

SEASONAL POPULATION DYNAMICS OF DARK-EYED JUNCOS FROM WESTERN OREGON

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Abstract.—Dark-eyed Juncos (*Junco hyemalis*) were captured in summer and winter in 1987–1990 near Corvallis, Benton Co., Oregon, and U.S. Fish and Wildlife Bird Banding Laboratory records (BBL) for the Willamette Valley of western Oregon were examined to assess seasonal population dynamics of these birds. Banding recoveries indicate that at least 2.2% of these juncos breed on or near wintering grounds. Winter juncos of both sexes had significantly longer wings than summer juncos and winter males had significantly longer tarsi, suggesting some immigration of larger birds or, conversely, some emigration of smaller birds. These data indicate that breeding and wintering populations of Willamette Valley juncos show a degree of overlap characteristic of a pattern of partial migration. The male/female sex ratio was 2.8:1 in winter and consisted of a significantly greater proportion of males than in the breeding population. The percentage of females in winter populations of these juncos, from the relatively mild winter climate of western Oregon, was higher than predicted values for this latitude derived from eastern junco populations. This is consistent with predictions of the body size hypothesis for skewed winter sex distributions. Thus, the variable effects of winter climate on survival relative to body size are probably an important determinant of winter distribution in Dark-eyed Juncos.

DINÁMICA POBLACIONAL ESTACIONAL DE INDIVIDUOS DE JUNCO HYEMALIS DEL OESTE DE OREGÓN

Sinopsis.—De 1987–1990 se capturaron individuos de *Junco hyemalis* durante el invierno y el verano en una localidad cerca de Corvallis, Benton Co., Oregon, y se examinaron los registros del Laboratorio de Anillamiento del Departamento de Pesca y Vida Silvestre de los Estados Unidos correspondientes al Valle de Willamette del oeste de Oregón para evaluar la dinámica poblacional estacional de estas aves. Al recobro de anillas indica que al menos 2.2% de los juncos se reproducen en o muy cerca de los lugares en donde pasan el invierno. Durante el invierno juncos de ambos sexos tienen las alas significativamente más largas que los individuos en el verano, y en el invierno los machos tienen tarsos significativamente más largos, lo que sugiere ya sea inmigración de individuos de mayor tamaño, o sea emigración de individuos más pequeños. Los datos indican que las poblaciones reproductivas e invernales del Valle de Willamette, muestran un cierto grado de solapamiento, característico de un patrón de migración parcial. La proporción de sexos (macho/hembra) fue de 2.8:1 durante el invierno y consistió en una proporción mayor de machos que los encontrados en las poblaciones residentes. El porcentaje de hembras de las poblaciones invernales, para el clima moderado del oeste de Oregon, resultó mayor que los valores predecibles para esta latitud derivados para poblaciones orientales de juncos. Los resultados son consistentes con las predicciones de la hipótesis del tamaño corporal para distribuciones invernales con sesgo en la proporción de sexos. Por lo tanto, los efectos variables del clima de invierno en la supervivencia de las aves en relación a su tamaño, son probablemente determinantes importantes en la distribución invernal del ave.

Dark-eyed Juncos, *Junco hyemalis*, are common year-round residents in western Oregon. Wintering populations of juncos in the western United

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States apparently include both migratory and resident birds (Bent 1968, Gabrielson and Jewett 1940, Sabine 1955). Dark-eyed Juncos exhibit complex migratory patterns with different populations showing differing degrees of migratory behavior (Bent 1968, Ketterson and Nolan 1976, Rabenold and Rabenold 1985). The migratory patterns of western juncos are not well understood. Partial and differential migration probably operate, but distributions are complicated by the taxonomically diverse western subspecies (Balph 1979). The extent to which breeding and wintering populations overlap in western Oregon is not certain. This study uses banding recoveries to assess seasonal population turnover and breeding site fidelity in Dark-eyed Juncos in western Oregon to assist understanding of migratory patterns in western juncos.

In addition, seasonal trends in sex ratios were monitored to determine whether these juncos undergo patterns of partial or differential migration resulting in skewed winter sex ratios as documented for other populations of Dark-eyed Juncos (Balph 1975, Ketterson and Nolan 1976). Three distinct hypotheses have been proposed to explain partial and/or differential migration and skewed winter sex distributions among birds (for reviews see Gauthreaux 1982; Ketterson and Nolan 1983, 1985). The dominance hypothesis states that dominant birds restrict subordinates from a limiting food supply, thus forcing subordinates to migrate, or migrate farther. Recent evidence suggests that dominance does not play a major role in the determination of winter distribution in eastern Dark-eyed Juncos (Nolan and Ketterson 1990, Rogers et al. 1989). The arrival-time hypothesis contends that if early arrival on the breeding grounds leads to increased reproductive success, then the most competitive birds (males, and especially juvenile males, Ketterson et al., in press) should winter closest to breeding grounds. The body-size hypothesis suggests that variable effects of winter climate on survival relative to body size will result in larger birds (adult males in juncos, Nolan and Ketterson 1983) wintering closer to breeding grounds. The body-size hypothesis appears to function as the best predictor of winter distribution in partially migratory eastern House Finches (Belthoff and Gauthreaux 1991) and body size-climate relations may be important, although they are not the best predictor, in shaping the winter distribution of eastern Dark-eyed Juncos (Ketterson and Nolan 1978, 1983; but see Stuebe and Ketterson 1982). A corollary prediction of the body-size hypothesis is that areas with milder winter climates should show higher proportions of smaller birds (females) than areas with harsher climates. The mild winter climate of western Oregon affords an ideal opportunity to test this prediction for Dark-eyed Juncos.

METHODS

Dark-eyed Juncos were captured in mist nets and live-traps near Corvallis, Benton Co., Oregon (44°37'N, 123°18'W) in summers and winters from 1987 through 1990. Elevation at capture sites ranged from about 75 m to about 500 m. Juncos were more common at lower elevations in

winter and at higher elevations in summer (pers. obs.). Consequently, winter capture sites were generally at lower elevation than summer capture sites, although some trapping was conducted at certain sites throughout the year. Birds captured from 15 May–15 Sep. were considered “summering birds.” Those captured from 10 Dec.–10 Mar. were designated “wintering birds.” Banding efforts were concentrated on summering populations. The number of days on which banding was conducted during the summer season were 24 (1987), 37 (1988), 35 (1989) and 13 (1990). Juncos were trapped, but not banded, for 24 d (1987–1988), 15 d (1988–1989), and 4 d (1989–1990) in winter. Winter juncos were not banded because most birds at this season were sacrificed for metabolic experiments (Swanson 1990, 1991a,b). Sex of individual juncos was determined by hood color and wing length at both seasons (Balph 1975) and by presence of cloacal protuberance or brood patch in summer. Wing length was measured as unflattened wing chord. Individuals in which neither hood color nor wing length established sex conclusively (6% of the total sampled) were omitted from sex ratio calculations and seasonal morphometric comparisons. Age (hatching year [HY] or after-hatching year [AHY]) was established during the summer by plumage characteristics.

Banding recovery data for Dark-eyed Juncos in Oregon through 1988 were obtained from the U.S. Fish and Wildlife Service Bird Banding Laboratory (BBL). Only recoveries from the Willamette Valley region (defined here as the area encompassed by 43°50'N to the Columbia River and 122°W to 123°50'W) were included in the present study. Banding and recovery dates for BBL data were assigned to summering and wintering populations as follows: summering, 15 May–15 Sep.; wintering, 10 Dec.–10 Mar. Birds banded as members of summering populations and recovered during the winter period, and birds banded as wintering birds and recovered during the summer season were tallied to determine what proportion of the population summers on or near wintering grounds.

Numerical data are presented as means \pm SD. Sex ratios in breeding and wintering populations were compared by χ^2 test for goodness of fit. Student's *t*-test was used to compare seasonal morphometric measurements. Statistical significance was accepted at $P < 0.05$, except for mass and morphometric measurements where a sequential Bonferroni technique for α -level adjustment with multiple *t*-tests (Rice 1989) was applied between seasons ($k = 6$) and between sexes ($k = 6$).

RESULTS

Seasonal population turnover and site fidelity.—Percent recoveries at breeding sites varied with age, sex and year (Table 1). Of the 14 juncos recaptured, 13 were males, and of these, only one was recaptured at a season other than when banded. Males demonstrated much greater fidelity to breeding sites than females. The only recapture of a female occurred at a site approximately 2 km from the original banding site. All males were recaptured at banding sites.

TABLE 1. Percent recoveries^a in subsequent years at breeding sites for different age/sex classes^b of Dark-eyed Juncos in 1988–1990.

Year ^c	Adult males	HY males	HY females
1988	17.6 (3/17)	9.0 (3/33.5)	3.0 (1/33.5)
1989	44.4 (4/9)	4.9 (1/20.5)	0
1990	0	4.5 (3/67)	0

^a Parentheses give the number recaptured/total number of each age-sex class banded in the previous year.

^b Percent recoveries for HY birds were calculated assuming a 1:1 sex ratio of juveniles banded.

^c Adults were not banded in 1989, so no adult returns were noted in 1990. Recaptures from birds banded in 1987 and recaptured and released again in 1988 are included in recovery calculations for 1989 adult males. Total birds banded were 17 adult males (M), 14 adult females (F), and 67 hatching-year (HY) birds in 1987; 3 M, 2 F, and 41 HY in 1988; and 134 HY in 1989.

Of 504 total BBL returns for Dark-eyed Juncos in the Willamette Valley, 11 (2.2%) were recaptured in summer when banded in winter or in winter when banded in summer. There appeared to be a bias in the BBL data toward wintering populations. Of 504 recoveries, 43.1% were of birds banded between 10 Dec. and 10 Mar., while only 3.4% were of birds banded between 15 May and 15 Sep.

Morphometric measurements.—Mean masses for summer and winter juncos were: summer males, 18.0 ± 0.8 g ($n = 51$); winter males, 19.7 ± 1.1 g ($n = 65$); summer females, 17.4 ± 1.0 g ($n = 44$); winter females, 18.5 ± 1.3 g ($n = 23$). Males significantly outweighed females at both seasons (summer: $t = 3.23$, $df = 93$, $P = 0.002$; winter: $t = 4.06$, $df = 86$, $P < 0.001$). Winter juncos of both sexes were significantly heavier than their summer counterparts (males: $t = 9.20$, $df = 114$, $P < 0.001$; females: $t = 3.88$, $df = 65$, $P < 0.001$). Mean wing length was significantly greater in males than in females at both seasons (summer: $t = 9.97$, $df = 89$, $P < 0.001$; winter: $t = 8.26$, $df = 86$, $P < 0.001$). Mean winter wing length was significantly greater than in summer for both males ($t = 7.07$, $df = 111$, $P < 0.001$) and females ($t = 5.81$, $df = 64$, $P < 0.001$, Table 2). Considerable overlap in wing length existed between wintering and breeding populations, however (Table 2). Tarsus length was significantly greater in winter for males ($t = 2.68$, $df = 108$, $P < 0.01$) but not females (Table 2). Tarsus length was significantly greater in males than in females at both seasons (summer: $t = 2.81$, $df = 83$, $P < 0.01$; winter: $t = 2.82$, $df = 86$, $P < 0.01$, Table 2). These data suggest that wintering populations are made up of larger birds.

Seasonal sex ratios.—There was a significantly greater ($\chi^2 = 7.04$, $df = 1$, $P < 0.01$) proportion of males in the winter population than in the summer population. Sex ratios did not vary significantly between years, so sex ratio data from 1988–1990 were pooled. Seasonal sex ratios of all juncos captured in which sex was determinable were 51 males : 44 females in summer and 65 males : 23 females in winter. The sex ratio in winter,

TABLE 2. Seasonal morphometric data for Dark-eyed Juncos captured near Corvallis, Benton Co., Oregon.

Season	Sex	n	Wing length ^a (mm)		Tarsus length (mm)	
			Mean \pm SD	Range	Mean \pm SD	Range
Summer	M	48 ^b	71.9 \pm 1.9 ^d	67.6–76.6	22.4 \pm 0.7 ^c	20.2–23.8
Winter	M	65	74.6 \pm 2.2 ^{d,f}	70.0–79.8	22.7 \pm 0.6 ^{c,e}	21.0–24.4
Summer	F	43	67.8 \pm 2.0	64.2–72.4	21.9 \pm 0.8	20.2–23.5
Winter	F	23	70.6 \pm 1.5 ^f	68.2–72.8	22.3 \pm 0.7	20.6–23.5

^a Wing length was measured as unflattened wing chord.

^b Sample size for tarsus length in summer males was 45 rather than 48.

^{c-f} These superscripts indicate significant differences between sexes at $P < 0.01$ (c), between sexes at $P < 0.001$ (d), between seasons for the same sex at $P < 0.01$ (e) and between seasons for the same sex at $P < 0.001$ (f).

but not in summer, was significantly different from 1:1 ($\chi^2 = 19.10$, $df = 1$, $P < 0.001$).

DISCUSSION

Banding recoveries indicate that at least 2.2% of Dark-eyed Juncos are permanent residents in the Willamette Valley. These juncos are much more common at low elevations than at high elevations in winter, while the reverse is true in summer (pers. obs.). This distribution may be explained by altitudinal or latitudinal migration. Altitudinal migration has been documented in several populations of Dark-eyed Juncos (Ketterson et al., in press; Rabenold and Rabenold 1985), including the race present in western Oregon (Bent 1968). Altitudinal migration makes locating wintering localities for breeding birds difficult, even if they are in nearby areas, and thereby reduces summer–winter recaptures of birds remaining in the same general area. This reduction leads to an underestimate of birds wintering near breeding grounds by mark-recapture techniques. Furthermore, BBL data showed a pronounced winter bias in juncos banded and subsequently recovered in the Willamette Valley, which strongly suggests concentration of banding effort in winter relative to summer. This could lead to an underestimate of the numbers of juncos breeding on or near wintering grounds. Thus, I believe that 2.2% is an underestimate of the actual proportion of juncos that winter on or near breeding grounds in the Willamette Valley. These data indicate that Dark-eyed Juncos in the Willamette Valley are partial migrants.

Breeding site fidelity was much higher among males than females. This concurs with previous data from other junco populations (Rabenold and Rabenold 1985) and from many other species (see Gauthreaux 1982). The total percentage of site-faithful adult males recaptured in subsequent years was 26.9%, but was only 5.8% for juvenile males (assuming one-half of banded juveniles were males). This suggests that adult males show a greater degree of site fidelity than first-year birds (see Gauthreaux

1982), that adult males are capable of reoccupying previous territories and excluding first-year birds due to dominance relationships (Ketterson and Nolan 1983), or that adult males have higher survival rates than first-year males. Regarding the latter possibility, Ketterson and Nolan (1982) found no differences between sex-age classes in overwinter survival in eastern Dark-eyed Juncos.

Winter populations of Dark-eyed Juncos in this study demonstrated a 2.8:1 ratio of males to females. This was a significantly greater proportion of males than in the summer population. These data support other data suggesting latitudinal segregation of the sexes among western populations of wintering Dark-eyed Juncos (Balph 1975, 1979; Ketterson and Nolan 1979). Latitudinal segregation of the sexes resulting from differential migratory patterns has been documented for eastern juncos (Ketterson and Nolan 1976, 1979).

The data from this study do not agree with latitude-predicted sex ratios derived from eastern junco populations. Ketterson and Nolan's (1979) equation predicts that females should comprise only 17% of wintering populations at 45°N latitude. A similar underestimate of female proportions was also detected for junco populations wintering in eastern Washington (Ketterson and Nolan 1979). The mild winter climate of the Pacific coast states may allow increased numbers of females to overwinter at higher latitudes. A northward shift in wintering proportions of females relative to continental populations also appears to exist along the Atlantic coast states (Ketterson and Nolan 1976). These data are consistent with the prediction of the body size hypothesis, that milder climates should show higher proportions of wintering females than harsher climates. Thus, the body size hypothesis is not invalidated as playing an important role in shaping winter distributions in Dark-eyed Juncos. This winter distribution likely also reflects different breeding distributions and densities between coastal and continental populations, however, and winter distributions among western juncos are probably complicated by competition between the taxonomically diverse western subspecies (Balph 1979).

The winter increase in mean wing length in both sexes and the winter increase in tarsus length in males suggests an influx of larger birds into wintering populations or an emigration of smaller birds. In either case, larger birds appear to winter north of smaller birds in these juncos. This is contrary to studies on eastern juncos, if wing length is assumed to parallel body size, which show either no latitudinal variation in wing length within age-sex classes (Nolan and Ketterson 1983) or decreasing wing length from late fall into early winter (Chandler and Mulvihill 1990). Eastern juncos did show increased mass in northern populations (Nolan and Ketterson 1983). Large juncos tolerate exposure to extreme cold better than small juncos (Swanson 1990). As males are larger than females, presumably they are more cold resistant. Given sufficient food, however, Dark-eyed Juncos from western Oregon are physiologically capable of withstanding temperatures well below any experienced under

natural conditions (Swanson 1990). In this context, the factor limiting winter survival appears to be procurement of food, especially during periodic inhibition of foraging by severe winter weather (Ketterson and Nolan 1983; Marsh and Dawson 1989). When food is restricted, dominant juncos acquire more food than subordinates (Baker et al. 1981, Theimer 1987) and this may influence overwinter survival (Baker and Fox 1978). Thus, climatic effects relative to body size appear to interact with dominance relationships and/or breeding arrival time to determine sex structure in wintering populations of western Dark-eyed Juncos.

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