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## GEOGRAPHIC VARIATION AND ITS CLIMATIC CORRELATES IN THE SEX RATIO OF EASTERN-WINTERING DARK- EYED JUNCOS (*JUNCO HYEMALIS HYEMALIS*)<sup>1</sup>

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**Abstract.** The sex ratio of Dark-eyed Juncos wintering in the eastern and central United States and Canada varies clinally along a latitudinal gradient. The percentage of ♀♀ among both museum skins and live-caught birds is ≈ 70% in the south, 20% in the north. When abundance according to latitude is also considered, an average ♀ appears to winter farther south than an average ♂ and hence probably tends to migrate farther.

Latitude alone is an excellent predictor of sex ratio ( $r^2 = 85\%$ ), and latitude plus 13 other measures of climate explain virtually all the variation ( $r^2 = 96.6\%$ ). Extreme measures of climate, as compared to mean measures, are equally predictive. Principal component analysis indicates that snowfall, temperature, and latitude are the most important climatic variables associated with sex ratio.

Because ♂♂ average larger than ♀♀ and are concentrated northward, mean wing length increases with latitude and is significantly correlated with climatic measures that vary with latitude. Further, larger birds within each sex may select higher altitudes as wintering sites. Sex ratio does not vary measurably with date in wintering populations.

Among possible explanations for clinal variation in sex ratio are sex-associated differences in (1) advantages of early arrival on the breeding or wintering grounds, (2) impacts of inter- and intrasexual competition, and (3) effects of low temperature and intermittent food availability. Comparison of ♂♂ and ♀♀ with respect to potential fasting endurance, a size-related metabolic parameter, indicates that at 0°C an average ♂ should be able to fast 4% longer (1.6 h) than an average ♀ at standard metabolic rates. An extremely heavy ♂ might endure fasting up to 29% (10.7 h) longer than a very light ♀. These differences may confer greater survival ability upon the ♂ at latitudes where snow cover can often preclude feeding.

**Key words:** Bergmann's Rule; climate; eastern United States; fasting endurance; geographic variation; junco; overwinter survival; physiological ecology.

### INTRODUCTION

In a 17-yr study of Dark-eyed Juncos (*Junco hyemalis hyemalis*) that winter near Bloomington, Indiana, V. Nolan (*personal observation*) found that males are approximately twice as common as females during winter months; during both migrations the sex ratio of captured samples is nearer unity. These findings, which are supported by reports for other northern or central portions of the junco's winter range (Blake 1964, 1967, Dow 1966, Helms et al. 1967, Grant and Quay 1970, Balph 1975), led to the hypothesis that on the whole females winter farther south than males.

Differential winter distribution of the sexes, with males wintering farther north than females, has been reported for a number of bird species (Heydweiler 1936, Tree Sparrow, *Spizella arborea*, Nice 1937, Song Sparrow, *Melospiza melodia*, Chaffinch,

*Fringilla coelebs*, Blackbird, *Turdus merula*, Mockingbird, *Mimus polyglottos*, Cabanis' Woodpecker, *Dryobates villosus hyloscopus*, Prairie Chicken, *Tympanuchus cupido americanus*; Schäfer and de-Schauensee 1939:222-223, Gildenstadt's Redstart, *Phoenicurus erythrogaster*; Lack 1944, Robin, *Erithacus rubecula*; Quay 1951, Mourning Dove, *Zenaida macroura*; Howell 1953 Yellow-bellied Sapsucker, *Sphyrapicus varius*; Bellrose et al. 1961, various duck species; King et al. 1965, White-crowned Sparrow, *Zonotrichia leucophrys gambelii*; Senk et al. 1972, Skylark, *Alauda arvensis*). In most of these studies data were obtained either by analyzing the locations of recovery of banded individuals or by intensive sampling over a small portion of the range; however, King et al. sampled White-crowned Sparrows throughout much of the winter range.

The present study was begun in 1971 with two questions in mind: (1) Do female juncos tend to winter farther south than males, and (2) if so, why?

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## METHODS

*Taxonomic and seasonal considerations*

Wintering juncos were obtained from two sources: (1) museum skins taken during the 19th and 20th centuries east of 105°W longitude in the United States and Canada (see Acknowledgments for museums providing skins), and (2) birds caught from 1971–74 in Illinois, Indiana, Tennessee, Mississippi, Alabama, and Georgia.

The Dark-eyed Junco comprises what were thought until recently to be four species, Oregon (*J. oregonus*), White-winged (*J. aikini*), Guadalupe (*J. insularis*), and Slate-colored Juncos (*J. hyemalis*). The species as now conceived carries the binomen formerly held by the Slate-colored Junco (Comm. Class. Nomen. A.O.U. 1973). The subspecies *J. h. hyemalis* (whose English name is now Slate-colored Junco) breeds throughout the boreal forest and winters over much of the continental United States. However, it is most abundant during winter in eastern North America, where it is the only subspecies found in large numbers (Miller 1941). Therefore our live-caught samples almost surely consisted of *J. h. hyemalis*, and because only skins labelled "*Junco hyemalis*" or "Slate-colored Junco" were examined, the same is true of the museum samples. Skins labelled "*J. h. carolinensis*" were ignored, primarily because we had no experience with sex determination in this race. Henceforward we shall simply refer to either "juncos" or to *J. h. hyemalis*.

Consideration was further limited to juncos thought to be wintering where taken, i.e.; to birds caught or shot in December, January, and February. Reasons for believing that there is little or no migration during these months follow:

- 1) At Bloomington, Indiana, 39°N latitude and about the center of the winter range, 17 yr of daily banding in the period November–April suggest no migration between 1 December and 1 March (V. Nolan, *personal observation*).
- 2) In Massachusetts fall migration terminates in late November, and spring migration begins the second or third week of March (Helms and Drury 1960).
- 3) In northern Michigan fall migration peaks 16–18 October; spring migration peaks 10–12 April (Stack and Harned 1944).
- 4) In the District of Columbia and Maryland, normal fall migration lasts from late September to 20–30 November, with an extreme departure date of 5 December; normal spring migration lasts from 1–10 March to 1–10 May with an extreme arrival date of 25 February (Stewart and Robbins 1958).

- 5) In Winston-Salem, North Carolina, "local juncos begin to diminish by the end of March" (Johnston 1962).

Additional migration dates may be found in Bent (1968). In summary, few of the 1,089 birds considered in this paper are likely to have been migrating.

*Sexual dimorphism; Accuracy of methods of sexing*

In *J. h. hyemalis* the sexes are sufficiently similar to preclude confident field determination of sex of many individuals. While some workers (Helms et al. 1967) have stated that proper sex determination of more than  $\approx 75\%$  of hand-held specimens requires laparotomy, Dow (1966) indicates otherwise. Our data corroborate Dow. No single character differentiates males from females; but males tend to be darker, have longer wings, and have somewhat different crown markings. Together these differences let us accurately determine the sex of 93% of specimens examined in the hand. A summary of sexual differences and methods of sexing follows:

- 1) Coloration. Male plumage is more often dark slate as opposed to slate or light slate, and males usually lack or have little brown wash on the head and/or back and/or sides; brown on these regions is characteristic of females (Miller 1941). Grant and Quay (1970) classified 71 specimens according to a seven-gauge scale ranging from "no brown" to "very brown." Females varied from "some brown" (gauge 4) to "very brown" (gauge 7), males from "no brown" (gauge 1) to "rather brown" (gauge 5). See also Balph (1975).
- 2) Size. Mean length of the flattened wing of migrating and wintering males at Bloomington, Indiana, is  $\approx 81$  mm, mean female wing length  $\approx 76.5$  mm (V. Nolan, *personal observation*; see also Balph 1975). Helms et al. (1967) in a study of body components of 159 juncos captured near Lewisburg, Pennsylvania, found that males had significantly longer wings than females (difference between sample means, 3.6 mm; mean wing length of sexes pooled, 78.8 mm), greater wet weight (difference, 1.22 g; pooled mean, 21.1 g), more total water, and greater dry fat-free weight. Sexual differences were nonsignificant in total fat (pooled mean, 2.67 g), fat as a percentage of wet weight, fat index, and visible fat. Although it is usually assumed for individuals of the same population that differences in wing length indicate differences in body mass, Helms et al. found that dry fat-free weight was a linear function of wing length in females but not males. Within

TABLE 1. Live-caught juncos: Sources, associated dates, sample sizes, methods of capture, and weather

Location	Dates	<i>n</i>	Capture method	Weather
LaGrange, Illinois	5 Dec 1971, 1–2 Jan 1972	84	nets	–7° to –1°C, light snow
Bloomington, Indiana	1 Dec 1971–1 Mar 1972 1 Dec 1972–1 Mar 1973	151	nets and traps	–12° to 18°C, dry, rain, snow
Olivehill, Tennessee	9–11 Jan 1973	88	primarily traps, some nets	aftermath of severe snowstorm, snow cover, –12° to –7°C
Noxubee County, Mississippi	19 Dec 1972	1	net	both rainy and clear, > 10°C
Birmingham, Alabama	12–14 Jan 1974	57	nets	both rainy and clear, > 10°C
Columbus, Georgia	15–18 Jan 1974	92	primarily nets, some traps	both rainy and clear, > 16°C

the range of overlapping wing lengths, males were significantly heavier (wet weight) than females.

- 3) Crown markings. Crown feathers of many juncos show concentrations of dark pigment that result in patterns tending to differ according to sex (Dow 1966). Males' crown feathers are often darker at base than tip, giving a laterally barred appearance to the crown. Female crown feathers are often darker adjacent to the rachis than marginally, resulting in anterior-to-posterior streaking; males occasionally show this streaking. Some individuals of both sexes show both patterns, barred anteriorly, streaked posteriorly; and some show no crown pattern.

In general we relied upon a Gestalt of size, coloration, and crown-pattern characteristics for sex determination. Occasionally an individual's characteristics provided conflicting information about its sex. Usually, if the wing length was above the male mean or below the female mean, that alone controlled our decision as to sex; in the remainder of cases color and crown pattern were more influential. The latter were particularly useful when dealing with museum skins, where difficulty in measuring the wing and possible shrinkage affected the reliability of measurement. (In both sexes our measurements of museum skins averaged smaller than those of live-caught birds from the same latitudes.)

Any freshly dead juncos obtained during the study were first sexed by the methods described, then by examination of the gonads. Most of these birds died accidentally, but  $\approx 20\%$  were killed because their external sex-associated characters were indeterminate. Therefore the sample was biased toward juncos difficult to sex. A correct determination was made 102 of 110 times (93% accuracy). Museum skins were sexed prior to examination of the labels. When a label stated sex and revealed that the gonads had been seen by the collector, the bird was used to determine accuracy of sexing of museum skins; there were 4 errors in 52 cases (92% accuracy). We found

that use of external characters is equally reliable for both sexes (4 females wrong of 63, 8 males wrong of 99,  $\chi^2 = 0.12$ ;  $0.9 > p > 0.5$ ), for museum skins and freshly killed specimens ( $\chi^2 = 0.01$ ;  $0.9 > p > 0.5$ ), and for birds taken in Indiana as opposed to other localities (7 of 101 Indiana juncos incorrectly sexed, 5 of 61 from outside the state,  $\chi^2 = 0.01$ ;  $0.9 > p > 0.5$ ). (However, composition of outside-Indiana and museum samples overlaps by 94%.) In summary, external sexual differences in the populations studied permitted sexing with a minimum accuracy of 93%, with no reason to suspect variation in accuracy according to sex, source, or location.

#### *Source and treatment of sample*

Between 1971 and 1974 and at six locations, 473 juncos were netted or trapped, banded, and measured (flattened wing to the nearest whole millimeter). Details of dates, methods, and weather conditions appear in Table 1. Both authors processed the samples from Alabama and Georgia. Ketterson alone processed all others except birds from Illinois; these were captured, sexed, and measured by Michael Monahan, a colleague who employed our methods. Before relying on his data, we compared juncos ( $n = 93$ ) Monahan had sexed and measured at Bloomington with corresponding information collected (on different individuals) by Ketterson from the same location in 2 later years. Both Monahan's and Ketterson's samples were sexed as 32% female; wing length means (sexes pooled) differed by 0.17 mm ( $t = 0.48$ , NS). Additionally, Monahan made independent determinations of sex of  $\approx 50$  freshly dead juncos that we also sexed, with no differences in result. We therefore feel justified in using his Illinois data.

Museum skins numbered 616 and were treated (by Ketterson) like live-caught birds in all relevant ways. They represent 31 states and 1 province.

#### *Environmental data*

To determine whether sex ratio is geographically variable and, if so, with respect to what environmental

parameters, geographic and climatic data for every location where birds originated were assembled. With the exception of Canadian specimens, for which climatic data were not readily available, values for 14 variables were assigned to each bird. Closest latitude and longitude were determined from the Rand McNally Collegiate World Atlas (1962), with minutes rounded to the nearest degree. Altitude and values for 11 climatic variables were obtained from the U.S. Weather Bureau Bulletin W, Climatology of the United States (1932), which reports long-term (1899–1930) monthly and annual means of precipitation, snowfall, and temperature for most counties and often for several locations within a county. Information on sunshine, extreme snowfall, and numbers of cold days is reported only for larger cities ( $\approx$  1–6 per state); with respect to these measures of climate, juncos were assigned values from the closest reported location. Descriptions of the climatic variables and their determinations appear in the U.S. Department of Agriculture Yearbook of Agriculture (1941).

A brief description of the 14 variables follows, preceded by code designations to be used in the remainder of the paper: (1) WINTEM = average winter (Dec–Feb) temperature; (2) JANTEM = average of daily minimum temperatures during January; (3) WINPPT = average moisture falling during winter as rain, snow, hail, or sleet; measured as rain plus water equivalents of snow, hail, etc.; (4) ANSNOW = average annual snowfall; (5) WINSUN = average hours sunshine during winter; (6) SUNPCT = average hours sunshine during winter as percentage of total possible hours; (7) DAYS32 = average days per year temperature below 32°F; (8) DAYSBO = average days per year temperature below 0°F; (9) SNODAY = average days snowfall per year; (10) MINTEM = lowest temperature ever recorded; (11) LATITU = latitude; (12) LONGIT = longitude; (13) ALTITU = altitude; (14) SNOW24 = greatest snowfall ever recorded in 24 h.

*Regression analyses*

Computer cards for each case (individual) were grouped in one of 72 possible cells of a matrix (Table 2) whose rows consist of bands of latitude 3° wide, from 28° to 51°N latitude, and whose columns consist of bands of longitude 4° wide, from 70° to 105°W longitude. In 27 cells there were 5 or more cases (total 1,089); the data in these cells were analyzed for variation in wing length. Seventeen cells contained at least 10 cases (total 991), and these data were analyzed for variation in sex ratio.

Percent female, mean wing length, and mean values for each of the 14 environmental variables were calculated for each of the 27 cells. Mean wing

TABLE 2. Sample size (\*) and sex ratio in percent ♀♀ (\*\*), according to latitude and longitude. Localities in the United States where  $n \geq 5$  are indicated by capital letters.

LATITUDE	LONGITUDE									
	70-73	74-77	78-81	82-85	86-89	90-93	94-97	98-101	102-105	
28-30					A 9* 56%**	B 13 69%		C 20 70%		
31-33			D 9 89%	E 100 87%	F 5 100%	G 7 57%	4 75%	4 100%		
34-36			H 32 56%	I 118 49%	J 145 48%	K 16 69%	L 20 50%	M 17 41%		
37-39		N 52 29%	O 5 20%	2 50%	P 161 34%		Q 40 30%		R 5 40%	
40-42	S 68 34%	T 50 38%	U 9 22%	V 36 22%	W 89 18%	X 8 25%				
43-45	Y 6 66%		17 35%	1 0%		Z 14 21%	AZ 5 0%			
46-48										
49-51								2 0%		

length and sex ratio were then regressed upon the values for the environmental variables of the 27 or 17 appropriate cells (BMD02R stepwise regression, Dixon 1970). The data representing the environmental variables were analyzed by principal component analysis (BMD02M regression on principal components, Dixon 1970), and sex ratio was regressed upon the first three resulting components. Parametric tests were used in all these analyses: none of the 16 variables was significantly nonnormally distributed (under Kolmogorov-Smirnov  $d_{max}$  test, Sokal and Rohlf 1969,  $p > 0.2$ , except DAYSBO  $p > 0.1$ ).

*Abundance*

Interpretation of geographic variation in the winter sex ratio of juncos requires that something be known of relative density of populations in the winter range. We therefore analyzed 716 National Audubon Society Christmas Bird Counts taken in 1970–71. The primary advantage of these data is their quantity, accuracy of species identification, and uniformity of area covered (Arbib 1972). Disadvantages include wide local variation in hours spent counting, in number and abilities of participants, and in habitats visited. Nevertheless, “the counts have been shown to be reliable indices of large-scale population fluctuations and distribution” (Bock and Lepthien 1974).

With the exception of purely pelagic counts, all counts east of the western boundaries of Texas, Oklahoma, Kansas, Nebraska, South Dakota, North Dakota, and Ontario were included. No corrections were made for variation with respect to habitats visited. The number of juncos, reported as Slate-

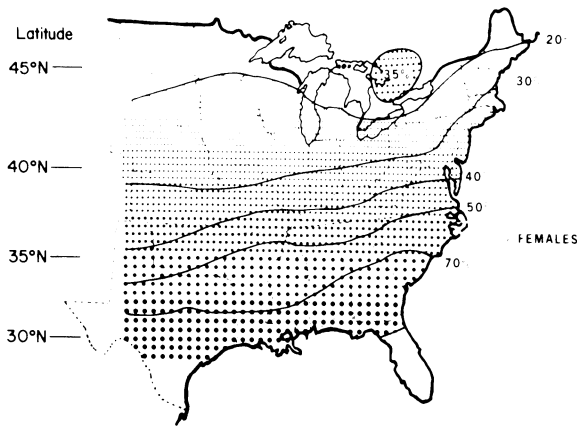


FIG. 1. Schematic map of geographic variation in the sex ratio of Dark-eyed Juncos wintering in the eastern United States. Percentage of ♀♀ based on both live-caught juncos and museum specimens was calculated for each cell formed by a matrix of latitude-longitude intersections (see text and Table 2) and regions of similar sex ratio were demarcated by hand. Percentage of ♀♀ may be seen to increase with decreasing latitude.

colored Juncos, seen per party hour in the field (i.e., total number reported for a count divided by number of party hours spent counting) was calculated for each count, with fractions rounded to the nearest whole. The latitude for each count was rounded to the nearest degree, and counts were grouped as in the analysis of sex ratio. Thus there were nine groups or categories of latitude, each 3° wide, between 25° and 51°N latitude (longitude was not considered). The median and mean values for juncos seen per party hour were determined for each latitudinal band.

*Seasonal variation in sex ratio*

To determine whether sex ratio varied over the winter, museum specimens killed 1 December–15 January (considered early) were separated from those taken thereafter (considered late). Early and late samples were further divided according to latitude of point of collection using the method described in the preceding paragraph.

**RESULTS**

Figure 1 is a schematic map depicting geographic variation in sex ratio based on data for localities with 10 or more individuals (see Table 2). Sex ratio appears to vary clinally with latitude from ≈ 20% to 70% females, north to south. The correlation between latitude and percentage of females is highly significant (Pearson's  $r = 0.922$ ,  $df = 15$ ,  $p < 0.01$ ).

Before concluding, however, either that the average female winters farther south than the average male, or that females migrate farther on the average than do males, relative winter abundance of juncos

TABLE 3. Abundance and sex ratio of juncos by latitude according to Audubon Christmas Bird Count, 1970–71

Latitude	Median/h <sup>1</sup>	Ex-tremes <sup>1</sup>	n <sup>2</sup>	% ♀♀ <sup>3</sup>	n <sup>4</sup>
25°–27°	0	0–0	23		0
28°–30°	0	0–4	41	0.666	42
31°–33°	4	0–30	45	0.705	129
34°–36°	5	0–27	60	0.500	348
37°–39°	6	0–33	115	0.324	265
40°–42°	5	0–56	219	0.315	260
43°–45°	1	0–44	169	0.209	43
46°–48°	0	0–1	37		0
49°–51°	0	0–0	7	0.000	2

<sup>1</sup> Median and extreme numbers of juncos per party hour for all Christmas Bird Counts within each band of latitude; see text.

<sup>2</sup> Number of 1970–71 Christmas Bird Counts in sample; see text.

<sup>3</sup> Percentage of females among museum skins and live-caught juncos within bands of latitude, obtained from Table 2.

<sup>4</sup> Number of individuals upon which percentages of females are based; see footnote 3.

at various latitudes must be investigated. Clearly, if a southern latitudinal band were to support a greater proportion of females than a northern one but were also to be inhabited by a much smaller population, then in absolute terms the northern band could be inhabited during winter by more females. Such a situation would call for a different interpretation than would one in which juncos were equally numerous at both latitudes.

Table 3 relates latitudinal data on abundance and sex ratio. Given are median and extreme numbers per party hour for each band of latitude, number of Christmas Bird Counts on which the median is based, percentage of females in each band, and number of museum and live specimens from which this percentage was calculated. Figure 2, based on Table 3, graphs relative abundance of juncos and percentage of each sex according to latitude; for example, males per party hour at any latitude is the product of the relevant median abundance and percentage of males.

Juncos appear (1) rare above 45°N and below 31°N, and (2) most abundant at 37°–39°N, the center of the winter range. Abundance falls off more gradually to the north than to the south of the center. To determine the statistical significance of the data showing these trends, a Kruskal-Wallis one-way analysis of variance (Siegel 1956) was applied to data from various combinations of latitudinal bands. The two northernmost and two southernmost bands are homogeneous with respect to abundance ( $H = 1.76$ ,  $p = 0.623$ ); that is, numbers per party hour were statistically equivalent north of 45°N latitude and south of 31°N latitude. Bands 3, 4, 5, and 6 (31°–42°N) also do not differ significantly in hourly numbers ( $H = 7.05$ ,  $p = 0.07$ ); the bulk of juncos wintering in eastern

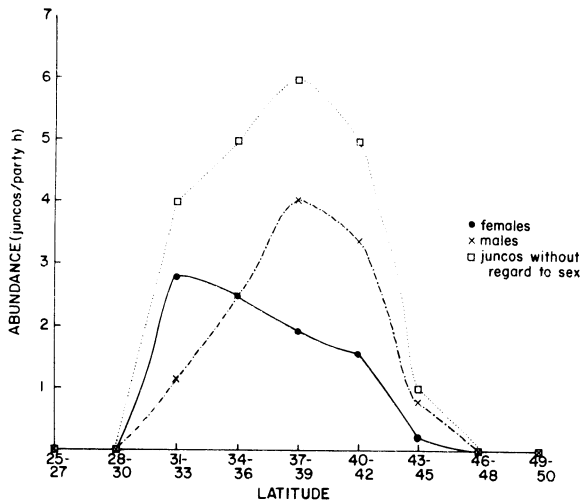


FIG. 2. Relationship of abundance and latitude. To determine abundance, number of juncos per party hour was calculated for each Christmas Bird Count. Counts were grouped according to 3° bands of latitude and the median determined for each band. Those medians are joined by the dotted line in the figure. Abundance of each sex was determined by multiplying the median number of juncos per party hour by the percentage of that sex found at that latitude, as determined from both live-caught juncos and museum specimens grouped in the same 3° bands of latitude. Male abundance may be seen to peak at a higher latitude than ♀ abundance; see text for further details.

North America appears to occur here. Band 7 (43°–45°N) is in a category by itself, differing from all other combinations (bands 3, 4, 5, 6, 7:  $H = 96.74$ ,  $p = 0.00$ ; bands 1, 2, 8, 9, 7:  $H = 107.72$ ,  $p = 0.00$ ; bands 3, 7:  $H = 7.93$ ,  $p = 0.005$ ). This suggests intermediate to low numbers north of the center of the range; that is, abundance falls off less rapidly toward the north.

Thus the trends suggested by the medians are borne out by the tests of significance, and absolute numbers of juncos at latitudes where females outnumber males evidently are about as large as absolute numbers where males predominate. We conclude that the average female winters farther south than the average male. Assuming that sex ratio, whether 1:1 or not, is unvarying throughout the breeding range (an assumption lacking supporting data), a further implication of our results is that the average female migrates a greater distance than does the average male.

If, for each sex, median abundances per latitudinal band in numbers per party hour are summed from north to south (see Fig. 2, Table 3) and the totals per sex compared, males outnumber females 11.95:9.05. Means per party hour were not used as an estimate of abundance because within some latitudinal bands the distribution of hourly numbers was

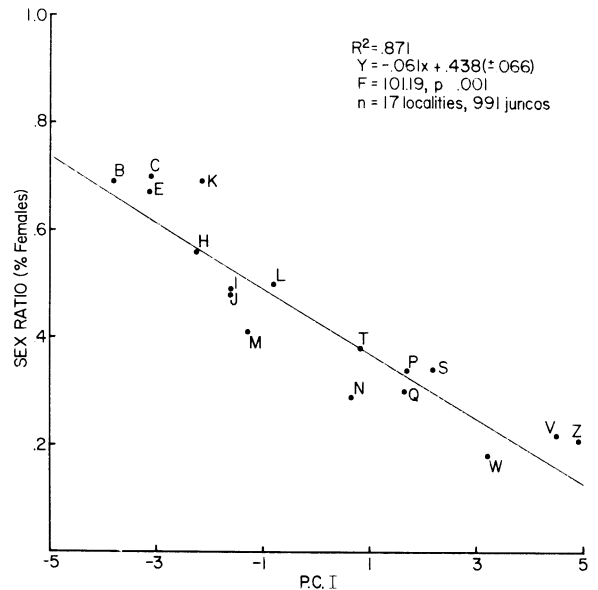


FIG. 3. Relationships of sex ratio (in % ♀♀) and values of principal component I (P.C. I) per locality. High values of the component are associated with localities characterized by high latitude, high annual snowfall, numerous days with snow, and both average and extreme low winter temperatures. The letters represent different localities, identified by the same letters in Table 2. For further details see text. The percentage of ♀♀ may be seen to decrease with increasing values of P.C. I.

strongly skewed to the right; but when mean, rather than median, is multiplied by sex ratio, the difference between totals increases, 16.7:12.1.

At least equally as interesting as the implication that the average female migrates farther than the average male is the fact that she spends the winter in a different climate, for latitude certainly correlates with climatic variation over the region studied. Therefore we investigated the predictive role of climate.

Sex ratio (percent females) and all 14 environmental variables except WINSUN, SUNPCT, LONGIT, and ALTITU correlate at or beyond the 0.05 level; at the 0.01 level WINPPT is no longer correlated (Table 4). In short, percentage of females increases with precipitation and temperature and decreases with latitude and with measures of snowfall. Table 5 relates sex ratio to the environmental variables in stepwise regression. LATITU, the first variable entered, explains 85% of the variation in sex ratio ( $r^2 = 0.851$ ). WINPPT is second and explains another 3%, or 26% of the variation not attributable to latitude. Together the 14 variables account for 96.6% of sex-ratio variation.

We pursued the possibility that climatic extremes might have been major determinants in the evolution of clinal variation in sex ratio, under the hypothesis

TABLE 4. Pearson's product-moment correlation coefficients (*r*) relating percent ♀♀ and mean wing lengths (sexes pooled) to 14 environmental variables. See text for codes

Variable	% ♀♀	Wing length <sup>1</sup>
WINTEM	0.922**	-0.722**
JANTEM	0.890**	-0.685**
WINPPT	0.523*	-0.395*
ANSNOW	-0.864**	0.650**
WINSUN	0.415	-0.416*
SUNPCT	0.227	-0.290
DAYS32	-0.648**	0.591**
DAYSB0	-0.731**	0.554**
SNODAY	-0.736**	0.575**
MINTEM	0.837**	-0.691**
LATITU	-0.922**	0.729**
LONGIT	0.243	0.036
ALTITU	-0.242	0.408*
SNOW24	-0.659**	0.579**

<sup>1</sup>\*\* designates significance at the 0.01 level; \* at the 0.05 level; df = 15 in case of % ♀♀, df = 25 in case of wing length.

that extremes may have the greatest impact on survival (see Tinbergen 1957:25, Johnston et al. 1972, Jenkins et al. 1965:373). In the framework of the present problem, the effects of extreme cold or snowfall operating upon any sexual differences in tolerance to winter storms (e.g., differences in fasting ability, see below) could exert differential pressures on the sexes, producing the distributional differences shown. Results of a stepwise regression of SNOW24, DAYSB0, and MINTEM on percent females (Table 6) indicate that each of these variables is a good predictor of sex ratio when the others are not permitted to vary; together they account for 86.7% of the total variation in the dependent variable. This coefficient of determination is comparable in magnitude to that of latitude alone.

TABLE 5. Stepwise regression of sex ratio against environmental variables. Variables are listed in order of their entrance into the stepwise regression; see text for codes

Variable	Coefficient	SE	Increase in <i>r</i> <sup>2</sup>
LATITU	0.0440	0.108	0.851
WINPPT	0.0099	0.024	0.030
DAYSB0	-0.0323	0.025	0.011
SNOW24	-0.0124	0.012	0.012
SUNPCT	0.0578	0.056	0.011
WINSUN	-0.0060	0.006	0.020
DAYS32	-0.0004	0.002	0.008
LONGIT	0.0161	0.014	0.004
WINTEM	0.0333	0.091	0.009
MINTEM	0.0037	0.014	0.006
ANSNOW	0.0022	0.015	0.004
JANTEM	-0.0076	0.042	0.000
ALTITU	-0.0002	0.002	0.000
SNOWYR	-0.00002	0.007	0.000
Constant	= -3.579		
Multiple <i>r</i>	= 0.966		
SE of estimate	= 0.092		
<i>F</i> -ratio	= 4.124 (df = 14, 2); <i>p</i> < 0.05		

TABLE 6. Stepwise regression of three measures of extreme climatic conditions and percent ♀♀. Variables are listed in order of their entrance into stepwise regression; see text for codes

$Y = 0.006(\text{MINTEM}) - 0.013(\text{SNOW24}) - 0.029(\text{DAYSB0}) + 0.742$		
$F = 28.2, p < 0.01$		
$r^2 = 0.867$		
Partial regression coefficients, tests of their significance, and cumulative <i>r</i> <sup>2</sup> :		
Code	<i>p</i>	<i>R</i> <sup>2</sup>
MINTEM	<i>t</i> = 2.80, <i>p</i> < 0.02	0.7008
SNOW24	<i>t</i> = 3.14, <i>p</i> < 0.01	0.7840
DAYSB0	<i>t</i> = 2.86, <i>p</i> < 0.02	0.8670

Because extremes of climate are highly intercorrelated with certain means, a principal component analysis was performed on the independent variables in order to extract a smaller number of composite, orthogonal variables. Table 7 lists the first three components derived in this manner and the proportion of the total variance in the correlation matrix formed by the environmental variables explained by each. Also given are the largest loadings on the components from the original variables and the proportion of variation in sex ratio that each of these explains.

Localities at which the first principal component (P.C. I) has a large value are characterized by high latitude, heavy annual snowfall, and low average and extreme winter temperatures. A high value of the component is associated with a low proportion of females (Fig. 3;  $F = 101.2, p < 0.001, r^2 = 0.871$ ). Comparison of coefficients of determination shows that P.C. I correlates with sex ratio comparably to latitude alone; however, it does identify the most informative aspects of climate that vary with latitude.

P.C. II suggests that independently of snow, temperature, and latitude, locations vary with respect to precipitation and sunshine received. Locations low

TABLE 7. Principal components derived from analysis of correlation matrix of 14 environmental variables. See text for codes

Principal Components (heaviest loadings)		
P.C. I	P.C. II	P.C. III
-0.368 WINTEM	-0.458 WINPPT	0.459 SNOW24
-0.360 JANTEM	0.492 WINSUN	0.313 SUNPCT
0.339 ANSNOW	0.507 SUNPCT	-0.538 LONGIT
-0.322 MINTEM		-0.441 ALTITU
0.354 LATITU		
Proportion of environmental variance explained		
0.53	0.16	0.14
<i>r</i> <sup>2</sup> sex ratio		
0.87	0.002	0.009



in precipitation tend to be sunny, but this aspect of climate when regressed on sex ratio explains only 2% of the variation in that ratio. P. C. III is not easily interpreted but in any event tells little about sex ratio, and we ignore it.

Because male juncos have longer wings than females and are more abundant in the north, it might be expected that mean wing length of junco populations would increase with latitude and vary accordingly with climatic measures associated with latitude. This expectation is largely fulfilled (Table 4). The respective correlations of mean wing length and of sex ratio with the 14 environmental variables differ in only two respects: Whereas WINSUN and ALTITU do not correlate significantly with sex ratio, they do so with mean wing length. Positive correlation of wing length and altitude, but not of sex ratio and altitude, may indicate that larger birds within each sex are selecting higher altitudes and thereby experiencing slightly more demanding environments than smaller individuals. The significant correlation of WINSUN with wing length but not with sex ratio is probably simply a reflection of the larger sample size used in the analysis of wing length, since the magnitudes of the respective correlation coefficients differ only slightly.

The museum data, collected during many winters, lend themselves to analysis of one further question: Does sex ratio vary over the winter? That is, on the assumption that changes in sex ratio between 1 December and 1 March would not be caused by migration, does it appear that one sex has a higher mortality rate at any latitude? In response, at no latitude (3° band) did the sex ratio of birds collected early differ significantly from that of birds collected late.

#### DISCUSSION

Having shown that most male juncos winter farther north than most females, we consider how such a system might have evolved. Choice of a wintering site presumably involves a compromise tending to optimize fitness by balancing selective impacts of various environmental factors. Because differences in fitness reflect differential mortality and/or differential reproduction, understanding of the compromise requires consideration of the influence of the environment on both these processes (von Haartman 1968). If factors differ in impact according to sex, it is necessary to treat the sexes separately when considering relative fitness. Note that if the system regulating geographic variation in sex ratio is in equilibrium and the environment is stable, average fitness of each population along the latitudinal cline should be the same; what changes along the cline is the relative impacts of the environmental factors. In the paragraphs to follow we shall ask what are the relevant

environmental factors, how might their impact vary geographically, and how might the sexes be differentially affected by them.

Important factors influencing fitness seem likely to be (1) cost of migration as determined by distance separating breeding and wintering sites; (2) arrival and departure times at breeding and wintering sites as affected by the distance between them; (3) intra-specific competition as determined by quantity and quality of birds wintering at the same site; (4) climate of the winter site selected. Geographic variation in predation pressure, interspecific competition, parasite and pathogen occurrence and density, and net primary production may also play a role in determining geographic variation in sex ratio. However these will not be considered here because we cannot elaborate on them.

#### *Direct cost of migration*

Because migration requires time and energy, we might assume that its caloric cost increases with distance traveled. However, Dolnik (1971a) has noted that thermoregulatory requirements on a seasonal basis are lower at lower (warmer) latitudes, and a comparison of calories spent on migration with calories saved on thermoregulation shows they often balance. Even if we limit concern to the days a bird is actually engaged in migratory flight, it might still be argued that the caloric cost of migration is not large; Dolnik (1971b), for example, indicates that the cost of migration in units of existence energy per day is no more than that for molt or breeding.

The cost of migration, however, is more than the caloric cost of flight. In many species, migration is interrupted by stopovers lasting several days (King 1961, Dolnik and Blyumenthal 1967) during which the migrant is in unfamiliar areas where locations of food sources and potential predators are probably unknown to him. Although Helms et al. (1967) estimate that in early April the average junco near Lewisburg, Pennsylvania, has sufficient fat to reach the nearest suitable breeding habitat in a single flight, both Johnston's (1962:395) data from North Carolina and the great sizes of the junco's breeding and winter ranges indicate that most individuals must interrupt migration with stopovers. Our trapping in Indiana also suggests this: During both fall and spring migrations we catch many juncos repeatedly for several days, then never see them again. Added evidence of junco stopovers during migration is provided by banders' recoveries far from original capture sites. These indicate that the summer and winter quarters of at least some individuals are separated by minimum distances of 1,000–1,500 km (Low 1931, Daley 1931, Beals 1939, Broun 1943, Cooke 1943, Stevens 1944, Gray 1948). (Because activity

of bird banders is largely at and south of the southern limits of the breeding range, migrations much longer than 1,500 km could take place with very little likelihood of being detected.) Therefore, perhaps more important than the energetic cost of migration is the risk involved, and while we know of no data comparing predation losses of migrants and local residents, we suggest that the difference may be substantial. Yet another risk of migration is severe weather, which at times causes massive bird kills (Roberts 1907, Saunders 1907). Each of these risks may be in rough proportion to the time (distance) spent migrating.

We can imagine no reason why the sexes should *a priori* be differentially affected by migration costs and risks per unit time or distance traveled. If there is no such sexual difference, and therefore the average female's migration is more demanding and hazardous than the average male's, she must gain compensating advantages on her more southerly wintering site.

#### *Arrival and departure times*

Birds with shorter distances to travel may be better able to time their comings and goings to maximize advantages at their seasonal destinations. Such advantages have been associated primarily with early arrival on the breeding grounds (but not too early, see Vepsäläinen 1968), and reported cases concern males. Among Great Tits (*Parus major*) first arrivals occupy preferred habitat (Kluyver and Tinbergen 1953); among Chaffinches (*Fringilla coelebs*) late arrivals acquire smaller territories (Bergman 1953); among Yellowhammers (*Emberiza citrinella*) territories established in March are superior to those established in April (Wallgren 1956); among Prairie Warblers (*Dendroica discolor*) early-arriving males obtain mates sooner, nest sooner, and thus have longer breeding seasons (V. Nolan, *personal observation*). Since in the reported partially migratory species and species exhibiting geographic variation in sex ratio it is the males that are nonmigratory or that winter farther north (Lack 1943, 1944, Selander 1966, Dolnik and Blyumental 1967, von Haartman 1968), it seems probable that this behavior confers particular reproductive advantage on the sex that takes the initiative in establishing and maintaining territory. In this vein, von Haartman (1968), while speculating about the origin of the sedentary habit in bird species, has suggested that sedentary individuals in a partially migratory species may compensate for lowered life expectancy due to harsh climate by out-competing migrants for breeding resources and thereby raising more young. This logic may be extended to geographic variation in sex ratio: Males, by wintering farther north, may risk greater mortality but may compensate for such losses by arriving on

the breeding grounds at the optimum time. However, we emphasize that we are aware of no data supporting the contention that wintering closer to the breeding grounds promotes timely arrival. Obviously, individuals wintering farther south could initiate migration earlier and pace their stopovers en route to eliminate any timing advantage accruing to northern individuals.

Turning to females, little is known of the level of female competition for breeding resources. The fact that midseason replacement of females experimentally removed from breeding populations occurs in some species (von Haartman 1971) may suggest a surplus of nonbreeders that are unable to find mates. Other evidence, however, implies a shortage of breeding females relative to males (Snow 1954, Tompa 1964, Bulmer and Perrins 1973); and our own calculations (above) suggest there may be fewer female than male juncos in the eastern and central United States during winter. Even if all female juncos do obtain mates, it seems reasonable to assume that early arrivals might have a wider choice of both males and territories and thereby enjoy a reproductive advantage. In any event, it is critical only that a female arrive before others of her sex; wintering farther south than males should not influence fitness in this context.

Time of arrival on the wintering grounds may also influence fitness. Sabine (1959) and E. Ketterson (*personal observation*) found early arrival to be positively correlated with rank in dominance hierarchies among wintering juncos visiting baited areas, and Fretwell (1969) reports that high rank increases chances of overwinter survival. Again we add that we are aware of no evidence that shorter-distance migrants do in fact arrive earlier or at the optimum time.

#### *Intraspecific competition*

According to Lack (1966) and Fretwell (1972), insufficient food during winter is the most likely factor controlling density of temperate bird populations. Thus competition for food is a possible contender as a cause of geographic variation in sex ratio. Further, because females of many bird species tend to lose aggressive encounters to males during winter (Tordoff 1954, Brown 1963, Martin 1970, Ralph 1975), we might expect disadvantages stemming from intraspecific competition to be greater for the female. Female juncos frequenting baited stations near Bloomington, Indiana, lose in aggressive encounters with males, and such encounters occur most frequently under adverse weather conditions that we surmise increase food needs (E. Ketterson, *personal observation*). Fretwell (1969) reports that dominant juncos in North Carolina have longer wings (= males?)

and are more likely to be recaptured (= survive?) at the end of a winter than subdominants (= females?). Fretwell's interpretation is that "dominance behavior in the flock is a natural factor regulating food utilization, distribution, and mortality in juncos." If food is limiting, both Ketterson's and Fretwell's findings suggest that the resulting competition could lead to geographic variation in sex ratio.

We think it likely that reduction of intersexual competition for winter resources has been an ultimate factor in the differential winter distribution of the sexes. However, forces other than this competition have probably contributed to the pattern, and clinal variation in sex ratio rather than strict allopatry of the sexes is not unexpected. For example, recalling that the breeding range is extensive, it seems especially likely that females originating in northern portions of that range may achieve optimal fitness by selection of a winter site north of the latitude of modal female abundance. Further, there may be a point at which the intensity of intrasexual competition exceeds that of intersexual, making it advantageous to overwinter with a larger proportion of males than would be encountered if migration were extended.

#### *Climate*

Because climatic measures are highly correlated with sex ratio, it may follow that fitness is in part a function of climate at the wintering site and that the sexes are differentially affected by climate. The lower temperatures and heavier snows associated with sites to the north imply both increased food demands for wintering birds and also, for ground-feeding species like the junco, greater difficulty in obtaining that food. Several factors, however, have led some investigators (e.g., King and Farner 1966, Newton 1966, Evans 1969) to doubt whether winter weather plays a significant role in mortality: (1) Dead birds are rarely encountered in the field. (2) In many temperate passerines, winter body weight is inversely related to air temperature (Baldwin and Kendeigh 1938, Helms and Drury 1960, King and Farner 1966, Evans 1969). (3) Laboratory studies indicate that many avian species can maintain energy balance at air temperatures considerably lower than those they are likely to encounter in nature.

King and Farner (1966) "find it difficult to envision that natural selection should operate to produce a population existing at the margin of trophic crisis for any large fraction of its annual cycle" and conclude that "permissive factors (food availability, day length, thermoregulatory expenditure) only rarely become limiting in moderate temperate environments." Nevertheless, environmental conditions encountered only rarely may have been met sufficiently

often to effect adaptation. Fretwell (1972:177) has noted that "it does a bird no good to survive very efficiently for 99 percent of the winter days if it is likely to die on the remaining 1 percent," and Tinbergen (1957:25) has stated that "selection acts when situations are critical. It is the days when food is exceptionally scarce" that require study.

Assuming that climate has been partly responsible for adaptation in juncos, we may ask the nature of the adaptation to be expected. Reports of bird mortality in response to severe weather usually attribute death to one of three causes: icing, prolonged snow cover accompanied by subnormal temperatures, or rapidly falling temperatures associated with high winds and precipitation (Bumpus 1899, Odum and Pitelka 1939, Scott and Baskett 1941, Larsen and Lahey 1958, Roseberry 1962, Hanson and Kossak 1963:101, Dobinson and Richards 1964, Macdonald 1965, Hilden and Koskimies 1969, McGowan 1969, Johnston et al. 1972, Rising 1973). Victims of the first two causes probably starved because food was inaccessible while thermoregulatory demands were high. Death from the third cause suggests that heat loss greatly exceeded heat production for a relatively short time until the birds froze. When ice and snow are the causes of mortality we expect that selection should favor those individuals with a greater ability to acquire food, or to store it, or to use it conservatively; conditions causing death by freezing should select for individuals of greater summit metabolism. We shall concentrate on adaptation to icing and snow cover, because there is field evidence that juncos encounter and sometimes die in such weather. Roseberry (1962) counted 5 dead juncos among 112 carcasses (12 species) found during a period of extended cold and snow cover in Illinois. Johnston (1962) reported that during the same winter (1960) juncos in North Carolina showed a mid-February weight loss. He attributed the loss to low temperatures and a period of heavy snow lasting more than 2 weeks and stated, "a few juncos expired in their cages and others were found dead in the snow near the nets, their carcasses being extremely emaciated."

The best known morphological correlate of climate is described by Bergmann's Rule (as interpreted by Mayr 1963), which states that larger individuals of a species are found in cooler climates or, as recently reinterpreted by James (1970), in cooler and/or drier climates. Occurrence of larger individuals in the northern part of the range has been described for numerous breeding birds, both migratory and sedentary species (Snow 1954, Hamilton 1961, Rand 1961, Johnston and Selander 1971, Power 1969, James 1970), and Bergmann's Rule may therefore be said to have empirical validity for populations of breeding birds on an intraspecific level.

Our data on clinal variation in wing length among wintering juncos are reminiscent of Bergmann's Rule, although they can be explained in terms of the males' greater size and the clinal variation in sex ratio. Under the rule we expect larger individuals within each sex to winter further north (compare Diamond 1973), but analysis of our wing-length data reveals no such latitudinal trend. However, Helms et al. (1967) have reported for the junco that "significant shifts in size and weight between fall migration, winter, and spring migration indicate that smaller and lighter birds tended to winter farther south. This conclusion is supported by parallel shifts in size and weight within each sex." We are continuing our investigation of intrasexual size differences in wintering juncos, a matter we consider important in view of the absence of detailed studies of such differences in winter bird populations.

Another empirical rule, the size-metabolism relationship, which states that body size is inversely related to metabolic rate per gram, has often been cited as the physiological basis for Bergmann's Rule. But because birds rarely exist in one-gram units, the level at which the advantage is achieved, the importance of the size-metabolism relationship in this context has been questioned (Scholander 1955, McNab 1971). According to Selander (1971:82), "the advantage of larger body size . . . in relation to body temperature regulation may be offset by greater requirements for food, and thus Bergmann's Rule will be expressed only when the physiological advantages outweigh the ecological disadvantages." If food is limiting either in absolute amount or availability, we might even expect selection for minimum body size, as has been proposed by Fretwell (1972); yet just the opposite pattern is observed. Kendeigh (1969) suggests, on the interspecific level, an advantage of large size in colder climates: With increasing size the rate of increase in metabolic rate per degree drop in temperature becomes smaller. Even so, and even if this relationship holds true within a species, the food requirements of the smaller of two conspecifics would still be lower in snowy, cold weather.

A solution to the problem has recently been proposed by Calder (1974, 1975; see also Lindsey 1966, Rosenzweig 1968). Fasting endurance, or the length of time an individual can survive on stored energy in the absence of food, may be the critical size-related variable causally linking the size-metabolism relationship to Bergmann's Rule. The greater the amount of energy stored in fat relative to metabolic rate, the longer a bird is able to endure fasting. If ice and snow temporarily prevent access to food, then those individuals best able to wait out inclement conditions may be favored; and if those favored

are larger, Bergmann's Rule may be accounted for. Calder (1974) expressed fasting endurance allometrically as follows: Because existing data from a variety of small birds during winter suggest that the proportion of body weight composed of fat does not vary with body size, the slope relating stored fat to body size is 1. According to Kendeigh (1969), the rate of increase in standard metabolic rate with body weight at 0°C among passerines is 0.417, i.e., < 1. Therefore the ratio of energy stored as fat to rate of use, i.e., fasting endurance, increases with size.

To apply these considerations to juncos, it is notable that on a population basis juncos show the typical inverse relation between air temperature and body weight (Helms and Drury 1960); see point (2) above. Despite this, in extreme conditions some individuals die, and those that survive may do so because they are better adapted to dealing with cold and snow. Two primary reasons for thinking that males might be better able to cope with such conditions are (1) their larger size and consequent advantage in aggressive encounters for food (see previous section), and (2) the greater fasting endurance associated with larger size. If males do indeed enjoy these advantages, geographic sex-ratio variation like that observed might be expected.

We have calculated fasting endurance for four hypothetical juncos thought to represent average and extreme differences between the sexes. The following procedure was used.

TABLE 8. Estimated fasting endurance of wintering juncos. Fasting endurance = Energy stored (0.15w) / Metabolic rate (19.967w<sup>0.417</sup>), where w = wet weight. See text for methods

Wet weight (g)	18.0	21.0	22.5	28.0
Utilizable stored fat (g) (94% of 0.15w)	2.54	2.96	3.17	3.95
Utilizable stored fat (kJ)	101.01	117.85	126.27	157.13
Metabolic rate (kJ/day)	66.644	71.069	73.143	80.127
Fasting endurance (h)	36.38	39.80	41.43	47.06

*Weight*

Helms and Drury (1960) found afternoon weights of juncos in Massachusetts to range from 18–28 g during December, January, and February, when mean population weights ranged from 21.5–25 g. Helms et al. (1967), who shot rather than trapped their birds and combined morning and afternoon samples, found wintering juncos in Pennsylvania to average ≈ 22 g, males averaging 1.22 g heavier than females on a season-long basis (November–April). Accordingly we selected 18 g and 28 g to represent the extreme difference between the sexes and 21 g and 22.5 g to represent average sexual

difference among members of the same wintering population.

#### *Fat as a percent of wet weight*

This variable does not differ significantly between the sexes in the junco, but neither does the absolute amount of fat (Helms et al. 1967). In general, however, fat has been found to constitute a constant proportion of wet weight (Calder 1974), and we assume for the purposes of this argument that fat as a percentage of wet weight is similar for the sexes. Helms et al. (1967) report that the mean percentage varies seasonally from 8% to 17%. For a reasonable maximum, likely to obtain on colder days, we chose 15%. The energy equivalent of 1 g of fat is 39.8 kJ (9.5 kcal), 94% of which is utilizable as fuel (Helms et al. 1967).

#### *Metabolic rates*

Kendeigh's (1969) equation estimating standard metabolism at 0°C for passerines of any weight converted to S.I. units is  $M.R. = 19.967w^{0.417}$  (kJ/day), where  $w$  is wet weight in grams ( $= 4.769w^{0.417}$  kcal/day).

Using these assumptions and related values, the equation for fasting endurance was solved (Table 8). Solutions ranged from 36–47 h. A male of average size should be able to endure fasting 1.63 h or 4% longer at 0°C than an average-size female; very fat birds may be able to fast as much as 29% longer than very light ones. Differences should increase as air temperatures fall below 0°C, because metabolic stress per degree drop in temperature is inversely related to body size (Kendeigh 1969). Although a difference of less than 2 h may appear inconsequential, under certain not unusual circumstances it could be critical. For example, birds finishing feeding at  $\approx 1700$  after a normal midwinter day might awake the following morning to conditions precluding feeding for the entire day. Roosting on the second night would begin with the birds having fasted for 24 h. Even if the third day dawned clear at  $\approx 0800$  and food were again available in normal quantities, individuals that began the fast with fat stores sufficient to last 39 h would be dead or too weak to forage, whereas individuals capable of fasting for 41 h could start feeding. In any winter conditions, the importance of small differences in fasting endurance would be magnified if the less enduring individuals, here females, also tend to lose aggressive encounters over food.

Our estimates of fasting endurance may be compared to some previously reported. Kendeigh (1945) starved juncos in the dark and without water. At  $-14^\circ\text{C}$  time to death averaged 37 h (initial weight 21.8 g,  $n = 12$ ); at  $-3^\circ\text{C}$ , 51 h (initial weight 21.8 g,  $n = 20$ ); and at  $35^\circ\text{C}$ , 54 h (initial weight 20.7 g,  $n$

$= 4$ ). Helms and Drury (1960) held one junco for 45 h before releasing it with no apparent long-term ill effects. Nolan has several times held juncos at room temperature for 48 h without causing death. By comparison with other species that encounter severe weather, the junco's insurance against food shortage appears to be unusually great. High percentages (90% or more) of wintering populations of Rosy Finches (*Leucosticte tephrocotis*, King and Wales 1964), Black-capped Chickadees (*Parus atricapillus*, Chaplin 1974), Yellowhammers (Evans 1969), and White-crowned Sparrows (King and Farner 1966) are estimated to carry fat sufficient to fuel an overnight fast and also flight to the feeding area the following morning. But few individuals are thought to have enough fat to survive the following 24 h without food.

Of particular relevance here are findings of Ivacic and Labisky (1973), who tested Mourning Doves under simulated winter conditions of low ambient temperatures and absence of food. Adults, particularly males, showed greater potential survival ability than immatures, particularly females. These facts, plus evidence that male Mourning Doves predominate in northern portions of the winter range (Quay 1951), support the notion that climate might play a causal role in effecting geographic variation in sex ratio. Similarly, White-crowned Sparrows exhibit differential fasting ability of the sexes (males longer than females, E. Ketterson and J. R. King, *personal observation*) and geographic variation in sex ratio (King et al. 1965).

Sexual differences in fasting endurance, suggested by our calculations, give added significance to the finding that extreme measures of climate predict sex ratio fully as well as does latitude alone. At higher latitudes during and after severe storms, food may be unobtainable or may be present only in small scattered patches which are likely to be dominated by males; further, all individuals must fast longer because of the longer interval of darkness. The ability to endure such rigors sustained by fat reserves may determine which birds survive, and because of average larger size, males may have a greater probability of succeeding.

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#### LITERATURE CITED

- Arbib, R. S. Jr. [ed.] 1972. 72nd Christmas Bird Count. *Am. Birds* **26**:135-550.
- Baldwin, S. P., and S. C. Kendeigh. 1938. Variations in the weight of birds. *Auk* **55**:416-467.
- Ralph, M. H. 1975. Wing length, hood coloration, and sex ratio in Dark-eyed Juncos wintering in northern Utah. *Bird-Banding* **46**:126-130.
- Beals, M. V. 1939. Ten years of banding at Birdwood. *Bird-Banding* **10**:1-15.
- Bellrose, F. C., T. G. Scott, A. S. Hawkins, and J. B. Low. 1961. Sex ratios and age ratios in North American ducks. *Ill. Nat. Hist. Surv. Bull.* **27**:391-474.
- Bent, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies; order Passeriformes: family Fringillidae. O. L. Austin, Jr. [ed.] *U.S. Natl. Mus. Bull.* **237**(2).
- Bergman, G. 1953. Über das Revierbesetzen und die Balz des Buchfinken *Fringilla coelebs* L. *Act. Soc. Fauna Flora Fenn.* **69**:1-15.
- Blake, C. H. 1964. Color and wing length in the Slate-colored Junco. *Bird-Banding* **35**:125-127.
- . 1967. More on the wing length of the Slate-colored Junco. *Bird-Banding* **38**:234.
- Bock, C. E., and L. W. Lepthien. 1974. Winter patterns of bird species diversity and abundance in the United States and southern Canada. *Am. Birds* **28**:556-562.
- Broun, M. 1943. A longevity-recovery record of a Slate-colored Junco. *Bird-Banding* **14**:46.
- Brown, J. L. 1963. Aggressiveness, dominance and social organization in the Steller Jay. *Condor* **65**:460-484.
- Bulmer, M. G., and C. M. Perrins. 1973. Mortality in the Great Tit *Parus major*. *Ibis* **115**:277-281.
- Bumpus, H. C. 1899. The elimination of the unfit as illustrated by the introduced sparrow, *Passer domesticus*. *Biol. Lectures, Mar. Biol. Lab., Woods Hole, Massachusetts*, p. 209-226.
- Calder, W. A. 1974. Consequences of body size for avian energetics, p. 86-144. In R. A. Paynter [ed.] *Avian energetics*. Nuttall Ornithological Club Publ. No. 15. Cambridge, Massachusetts.
- . 1975. Daylength and the hummingbirds' use of time. *Auk* **92**:81-97.
- Chaplin, S. B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus*, in winter. *J. Comp. Physiol.* **89**:321-330.
- Committee on Classification and Nomenclature. 1973. Thirty-second supplement to the American Ornithologists' Union Check-list of North American birds. *Auk* **90**:411-419.
- Cooke, M. R. 1943. Returns from banded birds: Some miscellaneous recoveries of interest. *Bird-Banding* **14**:67-74.
- Daley, F. K. 1931. Song Sparrow, junco and Purple Finch recoveries. *Bird-Banding* **2**:83.
- Diamond, A. W. 1973. Altitudinal variation in a resident and a migrant passerine on Jamaica. *Auk* **90**:610-618.
- Dixon, W. J. [ed.]. 1970. BMD biomedical computer programs. Univ. of Calif. Publ. in Automatic Computations **2**:1-600.
- Dobinson, H. M., and A. J. Richards. 1964. The effects of the severe winter of 1962/63 on birds in Britain. *Br. Birds* **57**:373-434.
- Dolnik, V. R. 1971a. Comparative energy expenditure in migration and wintering of birds. *Ekologiya* **2**:88-89. (In Russian)
- . 1971b. The degree of productive energy of birds at different phases of the annual cycle. *Ekologiya* **2**:89-91. (In Russian)
- Dolnik, V. R., and T. I. Blymental. 1967. Autumnal premigratory and migratory periods in the Chaffinch (*Fringilla coelebs coelebs*) and some other temperate-zone passerine birds. *Condor* **69**:435-468.
- Dow, D. D. 1966. Sex determination of Slate-colored Juncos by means of plumage characters. *Ont. Bird Banding* **2**:1-14.
- Evans, P. R. 1969. Winter fat deposition and overnight survival of Yellow Buntings (*Emberiza citrinella* L.). *J. Anim. Ecol.* **38**:415-423.
- Fretwell, S. D. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). *Bird-Banding* **40**:1-25.
- . 1972. Populations in a seasonal environment. *Monographs in population biology*, No. 5. Princeton Univ. Press, Princeton, New Jersey. 217 p.
- Grant, G. S., and T. L. Quay. 1970. Sex and age criteria in the Slate-colored Junco. *Bird-Banding* **41**:274-278.
- Gray, H. R. 1948. Banding data from Wilton, North Dakota. *Bird-Banding* **19**:159-162.
- Haartman, L. von. 1968. The evolution of resident versus migratory habit in birds. Some considerations. *Ornis Fenn.* **45**:1-7.
- . 1971. Population dynamics, p. 391-459. In D. S. Farner and J. R. King [ed.] *Avian biology I*. Academic Press, New York. 586 p.
- Hamilton, T. H. 1961. The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. *Evolution* **15**:180-195.
- Hanson, H. C., and C. W. Kossack. 1963. The Mourning Dove in Illinois. *Tech. Bull. No. 2*, Illinois Dept. of Conservation and Illinois Natural History Survey. Southern Ill. Univ. Press, Carbondale. 133 p.
- Helms, C. W., and W. H. Drury, Jr. 1960. Winter and migratory weight and fat: Field studies on some North American buntings. *Bird-Banding* **31**:1-40.
- Helms, C. W., W. H. Aussiker, E. B. Bower, and S. D. Fretwell. 1967. A biometric study of major body

- components of the Slate-colored Junco, *Junco hyemalis*. *Condor* **69**:560-578.
- Heydweiler, A. M. 1936. Sex, age, and individual variation of winter Tree Sparrows. *Bird-Banding* **7**: 61-68.
- Hilden, O., and J. Koskimies. 1969. Effects of the severe winter of 1965/66 upon winter bird fauna in Finland. *Ornis Fenn.* **46**:22-31.
- Howell, T. R. 1953. Racial and sexual differences in migration in *Sphyrapicus varius*. *Auk* **70**:118-126.
- Ivacic, D. L., and R. F. Labisky. 1973. Metabolic responses of Mourning Doves to short-term food and temperature stresses in winter. *Wilson Bull.* **85**:182-196.
- James, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* **51**:365-390.
- Jenkins, D., A. Watson, and G. R. Miller. 1965. Population studies in Red Grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. *J. Anim. Ecol.* **32**:317-376.
- Johnston, D. W. 1962. Lipid deposition and gonadal recrudescence in response to photoperiodic manipulations in the Slate-colored Junco. *Auk* **79**:387-398.
- Johnston, R. F., and R. K. Selander. 1971. Evolution in the House Sparrow. II. Adaptive differentiation in North American populations. *Evolution* **25**:1-28.
- Johnston, R. F., D. M. Niles, and S. A. Rowher. 1972. Herman Bumpus and natural selection in the House Sparrow *Passer domesticus*. *Evolution* **26**:20-31.
- Kendeigh, S. C. 1945. Resistance to hunger in birds. *J. Wildl. Manage.* **9**:217-226.
- . 1969. Tolerance of cold and Bergmann's Rule. *Auk* **86**:13-25.
- King, J. R. 1961. The bioenergetics of vernal pre-migratory fat deposition in the White-crowned Sparrow. *Condor* **63**:128-142.
- King, J. R., and D. S. Farner. 1966. The adaptive role of winter fattening in the White-crowned Sparrow with comments on its regulation. *Am. Nat.* **100**: 403-418.
- King, J. R., and E. E. Wales. 1964. Observations on migration, ecology, and population flux of wintering Rosy Finches. *Condor* **66**:24-31.
- King, J. R., D. S. Farner, and L. R. Mewaldt. 1965. Seasonal sex and age ratios in populations of the White-crowned Sparrows of the race *gambelii*. *Condor* **67**: 489-504.
- Kluyver, H. N., and L. Tinbergen. 1953. Territory and the regulation of density in titmice. *Arch. Neerl. Zool.* **10**:265-289.
- Lack, D. 1943, 1944. The problem of partial migration. *Br. Birds* **37**:122-130, 143-150.
- . 1966. Population studies of birds. Clarendon Press, Oxford. 341 p.
- Larsen, J. A., and J. F. Lahey. 1958. Influence of weather upon a Ruffed Grouse population. *J. Wildl. Manage.* **22**:63-70.
- Lindsey, C. C. 1966. Body size of poikilotherm vertebrate at different latitudes. *Evolution* **20**:456-465.
- Low, S. H. 1931. A junco recovery. *Bird-Banding* **2**:82.
- Macdonald J. W. 1965. Post-mortem condition of birds found dead during the 1963 cold spell. *Br. Birds* **58**:301-302.
- Martin, S. G. 1970. The agonistic behavior of Varied Thrushes (*Ixoreus naevius*) in winter assemblages. *Condor* **72**:452-459.
- Mayr, E. 1963. Animal species and evolution. Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts. 797 p.
- McGowan, J. D. 1969. Starvation of Alaskan Ruffed and Sharp-tailed Grouse caused by icing. *Auk* **86**: 142-143.
- McNab, B. K. 1971. On the ecological significance of Bergmann's Rule. *Ecology* **52**:845-854.
- Miller, A. H. 1941. Speciation in the avian genus *Junco*. *Univ. Calif. Publ. Zool.* **44**:173-434.
- Newton, I. 1966. Fluctuations in the weights of Bullfinches. *Br. Birds* **59**:89-100.
- Nice, M. M. 1937. Studies in the life history of the Song Sparrow I. *Trans. Linn. Soc. N.Y.* **4**:1-247.
- Odum, E. P., and F. A. Pitelka. 1939. Storm mortality in a winter Starling roost. *Auk* **56**:451-455.
- Power, D. M. 1969. Evolutionary implications of wing and size variations in the Red-winged Blackbird in relation to geographic and climatic factors: A multiple regression analysis. *Syst. Zool.* **18**:363-373.
- Quay, T. L. 1951. Mourning Dove studies in North Carolina. North Carolina Wildl. Resources Comm. Raleigh, North Carolina. 90 p.
- Rand, A. L. 1961. Some size gradients in North American birds. *Wilson Bull.* **73**:46-56.
- Rand McNally Collegiate World Atlas. 1962. Rand McNally and Co., Chicago. 309 p.
- Rising, J. D. 1973. Age and seasonal variation in dimensions of House Sparrows, *Passer domesticus* (L.), from a single population in Kansas, pp. 327-336. In S. C. Kendeigh and J. Pinowski [ed.] Productivity, population dynamics and systematics of granivorous birds, Proc. General Meeting of the Working group on Granivorous Birds, IBP, PT Section. The Hague, Holland, September 6-8, 1970.
- Roberts, T. S. 1907. A Lapland Longspur tragedy. *Auk* **24**:369-377.
- Roseberry, J. L. 1962. Avian mortality in southern Illinois resulting from severe weather conditions. *Ecology* **43**:739-740.
- Rosenzweig, M. L. 1968. The strategy of body size in mammalian carnivores. *Am. Midl. Nat.* **80**:299-315.
- Sabine, W. S. 1959. The winter society of the Oregon Junco: intolerance, dominance, and the pecking order. *Condor* **61**:110-135.
- Saunders, W. E. 1907. A migration disaster in western Ontario. *Auk* **24**:108-110.
- Schäfer, E., and R. M. deSchauensee. 1939. Zoological results of the second Dolan expedition to western China and eastern Tibet, 1934-1936. Pt. II—Birds. *Proc. Acad. Nat. Sci. Philadelphia* **90**:185-260.
- Scholander, P. F. 1955. Evolution of climatic adaptations in homeotherms. *Evolution* **9**:15-26.
- Scott, T. G., and T. S. Baskett. 1941. Some effects of the 1940 Armistice Day storm on Iowa's wildlife. *Iowa Bird Life* **11**:23-29.
- Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* **68**:113-151.
- . 1971. Systematics and speciation in birds, p. 57-147. In D. S. Farner and J. R. King [ed.] Avian biology I. Academic Press, New York. 586 p.
- Senk, R., A. Senk, and H. Wörner. 1972. Zur Frage: Überwintern nur männliche Feldlerchen (*Alauda arvensis*) in Westdeutschland. *Die Vogelwarte* **26**: 314.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 312 p.

- Snow, D. W. 1954. Trends in geographical variation in the Palearctic members of the genus *Parus*. *Evolution* **8**:19-28.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. W. F. Freeman and Co., San Francisco. 776 p.
- Stack, J. W., and R. L. Harned. 1944. Seventeen years of banding White-throated Sparrows and Slate-colored Juncos at Michigan State College. *Bird-Banding* **15**: 1-14.
- Stevens, O. A. 1944. Fifteen years banding at Fargo, North Dakota. *Bird-Banding* **15**:139-144.
- Stewart, R. E., and C. S. Robbins. 1958. Birds of Maryland and the District of Columbia. *North Am. Fauna* **62**.
- Tinbergen, N. 1957. The functions of territory. *Bird Study* **4**:14-27.
- Tompa, R. 1964. Factors determining the numbers of Song Sparrows, *Melospiza melodia* (Wilson), on Mandarte Island, B. C., Canada. *Act. Zool. Fenn.* **109**:1-73.
- Tordoff, H. B. 1954. Social organization and behavior in a flock of captive, nonbreeding Red Crossbills. *Condor* **56**:346-358.
- U.S. Department of Agriculture. 1941. *Climate and man*. (Yearbook of Agriculture.) U.S.D.A., Washington, D.C.
- U.S. Weather Bureau Bulletin W. 1932. *Climatology of the United States*, Sections 1-106.
- Vepsäläinen, K. 1968. The effect of the cold spring 1966 upon the Lapwing (*Vanellus vanellus*) in Finland. *Ornis Fenn.* **45**:33-47.
- Wallgren, H. 1956. Zur Biologie der Goldammer, *Emberiza citrinella* L. *Act. Soc. Fauna Flora Fenn.* **71**: 1-44.