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Commentary

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DIAGNOSABILITY OF SUBSPECIES: LESSONS FROM SAGE SPARROWS (*AMPHISPIZA BELLI*) FOR ANALYSIS OF GEOGRAPHIC VARIATION IN BIRDS

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The validity and utility of subspecies is an enduring subject of controversy in systematic ornithology. In a set of commentaries in *The Auk* more than two decades ago, numerous authors contributed personal views on avian subspecies and reaffirmed the validity of the concept despite its frequent misapplication (Barrowclough 1982, Gill 1982, Johnson 1982, Lanyon 1982, Mayr 1982, Monroe 1982, O'Neill 1982, Parkes 1982, Phillips 1982, Storer 1982, Zusi 1982). More recently, the subspecies rank was reviewed in light of molecular data (Zink 2004), with the conclusion that named subspecies commonly mislead taxonomy, evolutionary studies, and conservation policy. Because morphology and molecules may show discordant patterns of geographic variation (e.g. Zink 1996, Fry and Zink 1998), and because subspecies are traditionally defined on the basis of morphological criteria, rigorous analysis of morphology is crucial for proper classification at the subspecies level.

Patten and Unitt (2002) reviewed the debate and contended that taxonomists too often have diagnosed avian morphological subspecies on the basis of calculated mean differences among populations rather than an objectively defined level of diagnosability. Although admitting that "the lower boundary for defining a valid diagnosable subspecies is arbitrary" (Patten and Unitt 2002:28), they proposed that the level of diagnosability should be defined formally for the trait of interest so that 75% of its distribution in one set of populations falls outside of 99% of the distribution of the other set of populations being compared (the "75% rule"; Amadon 1949). Patten and Unitt (2002) used museum specimens of subspecies of Sage Sparrow (*Amphispiza belli*) to illustrate their thesis and claimed that *A. b. canescens* Grinnell, 1905—a name long applied to breeding populations in the San Joaquin Valley and Mojave Desert of California and the Grapevine Mountains of Nevada—is not diagnosable from *A. b. nevadensis* by the 75% rule despite significant differences in size (mainly wing length), as demonstrated in their study and others (Grinnell 1905, Johnson and Marten 1992). Hence, they synonymized *A. b. canescens* under *A. b. nevadensis.*

Overall, we agree with Patten and Unitt (2002) regarding the importance of diagnosability, and we recommend their review to systematists and others wishing to place morphological subspecies on a more objective footing than has often been the practice. However, because their results for *A. b. canescens* and *A. b. nevadensis* are at such variance with morphological differences reported by Johnson and Marten (1992) for specimens in the Museum of Vertebrate Zoology (MVZ, University of California, Berkeley), as well as with data for additional males and females from this collection, we suspected that their analyses and findings masked real patterns of geographic variation.

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In particular, two important issues stood out: (1) measurements were lumped by subspecies across the geographic range of specimens examined (presumably classified according to existing identifications on specimen labels), and (2) specimens were noted to be from the "breeding range" but apparently included times of the year when Sage Sparrows are not breeding (e.g. reference to "breeding males of *A. b. canescens*" from 28 July in southern California, or to "*A. b. nevadensis*" from 9 September in eastern California [Patten and Unitt 2002:32]; both of these dates are well outside the known breading season for these subspecies [Johnson and Marten 1992, Martin and Carlson 1998]).

We reiterate a long-standing truth that "unless specimens are clearly from a known breeding population they are *irrelevant* for analyses of geographic variation" (Zink and Dittmann 1992:765). Failure to restrict analyses to such individuals obscures potential variation within subspecies, such as clinal variation from northern to southern populations of the wide-ranging *A. b. nevadensis*. Furthermore, the null hypothesis in such studies should be that the species is geographically invariant (Johnson 1980, Cicero 1996). Accordingly, the existence of any variation must first be proved by examining geographic areas of breeding birds without regard to named subspecies, and then evaluated in light of the distributional limits of those taxa. This is the only approach that allows investigators to exclude potentially contaminating foreign specimens from local gene pools or demes in which variation is being assessed. Finally, *a priori* reliance on specimen identifications from museum labels to establish limits of trait variation for a particular subspecies is circular.

To clarify the findings of Patten and Unitt (2002), we requested copies of their original data, and they graciously complied. We reciprocated by sending copies of our own data sheets for measurements of Sage Sparrows (Johnson and Marten 1992, C. Cicero and N. K. Johnson unpubl. data). In addition to photocopies from Patten's notebook with data on museum specimens examined, they sent a spreadsheet that included "every specimen…used in [their] analysis" (M. A. Patten pers. comm.) with the exception of four individuals (he was unable to determine which four were missing). Patten also provided new means and standard deviations for wing chord from these data, which "do not differ materially from those in [the] published analysis" (M. A. Patten pers. comm.). We corroborated that statement by recalculating means and standard deviations for the data provided in the spreadsheet and then comparing them to the published data (table 2 in Patten and Unitt 2002); the only differences were a mean wing chord of 70.7 ± 2.81 (n = 43) versus 70.9 ± 2.88 (n = 45) for male *A. b. canescens*, and 66.9 ± 2.41 (n = 40) versus 67.2 ± 2.77 (n = 42) for female *A. b. canescens*.

Data included labeled identification of taxon, museum acronym and catalogue number, sex as written on the label, date and locality of collection, and measurements of wing and tail. The notebook data included additional specimens not listed in the spreadsheet and not analyzed; therefore, we restricted further examination to the spreadsheet. Of the 151 specimens included in the spreadsheet (40 female *A. b. canescens,* 43 male *A. b. canescens*, 30 female *A. b. nevadensis*, and 38 male *A. b. nevadensis*), 98 were from the MVZ; the remaining specimens were from the San Diego Museum of Natural History (n = 28), Los Angeles County Museum of Natural History (n = 17), and Western Foundation of Vertebrate Zoology (n = 8).

To assess whether the specimens were breeding or nonbreeding, we converted specimen dates to Julian dates and plotted them as histograms by subspecies (males and females were plotted separately and combined). For comparison, we also plotted Julian collecting dates for our morphological data set, which included 84 *A. b. canescens* (56 males, 28 females) and 202 *A. b. nevadensis* (159 males, 43 females) from 20 geographically organized sample areas within their active nesting ranges (Appendix). To be conservative, our data set included only adult specimens with enlarged reproductive organs. Therefore, we omitted from analysis many specimens of potential breeders (judging from collecting date) that lacked gonad information or had small gonads.

Specimens analyzed by Patten and Unitt (2002) showed a much broader range of dates than those in our study (Fig. 1 and Table 1), with histograms that differed significantly (Kolmogorov-Smirnov two-sample test, $P < 0.001$) for all comparisons by subspecies and sex; within each data set, the shape of the histograms did not differ significantly between

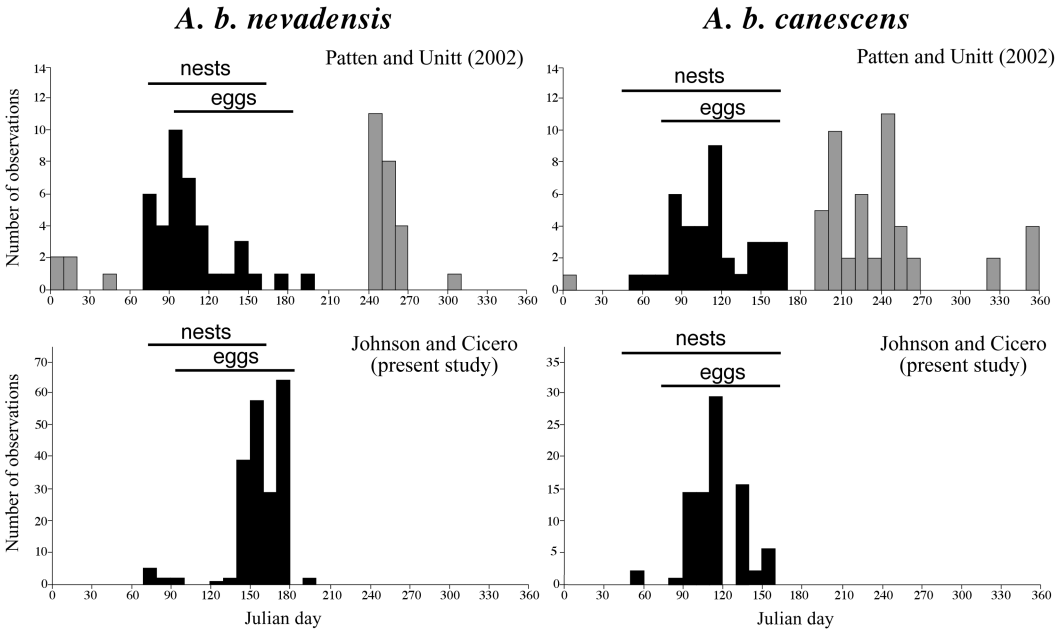

FIG. 1. Histograms of Julian dates for museum specimens of *A. b. canescens* and *A. b. nevadensis* examined by Patten and Unitt (2002) and Cicero and Johnson (present study). Black bars indicate timing of enlarged gonads based on this study; gray bars illustrate specimens collected outside of the breeding season. The active period for nests and eggs (Martin and Carlson 1998) is shown for comparison (horizontal bars). Sexes were combined because plots for males and females did not differ significantly within each subspecies (Kolmogorov-Smirnov two-sample test, $P > 0.10$).

TABLE 1. Dates of museum specimens examined for two analyses of morphological variation in *Amphispiza belli*.

Data set	Subspecies	Sex	*n*	Earliest date	Latest date
Patten and Unitt (2002)	*A. b. canescens*	M	43	21 February	25 December
	A. b. canescens	F	40	11 January	24 September
	A. b. nevadensis	M	38	5 January	7 November
	A. b. nevadensis	F	30	5 January	27 September
Cicero and Johnson (present study)	*A. b. canescens*	M	56	21 February	7 June
	A. b. canescens	F	28	31 March	5 June
	A. b. nevadensis	M	159	14 March	14 July
	A. b. nevadensis	F	43	10 April	25 June

males and females ($P > 0.10$). The histograms indicate that Patten and Unitt's (2002) analysis of diagnosability included a mixture of breeders and nonbreeders. In fact, 46 *A. b. canescens* (55%) and 29 *A. b. nevadensis* (43%)—about 50% of their total sample—were collected during periods of the year when interior forms of *A. belli* are not known to breed (mid- to late July through mid-February [*A. b. canescens*] or mid-March [*A. b. nevadensis*]; Fig. 1). The remaining 76 specimens represent possible or probable breeders judging from collecting date, but their data did not include reproductive information. To further evaluate breeding status, we examined the labels for all MVZ specimens ($n = 98$, 65%) analyzed by Patten and Unitt (2002) and found that 84 (86%) lacked gonad data. In addition, 19 (19%) contained data that showed nonbreeding (e.g. "molt," "nonbreeder"), and 16 (16%) were explicitly labeled as either juvenile

or immature (only one of these had gonad information). Gonad data are crucial both for providing insight into reproductive condition and for correct determination of sex, which can be especially difficult when dealing with nonbreeding or young birds.

Because Patten and Unitt's (2002) data led to the conclusion that *A. b. canescens* is not diagnosable from *A. b. nevadensis* using the 75% rule, despite significant mean size differences, we further compared the two data sets by applying the same statistical methods to our morphological measurements. These included: (1) *t*-tests of mean differences in wing and tail characters; (2) box plots to visualize differences in wing-chord distributions among subspecies and sample areas (Appendix; only samples with $n \geq 5$ were plotted in the geographic analysis); (3) discriminant function analysis to maximally separate the two subspecies on the basis of wing and tail measurements combined; and (4) the diagnosability index D_{ij} developed by Patten and Unitt (2002) to formally quantify the diagnosis of a subspecies using the 75% rule. Measurements in our data set were taken according to methods described in Johnson (1980), and analyses were performed separately on each sex using STATISTICA for Windows, version 5.1 (StatSoft, Tulsa, Oklahoma).

The *t*-tests were significant ($P < 0.001$) for all comparisons between *A. b. canescens* and *A. b. nevadensis*, indicating significant mean differences in wing and tail length within sex. Although this finding agrees with that of Patten and Unitt (2002; their table 2), our other analyses differed in conclusions of diagnosability. Among subspecies and geographic samples (Fig. 2 and Appendix), the 75th percentile for box plots of wing chord fell outside the range of the other subspecies (except for an unusually large male *A. b. canescens* from Jawbone Canyon; MVZ 169353), indicating that that they are diagnosable under the 75% rule. The only overlap was between *A. b. nevadensis* from Benton Valley (site 13) and *A. b. canescens* from Coso Junction (site 16). However, these samples represent ends of a zone where the subspecies approach in possible secondary contact in eastern California (Johnson and Marten 1992; C. Cicero and N. K. Johnson unpubl. data); therefore, it is not surprising that morphological diagnosability is limited in that region because of current or past gene flow.

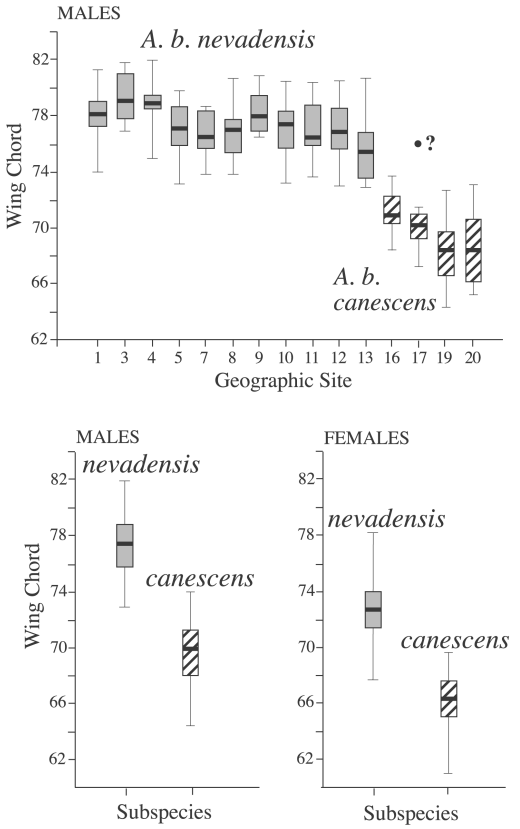

FIG. 2. Box plots of wing-chord variation in *A. b. canescens* and *A. b. nevadensis*, by subspecies (males and females) and across geographic sample areas (males only). For the geographic analysis, only sites with samples with $n \geq 5$ were included; females showed the same general pattern, although sample sizes were smaller. Site numbers correspond to samples areas in the Appendix. Boxes show the median line and the 25th and 75th percentiles; bars show the range of variation. Wing chord of an unusually large male *A. b. canescens* from Jawbone Canyon (MVZ 169353, site 17) is shown with a question mark; unfortunately, this measurement could not be corroborated because the specimen is a skeleton.

Patten and Unitt (2002; their fig. 4) found broad overlap in discriminant function scores (wing plus tail) between *A. b. canescens* and *A. b. nevadensis*, with <75% of individuals correctly classified according to subspecies within each sex. By contrast, we found strong discrimination and essentially no overlap of both males and

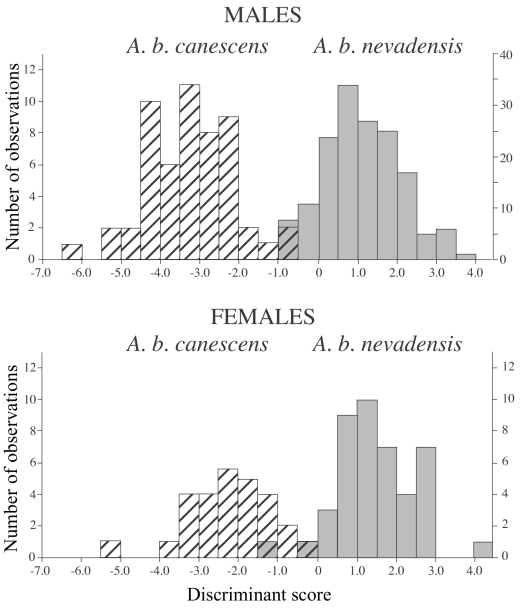

FIG. 3. Histograms of discriminant function scores for males and females of *A. b. canescens* and *A. b. nevadensis*. Number of observations for *A. b. canescens* and *A. b. nevadensis* are given on left and right axes, respectively; note the different scale for male *A. b. nevadensis*. Means and standard deviations of discriminant scores are: male *A. b. canescens*, –3.222 ± 1.095; male *A. b. nevadensis*, 1.101 ± 0.966; female *A. b. canescens*, –2.198 ± 1.053; female *A. b. nevadensis*, 1.431 ± 0.964. The distributions of subspecific scores were significantly different for both males and females (Kolmogorov-Smirnov two-sample test, $P < 0.001$).

females (Fig. 3), with >96% correct classification (Table 2). Individuals incorrectly assigned to subspecies were: males, MVZ 170336 (Coso Junction) and MVZ 169353 (Jawbone Canyon); females, MVZ 166953 (Queen Valley) and MVZ 170321 (Coso Junction). Three are *A. b. canescens* classified as *A. b. nevadensis*, and mitochondrial DNA data (C. Cicero and N. K. Johnson unpubl. data) confirmed that these birds have haplotypes characteristic of *A. b. canescens*; we lack haplotype data for the *A. b. nevadensis* from Queen Valley, but this bird was laying with an incubation patch and thus appears to be an uncharacteristically small female.

When Patton and Unitt (2002) applied their diagnosability index (D_{ij}) to interior subspecies of the Sage Sparrow, they obtained values less than zero for all four sex–subspecies classes. According to their criteria, this indicates nondiagnosability of the two forms. Again, our findings are at odds with these results. To confirm that we were using the index correctly, we recalculated D_{ij} for wing statistics of males measured by Patten and Unitt (2002; their table 2) and obtained identical results ($D_{nc} = –1.0532$, $D_{cn} = –0.9424$). We then used the same method to calculate D_{ij} for our data set and obtained positive values in all cases: males, $D_{nc} = 0.3983$ and $D_{cn} = 1.0045$; females, $D_{nc} = 0.3489$, $D_{cn} = 0.3771$. As stated by Patten and Unitt (2002), $D_{ij} > 0$ indicates that population *i* is diagnosable from population *j* according to the 75%-rule; performing the test in both directions confirms the diagnosability of the two groups.

In our opinion, several interrelated reasons explain Patten and Unitt's (2002) conclusion that

TABLE 2. Actual versus predicted classification of *A. b. canescens* and *A. b. nevadensis* based on stepwise discriminant-function analysis of wing and tail measurements (n = 212 males,[a] 71 females).

Actual group	Predicted: *A. b. canescens*	Predicted: *A. b. nevadensis*	Correct classification (%)
	Males		
A. b. canescens	52	2	96.3
A. b. nevadensis	0	158	100.0
	Females		
A. b. canescens	27	1	96.4
A. b. nevadensis	1	42	97.7

[a] Three specimens were omitted because of missing data (tails not measurable).

A. b. canescens and *A. b. nevadensis* are not diagnosable according to their criteria, despite significant mean size differences. First, the samples on which Patten and Unitt (2002) based their analysis were contaminated by a large proportion (~50%; Fig. 1) of nonbreeding birds, many of which were molting, as well as some specimens clearly labeled as juvenile or immature. Patten and Unitt selected specimens on the basis of the species' biology, and thus included molting individuals because Sage Sparrows reportedly molt on the "breeding" grounds (Martin and Carlson 1998); implicit here is the assumption that molting birds also represent the breeding population. Although Pyle (1997) noted that Sage Sparrows molt on the "summer" grounds, he purposely used this term to account for "post-breeding dispersal away from the breeding grounds but as distinct from those that go all the way to the winter grounds to molt" (P. Pyle pers. comm.). Such movements—which may range from upslope dispersal or other localized movements to migration to molt-stopover sites—are now known for numerous avian species, especially those breeding in areas that become very hot and dry in July–August (P. Pyle pers. comm.), and have been documented for Sage Sparrows (Johnson and Marten 1992). Another important consideration is timing of breeding of different subspecies. Because *A. b. canescens* typically nests earlier than *A. b. nevadensis* (see Fig. 1), nonbreeding individuals of the latter subspecies migrate north through the active nesting range of *A. b. canescens*. Therefore, they could easily be incorporated improperly into putative samples of *A. b. canescens*, especially those nesting in the northern Mojave Desert, where both subspecies winter. These patterns emphasize the importance of relying on objective assessments of reproductive condition (e.g. enlarged gonads) and nesting behavior to provide proof or strong inference of breeding in studies of geographic variation. All nonbreeding movements—whether migratory, irruptive, or dispersal-related—can seriously confound such studies. Even tropical species that are assumed to be sedentary may show periodic large-scale geographic movements (e.g. Winker et al. 1997). Thus, geographic position alone does not define a subspecies, nor is it sufficient to categorize an individual to subspecies. Studies that assume breeding on the basis of nonreproductive criteria, such as time of year, locality, or "summer" molt, use faulty methodology and can obscure real patterns of variation.

Another problem with using nonbreeding specimens in studies of geographic variation is that such material likely contains an uncertain number of missexed birds. Because gonads are small during the nonbreeding season in adult birds and are undeveloped in immatures during their first year, missexed individuals are expected with far greater frequency than specimens from the breeding grounds. Furthermore, this problem is compounded by damage to reproductive organs that routinely results during collecting. The lack of gonad data for many specimens in Patten and Unitt's (2002) data set exacerbates the potential for missexing. In Sage Sparrows, interior subspecies are characterized by a descending mean size series from large male *A. b. nevadensis* to female *A. b. nevadensis*, male *A. b. canescens*, and finally small female *A. b. canescens*. Thus, correctly sexed male *A. b. nevadensis* are completely distinguishable in size from correctly sexed female *A. b. canescens*, whereas definite female *A. b. nevadensis* can overlap in size with definite male *A. b. canescens*. Missexing of such individuals could easily result in identification to the wrong subspecies, especially for specimens from nonbreeding areas, because of potential mixing of different forms.

The only reasonable basis for the discrepancy between our results and those of Patten and Unitt (2002) is the different composition of samples in the two data sets (i.e. breeding vs. nonbreeding, adults vs. immatures) and the likelihood that at least some of their birds were missexed (for reasons given above). To illustrate the problem, we refer to several examples given by Patten and Unitt (2002:32) of "summer specimens from within the range of either subspecies [that] demonstrate the broad overlap in size." The two "breeding males of *A. b. canescens"* from Tulare County, California (wing chords = 76 mm; MVZ 20461–20462) are clearly nonbreeders, judging from the late date (28 July) and the fact that they are molting; both lack gonad data and are probably misidentified, postbreeding *A. b. nevadensis*. Similarly, the small female "*A. b. nevadensis*" from Mono County (wing chord = 68 mm; MVZ 28408) with a date of 9 September is labeled in the collection as *A. b. canescens*, the original identification; this measurement fits with other females of that subspecies, although both taxa could occur there in

the fall—with *A. b. canescens* moving north during postbreeding dispersal. Patten and Unitt (2002:32) also commented on a small male "*A. b. nevadensis*" from Garden Valley, southern Nye County, Nevada (wing chord = 73 mm; MVZ 163098). The specimen label indicated that this bird had small testes (2.5 × 1 mm) and "post-breeding molt," and thus was not breeding. We measured the wing chord as 75.5 mm, which is slightly smaller than two other males collected in early June in Garden Valley (wing chord = 76.6 and 77.7 mm; neither with reproductive data; MVZ 61223–61224). The latter two compare closely with other *A. b. nevadensis* in size. Because this location is at the southern limit of *A. b. nevadensis* in east-central Nevada, the measurements may represent the end of a size cline in that subspecies. Alternatively, MVZ 163098 may be an individual of *A. b. canescens* that moved into the valley after breeding elsewhere. All these questionable identifications should be confirmed with molecular data.

Because a proper understanding of geographic variation is crucial to many studies (e.g. systematics, evolution, taxonomy, biogeography, dispersal, migration), and described subspecies often form the basis for conservation policy decisions (e.g. Zink et al. 2000, Pruett et al. 2001, Chan and Arcese 2002), diagnosis using morphological characters must adhere to the strictest standards. Thus, in summary, we agree with Patten and Unitt (2002) that general standards for the recognition of subspecies should be upgraded so that formally named geographic forms are diagnosable at a strictly defined operational level. We also agree with their statement that "the vast majority of attacks on the subspecies concept have resulted from displeasure with its improper application, not from serious flaws in the concept itself" (Patten and Unitt 2002:26). However, Patten and Unitt's (2002) choice of the Sage Sparrow to illustrate their thesis, and the data set which they used to argue against diagnosability using the 75% rule, unfortunately provides another lesson in improper application. The contamination of their data with a significant proportion of nonbreeding specimens representing unknown nesting localities and the lack of attention to gonad information, both of which increase the likelihood of missexed or misidentified birds, are misleading and cannot support their case for synonymizing *A. b. canescens* under *A. b. nevadensis*. On the contrary, our analysis of specimens with enlarged gonads, collected when they were settled for breeding, unequivocally demonstrate that *A. b. canescens* and *A. b. nevadensis* are diagnosable at a level far above Patten and Unitt's (2002) explicitly defined minimum standard. In fact, these subspecies of Sage Sparrow are among the most distinctive forms in the North American avifauna. This study underscores the importance of proper and stringent systematic methodology, especially sampling based on geographically organized specimens known to be breeding at the time of collection, when characterizing variation and diagnosing subspecies of birds.

Postscript.—For the past decade, we have recorded songs and collected breeding male Sage Sparrows at a series of sites where *A. b. nevadensis* and *A. b. canescens* approach in Owens Valley, eastern California. Preliminary molecular and morphological data (C. Cicero and N. K. Johnson unpubl. data) point to strong differences between the two forms and suggest probable secondary contact in this region. The conclusion that these two forms are fully diagnosable subspecies can no longer be doubted. Instead, the question to be answered now is whether they are biological species.

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Appendix. Breeding specimens of *A. b. nevadensis* (sample areas 1–13) and *A. b. canescens* (sample areas 14–20) measured for wing- and tail-length variation (M = male, $n = 215$; F = female, $n = 71$). Data on specific localities, dates of collection, and reproductive condition are available from the MVZ database (www.elib.berkeley.edu/mvz) or from C. Cicero. MVZ = Museum of Vertebrate Zoology, University of California, Berkeley.

Sample area	*n*	MVZ catalogue numbers
A. b. nevadensis		
(1) Moxee, Yakima County, Washington [a]	8 M, 1 F	122566, 125121, 125732–125733, 130598, 131390–131391, 131393–131394
(2) Prineville, Cook County, Oregon [a]	3 M, 1 F	74034–74037

Appendix. Continued.

Sample area	*n*	MVZ catalogue numbers
(3) Plush, Lake County, Oregon [b]	13 M, 5 F	170233–170250
(4) Northwestern Nevada [a]	14 M, 2 F	8746–8747, 8750–8752, 8756–8763, 8765–8766, 40961
(5) Denio, Humboldt County, Nevada [b]	15 M, 5 F	170339–170358
(6) Central and eastern Nevada [a]	4 M, 0 F	133319, 147880, 163078, 163098
(7) Pioche, Lincoln County, Nevada [b]	14 M, 6 F	167144–167163
(8) Paradise Range, Nye County, Nevada [b]	12 M, 3 F	166933–166947
(9) Wellington, Lyon County, Nevada [a]	9 M, 0 F	163068–163069, 163071–163077
(10) Rattlesnake Flat, Mineral County, Nevada [b]	25 M, 2 F	163080–163091, 168571–168580, 166948–166952
(11) Mono Valley, Mono County, California [b]	14 M, 2 F	165428–165437, 168551–168556
(12) Queen Valley, Mineral County, Nevada [b]	15 M, 8 F	135387, 163092–163097, 165732, 165734–165741, 166953–166959
(13) Benton Valley, Mono County, California [a, b]	13 M, 8 F	85414–85415 [a], 165742–165746 [b], 168557–168570 [b]
A. b. canescens		
(14) Grapevine Mountains, Nye County, Nevada [a]	4 M, 2 F	80386–80390, 163099
(15) Southern Owens Valley and Argus Mountains, Inyo County, California [a]	2 M, 4 F	40618, 80384–80385, 85401, 85404, 85413
(16) Coso Junction, Inyo County, California [b]	8 M, 10 F	170321–170338
(17) Jawbone Canyon, Kern County, California [b]	11 M, 4 F	169351–169354, 170283–170293
(18) Southern San Joaquin Valley, Fresno and Kern counties, California [a]	3 M, 1 F	60094, 60097, 83063, 140471
(19) Caliente Range, San Luis Obispo County, California [b]	16 M, 2 F	169089–169094, 169097–169099, 169342–169350
(20) Panoche Hills, Fresno County, California [b]	12 M, 5 F	169326, 169355–169357, 170270–170282

[a] Specimens from populations not sampled by Johnson and Marten (1992). An additional 66 specimens (42 males, 24 females) from probable breeding areas were measured but were excluded from analysis because of undeveloped gonads or lack of gonad data to verify breeding and sex. In every instance except one (a probable incorrectly sexed bird, MVZ 8760), these specimens corroborated the differences reported here between *A. b. nevadensis* and *A. b. canescens* and between the sexes of each taxon.

[b] Sample areas included in Johnson and Marten (1992). Only measurements of males (n = 153 from this data set) were analyzed in that study.