



USE OF JUVENAL PLUMAGE IN DIAGNOSING SPECIES LIMITS: AN EXAMPLE USING BUNTINGS IN THE GENUS *PLECTROPHENAX*

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ABSTRACT.—Species limits in the genus *Plectrophenax* have been difficult to assess. McKay's Buntings (*Plectrophenax hyperboreus*) are very similar both morphologically and behaviorally to Snow Buntings (*P. nivalis*). However, their breeding ranges are allopatric, and there is limited evidence of gene flow. The juvenal plumage of McKay's Buntings has never been described as different from that of Snow Buntings. Comparison of a series of McKay's Buntings in juvenal plumage with a series of Snow Buntings in juvenal plumage showed clear differences between the two forms. We used color spectrophotometry to quantify the differences between the two taxa in two areas of the body that appeared to be consistently different, the throat and back. The relative magnitude of the difference between McKay's and Snow buntings was greater than homologous differences between two subspecies of Snow Bunting (*P. n. nivalis* and *P. n. townsendi*). Four out of six variables were significantly different between McKay's and Snow buntings, whereas none of the variables were significantly different between the two subspecies of Snow Bunting. Bonferroni corrected *t*-tests of sexual dimorphism and regression of the variables against year of collection showed that these factors were not associated with these differences. Discriminant analysis accurately separated 100% of the specimens into their respective groups. These differences are notable given the evolutionarily conservative nature of juvenal plumage. Our results support continued recognition of McKay's Bunting as a species and reconfirm the use of juvenal plumage to help determine species limits. Received 7 December 2005, accepted 25 July 2006.

Key words: discriminant analysis, juvenal plumage, *Plectrophenax*, reflectance spectrophotometry, species limits.

Uso del Plumaje Juvenil para Diagnosticar los Límites entre Especies: un Ejemplo en el Género *Plectrophenax*

RESUMEN.—Los límites entre especies del género *Plectrophenax* han sido difíciles de establecer. *Plectrophenax hyperboreus* es muy similar en morfología y comportamiento a *P. nivalis*. Sin embargo, sus rangos de cría son alopatricos y la evidencia de flujo genético es limitada. El plumaje juvenil de *P. hyperboreus* nunca ha sido descrito como diferente del de *P. nivalis*. Una comparación de series de especímenes de *P. hyperboreus* y *P. nivalis* en plumaje juvenil mostró claramente que existen diferencias entre las dos formas. Utilizamos espectrofotometría de color para cuantificar las diferencias entre los dos taxones en dos regiones del cuerpo que parecían diferir consistentemente, la garganta y la espalda. La magnitud relativa de la diferencia entre *P. hyperboreus* y *P. nivalis* fue mayor que la de diferencias homólogas observadas entre dos subspecies de *P. nivalis* (*P. n. nivalis* y *P. n. townsendi*). Cuatro

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de seis variables fueron significativamente diferentes entre *P. hyperboreus* y *P. nivalis*, mientras que ninguna de las variables fue significativamente diferente entre las dos subespecies de *P. nivalis*. Pruebas de *t* corregidas mediante Bonferroni para evaluar dimorfismo sexual y análisis de regresión de las variables contra el año de colección, mostraron que esos factores no están asociados con las diferencias. Análisis discriminantes separaron el 100% de los especímenes con exactitud en sus grupos respectivos. Estas diferencias son notables dada la naturaleza evolutivamente conservada del plumaje juvenil. Nuestros resultados apoyan el reconocimiento continuado de *P. hyperboreus* como una especie, y reafirman el uso del plumaje juvenil para ayudar a determinar los límites entre especies.

IN CLOSELY RELATED forms that have distinct but subtly different adult characters, juvenal plumage differences can be a useful indicator of species limits. Phillips and Dickerman (1965) argued that in certain instances juvenal plumage is just as useful as adult plumages for diagnosing taxon limits and evolutionary affinities, especially in taxa that have extremely similar adult plumages. In passerines, consistent juvenal plumage differences in the complete absence of adult differences have been used to separate forms into subspecies (Phillips and Dickerman 1965). The primary reason for this utility is the evolutionarily conservative nature of the juvenal plumage. Juvenal plumage is considered more evolutionarily conservative than adult plumages because it is generally worn for a brief period, and selection at this stage is likely to be strong to maintain cryptic plumage for avoiding predator detection. Also, this plumage is probably not subjected to sexual selection, because birds molt the juvenal plumage well before reaching sexual maturity. Passerines offer clear examples of this evolutionary conservatism, such as among the Turdidae, in which spot-breasted juvenal plumage is essentially ubiquitous, even among species in which adults have no breast-spotting. The evolutionarily conservative nature of juvenal plumage makes it a potentially useful source of characters for determining species limits, especially in groups of birds that are closely related or have subtle adult plumage differences.

Phillips (1969) demonstrated that the juvenal plumages of Russet Nightingale-Thrush (*Catharus occidentalis*) and Ruddy Nightingale-Thrush (*C. frantzii*), two sympatric species that are difficult to distinguish as adults, show distinct differences, enough to support the recognition of these two forms as distinct species. Shortt (1951) noted that juvenal plumages

of the two North American species of *Anthus* are much more distinct than their adult plumages. Some families are characterized by evolutionarily conservative juvenal plumage, and within these families this plumage can have characters that are unique and independent of adult plumages (e.g., Turdidae: Traylor 1972; Emberizidae: Graber 1955, Paynter 1964). This previous work has demonstrated the usefulness of juvenal plumage for determining species limits in closely related forms of passerines. However, these studies analyzed juvenal plumages qualitatively, not quantitatively as we have done here.

Species limits in buntings (*Plectrophenax* spp.) have long been contentious. The American Ornithologists' Union (AOU 1998) recognizes two species within the genus: McKay's Bunting (*P. hyperboreus*) and Snow Bunting (*P. nivalis*). Both species breed at high latitudes. The Snow Bunting is distributed throughout the Holarctic, whereas McKay's Bunting breeds allopatrically from the Snow Bunting on two islands in the Bering Sea, St. Matthew and Hall islands. Hall Island is very small, located a few kilometers to the northwest of St. Matthew Island. McKay's Bunting has been discussed as a strongly demarcated subspecies on the basis of plumage similarity and evidence of hybridization (Sealy 1969; see Paynter and Storer 1970). Other authors have referred to McKay's Bunting as a subspecies of Snow Bunting without explanation (Salomonsen 1931, Vaurie 1959). These treatments of species limits in *Plectrophenax* have never resulted in the submersion of *hyperboreus* into *nivalis* by the AOU (1957, 1983, 1998), but most of these publications stressed the need for further research. Indeed, the adult plumage characteristics of the two taxa enabling diagnosis are subtle except for a single striking difference between adult males: the back is white

in *hyperboreus* and black in *nivalis*. Other than slight and variable differences in the extent of black on the wing, tail, and crown, females are easily separable only in basic plumage; *hyperboreus* are considerably paler. Evidence of hybridization, coupled with recognized plumage differences that are no more pronounced than among many passerine subspecies, leaves open the question of species limits.

While in the field collecting specimens for this question of species limits in these taxa, one of us (K.W.) was struck upon arriving on St. Matthew Island that juvenal-plumaged birds looked paler than *nivalis* populations in the same plumage on the Pribilof Islands and on the Alaska mainland. Knowledge of Phillips's (1969) and Phillips and Dickerman's (1965) insightful uses of juvenal plumage suggested that this unexpected avenue might be useful here as well, and so we began this study.

The original description of McKay's Bunting (Ridgway 1884) was based on two adult males and two adult females in basic plumage, which were collected on the wintering grounds of western Alaska. The juvenal plumage of McKay's Buntings has been marginally discussed in the literature and usually on the basis of little or no information. The first mention came from Ridgway (1901:153). He noted: "*young* very similar to that of *P. n. townsendi*, and not with certainty distinguishable" (original italics). He made no mention of the specimens used for this statement, but in an earlier publication he noted the first juvenal-plumaged specimen collected on Hall Island in 1885 by C. H. Townsend (Ridgway 1886) and mentioned his imminent description of this specimen. But this was apparently never published; he made no other mention of juvenal-plumaged buntings until 1901. Lyon and Montgomerie (1995a, b) purportedly described the juvenal plumage of *hyperboreus*, but they confused a source (cited as Anonymous 1980, but here cited as Arbib 1980). This source (Arbib 1980) did not report on juvenal-plumaged McKay's, but described *juvenile* plumage (which we recognize as first basic), not *juvenal* plumage, as suggested (for definition, see Eisenmann 1965). The specimens used by Arbib (1980) were collected in Nome and are deposited at the University of Alaska Museum (UAM); they are in first basic plumage.

Here, we conducted a thorough analysis of the juvenal plumages of McKay's and Snow

buntings. Our null hypothesis was that there is no difference between the juvenal plumages of McKay's and Snow buntings. We contrasted differences between currently recognized subspecies of Snow Bunting (described based on adult measurements) and the relative differences between McKay's and Snow buntings. We also tested for other factors that could be influencing our analyses (e.g., year specimen was collected and sexual differences). We quantified observed visual differences between the juvenal plumages of these two forms using reflectance spectrophotometry and demonstrated that they can be quantitatively and confidently separated. We also demonstrated the utility of juvenal plumage in providing characters that can be used to define species limits within a group by applying classic concepts (Mayr 1969) on relative differentiation between forms.

METHODS

Fifty juvenal-plumaged bunting specimens were assembled for our spectrophotometric analyses. All 20 McKay's Buntings were from St. Matthew Island, Alaska. The 30 Snow Buntings were from a variety of locations in Alaska and Canada (see Appendix). Individuals were selected for analysis only if they clearly retained the major part of their juvenal plumage (determined by visual comparison with birds in first basic plumage) and possessed unbroken juvenal plumage on the back and throat. Most of the specimens (48) were collected in July and August; just two were collected in early September. Specimens ranged from nestlings with some downy feathers to fledged birds that had just begun their first prebasic molt.

Spectrophotometry has been used to quantify subtle plumage differences in a variety of taxa (e.g., Graves 1997, Winker 1997). We used the Colortron II digital color ruler (Light Source Computer Images, San Rafael, California) to obtain reflectance measurements. This instrument has been demonstrated to quantify subtle plumage differences accurately (Hill 1998, 2000; McGraw and Hill 2001). Colors are measured precisely with a 3 × 3 mm measurement aperture, and the quantified values are then compared objectively using the colorimeter function in the accompanying COLORSHOP software (Light Source Computer Images). The software can output a variety of variables describing

color. We followed Graves (1997) and Winker (1997) in choosing the set that most accurately represented light–dark and color: CIE Lab (Light Source 1996). Three variables were obtained for each measurement: *L* (dark-to-light), *a* (red-to-green), and *b* (blue-to-yellow). The *L* value represents light reflectance on a scale from 0 to 300 (0 = no light reflected, 300 = all light reflected), and the *a* and *b* values are chromaticity coordinates on axes with scales from –300 to 300 (Light Source 1996, Graves 1997).

Visual examination of specimens suggested that the back and throat plumage were the most consistently different between *hyperboreus* and *nivalis*. We saw no evidence of any plumage soiling that might affect the outcome of our study. Light reflectance spectrophotometric analysis was conducted on these two areas. On the back, three areas (upper, middle, and lower) were chosen, and reflectance values averaged to minimize the influence of streaking and to obtain a more robust value per specimen (Graves 1997, Hill 1998). Each specimen was placed against the aperture, measured, and then removed and placed back against the aperture for each successive measurement. Three sequential measurements were made for each area, giving a total of nine measures of the back per specimen. The throat was more uniform than the back, but to incorporate light streaking, six sequential measurements were made, again removing and repositioning the specimen for each measurement. Specimens were chosen at random, regardless of species. All measurements were made on the same day under uniform conditions.

A total of 750 measurements was made on the 50 specimens, resulting in 2,250 values in the data set (3 values per measurement). Measurements were then averaged to give six values per specimen—back: *L*, *a*, and *b*; and throat: *L*, *a*, and *b*. These values were classified into two separate groups representing each species. Levene's test for equality of variances was conducted first to determine the appropriate assumption of variance for *t*-tests (Brown and Forsythe 1974). Independent sample *t*-tests, assuming either equal or unequal variance depending on the results of Levene's test, were conducted for each pair of values using SPSS, version 13.0 (SPSS, Chicago, Illinois) to test for differences between the two species. In all cases using multiple tests, we used Bonferroni correction to maintain an

experiment-wise $\alpha = 0.05$ (Johnson and Wichern 1988, Beal and Khamis 1991).

Snow Bunting specimens were classified into two currently recognized subspecies, determined by the collection locality and the last AOU *Check-list* to treat subspecies (AOU 1957). Because our specimens were all in juvenal plumage and not fully grown, we had to exclude measurements and use geographic range to classify the subspecies, which were described on the basis of adult plumage and morphometric characteristics. We examined specimens of *P. n. nivalis* ($n = 16$) and *P. n. townsendi* ($n = 14$). Levene's test and independent-sample *t*-tests were again conducted to test for differences. To help visualize the relative difference between species and between subspecies, we plotted the three most significant variables between McKay's and Snow buntings and the mean value per form on a 3-D scatterplot for both the species-level and subspecies-level comparisons using STATISTICA, version 5.5 (StatSoft, Tulsa, Oklahoma).

Because sexual dichromatism, foxing, or both, could have biased our results, we tested for these effects. We used Levene's test and independent-sample *t*-tests to test for sexual differences within subspecies and species, after which we combined all of the specimens to test for overall sexual differences. Because specimens of some species are known to change color over time, whether through fading or through foxing (for definitions, see Gabrielson and Lincoln 1951), we examined reflectance variables against the year the specimen was collected using linear regression.

We first tested for significant differences between the two forms, then determined how well the reflectance characters separated these taxa using a discriminant analysis conducted with SPSS. Discriminant analysis is a useful statistical tool for determining the ability of overlapping characters to be used to separate groups (e.g., Mayr and Ashlock 1991, Winker 1997, Figuerola et al. 1999). Analyses were conducted using both equal prior probabilities and probabilities calculated using group size.

RESULTS

When compared visually, the juvenal plumages of McKay's and Snow buntings appeared to have clear "average" differences in the

shades of throat and back plumage (Fig. 1). Light reflectance spectrophotometry revealed overlap in every measured character (Table 1). However, McKay's Buntings were significantly lighter than Snow Buntings on the back and the throat (variable L in Table 1). They were also a significantly different shade (lighter brown) on one axis of color for the throat (variable a in Table 1), and on one axis of color (brown) on the back (variable b in Table 1). We thus rejected our null hypothesis of no differences; the juvenal plumages of McKay's and Snow buntings were significantly different.

To compare the level of differentiation between McKay's and Snow buntings with the level of differentiation between the two subspecies of Snow Bunting sampled, we hypothesized that nominate *nivalis* was not significantly different from *P. n. townsendi*. The subspecies *townsendi* was based primarily on larger morphological measurements (Ridgway 1887). The six variables examined did not differ, though for both the throat and the back a was significantly different between the two subspecies before multiple test corrections (variable a in Table 2). This difference was not consistently evident visually. Here, we could not reject the null hypothesis that these two subspecies are not different. A multivariate plot of three variables showed that the degree of difference between McKay's and Snow buntings was greater than that between the two subspecies of Snow Bunting (Fig. 2).

We also tested for sexual dichromatism within McKay's Buntings on the back and throat. We next tested for sexual dichromatism in Snow Buntings, after which we combined all specimens. We found no sexual dichromatism in any analysis (before or after Bonferroni-correction of α), in throat or back plumage (Table 3). Here, we could not reject the null hypothesis that there are no sexually dichromatic differences in the measured aspects of the juvenal plumage of buntings (*Plectrophenax* spp.).

Regression of the reflectance variables against the year of specimen collection showed that only one of the six variables had a significant relationship with the year the specimen was collected. Variable a on the back was significantly positively correlated with specimen age after Bonferroni-correction of α ($F = 14.598$, $P = 0.0004$; all other values, $F < 3.5000$, $P > 0.0670$). Visual examination of the specimens indicated that slight foxing (browning) may account for this relationship. This character did not differ between McKay's and Snow buntings (Table 1).

Discriminant analysis was able to classify 100% of the specimens into the correct species group using all six variables. The analysis was conducted using prior probabilities computed from group size and assuming all groups equal; both yielded 100% correct classification. This supports the suggestion that McKay's and Snow buntings are consistently different in juvenal



FIG. 1. McKay's Buntings (top row) and Snow Buntings (bottom row) in juvenal plumage. Note that McKay's Buntings are consistently lighter. Snow Buntings are larger because they were collected, on average, several days later than the McKay's Buntings, but both species are in juvenal plumage.

TABLE 1. Statistical summary of reflectance values (*L*, *a*, and *b*) of throat and back of McKay's and Snow buntings in juvenal plumage.

Character	McKay's Buntings (20)			Snow Buntings (30)			<i>t</i> ^a	<i>P</i>
	Mean ± SD	(Minimum to maximum)	Mean ± SD	(Minimum to maximum)				
Throat	<i>L</i>	47.98 ± 4.83 (38.85 to 55.80)	41.87 ± 4.4 (34.48 to 51.61)	-4.63	<0.0005			
	<i>a</i>	-1.46 ± 0.63 (-2.81 to -0.48)	-0.97 ± 0.6 (-2.29 to 0.39)	2.78	0.0077			
	<i>b</i>	6.52 ± 1.63 (2.92 to 8.62)	6.32 ± 2.55 (3.02 to 11.09)	-0.30	0.7623			
Back	<i>L</i>	38.38 ± 3.27 (33.97 to 46.19)	33.38 ± 1.9 (29.09 to 37.60)	-6.17 ^b	<0.0005			
	<i>a</i>	-0.26 ± 0.49 (-1.03 to 0.67)	0.04 ± 0.43 (-0.59 to 0.92)	2.28	0.0269			
	<i>b</i>	7.02 ± 1.34 (5.04 to 9.77)	4.92 ± 1.55 (2.34 to 8.27)	-4.94	<0.0005			

^aThe *t*-value and associated *P*-value from an independent-sample *t*-test. Bonferroni-corrected $\alpha = 0.0083$.

^bThe two species' variances were significantly different based on Levene's test; the *t*-test was performed assuming unequal variance.

TABLE 2. Statistical summary of reflectance values (*L*, *a*, and *b*) of throat and back of Snow Bunting subspecies in juvenal plumage.

Character	<i>P. n. townsendi</i> (14)			<i>P. n. nivalis</i> (16)			<i>t</i> ^a	<i>P</i>
	Mean ± SD	(Minimum to maximum)	Mean ± SD	(Minimum to maximum)				
Throat	<i>L</i>	42.71 ± 4.68 (35.57 to 51.61)	41.14 ± 4.14 (34.48 to 48.66)	0.97	0.3395			
	<i>a</i>	-1.20 ± 0.49 (-2.29 to -0.6)	-0.77 ± 0.63 (-2.06 to 0.39)	-2.06	0.0492			
	<i>b</i>	5.80 ± 2.57 (3.02 to 10.73)	6.78 ± 2.53 (3.67 to 11.09)	-1.06	0.2983			
Back	<i>L</i>	33.97 ± 1.44 (30.83 to 35.85)	32.86 ± 2.13 (29.09 to 37.60)	1.64	0.1128			
	<i>a</i>	-0.14 ± 0.38 (-0.59 to 0.57)	0.20 ± 0.42 (-0.55 to 0.92)	-2.38	0.0243			
	<i>b</i>	4.67 ± 1.55 (2.34 to 7.30)	5.13 ± 1.57 (2.36 to 8.27)	-0.79	0.4337			

^aThe *t*-value and associated *P*-value from an independent-sample *t*-test. Bonferroni-corrected $\alpha = 0.0083$.

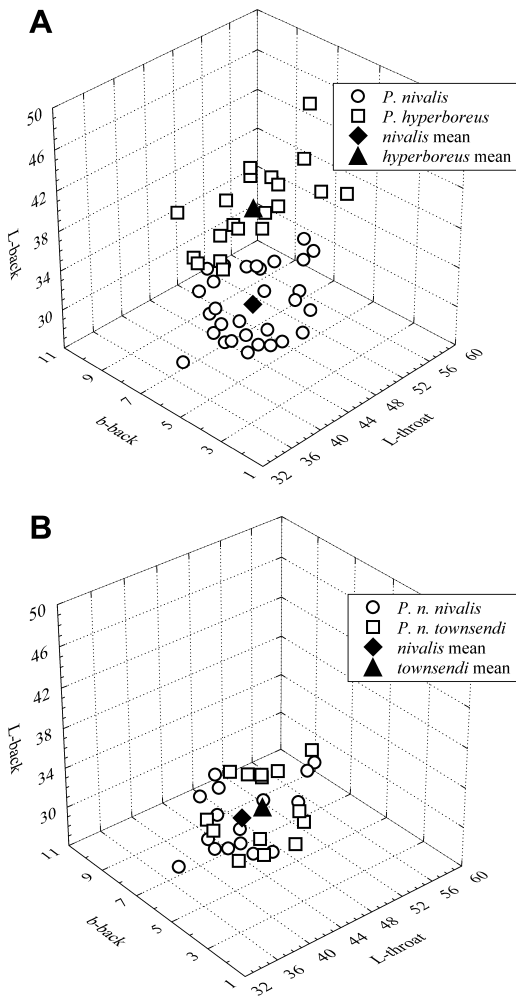


FIG. 2. Two 3-D scatter plots showing the difference between (A) clusters of species and (B) subspecies and relative positions of means within those clusters.

plumage. If they were not different, we would have expected a considerable number to be misclassified.

DISCUSSION

The juvenal plumages of McKay’s and Snow buntings are significantly different, both visually and quantifiably using reflectance spectrophotometry. Visually, on the back, Snow Buntings look dark gray, whereas McKay’s Buntings are light brown–gray. On the throat, this difference appears to be caused by a lack of dark pigment in most McKay’s Buntings, whereas Snow Buntings generally have a dark bib that is gray with buff feather edges.

Two factors could potentially bias our results: sexual dichromatism and plumage changes over time (e.g., foxing). Several species that have sexually dichromatic adult plumages also exhibit such differences in juvenal plumage (Graber 1955). Buntings (*Plectrophenax* spp.) also have sexually dichromatic adult plumages. These differences are obvious in the remiges and rectrices of birds in first basic plumage, but we determined that sex did not bias the analysis of the throat and back plumage. Slight foxing did not bias our results, because each species shared an equal proportion of older specimens; 20% of the specimens of each species were collected >100 years ago. Further, both between the two species and in the subspecific comparison this variable (*a* on the back) was not significant after multiple-test adjustment of α (Tables 1 and 2). Neither sexual differences nor foxing in the throat and back plumage contributed to the differences observed.

Analyses of subspecific differences within the Snow Bunting provided a comparison of the level of differentiation between subspecies and putative species in buntings (*Plectrophenax* spp.).

TABLE 3. Values of *P* of independent-sample *t*-tests for sexual dichromatism in the plumage color of buntings in the genus *Plectrophenax*. Specimens that were unsexed were excluded from analyses.

Species	<i>n</i>	Character					
		Throat			Back		
		<i>L</i>	<i>a</i>	<i>b</i>	<i>L</i>	<i>a</i>	<i>b</i>
<i>P. hyperboreus</i>	27	0.3763	0.1660	0.8602	0.8635	0.1406	0.9209
<i>P. nivalis</i>	17	0.2154	0.5665	0.7316	0.7793	0.3663	0.8619
Combined	44	0.3505	0.2845	0.7214	0.6096	0.1729	0.8257

Bonferroni-corrected $\alpha = 0.0083$.

These analyses showed that one set of differences (McKay's vs. Snow) was strong and consistent, in contrast to homologous, nonsignificant (or at best very slight) differences between the subspecies *nivalis* and *townsendi* (Fig. 2). Mayr (1969) discussed the clustering of forms and the relative positions of the means within those clusters as an accurate way to judge relationships between taxonomic groups. He described differences as being scalar from higher to lower taxonomic rank and recommended comparing differences between ranks as the best way to judge species limits within a group. On the basis of Mayr's (1969) reasoning and our data showing pronounced and consistent differences in several characteristics of juvenal plumage (Fig. 2), we conclude that McKay's Buntings and Snow Buntings are different species.

Juvenal plumage is largely overlooked in systematic studies of closely related species. Because juvenal plumage is worn for such a brief time, and perhaps because collectors do not realize that this plumage is useful in systematic studies, specimens in this plumage tend to be rather rare in collections. Our results suggest that juvenal plumage can be useful for examining species limits, and an effort should be made to fill this collection gap. By analyzing this plumage between subspecies and putative species, we can obtain a relative scale for defining species limits using the associated informative characters. Quantifying these differences using spectrophotometry allows for rigorous statistical analyses of differences and potential biases. Analysis of juvenal plumage in other groups should also be considered useful in determining species limits, especially when adult plumage characters are only slightly different or equivocal between populations.

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APPENDIX. Museum specimens used.

Species and locality	Specimen voucher number ^a
<i>Plectrophenax nivalis</i>	
Aleutian Islands	UAM 7275, 8425–8428, 8430, 13180.
Pribilof Islands	UAM 8478, 18516, 20644, 20645, 20723. USNM 496873, 496874.
Nunivak Island	UAM 11095, 11128, 11129.
Point Barrow	USNM 93114, 93117, 93118.
Canadian Arctic Archipelago	USNM 161877, 161879, 377129, 399703, 399704; 401098, 401100, 423059, 423060, 572745.
<i>Plectrophenax hyperboreus</i>	
St. Matthew Island	UAM 4888, 11094–11096, 17490, 18042, 20646; 20647, 20649–20651. USNM 164885, 164887, 595515, 595524–595526.
Hall Island	UAM 20648; USNM 164889, 164890.

^a Abbreviations: UAM = University of Alaska Museum, USNM = U.S. National Museum.