VARIATION IN THE EXTENT OF THE FIRST PREBASIC WING MOLT OF DARK-EYED JUNCOS

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Abstract.—We studied geographical and sexual variation in the extent of the first prebasic wing molt of Dark-eyed Juncos (*Junco hyemalis*) using data from migrant "Northern" juncos (*J. h. hyemalis; n =* 679) and resident juncos from "Pennsylvania" and "Southern" Appalachian populations (*J. h. carolinensis; n =* 150). In addition, we used skull pneumatization data to assess possible effects of hatching date on molt extent and migration timing of Northern juncos caught at Powdermill Nature Reserve in southwestern Pennsylvania. At a maximum, immature juncos replaced the lesser, median, greater secondary and carpal coverts, proximal and middle feathers of the alula, and proximal three secondaries (i.e., tertials) during their first prebasic wing molt. There were no differences in average molt extent between the Pennsylvania and Southern samples, but juncos in both these samples molted significantly more feathers than Northern juncos. Modal pattern of wing molt in the Northern sample (lesser, median, greater secondary and carpal coverts) was approximately the minimum observed for the Pennsylvania and Southern samples. Within all three samples males accomplished slightly more molt than females, although the difference was not statistically significant for the Southern sample. Juncos in the Northern sample caught during the second half of the spring and fall migration seasons had molted significantly fewer feathers than juncos caught during the first half of those seasons. Because there was little or no relationship between relative hatching date (estimated from skull data) and molt extent and migration timing, we attribute the observed intraseasonal variation to geographical variation within the Northern sample. Within the latitudinal range represented by this sample, juncos from more northerly areas likely molt less and migrate through Powdermill later in both the spring and fall compared to juncos from farther south.

VARIACIONES EN LA EXTENSIÓN DE LA PRIMERA MUDA PREBÁSICA DEL ALA EN *JUNCO HYEMALIS*

Sinopsis.—Estudiamos variaciones geográficas y sexuales en la extensión de la primera muda prebásica del ala en *Junco hyemalis* usando datos de los migrantes "norteños" (*J. h. hyemalis; n =* 679) y de las poblaciones residentes de "Pennsylvania" y del sur de los Apalaches (*J. h. Carolinensis; n =* 150). Además, usamos datos de pneumatización craneal para notar posibles efectos de la fecha de eclosión en la extensión de la muda y del tiempo de la migración de la población migrante tomados en la Reserva Natural de Powdermill en el suroeste de Pennsylvania. A lo máximo, los inmaduros reemplazaron las secundarias menores, medias y superiores y las cubiertas carpales, plumas proximales y medias de la alula, y las tres secundarias proximales (i.e., terciarias) durante su primera muda prebásica del ala. No hubo diferencias en la extensión promedio de la muda entre las muestras de Pennsylvania y del sur, pero hubo en ambas poblaciones aves que mudaron significativamente mas plumas que las aves norteñas. El patrón modal de la muda en la muestra norteña (secundarias menor, mediana y mayor y cubiertas carpales) se aproximó al mínimo observado en las muestras de Pennsylvania y del sur. En las tres muestras los machos mudaron ligeramente más que las

hembras, aunque la diferencia no fué estadísticamente significativa para la muestra del sur. Aves de la población norteña capturados durante la segunda mitad de las estaciones migratorias de primavera y de otoño habían mudado significativamente menos plumas que aves capturadas durante la primera mitad de estas estaciones. Debido a la poca o ninguna relación entre la fecha de eclosión (estimada de datos craneales) y la extensión de la muda o el tiempo de la migración, atribuimos las variaciones intraestacionales a la variación grográfica dentro de la muestra norteña. En la extensión latitudinal representada por esta muestra, aves de las poblaciones más norteñas probablemente mudan menos y migran a través de Powdermill más tarde durante ambas migraciones primaveral y otoñal en comparación con aves de áreas más al sur.

The first prebasic molt of most passerines is incomplete (Dwight 1900, Ginn and Melville 1983, Jenni and Winkler 1994, Mulvihill 1993, Pyle et al. 1987, Stresemann and Stresemann 1966, Svensson 1992). Within species the extent of this molt frequently varies with sex, hatching date, and/or geographical origin. Although this variation has been well documented for many European passerines (Jenni and Winkler 1994), detailed quantitative studies of individual variation in the extent of this molt currently are limited to a handful of North American species (Pyle 1995). This is unfortunate because knowledge of intraspecific variation in the pattern and extent of the first prebasic molt facilitates recognition of adult and immature age classes (Jenni and Winkler 1994, Mulvihill 1993, Pyle 1995), enabling researchers to account for an important variable in many studies of migration, population dynamics, reproductive and foraging ecology, and morphology (Mulvihill 1993).

The purpose of our study was to describe individual variation in the first prebasic molt of feathers in the upper alar (wing) tract of the Dark-eyed Junco (*Junco hyemalis*). Data were analyzed for possible differences in the extent of this molt related to sex, geographic origin, and hatching date of juncos in our sample.

<div align="center">MATERIALS AND METHODS</div>

We recorded the pattern and extent of the first prebasic molt of the major feathers (Fig. 1) of the upper alar tract of 829 immature Dark-eyed Juncos, mostly live birds ($n = 785$) trapped for banding, but also study skins in the collections of Carnegie Museum of Natural History (CMNH; $n = 17$) and U.S. National Museum (USNM; $n = 27$). The following comprised our geographic subsamples: (1) 679 individuals of the migrant northern subspecies, *J. h. hyemalis*, caught during the course of year-round banding operations from 1986–1988 at the field research station of CMNH (Powdermill Nature Reserve [PNR]) in the mountains of southwestern Pennsylvania (for details of the PNR banding program, see Leberman and Wood 1983); (2) 35 live birds banded in 1989 and 27 study skins of southern *J. h. carolinensis* from the mountains of Virginia, Tennessee, and North Carolina; and (3) 71 live birds banded from 1983–1989 and 17 study skins from a breeding population in the mountains of southwestern Pennsylvania. Juncos from this population also are ascribable to *carolinensis* (Mulvihill and Chandler 1991, Mulvihill 1992), which differs from
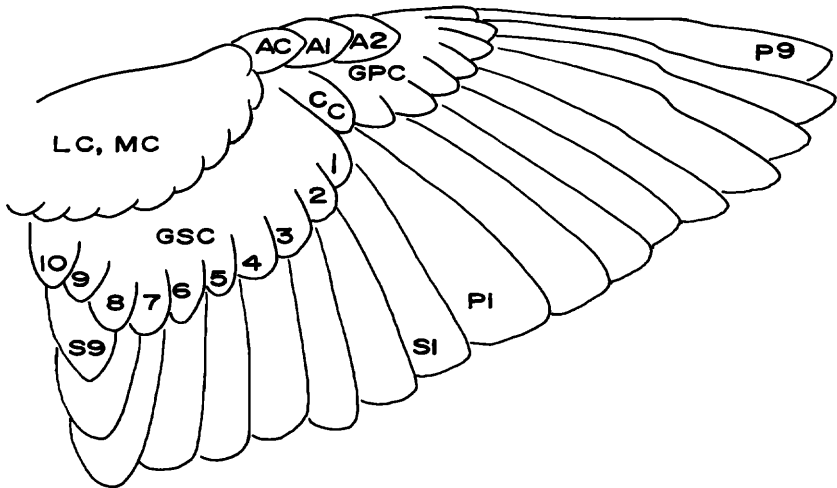
FIGURE 1.   Major feathers and feather groups of the upper alar tract of Dark-eyed Juncos:
LC (lesser coverts); MC (median coverts); AC (alula covert); A1 (middle alula feather);
A2 (distal alula feather); CC (carpal covert); GPC (greater primary coverts); GSC
(greater secondary coverts); P1–P9 (primaries one through nine); S1–S9 (secondaries
one through nine; S7–S9 are the "tertials").

nominate *hyemalis* in size, plumage color, and bill coloration (Miller
1941). These three groups were identified as Northern, Southern, and
Pennsylvania samples, respectively. Both the Southern and Pennsylvania
samples came from populations that are largely sedentary (Hostetter 1961,
Mulvihill and Chandler 1991, Rabenold and Rabenold 1985).

One problem in conducting a study such as this is the difficulty of dis-
tinguishing between retained juvenal and molted first basic feathers.
These two feather generations are similar in appearance in many small
emberizids, including juncos (Mulvihill 1993). However, under good light-
ing conditions differences between these feather generations in juncos
are discernable, making possible the accurate identification of immature
birds (hatching year [HY] or second year [SY] birds in banding terminol-
ogy) beyond the completion of skull pneumatization, until the latter
stages of the second (i.e., definitive) prebasic molt. First basic feathers
were recognized (in approximate order of importance) by color, luster,
wear, and size (see Mulvihill 1993). Retained juvenal feathers were always
browner (with narrow tan edging), less shiny, and noticeably more worn
than comparable molted feathers, which were usually lustrous dark gray,
with broad light gray edges. In addition, juvenal feathers were often
smaller than their first basic counterparts. They were particularly easy to
distinguish when a given feather group (e.g., greater secondary coverts,
alula, or tertials) was composed of both juvenal and recently grown first
basic feathers. Rarely, adult juncos may retain some feathers following

their usually complete prebasic molt (Yunick 1976). Four adult females caught during our study showed asymmetrical retention of one or more alular feathers, one or two greater primary coverts, and up to two secondaries. Such birds cannot be confused with immatures, however, because the retained, worn, brownish feathers are isolated in an otherwise entirely fresh plumage.

Juncos in our study were sexed by the presence in breeding (SY) individuals of a brood patch (female) or cloacal protuberance (male), or by a combination of wing length and plumage characters (summarized in Ketterson and Nolan 1976). Birds that could not be sexed by these criteria ($n = 65$; <10% of the total sample) were not included in the study.

Molt pattern and extent was determined for both wings of juncos in the sample by recording the major feathers of the upper alar tract that had molted. Individuals with asymmetrical molt were included in the sample if, after the exclusion of feathers that clearly were replaced adventitiously (i.e., feathers never observed to have been molted symmetrically by any junco in the sample), there was a difference of no more than two feathers between wings. The molt of the right wing of these birds ($n = 240$) was arbitrarily chosen for all analyses; for the majority of these (70%) the extent of molt differed by only one feather between wings.

Northern, Pennsylvania, and Southern samples were included in analyses of sexual and geographic variation. Statistical comparisons were made using Mann-Whitney *U*-tests; differences were considered to be significant at the $P \leq 0.05$ table-wide α-level (sequential Bonfrroni adjustment; Rice 1989).

Seasonal analyses were conducted only for the Northern sample, because comparable data were not available for the other samples. For these analyses, the migration seasons were defined as follows: spring, 5 March–5 May; fall, 10 October–15 December. The end of the spring and the beginning of the fall season represent the latest and earliest dates of capture, respectively, of immature juncos during the years of this study, prior to and following the species' summer-long absence at PNR. The onset of the spring migration and the end of the fall flight approximate the dates when the first and last non-wintering juncos are encountered at PNR (i.e., juncos that were neither banded nor recaptured during the intervening winter season). Therefore, with few exceptions juncos in the Northern sample were passing migrants, not local wintering birds. For intraseasonal analyses, spring and fall samples were divided chronologically into "Early" and "Late" half-seasons: these were calculated to be about 20 d for males and 25 d for females in the spring; fall half-seasons were about 30 d for both sexes.

We assessed the effects of differences in hatching date on seasonal variation in molt extent by analyzing the molt of fall migrant Northern juncos in relation to both capture date and skull pneumatization stage, which was scored on an scale of 1–6 (>80% unpneumatized to fully pneumatized). Because extent of skull pneumatization is largely a

function of a bird's age (Nero 1951, Winkler 1979), it provided information on relative hatching dates for juncos in our sample (cf. Jenni and Winkler 1994). Data from recaptures suggested that the interval between successive skull scores was about 35 d in juncos. Because the fall half-seasons were <35 d, we assumed that juncos at skull stage $n + 1$ were older than juncos at skull stage n within the Early and Late fall samples. Similarly, we assumed that birds caught at skull stage n in the Early half of the season were, on average, about the same age as birds caught at skull stage $n + 1$ in the Late half of the season. Seasonal differences in extent of molt were assessed using G-tests of independence (Wilkinson 1990); α-level was the same as for Mann-Whitney U-tests. There were no between-year differences in molt extent of male and female juncos in spring and fall; therefore data from 1986–1988 were combined for analyses.

<div align="center">RESULTS</div>

Extent of the molt.—At a minimum, the first prebasic molt in Dark-eyed Juncos replaced the lesser and median coverts (and not necessarily all of these) of the upper alar tract. This pattern was recorded for three female Northern juncos prior to the current study (no junco failed to molt at least two greater secondary coverts during this study; Fig. 2); in these individuals some retained body plumage was noted as well, including upper tail coverts and feathers in the scapular and/or capital tracts (none was actively molting). The maximum extent of molt observed during this study included the following 16 feathers in addition to all of the lesser and median coverts: all ten greater secondary coverts, the carpal covert, the alula covert, the middle feather of the alula, and all three tertials (Fig. 2). A molt this extensive was recorded for just three juncos during the study (one male each from the Northern, Pennsylvania, and Southern samples) and for one Northern female caught after the study. A Northern male caught after the study had additionally molted the large, distal feather of the alula on both wings. There was no evidence of normal (i.e., symmetrical) first prebasic molt of the primaries, greater primary coverts, secondaries (other than the tertials), or, with the single exception noted above, the distal feather of the alula.

The sequence of the molt.—Although all birds in this study had completed or nearly completed the first prebasic molt, an approximate sequence of feather replacement during this molt can be inferred from the following molt correlations. Of those birds that molted ≤5 greater secondary coverts ($n = 15$), only 20% ($n = 3$) replaced the carpal covert.; of those birds that molted >5 greater secondary coverts ($n = 814$), 92% ($n = 749$) replaced the carpal covert. Of those birds that molted one or more tertials ($n = 320$), all replaced the carpal covert, and 98% ($n = 313$) replaced all ten greater secondary coverts; of those birds that molted just one tertial ($n = 211$), 91% ($n = 191$) replaced the proximal tertial (secondary 9); of those birds that molted two tertials ($n = 85$), 92% ($n = 78$)

Minimum wing molt
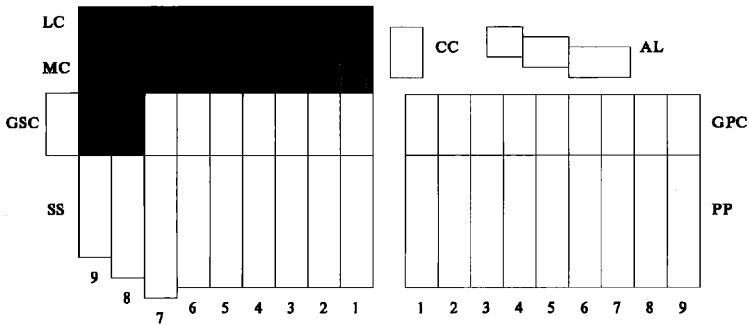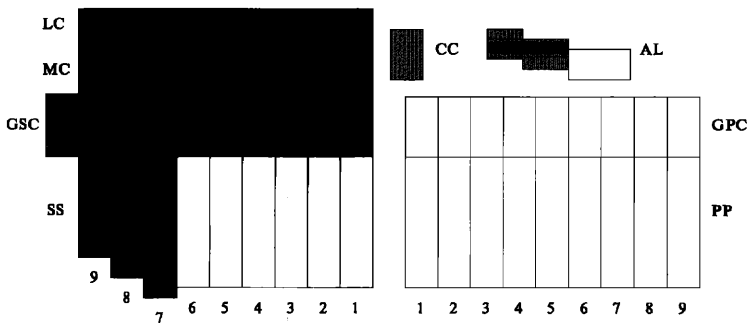

Maximum wing molt

FIGURE 2. Minimum and maximum molt (shaded areas) observed during the course of this study. LC = lesser coverts; MC = median coverts; CC = carpal covert; AL = alula; GSC = greater secondary coverts; GPC = greater primary coverts; SS = secondaries; PP = primaries.

replaced the inner two (secondaries 8 and 9). Of those birds that molted at least one alular feather ($n = 150$), 99% ($n = 149$) replaced all ten greater secondary coverts and the carpal covert; of those birds that molted only one alular feather ($n = 144$), 21% ($n = 30$) replaced no tertials, 37% ($n = 54$) replaced one tertial, and 42% ($n = 60$) replaced two or more tertials. Of those birds that molted one tertial ($n = 211$), 28% ($n = 60$) replaced at least one alular feather; of those birds that molted two or more tertials ($n = 109$), 59% ($n = 64$) replaced at least one alular feather. Lastly, of those birds that molted two alular feathers ($n = 6$), 16.7% ($n = 1$) replaced no tertials, 33.3% ($n = 2$) replaced one tertial, and 50% ($n = 3$) replaced all three tertials.

Based on these correlative patterns, we propose the following as a typical sequence of feather replacement during the first prebasic wing molt in Dark-eyed Juncos: lesser and median coverts, proximal greater secondary coverts (10 through 5), carpal covert, distal greater secondary coverts(4 through 1), proximal tertial (secondary 9), alula covert, middle tertial (secondary 8), distal tertial (secondary 7), and middle alula.

Geographic and sexual variation.—The number of wing feathers replaced by juncos during the first prebasic molt was variable within and among geographic regions (Fig. 3). In both sexes of Northern juncos, about 50% of the birds molted 11 upper alar feathers additional to the lesser and median coverts (ten greater secondary coverts and the carpal covert) (Fig. 3). The modal pattern for Northern juncos, however, was similar to the minimum for Pennsylvania and Southern juncos of either sex. The maximum extent of molt was the same across samples, while the minimum molt, as well as the average number of molted secondary coverts, alula feathers, and tertials differed markedly for the Northern sample compared to the Pennsylvania and Southern samples (Table 1). Both sexes of the Northern sample molted significantly fewer total feathers than their counterparts in the Pennsylvania and Southern samples; there were no differences between Pennsylvania and Southern juncos (Table 1). Within each geographic sample, males accomplished more molt than females, although not significantly so the Southern sample ($U = 360.0$, $P = 0.113$). Differences in the number of molted tertials contributed most to both the sexual and geographic variation in our sample of juncos (Table 1, Fig. 4).

Within-season variation.—Both male and female Northern juncos caught in the Late half of the spring and fall seasons molted significantly fewer feathers than their Early season counterparts (Table 2). By separating Early and Late fall samples according to skull stage we were able to assess the possible effects of hatching date, both on migration timing and molt extent in juncos. Comparison of the number of individuals at skull stage n in the Early fall samples and skull stage $n + 1$ in the Late samples provided little or no evidence that later hatched juncos in fact migrate later in the fall. The number of birds with lower and higher skull scores did not show large increases and decreases, respectively, between the Early and Late samples, as would be expected if later hatched birds migrated through PNR later in the season (Table 3). Furthermore, within each half-season there was no consistent trend for more extensive molt across skull stages, as would be expected if earlier hatched juncos had a more extensive molt than late-hatched juncos. For juncos of similar age, however, there was a consistent pattern of less extensive molt by juncos caught later in the season (compare average molt extent in Early skull stage n with Late skull stage $n + 1$; Table 3), in agreement with results obtained when differences in age were not taken into account (Table 2). There were no significant differences in molt extent between the fall and spring samples (Table 2).

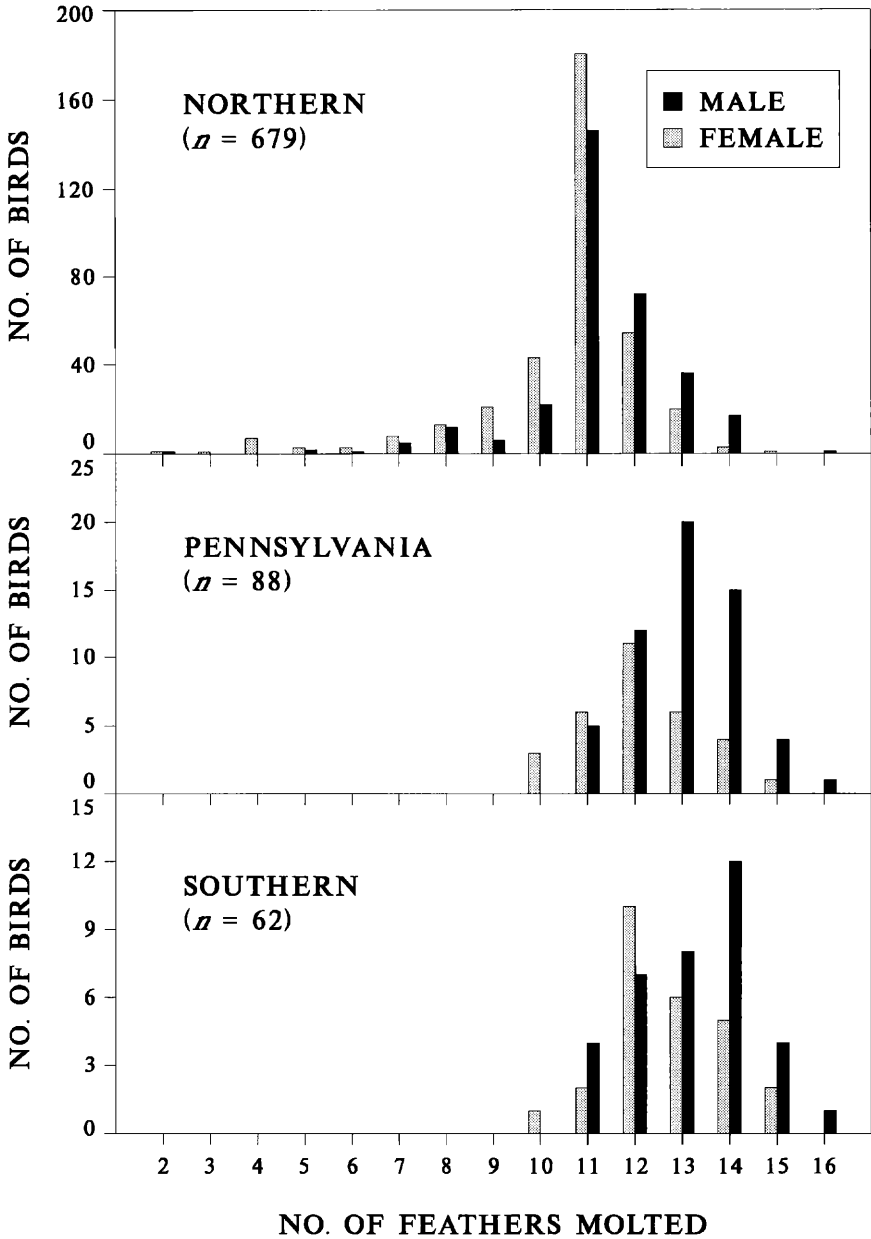R. S. Mulvihill and R. L. Winstead

FIGURE 3. Frequency distribution showing the extent of the first prebasic molt of upper wing feathers for male and female juncos from three geographic areas.

TABLE 1. Geographic and sexual variation in the extent of the first prebasic wing molt of the Dark-eyed Junco.

Sample		n	Mean no. feathers molted within feather-groups[a]				Total extent of molt[b]			Between-group comparisons[c]		
			GSC	CC	TT	AL	Mean	SD	Range			
Northern												
males	[NM]	321	9.7	0.9	0.5	0.2	11.3	1.6	2–16	NF***	PM***	SM***
females	[NF]	358	9.5	0.8	0.2	0.1	10.6	1.8	2–15	—	PF***	SF***
Pennsylvania												
males	[PM]	57	10.0	1.0	1.6	0.5	13.1	1.1	11–16	—	PF**	SM[ns]
females	[PF]	31	9.9	0.9	0.8	0.6	12.2	1.3	10–15	—	—	SF[ns]
Southern												
males	[SM]	36	10.0	1.0	1.7	0.5	13.2	1.3	11–16	—	—	SF[ns]
females	[SF]	26	10.0	1.0	1.4	0.3	12.7	1.2	10–15	—	—	—

[a] GSC = greater secondary coverts (max. 10); CC = carpal covert (max. 1); TT = tertials (max. 3); AL = alula (max. 3).
[b] max. 16.
[c] two-tailed Mann-Whitney U-tests: *** = $P < 0.001$, ** = $P < 0.01$, ns = not significant.

Northern Juncos (n = 679)
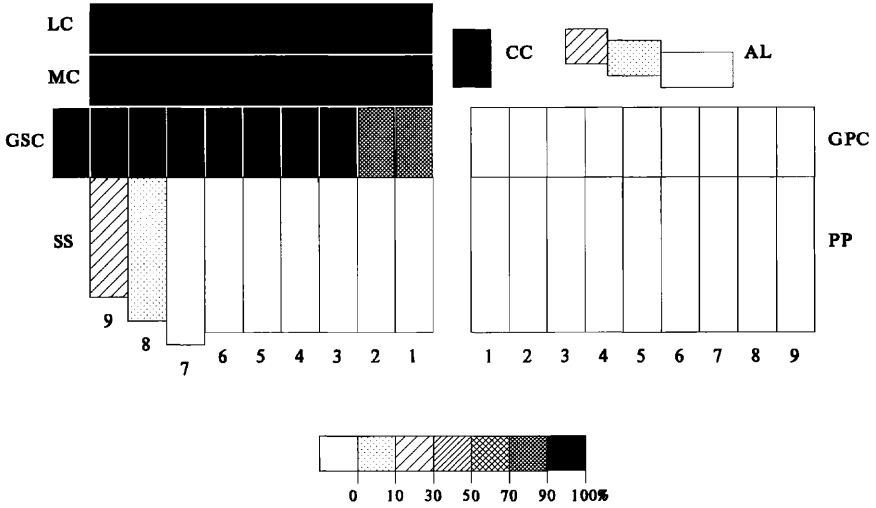
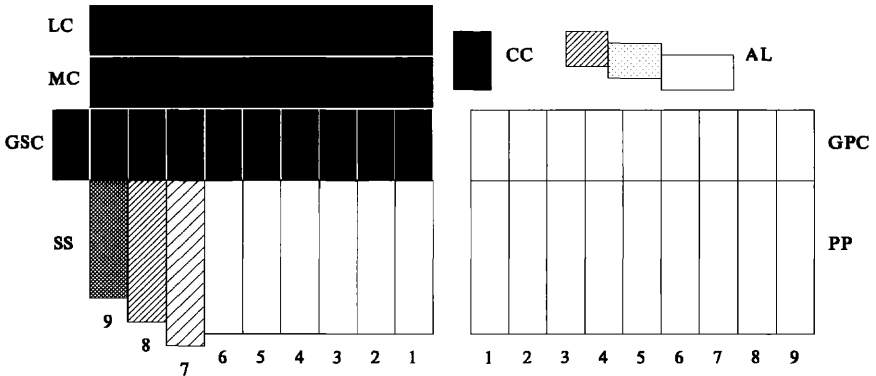## Pennsylvania & Southern Juncos (n = 150)

FIGURE 4.   Geographic variation in the percentage of juncos replacing various feathers dur-
ing the first prebasic molt. LC = lesser coverts; MC = median coverts; CC = carpal
covert; AL = alula; GSC = greater secondary coverts; GPC = greater primary coverts;
SS = secondaries; PP = primaries.

TABLE 2.   Inter- and intraseasonal comparisons of the extent of the first prebasic molt (number of feathers molted out of a possible 16) for female and male Northern juncos. Statistical comparisons are two-tailed Mann-Whitney *U*-tests.

Season	Females			Males		
	Mean	SD	*n*	Mean	SD	*n*
Spring[a]	10.8	1.7	157	11.5	1.4	117
Early[b]	11.0	1.6	90	11.8	1.4	54
Late[b]	10.5	1.9	67	11.3	1.3	63
Fall[a]	10.4	1.9	197	11.1	1.6	200
Early[c]	11.0	1.3	84	11.6	1.4	94
Late[c]	10.0	2.1	113	10.7	1.8	106

[a] females: $U = 16502.0$, $P = 0.176$; males: $U = 12977.0$, $P = 0.086$
[b] females: $U = 3643.0$, $P = 0.016$; males: $U = 2039.5$, $P = 0.047$
[c] females: $U = 5706.5$, $P = 0.004$; males: $U = 6635.5$, $P = 0.000$

DISCUSSION

Dwight (1900) described the postjuvenal (first prebasic) molt of Dark-eyed Juncos as including "the body plumage and wing coverts, but not the rest of the wings or tail." Yunick (1981) observed that a small percentage of immature juncos may replace 1–3 tertials. From Pyle et al. (1987) it can be inferred that from 1–5 distal greater secondary coverts may be retained in the first basic plumage. Based on the present study, the incomplete first prebasic molt of the Dark-eyed Junco typically replaces all of the body feathers, the lesser, median, greater secondary and carpal coverts; less often the alula covert and the proximal two tertials; rarely the middle alula feather and the distal tertial (Fig. 4). The pattern of the first prebasic molt in juncos is similar to that observed for several other North American and European emberizine finches (e.g., *Melospiza lincolnii, Spizella passerina, S. arborea, Zonotrichia albicollis,* Mulvihill unpubl. data; *Emberiza citrinella, E. cia,* and *E. schoeniclus,* Jenni and Winkler 1994). The within and between wing-feather tract sequence of feather replacement during the first prebasic molt in Dark-eyed Juncos inferred from our molt correlations is similar to that observed in many European passerines (Jenni and Winkler 1994:32ff) and to several North American emberizids examined while in active molt (Mulvihill, unpubl. data). Typically, the juvenal feathers replaced during an incomplete first prebasic molt are those that primarily have an insulatory, rather than aerodynamic, function; furthermore, they are the feathers most exposed to physical abrasion and most likely to become worn if they were retained until the definitive prebasic molt (Dwight 1900, Miller 1928).

It may be significant that in juncos the juvenal distal feather of the alula is virtually always retained until the definitive prebasic molt, despite its exposed position on the wing. In fact, this feather is commonly included in the partial molt of only a very few passerines (e.g., two out of 58 spe-

TABLE 3. Comparison of molt (mean number feathers replaced out of 16 possible) and sample sizes across skull stages between Early and Late halves of the fall migration season for Northern juncos. The distribution of birds among skull stages in the Late half of the season was compared to three null distributions, each of which described an expected average incremental increase of one skull stage between the Early and Late periods (see Methods). Differences were assessed with likelihood ratio chi-square statistics.

	Skull stage	Early		Late		Null distributions[a]		
		Mean	n	Mean	n	A	B	C
Females	1	10.8	15	10.5	6	0	3	5
	2	11.1	28	9.4	22	15	15	14
	3	10.8	30	10.0	36	28	25	24
	4	11.4	10	10.3	38	30	27	23
	5	11.0	1	10.3	11	10	12	13
	6	—	0	—	0	1	2	5
Probabilities						0.120	0.447	0.055
Males	1	10.8	18	8.5	10	0	3	6
	2	11.8	34	10.6	20	18	18	17
	3	11.5	31	11.1	40	34	30	27
	4	11.8	11	10.9	28	31	29	26
	5	—	0	10.9	8	11	12	15
	6	—	0	—	0	0	2	3
Probabilities						0.006	0.136	0.092

[a] Distributions based on null hypotheses that the number of birds in Late skull stage "n" equals: A) the number in Early skull stage $n - 1$; B) 1/6 the number in Early skull stages n and $n - 2$ and 2/3 of the number in Early stage $n - 1$; or C) 1/3 each of the number of birds in Early skull stage n, $n - 1$, and $n - 2$.

cies of European passerines studied by Jenni and Winkler 1994). Retention by juveniles of the large, distal feather of the alula may be due in part to its putative aerodynamic function as a wing slot, providing additional lift at slow flight speeds and facilitating take-offs (Kokshaysky 1973, Savile 1957). In juncos, the distal feather of the alula actually is slightly longer (by about 0.5 mm) in juveniles than adults (Mulvihill, unpubl. data), despite the fact that overall wing length is over 1 mm shorter on average in the immatures (Mulvihill and Chandler 1990). It is possible that a larger alula to wing length ratio gives an aerodynamic advantage to immature juncos (and probably immatures of other species as well; cf. Alatalo et al. 1984) sufficient to make replacement of the distal feather of the alula during the first prebasic molt disadvantageous. Additional lift provided by the longer juvenal alula may be especially important for immature juncos during the migration and winter seasons, because fat-related increases in body mass and wing loading are significantly greater in this age class than in adults (Chandler and Mulvihill 1992).

Geographic and seasonal variation.—Southern populations of juncos (represented by the Pennsylvania and Southern samples in this study) molted significantly more feathers than birds in the Northern sample.

Such geographical differences are common in passerines (e.g., Baillie and Swann 1980; Dwight 1900; Miller 1928, 1933; Pitelka 1945), and often are attributed to differences among populations in the onset of nesting (hence, hatching date differences) and or the date when molt necessarily ceases due to energetic demands associated with migration or survival in a cold environment (e.g., Hereward 1979, Mewaldt and King 1978, Miller 1933, Stangel 1985, Stresemann and Stresemann 1966).

Within a population earlier-hatched birds typically have a longer potential molt period and consequently a more extensive molt than later hatched birds (Dhondt 1973, Ligon and White 1974, Michener and Michener 1940, Scott 1967, Wiseman 1977). The effect of hatching date on molt extent, however, may be reduced or even eliminated for populations in which later-hatched birds both initiate molt sooner after hatching and molt more intensely and rapidly than their earlier hatched counterparts (e.g., Dolnik and Blyumenthal 1967, Dolnik and Gavrilov 1980, Michener and Michener 1940, Newton 1966). Given the absence of significant differences in molt extent between juncos at different skull pneumatization stages during each half of the fall migration (Table 4), there would appear to be factors promoting such molt synchronization in Northern juncos. This would also explain why molt extent for Northern juncos in this study was unimodal (Fig. 3), in spite of the fact that *J. h. hyemalis* occupies a wide latitudinal range and is double-brooded throughout that range (Bent 1968).

Within the Northern sample, male and female juncos caught during the second half of both migration seasons had molted significantly fewer feathers. This pattern of intraseasonal variation has been found in fall but not in spring samples of several migrant European passerines (Jenni and Winkler 1994:41). Such differences in the fall frequently are attributed to less extensive molt and later migration of late-hatched birds, birds from more northerly populations, or some combination of the two (Jenni and Winkler 1994:42). Because we observed no significant effects of hatching date on molt extent or migration timing, however, we tentatively attribute the pattern of reduced molt in Northern juncos caught during the second half of both the spring and fall migration seasons at PNR to less extensive molt and later migration by juncos from more northerly populations *within* the range represented by our Northern sample. Because the nominate race of the Dark-eyed Junco exhibits little morphological variation across most of its range (Miller 1941), we could not test the hypothesis of a relationship between molt extent, migration timing, and geographical origin using an independent morphological trait (e.g., wing length; Jenni and Winkler 1994:42).

Differences between the sexes in extent of molt.—A significantly more extensive first prebasic molt has been observed in males of several European passerines (Jenni and Winkler 1994:41), but this variation has been documented for only a few North American species (e.g., *Aphelocoma* spp.; Pitelka 1945). The magnitude of the sex differences in molt extent in jun-

cos (Table 1) is similar to that reported in thirteen species of European passerines (Jenni and Winkler 1994:41). Possible factors contributing to a slightly more extensive molt by male juncos include differences between the sexes in migratory behavior, social dominance interactions, and wintering environment.

The sex differences in molt observed for Northern juncos in this study are consistent with an hypothesis that migratory behavior affects the extent of the first prebasic molt by reducing the time available for molting, because females migrate about ten days earlier than males on average (Chandler and Mulvihil 1990, Mulvihill and Chandler 1991). However, because more extensive molt by males has been observed in several nonmigratory passerines (e.g., Dhondt 1973, Newton 1966, Pitelka 1945), as well as in the largely sedentary Pennsylvania juncos in this study, other factors also may contribute to this variation.

Jenni and Winkler (1994:41) proposed that for species in which the wing plumage of males is more brightly colored or conspicuously patterned, a sex difference in molt extent might be related to the importance of status signaling for males in social contests during winter and the succeeding nesting season. Although the wing plumage of male juncos is neither bright nor strongly patterned, retained brownish juvenal wing coverts and tertials are more conspicuous in the males than females (Mulvihill, pers. obs.). Because brown plumage may be associated with status signaling in juncos (Ketterson 1979a, 1979b), at least within their cohort, males that have replaced more juvenal plumage may be more likely to enjoy benefits associated with social dominance including increased access to food resources, decreased exposure to predation, and greater success in acquiring and defending a territory in the following breeding season (Rabenold and Rabenold 1985).

Differences in the levels of nutrient and energy stress also have been suggested as a possible cause for sex differences in the extent of molt (Jenni and Winkler 1994:41). Male juncos are socially dominant to females in winter (Ketterson 1979b), but whether or not male dominance in any way limits the access of female juncos to resources necessary for achieving maximum rates of feather synthesis during the course of their first prebasic molt is not known.

Because male juncos differentially winter in areas characterized by more severe climatic conditions than females (more northerly latitudes in *hyemalis*; higher elevations in *carolinensis*) (Ketterson and Nolan 1983, Rabenold and Rabenold 1985), a more extensive molt by this sex may be related to better insulation provided by the additional nonjuvenal wing feathers. In juncos, a difference between the sexes in the inclusion of tertials in the first prebasic molt accounts for most of the intersexual variation in all three samples. When a bird is at rest, with its wings folded over its back, the tertials, sometimes termed "shield feathers" (Svensson 1992), may have an important insulative function as a barrier against heat loss through the lateral apteria.

Finally, at least in the case of Northern juncos, sex differences in molt may simply reflect the within-sample geographical variation discussed above. Because Northern juncos exhibit differential migration, with many more immature females than males wintering to the south of PNR (Ketterson and Nolan 1985), the proportion of females passing through PNR from more northerly areas within the extensive geographic region represented by our "Northern" sample (i.e., from populations possibly characterized by less extensive molt) probably is greater than for males (Ketterson and Nolan 1982).

ACKNOWLEDGMENTS

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FIFTH INTERNATIONAL CONGRESS ON THE EFFECTS OF OIL ON WILDLIFE

The Fifth International Congress on the Effects of Oil on Wildlife will be held 3–6 Nov. 1997 in Monterey, California. It is hosted by the Oiled Wildlife Care Network, a joint program of the California Department of Fish and Game, Office of Oil Spill Prevention and Response and the University of California, Davis Wildlife Health Center. For information contact: Nancy Ottum, Oiled Wildlife Care Network, ITEH; University of California; Davis, California 95616; (916) 752-3809; 752-3318 (FAX); e-mail:ndottum@ucdavis.edu.

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