

**The Significance of Subspecies: A Case Study of Sage Sparrows
(Emberizidae, *Amphispiza belli*)**

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CHAPTER 9

THE SIGNIFICANCE OF SUBSPECIES: A CASE STUDY OF SAGE SPARROWS (EMBERIZIDAE, *AMPHISPIZA BELLI*)

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ABSTRACT.—Subspecies have been viewed as important biological entities that provide evidence of adaptation and early stages of speciation and that stimulate biological research on behavior, ecology, and other non-systematic questions. However, the history of subspecies and the lack of congruence with molecular data have led to questions about whether they help or hinder studies in avian biology and conservation. The Sage Sparrow (*Amphispiza belli*) provides a case study for examining the significance of subspecies. Of the five named subspecies, three breed in the continental United States (*A. b. belli*, *A. b. canescens*, *A. b. nevadensis*) and have been studied and debated for decades regarding their systematic relationships and status. I review this history and summarize our current understanding. In this particular case, subspecies have helped our understanding by alerting researchers to interesting geographic and behavioral patterns that otherwise might have been overlooked.

Key words: *Amphispiza belli*, geographic variation, intergradation, mitochondrial DNA, morphology, postbreeding movements, subspecies.

La Importancia de las Subespecies: Un Estudio de Caso sobre *Amphispiza belli* (Emberizidae)

RESUMEN.—Las subespecies han sido consideradas entidades biológicas importantes en el estudio de adaptaciones y estados tempranos de especiación. Además, su estudio ha estimulado investigaciones no sistemáticas relacionadas con la ecología o etología de los grupos estudiados. Sin embargo, la historia de las subespecies y la incongruencia que existe a veces entre datos moleculares y morfológicos, nos han llevado a preguntarnos si éstas facilitan o dificultan los estudios sobre la biología y la conservación de las aves. *Amphispiza belli* es un buen modelo para examinar la importancia de las subespecies. De las cinco subespecies conocidas, tres se reproducen en el área continental de los Estados Unidos (*A. b. belli*, *A. b. canescens*, *A. b. nevadensis*). Estudios sobre la relación filogenética entre estas subespecies han generado debates durante décadas. En este trabajo hago una revisión bibliográfica y resumo el estado actual de la información disponible. En este caso particular, las subespecies han ayudado al desarrollo de nuestro conocimiento, mostrándonos patrones geográficos y de comportamiento que de otra manera hubieran pasado desapercibidos.

THE SIGNIFICANCE OF subspecies has been hotly debated among ornithologists for decades (e.g., Wiens 1982, Zink 2004, Phillimore and Owens 2006, Rising 2007). In North America, this contentiousness can be attributed to several factors. First, most avian subspecies were described

in the late 1800s to early 1900s (Fig. 1), when relatively few specimens and characters were used compared to modern standards. Second, formal subspecies names have been applied to birds that vary “from groups of populations barely discernible on the basis of weak divergence in a single

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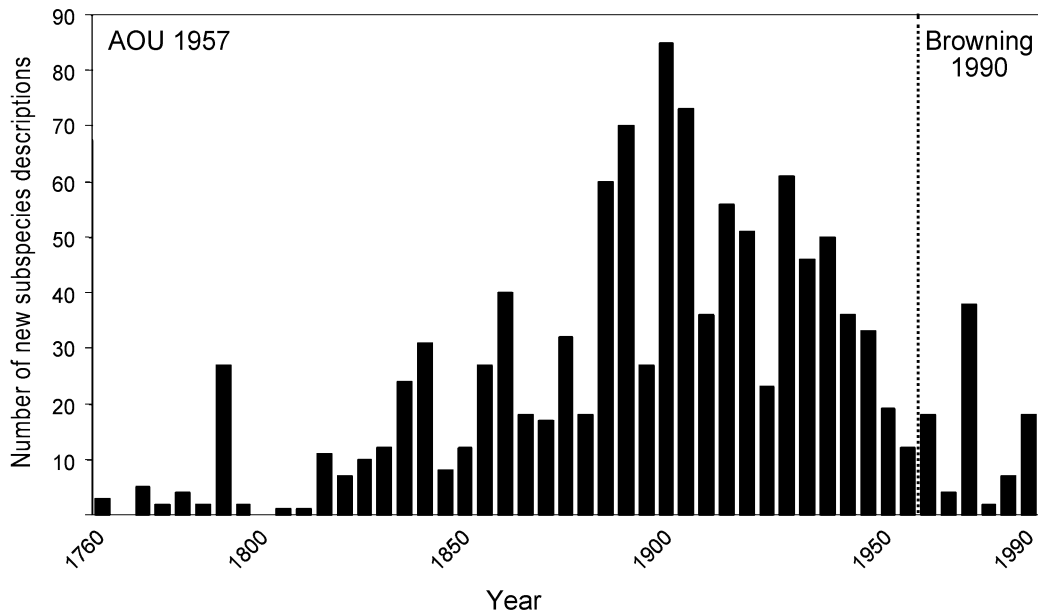


FIG. 1. Dates of descriptions of North American subspecies, in 5-year increments. Data are from American Ornithologists' Union (1957) and Browning (1990).

character to geographic forms that illustrate trenchant differences in morphology, coloration, and voice" (Johnson 1982:605). Third, molecular analyses often conflict with boundaries defined using traditional methods (Ball and Avise 1992, Greenberg et al. 1998, Zink 2004). Although incongruence between genetic data and subspecific characters based on phenotype is not surprising, such results have led to attacks on the concept of subspecies.

In a forum on the value of subspecies, Wiens (1982) posed a series of questions to several prominent American avian systematists to get their personal views on the topic. These questions focused on whether the concept of subspecies is useful and whether it should be revised, how subspecies should be defined, and whether subspecies exist as real biological units. Mayr (1982a:594–595) noted that subspecies "call attention to differences between geographically separated populations . . . that might have been overlooked otherwise" and that ornithologists who study ecology or behavior "often find the subspecies designations of the taxonomist useful as to clues to problems that might be studied profitably." Johnson (1982:605) echoed this sentiment when he wrote that subspecies names "function importantly as signposts calling attention to populations of significance for

their research potential." Johnson (1982:605) also noted that "some of these 'subspecies' will turn out after careful study to be full species."

Several examples illustrate the usefulness of subspecies for guiding research. Mennill (2001) studied song variation in two Yellow Warbler subspecies, *Dendroica petechia bryanti* and *D. p. aestiva*, with a goal of determining whether these subspecies, which were characterized by Browning (1994) on the basis of visual characteristics, show similar differences in song characteristics and singing behavior. His findings showed that the two subspecies are completely separable by song and that these differences, combined with geographic and morphological evidence, indicate strong divergence between them. In another study, Valkiūnas and Iezhova (2001) compared hematozoa of three subspecies of Yellow Wagtail (*Motacilla flava*) caught during spring migration to determine whether subspecies varied in their blood parasites, and found differences in the prevalence of infection which they attributed to differences in latitudinal range and breeding habitats used by each host subspecies. Other examples involve studies of differences in migratory routes and wintering areas between subspecies of Swainson's Thrush (*Catharus ustulatus*; Ruegg and Smith 2002) and Sharp-tailed

TABLE 1. Phenotypic, ecological, and behavioral differences among the five subspecies of Sage Sparrow (*Amphispiza belli*).

Subspecies	Size	Color	Primary habitat	Migration
<i>A. b. belli</i>	Small	Dark	Chaparral and coastal sage scrub	Nonmigratory
<i>A. b. cinereus</i>	Small	Pale	Arid and semi-arid scrub	Nonmigratory
<i>A. b. clementeae</i>	Small	Dark	Maritime desert scrub	Nonmigratory
<i>A. b. canescens</i>	Medium	Pale	Saltbush, shadscale desert scrub	Short-distance migrant
<i>A. b. nevadensis</i>	Large	Pale	Great Basin sagebrush	Long-distance migrant

Sparrows (*Ammodramus caudacutus* and *A. nelsoni*; Greenlaw and Woolfenden 2007), which can have important conservation implications (Greenlaw and Woolfenden 2007). In Swainson's Thrush, subspecific differences in migratory pattern are congruent with genetic, ecological, and acoustic divergences, and sharp concordant clines across a narrow hybrid zone provide evidence of barriers to gene flow that may justify recognition as sister species (Ruegg 2007).

Subspecies can be both a driving force and a challenge in evolutionary biology and conservation (Haig and D'Elia, this volume; Winker, this volume). Not surprisingly, close investigation using quantitative criteria may result in the elimination of some, and perhaps many, currently named subspecies. However, if subspecies are defined as phenotypically diagnosable breeding populations (Patten and Unitt 2002, Cicero and Johnson 2006), they can be useful taxonomic units that (1) provide evidence of early stages of allopatric speciation; (2) illustrate local adaptation in spite of ongoing gene flow; (3) alert researchers to differences other than traits originally considered, leading to recognition of some subspecies as full species; and (4) inform researchers about non-breeding movements of distinct portions of species' breeding ranges (Johnson 1982, Mayr 1982a, Rising 2007). Here, I use a case study of the Sage Sparrow (*Amphispiza belli*) to illustrate the value of subspecies in ornithology. Specifically, I review the history and current knowledge of Sage Sparrow systematics, and ask whether subspecies have been useful to researchers studying its biology and evolutionary relationships.

DEBATE OVER SAGE SPARROW SUBSPECIES

The Sage Sparrow provides a suitable case study on the significance of subspecies in ornithology because it shows strong geographic differentiation, has a long history (110 years) of

differing interpretations and debate about taxonomic relationships, and is of conservation concern as a result of habitat loss and degradation (Martin and Carlson 1998). Five subspecies are currently recognized (Table 1), with names dating back more than a hundred years: *A. b. belli* (Cassin 1850), *A. b. nevadensis* (Ridgway 1874), *A. b. cinerea* (Townsend 1890), *A. b. clementeae* (Ridgway 1898), and *A. b. canescens* (Grinnell 1905). Two subspecies are listed as federally threatened (*A. b. clementeae*) or of special concern in California (*A. b. belli*), and the species itself is listed as a species of special concern in several western states. I focus on the three subspecies that breed primarily in the continental United States (*A. b. belli*, *A. b. canescens*, and *A. b. nevadensis*; Figs. 2 and 3) because they have received the most systematic study. The two other subspecies (*A. b. cinerea* and *A. b. clementeae*) are resident in west-central Baja California, Mexico, and on San Clemente Island in the California Channel Islands, respectively.

Grinnell (1898b) collected *A. b. belli* and *A. b. nevadensis* (currently *A. b. canescens*) together in July 1897 in the mountains of central Los Angeles County, California (1,219–1,829 m elevation). He was surprised to find the two forms breeding in the same locality, and he collected adults and fully fledged young of both forms that showed no evidence of intergradation. On the basis of these observations, he argued that *A. b. belli* and "*A. b. nevadensis*" should be considered specifically distinct. Following this, Fisher (1898) countered that intermediates were collected on the east slope of the Sierra Nevada during the Death Valley Expedition in 1891 and that the birds Grinnell (1898b) collected were fully fledged and "had evidently wandered from their desert home." Thus, he concluded that the two forms were no more than subspecifically distinct.

Subsequent to these early reports, Grinnell (1905) described a new subspecies of Sage Sparrow (*A. b. canescens*) from the higher-elevation

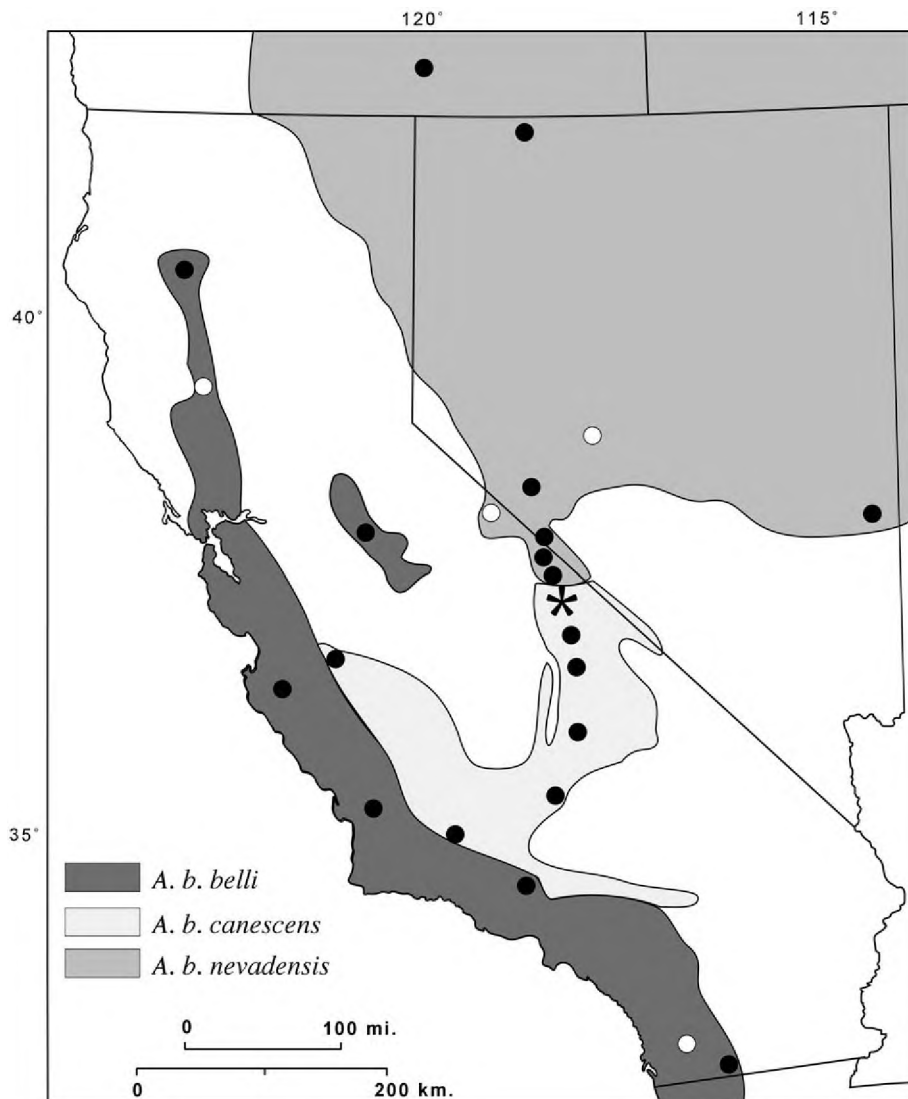


FIG. 2. Breeding distribution of three subspecies of *Amphispiza belli*. Closed circles show sites that have been studied for both allozymes (Johnson and Marten 1992) and mtDNA (Cicero and Johnson 2007, C. Cicero et al. unpubl. data); open circles show sites that were analyzed for allozymes only. Additional sampling and analyses have been done where *A. b. canescens* and *A. b. nevadensis* are in contact in northern Owens Valley, eastern California (shown by asterisk; see Cicero and Johnson 2007).

sage valleys of the southern Sierra Nevada and adjacent mountains of California and referred his earlier specimens from Los Angeles County to this subspecies. Although he described *A. b. canescens* as having characters intermediate between *A. b. belli* and *A. b. nevadensis*, he argued that all three forms were distinctive and that there were no intermediates between *canescens* and *belli* or

between *canescens* and *nevadensis*. In his examination of specimens from the 1891 Death Valley Expedition, he definitively assigned them to *canescens* and thus expanded the range of this form farther northward. Although Grinnell (1905:18–19) was convinced that *A. b. canescens*–*A. b. nevadensis* and *A. b. belli* should be considered species because of their distinctiveness, the apparent lack of



FIG. 3. Dorsal and ventral views of specimens of three of the five subspecies of *Amphispiza belli*. (Top) *A. b. nevadensis*. (Middle) *A. b. canescens*. (Bottom) *A. b. belli*. These forms have received the most attention because of confusion and debate over their relationships. Study skins are in the Museum of Vertebrate Zoology, University of California, Berkeley. (Photographs by Anand Varma.)

intermediates, and the thought that they bred in close proximity in the mountains of Los Angeles County, he stated: "current rulings being overwhelmingly against it . . . it is therefore only under protest that I use the combination *Amphispiza belli canescens* instead of *Amphispiza nevadensis canescens*."

The debate over how to treat phenotypically diagnosable forms of *A. belli* over a century ago, and their assignment as subspecies rather than species, catalyzed decades of interest and study aimed at understanding the evolutionary history and biology of this species. The extent to which populations move after breeding, as suggested by Fisher (1898), and whether or not different forms intergrade have received particular attention. In their analysis of the distribution of the birds of California, Grinnell and Miller (1944) countered earlier views on the lack of intergradation by reporting that *A. b. belli* and *A. b. canescens* intergrade on or near San Benito Mountain in the interior coastal range of San Benito County, California. They based this on specimens of *A. b. canescens* collected during June–July 1936 and August 1944 (housed in the Museum of Vertebrate Zoology, MVZ 69886–69904, 89797–89840), which they assumed were from breeding grounds. Their assertion that *A. b. belli* and *A. b. canescens* intergrade held for approximately half a century, until Johnson and Marten (1992) reexamined the specimens and emphasized that the birds were in non-breeding condition (i.e., small gonads, molt) and in flocks. Analysis of the series of specimens showed that they are

typical *A. b. canescens* in fresh, post-breeding plumage acquired after an uphill migration from nesting localities in the adjacent lowlands of the San Joaquin Valley. . . . Because these specimens are in fresh plumage and are therefore more richly colored and slightly darker than worn nesting individuals of typical *A. b. canescens*, Miller evidently viewed the increased pigmentation as evidence of intermediacy with *A. b. belli*. (Johnson and Marten 1992:17)

Thus, Johnson and Marten (1992) provided the first definitive evidence that individual *A. b. canescens* wander from their hot breeding grounds into the range of *A. b. belli* while the latter is still breeding. Their finding uncovered an interesting behavioral pattern that probably would not have

emerged if these forms had been treated as species per Grinnell's (1905) original inclination.

Grinnell and Miller (1944) also reported intergradation between *A. b. canescens* and *A. b. nevadensis* in the vicinity of Benton, Mono County, California. In a study of variation in allozymes and morphology, Johnson and Marten (1992) reported that populations at the northern end of the White Mountains, including those at Benton, are typical of *A. b. nevadensis*. Thus, they surmised that if contact and intergradation occurs during the breeding season, it must be somewhere in Owens Valley, eastern California, between what they reported to be the southernmost known *A. b. nevadensis* (Chalfant Valley, Mono County, ~33 km south of Benton) and the northernmost known *A. b. canescens* (Coso Junction, Inyo County). Subsequent study of populations from Benton to Coso Junction (Cicero and Johnson 2007) provided evidence that *A. b. nevadensis* and *A. b. canescens* meet in a narrow zone near Bishop, California, at the northern end of Owens Valley (about 15–20 km south of Chalfant Valley). This contact zone occurs in an area of ecological and bioclimatic transition between the Great Basin (*A. b. nevadensis*) and the Mojave Desert (*A. b. canescens*).

Johnson and Marten's (1992) study provided the first detailed analysis of population structuring in *A. b. belli*, *A. b. canescens*, and *A. b. nevadensis*. Their results showed strong morphological and genetic variation, especially between *A. b. canescens* and *A. b. nevadensis*. Reanalysis of size data combined from Johnson and Marten (1992) and Cicero and Johnson (2007) using discriminant function analysis (present study) supported the strong morphological separation between subspecies (Table 2 and Fig. 4), with the greatest overlap between *A. b. belli* and *A. b. canescens*. Although *A. b. belli* and *A. b. canescens* differ strongly in plumage, the allozyme data showed them to be genetically closely related, with some populations of *A. b. canescens* genetically closer to *A. b. belli* than to other populations of *A. b. canescens* (Johnson and Marten 1992: fig. 8). Because Johnson and Marten (1992) suggested that *A. b. canescens* and *A. b. nevadensis* putatively make contact in Owens Valley, they refrained from recommending taxonomic action that would split the subspecies into different species. Nonetheless, Rising (1996) used this study to treat *A. b. nevadensis* and *A. b. belli* as separate species, although he mistakenly placed *A. b. canescens* in "*A. nevadensis*." The American Ornithologists'

TABLE 2. Percent classification of three subspecies of *Amphispiza belli* based on specimens housed in the Museum of Vertebrate Zoology, Berkeley ($n = 275$ males). Analysis was based on seven linear measurements (wing length, tail length, bill length, bill depth, bill width, length of tarsus plus toe, and cube root of mass). Specimens included those studied by Johnson and Marten (1992) and Cicero and Johnson (2007), with the exception of those in the area of contact between *A. b. canescens* and *A. b. nevadensis* in northern Owens Valley, eastern California.

	<i>A. b. belli</i>	<i>A. b. canescens</i>	<i>A. b. nevadensis</i>	Percent correct classification
<i>A. b. belli</i>	59	3	0	95.2
<i>A. b. canescens</i>	10	76	3	85.4
<i>A. b. nevadensis</i>	0	2	122	98.4
Total	69	81	125	93.5

Union ([AOU] 1998) currently recognizes them as two groups within *A. belli*: "*A. nevadensis*" and "*A. belli*," with the latter including *A. b. belli*, *A. b. canescens*, *A. b. clementeae*, and *A. b. cinerea*. Both treatments correctly reflect the distinctiveness of *A. b. nevadensis* from the other forms in genotype, phenotype, and ecology, and future revision by the AOU is possible pending publication of additional molecular data (see below).

BREEDING VERSUS NON-BREEDING POPULATIONS IN DELINEATION OF SUBSPECIES

Debate over the taxonomic status of subspecies of *A. belli* has focused largely on *A. b. canescens*, which is geographically and phenotypically

intermediate between *A. b. belli* and *A. b. nevadensis* (Tables 1 and 2 and Figs. 2–4). This subspecies is most similar in size to *A. b. belli* (both forms are smaller than *A. b. nevadensis*), but it is most similar in color to *A. b. nevadensis* (both forms are paler than *A. b. belli*). The breeding distribution of *A. b. canescens* lies between that of *A. b. belli* and that of *A. b. nevadensis*, with its center in the western and southern San Joaquin Valley and in the western and northern Mojave Desert. As noted above, *A. b. canescens* has been reported to contact or intergrade with *A. b. belli* in Los Angeles County and in San Benito County (Grinnell 1898b, 1905; Grinnell and Miller 1944), although intergradation has not been established conclusively. Likewise, *A. b. canescens* and *A. b. nevadensis* contact one another

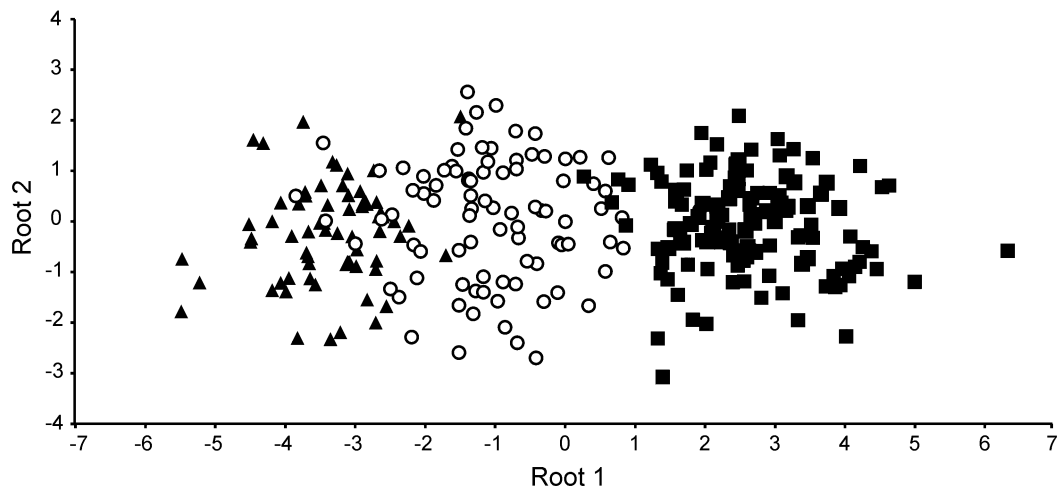


FIG. 4. Discriminant function scores for three subspecies of *Amphispiza belli*. Black triangles = *A. b. belli*, open circles = *A. b. canescens*, and black squares = *A. b. nevadensis*.

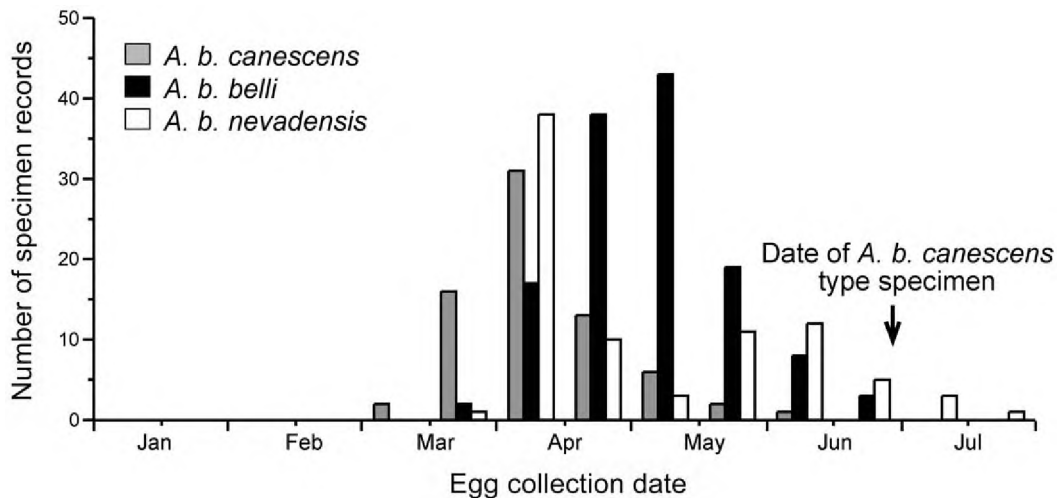


FIG. 5. Egg collection dates for three subspecies of *Amphispiza belli*, from specimen records in the Western Foundation of Vertebrate Zoology and the Museum of Vertebrate Zoology. Data were obtained from ORNIS (ornisnet.org, 1 March 2008) and from copies of egg data slips. Egg data were plotted as Julian dates in 15-day increments. Note the late (postbreeding) date of collection of the holotype of *A. b. canescens*.

narrowly in eastern California (Grinnell and Miller 1944, Johnson and Marten 1992, Cicero and Johnson 2007). The putative intergradation between *A. b. canescens* and *A. b. belli* is confounded by upslope, postbreeding movements of *canescens* into the range of *belli* while the latter is still breeding (Johnson and Marten 1992).

In reviewing the original description of *A. b. canescens* (Grinnell 1905), it is noteworthy that the type specimen (MVZ 35756) was collected at an elevation of 1,676 m on Mount Pinos, Ventura County, California, on 27 June 1904. Grinnell mistakenly assumed that this specimen was on its breeding grounds. Analysis of egg data (present study; Fig. 5) clearly showed that this was a postbreeding bird. Of the three subspecies, *A. b. canescens* breeds the earliest, with egg dates ranging from 14 March to 7 June ($n = 71$, median date = 12 April). By comparison, egg dates for *A. b. nevadensis* ranged from 25 March to 17 July ($n = 84$, median date = 19 April), and those for *A. b. belli* ranged from 25 March to 22 June ($n = 130$, median date = 2 May). Furthermore, the series of birds seen and collected by Grinnell at this locality were "moulting adults and fully fledged young . . . latter in companies in brush on summits of both Pinos and Sawmill peaks" (unpublished field notes in the archives of the Museum of Vertebrate Zoology). Thus, Fisher (1898) was correct in surmising that individuals collected in July

in the mountains of Los Angeles County, where Grinnell (1898b) postulated that *A. b. belli* and *A. b. canescens* bred sympatrically, were wandering (postbreeding) birds. Likewise, the individual *A. b. canescens* that Grinnell and Miller (1944) thought were intergrading with *A. b. belli* on the slopes of San Benito Mountain, San Benito County (see above), were clearly non-breeding individuals, given their dates of collection (13 June–7 August) and the fact that they had small gonads and were molting and in flocks (Johnson and Marten 1992).

The tendency of *A. b. canescens* to move upslope after breeding—not only into the coastal ranges but also into the Sierra Nevada and into the Inyo Mountains of Inyo County, eastern California (Squaw Flat sample of Johnson and Marten 1992:3)—has complicated interpretations and confounded prior studies of geographic variation. In a study of the morphological diagnosability of *A. b. canescens* versus *A. b. nevadensis*, Cicero and Johnson (2006) showed that incorporation of non-breeding individuals into samples when analyzing morphologic variation (Patten and Unitt 2002) distorted the results and led to incorrect conclusions regarding diagnosability. This behavior, in which birds show regional movements into other habitats after breeding, often during molt, appears to be especially common in western North America (Rohwer et al. 2005). Recent studies that

have highlighted this phenomenon (e.g., Rohwer et al. 2008) underscore the importance of paying close attention to breeding individuals when studying geographic variation (Zink and Dittman 1992), particularly when relying on museum specimens. Nevertheless, non-breeding birds may be relevant for subspecies studies in some cases (e.g., *Baeolophus inornatus* and *B. ridgwayi* [Cicero 1996], and *Branta canadensis* and *B. hutchinsii* [Anderson 2007]).

MITOCHONDRIAL DNA AS A TOOL FOR SUBSPECIES STUDIES

Mitochondrial DNA (mtDNA) has proved to be an extremely useful marker for delineating evolutionary lineages within species as well as at higher levels (Avisé 2004), and thus it has been the tool of choice for phylogeographic studies (Avisé et al. 1987, Avisé 2000). In a recent and controversial application, mtDNA has been used to develop short barcodes for species and to identify cryptic variation that might signal new species (Hebert et al. 2004, Moritz and Cicero 2004, Clare et al. 2007). Although mtDNA has many advantages, problems with gene trees have caused researchers to question whether mtDNA alone is sufficient for understanding the evolutionary history of species (Edwards and Beerli 2000, Funk and Omland 2003, Zink and Barrowclough 2008). Likewise, lack of congruence between mtDNA patterns and the boundaries of named subspecies has led some researchers to conclude that current subspecies do not reflect biological diversity (Zink 2004). On the other hand, phenotypic variation in the absence of concordant mtDNA variation can provide evidence of strong selection and local adaptation to different ecological conditions, leading to rapid phenotypic evolution (Greenberg et al. 1998, Hoekstra et al. 2005).

Analyses of mtDNA variation in *Amphispiza belli* (Cicero and Johnson 2007, C. Cicero unpubl. data) supported previous genetic data based on allozymes (Johnson and Marten 1992). As with the allozyme results, mtDNA clearly separated *A. b. canescens* from *A. b. nevadensis* and showed that populations of *A. b. canescens* in the San Joaquin Valley (e.g., Panoche Hills and Carrizo Plains; Johnson and Marten 1992: figs. 1 and 8) are genetically closer to coastal *A. b. belli* than to populations of *A. b. canescens* in the Mojave Desert (Fig. 6). Importantly, *A. b. canescens* from the San Joaquin Valley breeds in proximity to *A. b. belli*

but at an earlier date, and moves upslope after breeding into the range of *belli* without intergradation (see above). Thus, both the allozyme and mtDNA data suggest that these populations of *A. b. canescens* share an evolutionary history with *A. b. belli* that is distinct from other *A. b. canescens* and also from *A. b. nevadensis*. If *canescens* had been described originally as a subspecies of "*A. nevadensis*," there is a good chance that this unexpected relationship would still remain hidden. Nonetheless, phenotypic differences readily distinguish *A. b. belli* from *A. b. canescens*, even where their breeding ranges meet parapatrically and where they mix during the breeding and postbreeding seasons, respectively (Johnson and Marten 1992). Variation in plumage color between *A. b. belli* and *A. b. canescens* likely reflects adaptation to local ecological conditions.

A study of the contact between *A. b. canescens* and *A. b. nevadensis* (Cicero and Johnson 2007) also supported previous results from morphology and allozymes (Johnson and Marten 1992). In general, mtDNA showed congruence with morphology in the contact zone and in adjacent populations of both forms. Ecological niche models revealed that the sharp cline in mtDNA and morphology in this region is closely associated with bioclimatic changes that favor one form over the other (Cicero and Johnson 2007).

HAVE SUBSPECIES BEEN USEFUL FOR UNDERSTANDING RELATIONSHIPS IN *AMPHISPIZA BELLI*?

Over a century ago, Grinnell (1898b, 1905) argued that coastal and interior populations of Sage Sparrow (*A. b. belli* and *A. b. canescens*–*A. b. nevadensis*) should be recognized as full species. He based this argument on the (incorrect) perception that they breed sympatrically—or nearly so—in southwestern California and that phenotypically divergent forms do not intergrade where they supposedly make contact. If these taxa had been recognized as species over the past 100 years, it is unlikely that modern studies at the population level would have been undertaken. Because of their subspecies status, a series of detailed studies that began in the mid-1970s with collection of specimens for genetic and morphological analyses (Johnson and Marten 1992; Cicero and Johnson 2006, 2007; C. Cicero unpubl. data) are ongoing. These studies have yielded several important findings to date: (1) the common postbreeding

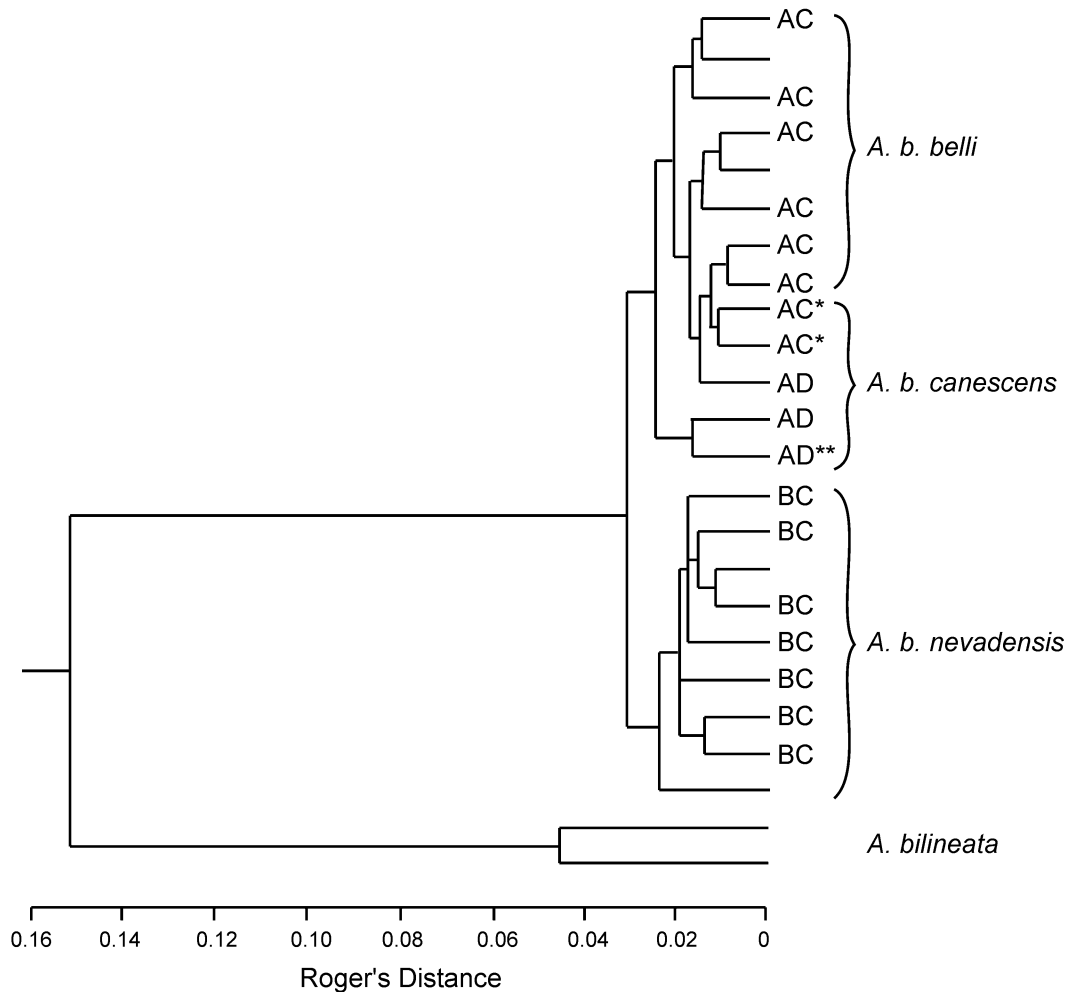


FIG. 6. UPGMA (unweighted pair group method with arithmetic mean) cluster analysis of Rogers's (1972) genetic distances among 22 population samples of *A. belli*, using *A. bilineata* as an outgroup (from Johnson and Marten 1992). The letters at the tips of branches (AC, AD, BC) show major mtDNA haplotype groupings superimposed onto the tree (Cicero and Johnson 2007, C. Cicero et al. unpubl. data) for 18 of the same populations. All are breeding populations except for one (AD**), which is from Squaw Flat, Inyo County, and contains post-breeding individuals of *A. b. canescens* that have moved upslope. The two populations of *A. b. canescens* that are genetically closer to *A. b. belli* than to other *A. b. canescens* (AC*) are also geographically closest (Panoche Hills and Carrizo Plains; see Johnson and Marten 1992: fig. 1).

upslope movement by *A. b. canescens* into the range of breeding *A. b. belli*; (2) the closer genetic relationship of *A. b. canescens* to *A. b. belli* than to *A. b. nevadensis*, contrary to treatments based on similarity in plumage color that placed *A. b. canescens* with *A. b. nevadensis* (Grinnell 1905, Rising 1996); and (3) the geographic position and extent of contact between *A. b. canescens* and *A. b. nevadensis* in Owens Valley, eastern California. Thus, as predicted by Mayr (1982a) and Johnson

(1982), the recognition of *A. b. belli*, *A. b. canescens*, and *A. b. nevadensis* as subspecies called attention to interesting geographic and behavioral patterns that otherwise might have been overlooked.

Cicero et al. (unpubl. data) have focused on variation in mtDNA sequences, microsatellite loci, and bioclimatic niches across populations of the three subspecies, and on song divergence between *A. b. canescens* and *A. b. nevadensis* where they come into contact in Owens Valley. Vocal

differences between *A. b. belli* and *A. b. canescens* also would be worth pursuing, given that the two forms mix in different stages of their annual cycle (breeding and postbreeding, respectively) and that some populations of *A. b. canescens* are more similar genetically to *A. b. belli* than to other *A. b. canescens*. In addition, a comparison between the three continental subspecies studied here and the other two forms—especially *A. b. clementeae*, which is endemic to San Clemente Island and federally threatened—would add valuable information to the overall picture of diversification in the Sage Sparrow complex.

Are Sage Sparrow subspecies worthy of species recognition? Evidence to date suggests that *A. b. canescens* and *A. b. nevadensis* represent different evolutionary units with limited gene flow between them (Cicero and Johnson 2007). These forms are morphologically and genetically diagnosable, and secondary contact is limited to a narrow zone in northern Owens Valley where their major bioclimatic and ecological associations—the Mojave Desert and Great Basin,

respectively—meet (Cicero and Johnson 2006, 2007). Although microsatellite and bioacoustic analyses (C. Cicero et al. unpubl. data) within the contact zone should shed additional light on patterns and processes of divergence, *A. b. nevadensis* clearly deserves species status. Whether *A. b. canescens* should be recognized as a species distinct from *A. b. belli* remains to be determined. Further molecular work will hopefully answer this question.

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