# SEASONAL, ANNUAL, AND GEOGRAPHIC VARIATION IN SEX RATIO OF WINTERING POPULATIONS OF DARK-EYED JUNCOS (*JUNCO HYEMALIS*)

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Abstract.—Previously published data pooled over entire winters showed clinal variation in the winter sex ratio of *Junco h. hyemalis*. Females were less numerous than males in the north and progressively more numerous southward.

In this study, regression coefficients calculated from the published data, with latitude and certain climatic measures as independent variables, accurately predicted the winter sex ratio of locations not previously sampled. Annual variation in sex ratio was nonsignificant. The pattern of distribution was established by the end of fall migration, before differential mortality could have accounted for it. Temperature rather than latitude, snowfall, or probable distance from the nearest breeding grounds correlated best with percentage of females in winter populations. It is suggested that climate has acted primarily indirectly to produce the sex-associated difference in winter distribution. Under this hypothesis, as climate becomes harsher, the impact of male dominance over females becomes more severe, resulting in increasing withdrawal by females from locations settled by males and thus in clinal variation in sex ratio. *Received 15 December 1978, accepted 27 February 1979.*

We earlier reported that the sex ratio of Dark-eyed Junco (*Junco hyemalis*) populations wintering in the eastern United States varies clinally, with the percentage of females increasing progressively toward the south (Ketterson and Nolan 1976). Latitude and a set of climatic variables accounted for more than 93% of the variation in sex ratio found in the 1976 data set. That sample consisted of 616 museum specimens and 473 live-caught birds, the former group collected over many winters, the latter banded by us during four winters. Only cases from the period December through February were considered, and these were combined for analysis. Climatic variables were based on weather averaged over 50 yr (U.S. Weather Bureau 1932). Thus the pattern of geographic variation that we described was based on long-term sampling of winter populations and weather. This approach left a number of interesting questions unanswered, and we now state these and present our recent efforts to answer them.

Objectives of this research were as follows:

(1) to predict sex ratios of winter junco populations at previously unstudied sites using equations derived from our earlier work, to capture samples at those sites, and to compare observed and expected ratios, i.e. to learn whether our initial results had predictive value;

(2) to sample sex ratios from several locations over more than 1 yr and thus to investigate the question of annual variation;

(3) to compare sex ratios obtained in December alone with ratios obtained by pooling data from entire winters, as described above, and thus to learn whether the basic pattern of distribution is established by the settlement of juncos arriving in the winter range or by subsequent differential winter mortality according to sex; and

(4) to determine the relative accuracy of various environmental variables in predicting sex ratio, i.e. to pursue investigation of the ultimate selective factor(s) responsible for geographic differences in winter sex ratio.

We therefore obtained new field information from six sites and found published

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TABLE 1. Percentages of females in seven wintering junco populations, according to year.[a]

| Location[b] | Date | N | Sex ratio (%♀♀) | $\chi^{2c}$ |
|---|---|---|---|---|
| Pullman, Washington (WA) (47°N, 117°W) | Dec–Feb 1974/75 | 168 | 28.0 | — |
| Logan, Utah[d] (UT) (42°N, 112°W) | Nov–Feb 1972/73, 1973/74 | 221 | 23.8 | — |
| Kalamazoo, Michigan (MI) (42°N, 86°W) | Dec 1976 | 111 | 22.5 | 0.67 |
| | Dec 1977 | 105 | 17.1 | |
| | *Total* | *216* | *19.9* | |
| Portage, Ohio (OH) (41°N, 84°W) | Dec–Feb 1975/76 | 46 | 37.0 | 0.30 |
| | Dec–Feb 1976/77 | 68 | 32.4 | |
| | Dec 1977 | 22 | 36.4 | |
| | *Total* | *136* | *34.6* | |
| Bloomington, Indiana (IN) (39°N, 87°W) | Dec–Feb 1973/74 | 160 | 31.9 | 2.14 |
| | Dec–Feb 1976/77 | 253 | 28.5 | |
| | Dec 1977 | 361 | 25.8 | |
| | *Total* | *774* | *27.9* | |
| Clemson, South Carolina (SC) (35°N, 83°W) | Dec 1976 | 104 | 59.6 | 3.34 |
| | Dec 1977 | 88 | 45.5 | |
| | *Total* | *192* | *53.1* | |
| Birmingham, Alabama (AL) (33°N, 87°W) | Dec 1976 | 37 | 70.1 | 0.04 |
| | Dec 1977 | 14 | 78.6 | |
| | *Total* | *51* | *72.5* | |

[a] None of these data appear in Ketterson and Nolan (1976).
[b] Degrees latitude and longitude were rounded to the nearest whole degree.
[c] Chi-square statistic tests independence of numbers of males and females according to season at each site. For Ohio and Indiana, df = 2; for Michigan, South Carolina, and Alabama, df = 1 and $\chi^2$ is adjusted. In all cases, $P < 0.05$.
[d] Data are from Balph (1975).

data (Balph 1975) from one additional site. Two of these seven locations had supplied data for our 1976 paper. It will be apparent that no one site was useful in investigating all of the foregoing objectives.

## METHODS

Methods were as described in Ketterson and Nolan (1976), except as specified below. Locations supplying data are shown in Table 1. Because the point will become important in the discussion section, we state here that we believe, on the basis of distributions described in Bent (1968), that the Washington population belonged to the formerly accepted taxon *J. oreganus montanus,* now *J. hyemalis oreganus* (see Committee on Classification of Nomenclature 1973).

We sexed juncos with virtually 100% accuracy, using either external characters or, in cases of doubt, laparotomy (Ketterson and Nolan 1976). Because our previous work dealt only with eastern populations, we report that the Washington sample exhibited sexual differences in crown pattern similar to those of eastern juncos and that size dimorphism was also comparable to that of eastern juncos (mean male wing length = 81.0 mm, SD = 1.60, n = 121; mean female wing length = 76.0 mm, SD = 1.36, n = 47). Only one of 58 Washington juncos sexed by these external characters and then examined for gonads was incorrectly determined (<2% error). As far as we know, the accuracy of our method of sexing has not been previously reported in connection with western juncos. Utah birds were sexed by Balph (1975) on the basis of hood color and wing length, although 13% of the sample was not sexed by these criteria.

Table 2 presents regression equations, calculated from the data published in 1976, relating the junco's sex ratio to latitude (LATITU), average temperature for December–February (WINTEM), average daily minimum temperature in January (JANTEM), and average annual snowfall (ANSNOW). Table 3 shows observed sex ratios and those predicted by each regression equation.

## RESULTS AND DISCUSSION

*Predicted sex ratio.*—At the five previously unstudied sites (Table 1, WA, UT, MI, OH, SC) overall sex ratios, i.e. combined across years when sampling covered

TABLE 2. Descriptive equations relating sex ratio (% females) to environmental variables.[a]

| Independent variable[b] | Slope | Intercept | SE estimate | $F^{c}$ | $r^2$ |
|---|---|---|---|---|---|
| LATITU | −0.037 | 1.819 | 0.071 | 85.6 | .851 |
| WINTEM | 0.016 | −0.165 | 0.071 | 85.2 | .851 |
| JANTEM | 0.017 | −0.012 | 0.084 | 57.0 | .791 |
| ANSNOW | −0.010 | 0.608 | 0.092 | 44.1 | .746 |

[a] These equations are derived from data in Ketterson and Nolan (1976).
[b] See text for definitions of names of independent variables.
[c] df = 1, 15.

more than 1 yr, differed in only one case (Washington) from the ratios predicted by equations derived from our earlier paper (Tables 2 and 3). We therefore conclude that the equations have predictive power.

*Annual variation.*—Year-to-year variation in sex ratio ranged from 5% to 14% at the five sites supplying more than one winter's data; in no case was it significant (Table 1, MI, OH, IN, SC, AL).

*Date of establishment of winter sex ratio.*—The pattern of clinal variation in sex ratio is evident in eastern junco populations as early as December, as Table 1 shows. Ratios obtained in Indiana and Ohio when only December was sampled did not differ from ratios at the same locations in samples taken throughout winter in earlier years. In a test of independence of the Indiana December 1977 ratio and the pooled Indiana 1973/74, 1976/77 ratio, adjusted $\chi^2 = 1.35$; in a similar test of the Ohio December 1977 ratio and the pooled Ohio 1975/76, 1976/77 ratio, adjusted $\chi^2 = 0.00$. Further, all samples from Michigan, South Carolina, and Alabama were obtained in December alone, and, as indicated in the first paragraph of this section, sex ratios at these sites corresponded to those found in our pooled winter data published in 1976.

Thus the observed ratios do not, as Baker and Fox (1978) have suggested, arise each year from sexual differences in winter mortality. Rather, the pattern of distribution appears to be the result of the tendency of females to migrate to more southerly latitudes than males. This is not to say that mortality according to sex is uniform. Preliminary data indicate that differential mortality occurs in northern locations and by the end of winter serves to exaggerate the skewed ratio; but the basic distribution of sex classes is present prior to the period of severe weather (Nolan and Ketterson, unpublished data).

TABLE 3. Comparison of observed[a] and predicted winter percentages of female juncos at seven sites.

| Location | Observed sex ratio (%♀♀) | Predicted sex ratio (%♀♀) | | | |
|---|---|---|---|---|---|
| | | LATITU | WINTEM | JANTEM | ANSNOW |
| WA | 28.0 | 08.0[b] | 32.5 | 38.2 | 15.9 |
| UT | 23.8 | 26.5 | 24.6 | 26.0 | 10.2 |
| MI | 19.9 | 26.5 | 23.2 | 26.0 | 05.9 |
| OH | 34.6 | 30.2 | 26.1 | 27.5 | 31.6 |
| IN | 27.9 | 37.6 | 33.1 | 32.8 | 37.2 |
| SC | 53.1 | 52.4 | 53.4 | 54.6 | 57.5 |
| AL | 72.5 | 59.8 | 57.1 | 61.7 | 59.0 |

[a] Data on observed sex ratio were averaged across years (see Table 1).
[b] Indicates case where observed sex ratio differed from predicted sex ratio (at sites in Washington, Utah, Michigan, Ohio, South Carolina) by greater than 2 standard errors of the estimate (see Table 2). Because Indiana and Alabama were among the sources of data for the predictions, observed and predicted ratios at those locations were not compared.

*Comparison of environmental variables as predictors: selective factors responsible for differential migration.*—Temperature provided consistently better estimates of sex ratio than did latitude or snowfall: sex ratios at five locations were most accurately predicted by a temperature variable (Table 3). Snowfall was about as accurate as temperature at sites where snowfall is moderate or light, but in regions of heavy snow (Washington, Utah, Michigan) it tended to underestimate the proportion of females in the population.

We believe that the data from Washington are important in suggesting the ultimate factors responsible for the differences in winter distribution of the sexes. In our earlier paper we proposed that these factors included some combination of (1) increasing cost of migration with increasing distance traveled; (2) sex-associated differences in advantages of early arrival on the breeding and/or wintering grounds; (3) relative effects of low temperature and snow cover (i.e. intermittent restriction of food) on sex classes, which differ in body size (males larger than females); and (4) differential impact on the sexes of intersexual competition for winter food (see also Balph 1975, Gauthreaux 1978). With respect to these, Washington departs from the pattern prevailing in most of the eastern United States, where there is covariation among latitude, climate, and distance separating the junco's breeding range from sites in the winter range. Instead, Washington's latitude is higher than that of any other location sampled and its distance to potential breeding locations shorter, whereas its winter temperatures are like those much farther south (e.g. at the Indiana site). Although the breeding grounds of the Washington winter population are unknown, Bent (1968) describes that of *J. oreganus montanus* (see above) as lying near the Washington site to the east, north, and west (see also Jewett et al. 1953, Burleigh 1972).

Considering now that climate rather than latitude or distance to the breeding grounds proved the best predictor of sex ratio in Washington, climate may also be the critical variable affecting the clinal variation found in the east. The four factors listed in the preceding paragraph may have interacted as follows to produce the variation: For both sexes, settlement for winter in locations near the breeding grounds is advantageous in minimizing costs of migration and facilitating optimally timed arrival at both breeding and winter sites. Because they are subordinate to males and therefore probably suffer in intersexual competition for winter food, however, females tend to segregate themselves from males, and this segregation requires a longer migration. If the adverse impact on females of subordinance in intersexual competition varies with severity of climate, i.e. with food availability and energetic demands associated with temperature, then females would be expected to select sites close to the breeding range when the winter climate there is mild, but farther away when it is harsh. We believe this hypothesis could account for the occurrence at the Washington site of a greater proportion of females than was predicted from the close correlation between latitude and sex ratio in the eastern United States.

In our earlier analysis we placed greater emphasis on physiological considerations associated with climate—e.g. lesser fasting endurance of females as compared to males. It is, of course, evident that under sufficiently harsh conditions physiological differences could produce the variation in winter distribution of the sexes, even in the absence of male dominance over females. But given the rather small difference between the sexes in fasting endurance, as calculated (Ketterson and Nolan 1976) and observed (Ketterson and Nolan 1978) for juncos, we now propose for climate the additional and/or alternate role of modulating the effects of males on female winter distribution.

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LITERATURE CITED

BAKER, M. C., & S. F. FOX. 1978. Dominance, survival, and enzyme polymorphism in Dark-eyed Juncos, *Junco hyemalis*. Evolution 32: 697–711.

BALPH, M. H. 1975. Wing length, hood coloration, and sex ratio in Dark-eyed Juncos wintering in northern Utah. Bird-Banding 46: 126–130.

BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. No. 237, part 2.

BURLEIGH, T. D. 1972. Birds of Idaho. Caldwell, Idaho, The Caxton Printers.

COMMITTEE ON CLASSIFICATION AND NOMENCLATURE. 1973. Thirty-second supplement to the American Ornithologists' Union check-list of North American birds. Auk 90: 411–419.

GAUTHREAUX, S. A., JR. 1978. The ecological significance of behavioral dominance. Pp. 17–54 *in* Perspectives in ethology, vol. 3 (P. P. G. Bateson and P. H. Klopfer, Eds.). New York, Plenum Press.

JEWETT, S. G., W. P. TAYLOR, W. T. SHAW, & J. W. ALDRICH. 1953. Birds of Washington State. Seattle, Univ. Washington Press.

KETTERSON, E. D., & V. NOLAN JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). Ecology 57: 679–693.

———, & ———. 1978. Overnight weight loss in Dark-eyed Juncos (*Junco hyemalis*). Auk 95: 755–758.

U.S. WEATHER BUREAU. 1932. Climatography of the United States, sections 1–106. Bull. W.