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**Evidence of Differential Migration by Sex in White-throated Sparrows
(*Zonotrichia albicollis*)**

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ABSTRACT.—Differential migrants are species in which one population class migrates farther than an-

other. White-throated sparrows (*Zonotrichia albicollis*), which migrate into the southern United States each autumn in large numbers, have been proposed as a candidate differential migrant (Cristol et al. 1999). Using Bird Banding Lab data, we tested for latitudinal variation in the sex ratio of White-throated

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Sparrows in the Atlantic and central flyways. We found that the proportion of females increases with decreasing latitude in at least the Atlantic flyway, strongly suggesting that females migrate farther than males. Sex ratios calculated from those banding data were compared to those of museum specimens collected at the same latitudes, as well as single-season population samples at three latitudes in the heart of the winter range. Broad agreement was found using the three independent methods of sampling the sex ratio, so we conclude that White-throated Sparrows are differential migrants.

RESUMEN.—Se denomina migrante diferencial a una especie en la cual una clase de la población migra más lejos que la otra. *Zonotrichia albicollis*, especie que migra cada otoño en grandes números hasta el sur de los Estados Unidos, ha sido propuesta para ser considerada como migrante diferencial (Cristol et al. 1999). Empleando datos del Bird Banding Lab, analizamos la variación latitudinal en el cociente de sexos de *Z. albicollis* en los corredores de vuelo atlántico y central. Encontramos que la proporción de hembras incrementa con una disminución en la latitud, al menos en el corredor de vuelo atlántico, sugiriendo de modo contundente que las hembras migran más lejos que los machos. Los cocientes de sexos calculados a partir de los datos de anillado fueron comparados con aquellos de especímenes de museo colectados en las mismas latitudes, y con muestras de poblaciones tomadas durante una única estación en tres latitudes en el centro de las áreas de invernada. Encontramos resultados similares con los tres métodos independientes que usamos para muestrear el cociente de sexos, por lo que concluimos que *Z. albicollis* es un migrante diferencial.

In many species of migratory birds, different travel distances by members of each age or sex class during autumn migration result in wintering populations that are partially segregated (Ketterson and Nolan 1976). Factors responsible for evolution and maintenance of such differential migrations are not clearly understood despite the fact that it is a common phenomenon that has received considerable study. Worldwide, there are more than 50 well-documented species of differential migrants and almost 100 more candidate species for which rigorous documentation is lacking (Cristol et al. 1999).

The White-throated Sparrow (*Zonotrichia albicollis*) is one of the most familiar and well-studied birds in North America (Falls and Kopachena 1994). It breeds across most of eastern Canada and the northeastern United States, and migrates south as far as the Gulf of Mexico. The evidence suggesting that White-throated Sparrows are differential migrants with regard to sex consists of a skewed sex ratio among 45 tower-killed migrants in Florida, from which Odum (1958) deduced that first-year females probably winter farther south than adults in general, and males in

particular. We are not aware of any further published studies on wintering sex ratios of White-throated Sparrows. The objective of our study was to use data from birds banded after autumn migration but before spring migration to test the hypothesis that there is a detectable latitudinal cline in sex ratio of wintering White-throated Sparrow populations. A latitudinal cline in sex ratio is usually indicative of differential migration (Ketterson and Nolan 1976). We also assessed whether our findings from the U.S. Geological Survey, Patuxent Wildlife Research Center, Bird Banding Laboratory (hereafter "BBL") data were in agreement with two independent sources of information about wintering White-throated Sparrow sex ratios.

Methods.—To study the geographic distribution of wintering male and female White-throated Sparrows, we analyzed sex ratio in each 1° block of latitude using 20 years of winter banding data from the BBL. We also examined skin collections in 12 museums and calculated sex ratio for birds collected in winter at any latitude for which sufficient data were found. Finally, we determined sex ratio of free-living birds caught over the course of a single winter at three field sites near the center of the species' winter range.

We ensured that only wintering birds were included by using birds captured in January through March, which is well outside the period in which most members of that species migrate (Falls and Kopachena 1994). The vast majority of White-throated Sparrows are banded within the Atlantic and central flyways of the United States (as defined in U.S. Department of the Interior, Fish and Wildlife Service and Canadian Wildlife Service 1977), so only in those areas did we have a sufficient sample size to attempt analyses. We analyzed each flyway separately under the assumption that White-throated Sparrows may be funneled into different flyways to some extent, in which case sex ratios in each might represent independent entities. Because there has historically been lack of agreement as to how to determine sex in White-throated Sparrows, we used only birds banded from 1980 through 2000, decades after clarifications regarding sex and morph appeared in the literature (e.g. Lowther 1961, Vardy 1971).

For each flyway, we determined total number of males and females in each 1° latitudinal block, and arbitrarily excluded all latitudes at which fewer than 15 birds were sexed by banders. Before carrying out the analysis of sex ratios, we examined numbers of unsexed birds at each latitude, and tested for a cline using linear regression and ANOVA. That was necessary because the range of wing lengths that can be used to classify a bird as female is smaller than that for males, and thus a higher percentage of birds of unknown sex are undoubtedly female. Any latitudinal cline in percentage of unknown birds could produce a spurious change in the sex ratio. We tested

for a latitudinal cline in sex ratio by normalizing proportion of females using the natural log, and regressing that on the independent variable of latitude. ANOVA was used to test whether the relationship differed significantly from the null hypothesis.

Because only the Atlantic flyway BBL data provided a statistically significant result (see below), we restricted our comparison with other data sets to that region. First, we obtained data on sex ratios of birds collected at each latitude by measuring birds in museums or accessing their databases via the internet. We assumed that museum collections provided an unbiased sample of sex ratios because it is unlikely that collectors could have selectively obtained one sex in such a monomorphic species and if so, our large sample of museums should swamp out the biases of particular collections (see Acknowledgments for a list of museums). We studied only collections in which there were at least 100 White-throated Sparrows and used all birds collected between January and March ($n = 296$). Wing chord measurement was our primary method of sex determination because that is how many banders currently determine sex in White-throated Sparrows, and thus is likely to be most consistent with the BBL data set. We measured the un-flattened length of each specimen's right wing. We were unable to measure 31 specimens, but those had been sexed by examination of the gonads so we included them in the data set. We classified all birds with wings <69 mm as females and >71 mm as males, which has been shown to result in 92% accuracy for females and 96% accuracy for males in a field study where sex was confirmed using laparotomies (Piper and Wiley 1991). Because museum sample sizes were smaller than those in the BBL data set, we calculated sex ratio for any latitude at which >10 birds had been sexed.

To determine whether latitudinal sex ratios differed between the BBL and museum skin data, we used a chi-square contingency analysis to compare number of females collected at each latitude with number expected for that latitude as predicted by either (1) proportion of females banded at that latitude, or (2) proportion predicted by the regression equation for the BBL data across all latitudes. These are two alternative analyses using somewhat different expected values, the former directly from the BBL sample at a single relevant latitude, the latter using a prediction for each relevant latitude based on the entire BBL data set.

We also examined sex ratios at three sites where individual researchers had sexed large samples of winter-resident White-throated Sparrows in a small area within a single year: the Mason Farm Biological Reserve in Chapel Hill, North Carolina (1985/1986); the campus of the College of William and Mary in Williamsburg, Virginia (1999/2000); and the George Washington National Forest near Harrisonburg, Virginia (1999/2000). The sex ratio from the Chapel Hill

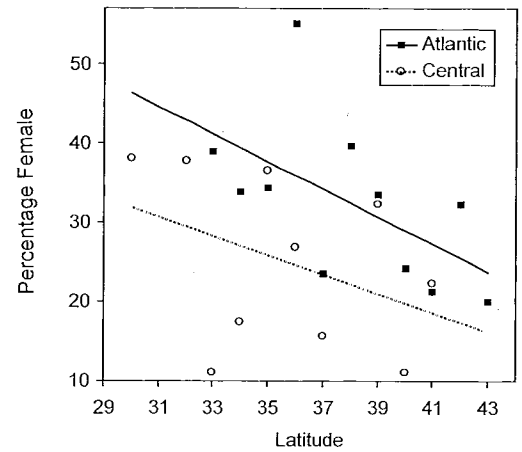


FIG. 1. Relationship between latitude and percentage of females in the wintering population for White-throated Sparrows in the Atlantic and central flyways. Graph is based on BBL data from 1980 to 2000. See text for statistical analysis of normalized data.

site was provided by Walter Piper (pers. comm.), and had been derived by laparotomy. We then used data published in Piper and Wiley (1991, fig. 1) to adjust the laparotomy-derived sex-ratio data to what it would have been if it had been derived from wing measurements. Data from the other two sites relied on the same wing-length criterion as we used for the museum specimens. The sex ratios at the three field sites were compared to expected values from the BBL data for the Atlantic flyway as described above for the museum data.

Results.—Banding lab data for the Atlantic flyway included 2,527 birds of known sex, 33% of which were classified as females, occurring in every 1° latitude block between 33 and 43°N. The proportion of females was significantly negatively related to latitude ($r = 0.61$, $F = 5.43$, $df = 1$ and 9 , $P = 0.04$; Fig. 1), indicating that sex ratios were more biased towards females at more southerly latitudes. The pattern appeared similar in the BBL data for the central flyway, but there were far fewer birds banded ($n = 94$, of which 29% were classified as females) and the result was not significant ($r = 0.37$, $F = 1.46$, $df = 1$ and 9 , $P = 0.23$; Fig. 1). The proportion of birds whose sex was unclassified was not related to latitude in either flyway (Atlantic: proportion unsexed = $0.5 \text{ latitude} + 45.1$, $r = 0.26$, $F = 0.66$, $df = 1$ and 9 , $P > 0.4$; central: proportion unsexed = $0.2 \text{ latitude} + 74.2$, $r = 0.10$, $F = 0.10$, $df = 1$ and 9 , $P > 0.5$).

To determine whether BBL sex-ratio data were comparable to that observed in museum collections, we located 154 skins collected during winter in the Atlantic flyway, of which we classified 25% as female. Those were collected between 30 and 40°N, and there

TABLE 1. Expected and observed proportions of females by latitude from museum skin data.

| Latitude | <i>n</i> | Observed | Expected ^a | Expected ^b |
|----------|----------|----------|-----------------------|-----------------------|
| 30.5 | 14 | 0.50 | — | 0.49 |
| 34.5 | 12 | 0.25 | 0.34 | 0.40 |
| 35.5 | 33 | 0.24 | 0.34 | 0.37 |
| 38.5 | 58 | 0.21 | 0.40 | 0.31 |
| 39.5 | 16 | 0.19 | 0.34 | 0.29 |
| 40.5 | 21 | 0.24 | 0.24 | 0.28 |

^a Based on BBL sample for same latitudes.

^b Based on prediction for same latitude from regression of BBL data.

were sufficient data at six latitudes to compare to the BBL data. The sex ratios at those latitudes did not differ from those found at the same latitudes in the BBL data ($\chi^2 = 7.5$, $df = 4$, $P > 0.1$; Table 1), or from that predicted by the regression equation for all BBL data ($\chi^2 = 4.8$, $df = 5$, $P > 0.1$; Table 1). Our power to detect a "medium" difference in these comparisons, as defined by Cohen (1988), was reasonably high (BBL sample: power = 86%; BBL regression: power = 83%).

We determined the sex ratio among live birds at three field sites located in the heart of the winter range of this species (38°20'N, 37°16'N, and 35°56'N). The sex ratios at those field sites matched closely those sampled from the same latitudes in the BBL data ($\chi^2 = 1.0$, $df = 2$, $P > 0.5$; Table 2). Our power to detect a "medium" difference (Cohen 1988) was high (>98%). However, field site samples differed significantly from those predicted for the same three latitudes by the regression equation based on all latitudes in the BBL data ($\chi^2 = 27.4$, $df = 2$, $P < 0.001$; Table 2). Proportion of females at the successively more southern field sites increased with decreasing latitude faster than predicted by the regression equation.

Discussion. Proportion of females in wintering populations of White-throated Sparrows increased at more southerly latitudes in the Atlantic flyway. Because we found that there was no relationship between number of unsexed birds and proportion of females, the relationship between latitude and proportion of females was not an artifact of latitudinal differences in the tendency for banders to classify birds as being of unknown sex.

The sex ratios derived from the BBL data did not differ from sex ratios of specimens in museum collections from the same latitudes, suggesting that BBL data provided a robust measure of the cline in the sex ratio across latitudes. In addition, the sex ratios among free-living birds at three field sites in the middle of the species' wintering range were remarkably similar to those of the same latitudes in the BBL data, although they differed from the sex ratios predicted by the regression equation on the basis of all latitudes in the BBL data set. That again suggests that the BBL data provided a robust measure of sex ratios

TABLE 2. Expected and observed proportions of females found at field sites.

| Location (latitude) | <i>n</i> | Observed | Expected ^a | Expected ^b |
|---------------------------|----------|----------|-----------------------|-----------------------|
| Harrisonburg, VA (38.5°N) | 52 | 0.33 | 0.40 | 0.31 |
| Williamsburg, VA (37.5°N) | 276 | 0.18 | 0.24 | 0.33 |
| Chapel Hill, NC (35.5°N) | 287 | 0.54 | 0.55 | 0.37 |

^a Based on BBL sample for same latitudes.

^b Based on prediction for same latitude from regression of BBL data.

at various latitudes, although sampling error due to small sample sizes at some latitudes, or confounding effects of unmeasured variables such as longitude or altitude, may have weakened the predictive power of that data set. Thus, three independent lines of evidence all support our hypothesis that sex ratios of White-throated Sparrows in winter differ depending upon latitude. Because each male-female pair begins migration at the location of their breeding site, and sex ratios of young can be assumed to be at parity in this socially monogamous species, a latitudinal cline in sex ratio during winter is best explained as the result of differential migration distance of the sexes.

Our much smaller sample size of BBL data from the central flyway was inconclusive. Relationship between proportion of females and latitude appeared similar to that in the Atlantic flyway, but we cannot determine from this sample whether there are real differences between flyways.

The three main hypotheses for differential migration are (1) the body size or cold-tolerance hypothesis; (2) the dominance or interclass-competition hypothesis; and (3) the arrival-time hypothesis (all reviewed in Cristol et al. 1999). The body-size hypothesis assumes that larger individuals are more likely than smaller ones to survive cold temperatures, and thus females should migrate farther south to avoid cold. The dominance hypothesis dictates that dominant birds force subordinates to migrate further from the breeding grounds. Finally, the arrival-time hypothesis proposes that there is a greater advantage of arriving early on the breeding grounds for the individuals that establish territories. It is not surprising that our data indicated that female White-throated Sparrows migrate farther than males in autumn, because that is the pattern predicted by each of these hypotheses. Male White-throated Sparrows are larger than females, are dominant in winter social hierarchies (Piper and Wiley 1989), and arrive one to two weeks earlier than females on breeding grounds to establish territories (Falls and Kopachena 1994). Thus, females might migrate farther because their small body size reduces their ability to withstand cold, because they benefit from avoiding competition with dominant males, because they do not benefit as much from being among the first to return

in the spring, or some combination of these and other factors.

In conclusion, our findings add the White-throated Sparrow to the list of documented differential migrants. The White-throated Sparrow is not an ideal species for differentiating between the three primary hypotheses for differential migration, because each makes the same prediction—that females will migrate farther than males. On the other hand, because their natural history is well studied, White-throated Sparrows would seem a very good species in which to investigate causes of this migration pattern through comparative studies or simulation modeling.

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