion that Patten and Unitt (2002) argued is insufficient for subspecies diagnosability—most, like *P. s. magdalenae* from Bahía Magdalena and *P. s. wetmorei* from Hacienda Chancol, Guatemala, have been described on the basis of impressions of differences that were not quantified in any way. Van Rossem (1938) described *P. s. wetmorei* from only five specimens collected in June 1897, and there seem to be no breeding specimens subsequently taken from south of Mexico. Hubbard (1974:14) noted that "Guatemalan specimens differ from Southwest specimens in being darker and ruddier brown above, with the streaking more extensive and darker; the yellow of the superciliary also tends to be darker and more extensive." In his description of *P. s. magdalenae,* van Rossem (1947:102) measured 16 males and 4 females and characterized this subspecies as similar to *P. s. guttatus* from Laguna San Ignacio "but lighter and more greenish (less grayish) olive; dorsal markings more prominent…due to lighter edgings." In his color plate (van Rossem 1947), *P. s. magdalenae* and *P. s. guttatus* appear to be very similar, as they do in the field (J. D. Rising pers. obs.).

None of the subspecies of Savannah Sparrow have been named following the mandates of any rule, and indeed, some have not been formally described (although perhaps described long after being first named). For example, Latham (AOU 1957) described the Sandwich Bunting from the Aleutian Islands, later named *Emberiza sandwichensis* by Gmelin in 1789; and in 1811, Wilson described *Fringilla savanna* from Savannah, Georgia. When these were synonymized, they became different subspecies of the same species, even though there was no formal description of their differences. In many instances, the subspecies represent only points on a clinal continuum (Rising 2001, Rising et al. unpubl. data). Only Hubbard (1974) attempted to delimit subspecies of Savannah Sparrows on the basis of the separability of adjacent populations. Several subspecies (e.g., *P. s. princeps, P. s. bradburyi, P. s. guttatus,* and *P. s. rostrata*) have been based on material taken from migrating or wintering individuals, and others have been based, in whole or in part, on nonbreeding individuals. Subspecific names should be given to populations or groups of populations that occupy a distinct breeding range and that are diagnosably distinct from other such populations (Mayr and Ashlock 1991, Patten and Unitt 2002, Cicero and Johnson 2006).

Among non-saltmarsh sparrows, the large and pallid Savannah Sparrows from Sable Island ("Ipswich Sparrow," *P. s. princeps*; Rising 2001) are the only ones that are consistently separable from all others. These birds are essentially 100% separable from mainland Savannah Sparrows using either size or color, although their mtDNA haplotypes are not distinctive (Zink et al. 2005). Among saltmarsh Savannah Sparrows, the birds from coastal Sinaloa and Sonora (*rostratus* group) are large and large-billed (Rising 2001) and differ in coloration (Rising et al. unpubl. data) from those along the coast of southern California and Baja California (*P. s. beldingi*); in my analyses, there is virtually no overlap between these sets of populations. Size and color variation along the coast of Sinaloa and Sonora is clinal, although color differences completely separate birds from Puerto Peñasco (*P. s. rostratus*) and Bahía Kino (*P. s. atratus*); birds from the Cabo Lobos region of Sonora are said to be intermediate (van Rossem 1947). Similarly, variation along the Pacific Coast is clinal in both color and size, although there is a gap between Morro Bay and Humboldt Bay (*P. s. alaudinus*) in California, and another between Guerrero Negro (*P. s. anulus*) and Bahía Magdalena (*P. s. magdalenae*) on the Baja California Peninsula. Lastly, Savannah Sparrows from Isla San Benito (*P. s. sanctorum*) are distinct from mainland birds morphologically (van Rossem 1947, J. D. Rising pers. obs.), in coloration (Rising et al. unpubl. data), and behaviorally (specimens collected in late April 1999 showed birds on different breeding cycles: laying eggs at Guerrero Negro, and clearly prereproductive on Isla San Benito). On the basis of size and coloration, van Rossem (1947) considered this population to be allied with those of the west coast of Sonora and Sinaloa. However, mtDNA analyses (Zink et al. 2005) do not support this conclusion, but rather ally them with Pacific Coast birds, as would be reasonable on geographical grounds. This suggests that the similarity in bill size between birds from San Benito and those from coastal Sinaloa and Sonora is attributable to convergence.

With regard to the question of what to do with these named subspecies, it is clear that we should neither accept them as named nor eliminate them altogether. Although many of the named subspecies clearly are not diagnosable, there is strong geographic variation that merits formal taxonomic recognition. On the basis of my research (Rising 2001; Zink et al. 1991, 2005; Rising et al. unpubl. data), which has led to a re-evaluation of these subspecies, I recommend that six subspecies be recognized with the following taxonomic synonymies:

Passerculus sandwichensis sandwichensis (Gmelin)

Emberiza sandwichensis Gmelin, Syst. Nat., 1, pt. 2, 1789, pl 875. Based on the Sandwich Bunting of Latham, Gen. Syn., vol. 2, pt. 1, p. 202 (In Unalaschca et sinu Sandwich = Unalaska, Alaska).

Fringilla savanna Wilson, 1811, Amer. Ornith., 3, p. 55, pl. 22, fig. 3 (Savannah, Georgia).

Passerculus alaudinus Bonaparte, 1853, Compt. Rend. Acad. Sci. Paris, 37, p. 918 (Californie = San Francisco).

Passerculus anthinus Bonaparte, 1853, Compt. Rend. Acad. Sci. Paris, 37, p. 920 (Kodiak = Kodiak Island, Alaska).

Passerculus anthinus (not of Bonaparte, 1853) Baird, 1858, Rep. Pacific R. R. Surv., ix, p. 445 (San Francisco, Benicia, and Petaluma, California).

Passerculus sandwichensis bryanti Ridgway, 1885, Proc. U.S. Nat. Mus., 7, p. 157.

Ammodramus (Passerculus) sandwichensis wilsonianus Coues, 1897, Auk, 14, p. 93 (new name for *Fringilla savanna* Wilson).

Ammodramus sandwichensis brunnescens Butler, 1888, Auk, 5, p. 265 (Valley of Mexico, Mexico).

Passerculus sandwichensis brunnescens Oberholser, 1930, Sci. Pub. Cleveland Mus. Nat. Hist., 1, p. 110 (Mexico).

Passerculus sandwichensis labradorius Howe, 1901, Contr. North Amer. Orn., vol. 1, Oct. 14, 1901, p. 1 (Lance [L'Anse] au Loup, Labrador).

Passerculus sandwichensis nevadensis Grinnell, Univ. California Publs. Zool. 5, no. 9, Feb. 21, 1910, p. 312 (Soldier Meadows, Humboldt County, Nevada).

Passerculus sandwichensis brooksi Bishop, 1915, Condor, 17, no. 5, Oct. 10, 1915 (Chilliwack, British Columbia).

Passerculus sandwichensis bradburyi Figgins, 1918, Proc. Colorado Mus. Nat. Hist., 2 no. 1, p. 2 (James Island, South Carolina).

Passerculus sandwichensis campestris Taverner, 1932, Proc. Biol. Soc. Washington, 45, p. 201 (Red Deer, Alberta).

Passerculus sandwichensis oblitus Peters and Griscom, 1938, Bull. Mus. Comp. Zool., 80, no. 13, p. 454 (Fort Churchill, Manitoba).

Passerculus sandwichensis crassus Peters and Griscom, 1938, Bull. Mus. Comp. Zool., 80, no. 13, p. 459 (Sitka, Alaska).

Passerculus sandwichensis wetmorei van Rossem, 1938, Bull. Brit. Ornith. Club, 58, p. 129 (Hacienda Chancol, 10,000 ft., Guatemala).

Passerculus sandwichensis mediogriseus Aldrich, 1940, Ohio J. Sci., 40, p. 4 (Andover, Ashtabula County, Ohio).

Passerculus sandwichensis rufofuscus Camras, 1940, Publ. Field Mus. Nat. Hist., Zool. Ser., 24, no. 15, p. 159 (Babicora, Chihuahua).

Passerculus sandwichensis princeps Maynard

Passerculus princeps Maynard, Amer. Nat., 6, no. 10, Oct. 1872, p. 637 (Ipswich, Massachusetts).

Passerculus sandwichensis beldingi Ridgway

Passerculus beldingi Ridgway, Proc. U.S. Nat. Mus., 7 (Feb. 25), 1885, p. 516 (San Diego, Cal[ifornia]).

Passerculus halophilus (not *Ammodramus halophilus* McGregor) Bancroft, 1927, Condor, 29, p. 56 (Scammon Lagoon, Baja California).

Passerculus rostratus halophilus Grinnell, 1928, Univ. Calif. Publs. Zool., 32, p. 163 (Scammon Lagoon, Baja California).

Passerculus rostratus anulus Huey, 1930, Trans. San Diego Soc. Nat. Hist., 6, no. 10, p. 204 (Scammon Lagoon, Lower California = Baja California).

Passerculus sandwichensis anulus Oberholser, 1930, Sci. Publs. Cleveland Mus. Nat. Hist., 1, p. 110 (Lower California); van Rossem, 1930, Trans. San Diego Soc. Nat. Hist., 6, p. 219 (Scammon Lagoon, Lower California).

Passerculus sandwichensis sanctorum Ridgway

Passerculus sanctorum Ridgway, Proc. U.S. Nat. Mus., 5, Apr. 3, 1883, p. 538 (Island of San Benito, Pacific coast of Lower California).

Ammodramus (Passerculus) sanctorum Coues, 1897, Auk, 14, p. 92 (San Benito Islands, Baja California).

Passerculus rostratus sanctorum Ridgway, 1901, Bull. U.S. Nat. Mus., 50, Part 1, p. 200 (San Benitos Islands).

Passerculus rostratus guttatus (not of Lawrence) Oberholser, 1919, Ohio J. Sci., 19, p. 349 (San Benito Islands).

Passerculus sandwichensis guttatus Lawrence

Passerculus guttatus Lawrence, Ann. Lyc. Nat. Hist. New York, 8, 1867, p. 473 (Lower California, San José [del Cabo]).

Ammodramus halophilus McGregor, 1898, Auk, 15, p. 265 (Abreojos Point [= Pond Lagoon], Lower California = Baja California Sur).

Passerculus rostratus halophilus Ridgway, 1901, Bull. U.S. Nat. Mus., 50, Part 1, p. 202 (Abreojos Point).

Passerculus sandwichensis halophilus van Rossem, 1930, Trans. San Diego Soc. Nat. Hist., 6, p. 219 (Abreojos Point south to Magdalena Bay).

Passerculus sandwichensis magdalenae van Rossem, 1947, Condor, 49, p. 97 (North Estero, Magdalena Bay, Baja California = Baja California Sur).

Passerculus sandwichensis rostratus (Cassin)

Emberiza rostrata Cassin, Proc. Acad. Nat. Sci. Philadelphia, Sept.–Oct. (Dec. 31) 1852, p. 184 (sea shore at San Diego, California).

Ammodramus rostratus Cassin, 1855, Ill. Birds Calif., Texas, etc., p. 226 (San Diego, Santa Barbara, San Pedro).

Passerculus rostratus Grinnell, 1905, Auk, 22, p. 16 (not breeding in California).

Passerculus sandwichensis rostratus van Rossem, 1930, Trans. San Diego Soc. Nat. Hist., 6, p. 219 (delta of Colorado River in Lower California and Sonora).

Passerculus sandwichensis atratus van Rossem, 1930, Trans. San Diego Soc. Nat. Hist., 6, p. 218 (Tobari Bay, Sonora).

Conclusions

Are subspecies useful according to the criteria that Johnson (1982) listed? First, can subspecies help us understand patterns of migration? The answer is a qualified "yes," if the subspecies are clearly defined and readily identifiable. In Savannah Sparrows, for example, the large, pale, distinctive birds that breed on Sable Island, Nova Scotia, likely winter along the Atlantic Coast, rarely away from the sand dunes and dune grass. However, many of the other populations, such as the dark and supposedly large *P. s. labradorius* from Labrador, are more difficult to follow. Although dark Savannah Sparrows are common in winter on the Gulf Coast of Texas, which suggests that they come from breeding populations in northeastern Canada, whether they are from Labrador is difficult to determine using conventional morphological criteria. To quote Todd (1963:673), in 1901

> Howe undertook to separate the Labrador birds as *labradorius.* He had just three Labrador specimens, and he based his new race mainly on the supposed larger size of the northern birds. Townsend and Allen (1907), however, relying on Oberholser's positive statement (in litt.) that their Labrador specimens were virtually indistinguishable from southern birds, declined to recognize the race, and this example was followed by most subsequent writers, down to Bangs (1930) who contended that in spite of all adverse criticism, 'the large dark Savannah Sparrow of Labrador is an excellent race.' [Austin (1932)], after examining and comparing his series of freshly collected specimens from the Labrador coast, reached the same conclusion. He defined its characters with considerable precision, stressing its general darker coloration, but discounting its supposed larger size as compared with southern specimens [note that this race was originally defined on the basis of size, and subsequently became defined on the basis of coloration].... Peters and Griscom (1932), with a series of 150 specimens before them, were able to thoroughly establish its validity, *although the majority of their specimens came from south of Labrador* [italics mine]."

Peters and Griscom also described a new subspecies, *P. s. oblitus*, with the type from Churchill, Manitoba. Todd (1963:673) commented,

> ...*labradorius* and *oblitus* are amazingly alike, but are distinguishable in series of seasonally comparable specimens. With only the two type-specimens in hand, I doubt that anyone would have ever considered them to belong to two different races.

On the basis of large series of specimens (Rising 2001, Rising et al. unpubl. data), *labradorius* appears to be darker, on average, than birds from farther to the west, and also slightly larger. However, as noted by Todd (1963), *labradorius* and *oblitus* are not distinguishable with small samples. Although geographic variation exists, the pattern is clinal. Thus, a dark Savannah Sparrow on the Gulf Coast of Texas may well have come from Labrador, but it also may have originated from any place in the James Bay or Hudson Bay lowlands. Mengel (1965) recognized a similar problem with American Robins (*Turdus migratorius*) wintering in Kentucky, where darker individuals could not be traced with certainty to Newfoundland.

Johnson's (1982) other three criteria can be considered together: Do subspecies represent early stages of allopatric speciation? Do they alert researchers to look for other differences? And can some subspecies, with further study, be found to be "good species"? The answer to all these questions, again, is a qualified "yes." If the subspecies have been described rigorously on the basis of sufficient breeding material, they can help us understand evolution (adaptations to local environments) and speciation. Again, to return to Savannah Sparrows, recent studies (Rising 2001, Rising et al. unpubl. data) have shown that some groups of populations are morphologically distinctive: "Ipswich" Sparrows breeding on Sable Island, Nova Scotia; "Belding's" Sparrows along the Pacific Coast of California and Baja California; "Large-billed" Sparrows on the coast of Sonora and Sinaloa; and the "San Benito" Sparrow on the Islas San Benito, Baja California. Genetic data (Zink et al. 1991, 2005) showed that west-coast birds form a distinct clade that contains no "typical" Savannah Sparrows, but that the "Ipswich" Sparrow is a "typical" Savannah Sparrow at the mtDNA level. Although "Ipswich" Sparrows are distinctive morphologically and behaviorally, doubtless those differences are based on genetic variation that has not yet been investigated. Likewise, there is no phylogeographic structure in mtDNA among "Belding's," "Large-billed," and "San Benito" sparrows, although there are morphological differences among them. These morphological "subspecies" have alerted us to look for other differences—which in some cases we have found, and in others not. Are these four groups incipient "biological" species? No doubt. They are mostly or completely allopatric, so the opportunity for interbreeding among populations is minimal. Should we recognize some of these subspecies as different species on the basis of the information that we have at present? I think that one could, but that becomes a matter of taxonomic judgment. The named subspecies, in some cases, have alerted us to the questions.

THE FUTURE

Many subspecies have been described on the basis of few specimens (in some cases, only one), and some on the basis of nonbreeding individuals. Clearly, an arbitrary rule (e.g., 75% or 95% diagnosability) cannot be applied to these without increased samples. Yet many agree that there is some virtue to the subspecies concept if subspecies are based on sufficient data (e.g., Phillimore and Owens 2006, Winker et al. 2007). Those faced with subspecies-level taxonomy need to have a sound basis for revision. Most named subspecies of North American birds are poorly differentiated, and many represent points on a cline. A large number is based on small samples, perhaps of migrants or wintering individuals, and their description is not based on a rigorous analysis of variation. Also, most of these subspecies will not be restudied. Those charged with revising taxonomies should re-evaluate the original descriptions and, when possible, examine material in museums. If a subspecies is defined on the basis of reasonably large samples of breeding birds (e.g., ≥10 specimens from each locality, preferably ≥25; J. D. Rising unpubl. data), combined with at least one diagnosable phenotypic character and preferably two or more, then it should be retained at least until an updated, quantitative study is published. If not, the subspecies name should be stricken from the books. Importantly, subspecies can mislead people about the amount of real geographic variation; for example, geographic variation among populations of Savannah Sparrows is strong but does not conform to 17–21 diagnosable units. In some cases (e.g., "Ipswich" Sparrow), the subspecies are so distinct that they should be retained even if not adequately defined by today's standards. Likewise, subspecies that are diagnosable morphologically but not by mtDNA should be retained because phenotypic differences are more likely than mtDNA to be the result of selection (Mumme et al. 2006). If we restrict subspecies to those that "predict" variation in ways not used in the original description, as Barrowclough (1982) demanded, the subspecies designation is useful. Otherwise, it is of no value and is potentially misleading.

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LITERATURE CITED

ALDRICH, J. W. 1940. Geographic variation in eastern North American Savannah Sparrows (*Passerculus sandwichensis*). Ohio Journal of Science 40:1–8.

AMADON, D. 1949. The seventy-five per cent rule for subspecies. Condor 51:250–258.

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American Birds, 5th ed. American Ornithologists' Union, Baltimore, Maryland.

American Ornithologists' Union. 1998. Check-list of North American Birds, 7th ed. American Ornithologists' Union, Washington, D.C.

Arbogast, B. S., S. V. Edwards, J. Wakely, P. Beerli, and J. B. Slowinski. 2002. Estimating divergence times from molecular data on phylogenetic and population genetic timescales. Annual Review of Ecology and Systematics 33:707–740.

Austin, O. L., Jr. 1932. The Birds of Newfoundland Labrador. Memoirs of the Nuttall Ornithological Club, no. 7.

Avise, J. C., and R. M. Ball, Jr. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Surveys in Evolutionary Biology 7:45–67.

Bangs, O. 1930. Types of birds now in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology 70:147–426.

Barrowclough, G. F. 1982. Geographic variation, predictiveness, and subspecies. Auk 99: 601–603.

Cicero, C., and N. K. Johnson. 2006. Diagnosability of subspecies: Lessons from Sage Sparrows (*Amphispiza belli*) for analysis of geographic variation in birds. Auk 123:266–274.

Cracraft, J. 1983. Species concept and speciation analysis. Pages 159–187 *in* Current Ornithology, vol. 1 (R. F. Johnston, Ed.). Plenum Press, New York.

Cracraft, J. 1997. Species concepts in systematics and conservation biology—An ornithological viewpoint. Pages 325–339 *in* Species: The Units of Biodiversity (M. F. Claridge, H. A. Dawah, and M. R. Wilson, Eds.). Chapman and Hall, London.

Edwards, S. V., and P. Beerli. 2000. Perspective: Gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. Evolution 54:1839–1854.

Funk, D. J., and K. E. Omland. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology, Evolution, and Systematics 34: 397–423.

Gill, F. B. 1982. Might there be a resurrection of the subspecies? Auk 99:598–599.

Hebert, P. D. N., M. Y. Stoekle, T. S. Zemlak, and C. M. Francis. 2004. Identification of birds through DNA barcodes. PLoS Biology 2: 1657–1663.

Hellmayr, C. E. 1938. Catalogue of Birds of the Americas. Field Museum of Natural History Publications, Zoology Series, vol. 13, part 11.

Hubbard, J. P. 1974. Geographic variation in the Savannah Sparrows of the inland southwest, Mexico, and Guatemala. Occasional Papers of the Delaware Museum of Natural History, no. 12.

Johnson, N. K. 1982. Retain subspecies—At least for the time being. Auk 99:605–606.

Johnson, N. K., and C. Cicero. 2004. New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. Evolution 58:1122–1130.

Johnson, N. K., J. V. Remsen, Jr., and C. Cicero. 1999. Resolution of the debate over species concepts in ornithology: A new comprehensive species concept. Pages 1470–1482 *in* Acta XXII Congressus Internationalis Ornithologici (N. J. Adams and R. H. Slotow, Eds.). BirdLife South Africa, Johannesburg.

Kerr, K. C. R., M. Y. Stoeckle, C. J. Dove, L. A. Weigt, C. M. Francis, and P. D. N. Hebert. 2007. Comprehensive DNA barcode coverage of North American birds. Molecular Ecology Notes doi:10.1111/j.1471-8286.2006.01670.x

Mayr, E. 1982. Of what use are subspecies? Auk 99:593–595.

Mayr, E., and P. D. Ashlock. 1991. Principles of Systematic Zoology. McGraw-Hill, New York.

McKitrick, M. C., and R. M. Zink. 1988. Species concepts in ornithology. Condor 90:1–14.

Mengel, R. M. 1965. The birds of Kentucky. Ornithological Monographs, no. 3.

Møller, A. P., and J. J. Cuervo. 1998. Speciation and feather ornamentation in birds. Evolution 52:848–858.

Monroe, B. L., Jr. 1982. A modern concept of the subspecies. Auk 99:608–609.

Moritz, C., and C. Cicero. 2004. DNA barcoding: Promise and pitfalls. PLoS Biology 2:1529–1531.

Mumme, R. L., M. L. Galatowitsch, P. G. Jabłoński, T. M. Stawarczyk, and J. P. Cygan. 2006. Evolutionary significance of geographic variation in a plumage-based foraging adaptation: An experimental test in the Slate-throated Redstart (*Myioborus miniatus*). Evolution 60: 1086–1097.

Patten, M. A., and P. Unitt. 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. Auk 119:26–35.

Paynter, R. A., Jr. 1970. Check-list of Birds of the World, vol. 13. Museum of Comparative Zoology, Cambridge, Massachussetts.

Peters, J. L., and L. Griscom. 1938. Geographic variation in the Savannah Sparrow. Bulletin of the Museum of Comparative Zoology 80:443–479.

Phillimore, A. B., and I. P. F. Owens. 2006. Are subspecies useful in evolutionary and conservation biology? Proceedings of the Royal Society of London, Series B 273:1049–1053.

Pyle, P. 1997. Identification Guide to North American Birds. Slate Creek Press, Bolinas, California.

REED, D. H., AND R. FRANKHAM. 2001. How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. Evolution 55:1095–1103.

REMSEN, J. V., JR. 2005. Pattern, process, and rigor meet classification. Auk 122:403–413.

RISING, J. D. 2001. Geographic variation in size and shape of Savannah Sparrows (*Passerculus sandwichensis*). Studies in Avian Biology, no. 23.

RISING, J. D., AND D. D. BEADLE. 1996. A Guide to the Identification and Natural History of the Sparrows of the United States and Canada. Academic Press, San Diego, California.

ROHWER, S. A., AND M. S. JOHNSON 1992. Differences in timing and number of molts for Baltimore and Bullock's orioles: Implications to hybrid fitness and theories of delayed plumage maturation. Condor 95:125–140.

SOL, D., D. G. STIRLING, AND L. LEFEBVRE. 2005. Behavioral drive or behavioral inhibition in evolution: Subspecific diversification in Holarctic passerines. Evolution 59:2669–2677.

STORER, R. W. 1982. Subspecies and the study of geographic variation. Auk 99:599–601.

TODD, W. E. C. 1963. Birds of the Labrador Peninsula and Adjacent Areas. University of Toronto Press, Toronto, Ontario.

TOWNSEND, C. W., AND G. M. ALLEN. 1907. Birds of Labrador. Proceedings of the Boston Society of Natural History 33:277–428.

VAN ROSSEM, A. J. 1938. Description of twenty-one new races of Fringillidae and Icteridae from Mexico and Guatemala. Bulletin of the British Ornithologists' Club 58:124–138.

VAN ROSSEM, A. J. 1947. A synopsis of the Savannah Sparrows of northern Mexico. Condor 49: 97–107.

WHEELWRIGHT, N. T., AND J. D. RISING. 1993. Savannah Sparrow (*Passerculus sandwichensis*). *In* The Birds of North America, no. 45 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

WIENS, J. A. 1982. Forum: Avian subspecies in the 1980's. Auk 99:593.

WILSON, E. O., AND W. J. BROWN, JR. 1953. The subspecies concept and its taxonomic application. Systematic Zoology 2:97–111.

WINKER, K., D. A. ROCQUE, T. M. BRAILE, AND C. L. PRUETT. 2007. Vainly beating the air: Species-concept debates need not impede progress in science or conservation. Pages 30–44 *in* Festschrift for Ned K. Johnson: Geographic Variation and Evolution in Birds (C. Cicero and J. V. Remsen, Jr., Eds.). Ornithological Monographs, no. 63.

ZINK, R. M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. Proceedings of the Royal Society of London, Series B 271:561–564.

ZINK, R. M., D. L. DITTMANN, S. W. CARDIFF, AND J. D. RISING. 1991. Mitochondrial DNA variation and the taxonomic status of the large-billed Savannah Sparrow. Condor 93:1016–1019.

ZINK, R. M., J. D. RISING, S. MOCKFORD, A. G. HORN, J. M. WRIGHT, M. LEONARD, AND M. C. WESTBERG. 2005. Mitochondrial DNA variation, species limits, and rapid evolution of plumage coloration and size in the Savannah Sparrow. Condor 107:21–28.

ZUSI, R. L. 1982. Infraspecific geographic variation and the subspecies concept. Auk 99:606–608.