

ACQUISITION OF PLUMAGE POLYMORPHISM IN WHITE-THROATED SPARROWS

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Abstract.—The White-throated Sparrow (*Zonotrichia albicollis*) was thought to be polymorphic in breeding plumage, having distinct white and tan phases that are bimodal in distribution and independent of sex. Vardy (1971), however, submitted evidence that plumage type is determined primarily by age, sex, and molt cycle. We reexamined this question by measuring plumage characteristics on a quantitative scale with the Munsell system of color notation. Using techniques of numerical taxonomy, we examined immature and adult birds before and after prenuptial molt. Winter plumages were basically unimodal and continuous in distribution, whereas spring plumages were bimodal, as the birds separated into two morphs independent of sex. Winter plumage was significantly more variable than spring plumage. We hypothesize that winter plumage variability could function to maintain stable social relationships in winter flocks. *Received 16 July 1979, accepted 22 October 1979.*

LOWTHER (1961) proposed that the White-throated Sparrow (*Zonotrichia albicollis*) is polymorphic in plumage and breeding behavior. In each sex there are bright and dull individuals. He qualitatively and subjectively examined museum specimens and live birds in breeding plumage. From these data he described a distinct bimodal distribution of individuals of each sex into two plumage types. One, the white morph, has a bright, white median crown stripe; a large percentage of black feathers in the lateral crown stripes; little chest streaking; a wide slate-gray chest band; a white throat patch with few dark markings; and large, bright, yellow superciliary stripes. In contrast, the tan morph has a dull, tan median crown stripe; a high percentage of brown feathers in the lateral crown stripes; moderate chest streaking; a narrow, pale, gray-tan chest band; a throat patch that is heavily marked with black; and small, dull yellow superciliary stripes. Lowther observed a system of selective mating in which white morphs, regardless of sex, bred almost exclusively with tan morphs.

Thornycroft (1966, 1975) was the first to support Lowther's findings. He studied the karyotypes of 397 White-throated Sparrows and found a chromosomal basis for plumage polymorphism. He discovered that the presence or absence of an autosome overrode the effects of age and sex in determining plumage characteristics. The bright plumage exhibited by white morphs was expressed phenotypically by immatures and by some adults only after the prenuptial molt. Ficken et al. (1978) reviewed this subject and suggested that there may be genetically determined differences in aggressive tendencies between the two morphs.

Vardy (1971), however, subjectively examined more than 600 individuals in both seasons and asserted that any plumage polymorphism was due solely to the sex and molt cycle of the bird. She did not find bimodal variation in crown plumage for any age or sex class in either breeding or winter plumage. She found: (1) males tended to be uniformly bright, and females uniformly dull; (2) in their first winter plumage immatures appeared duller than adults; and (3) after the prenuptial molt, both males and females were brighter, but males more so than females. Thus, plumage differ-

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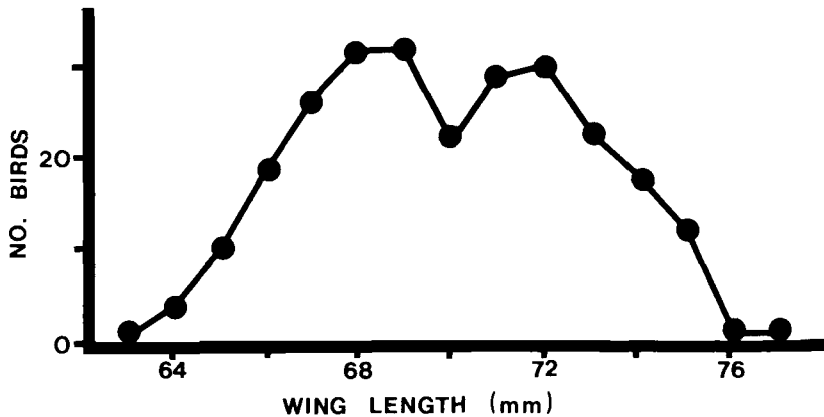


Fig. 1. Wing lengths of White-throated Sparrows captured in Pennsylvania for this and other studies during 1975.

ences, on the average, were related to sex. Kuenzel and Helms (1974) reinforced Vardy's finding of a lack of polymorphism when they conducted a study of the annual cycle of captive birds. They monitored body weight, lipid deposits, molt, cloacal protuberance, and nocturnal activity but failed to find any significant differences between white and tan morphs.

The purpose of our study was to determine whether or not plumage polymorphism exists within each sex by measuring plumage variation among birds on a quantitative scale.

MATERIALS AND METHODS

During autumn 1975, we mist netted 105 migrating White-throated Sparrows at the Reineman Wildlife Sanctuary in Perry County, Pennsylvania. We determined their age by the amount of skull ossification (Miller 1946). We housed the birds in two indoor aviaries and fed them finely ground, commercial, dry dog chow supplemented with lettuce, a commercial wild bird seed mixture, and grit.

In May 1976, we artificially increased the day length from 8L:16D to 12L:12D to induce prenuptial molt. After their prenuptial molt, we sexed the birds by noting the presence or absence of a cloacal protuberance and by measuring wing chord. A frequency histogram of wing lengths (Fig. 1) is bimodal with a median of 70 mm. We found that all birds with wing lengths of 72 mm or greater were males and those with 68 mm or less were females. Birds of questionable sex and all those with intermediate wing lengths were laparotomized.

Using the techniques of numerical taxonomy (e.g. West 1962), we ranked data for each plumage variable on a relative scale from 0 (dullest) to 10 (brightest). For example, the lowest observed percent black in the lateral crown stripes was 15% and the highest was 100%. We scaled these values to range from 0 to 10 (Figs. 2 and 3). Each plumage variable was similarly scaled and received equal weight in the analysis.

We measured color variables (hue, value, and chroma) with the Munsell system of color notation. Each of these components occupies a separate axis in a three-dimensional space (see Wood and Wood 1972). The Munsell system is quantitative and specifies a color numerically in orderly scales of nearly equal steps of perception to the eye. It is thus suited for statistical analysis.

Both Lowther (1961) and Vardy (1971) used a series of type specimens to classify birds as white or tan morphs. Our method of plumage measurement has the advantage of removing subjective interpretations of plumage variations, especially color, from the scales of measurement.

A plot of spring and winter color data for median crown stripe, superciliary stripe, and chest band revealed that hue varied little within each plumage characteristic; thus we discarded this axis and used only value and chroma to generate a two-dimensional comparison.

We ranked each of the color variables on a scale of 0 to 10 by calculating a regression line through a graph of value and chroma. Although the steps between the Munsell quantities are ordinal in nature, i.e.

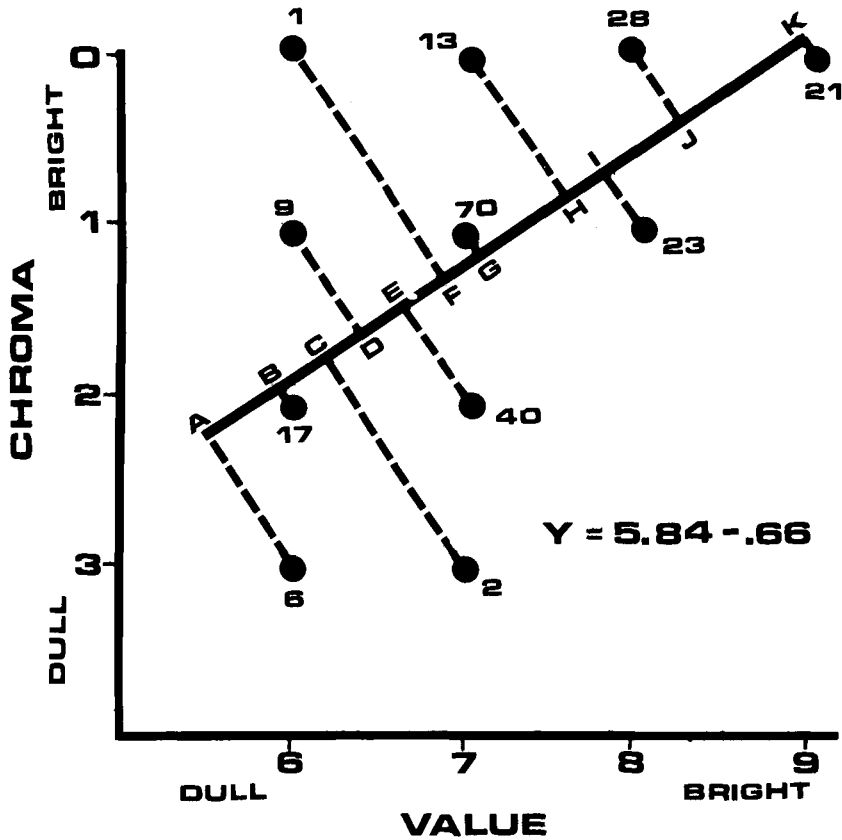


Fig. 2. An example, for the median crown stripe color, of the system for ranking color data on the relative plumage scale. Numbers next to data points indicate the number of individuals at each point. The length of each segment (AB, BC, . . . JK) of the regression line was proportionally converted (e.g. 100 AB/AK, etc.) to its corresponding value on a scale from 0 to 10 (Table 1). Designation of "Bright" and "Dull" is added by us to indicate relative perception of value and chroma.

they are not strictly equal, they are probably nearly so in the range in which we were working. From each data point on the graph, we drew a perpendicular to the regression line (the median crown stripe data are shown in Fig. 2). These perpendiculars broke the regression line into adjacent segments. The point where the lowest value intersected the regression line was ranked as "0" and where the highest intersected as "10." Intermediate intersections for other variables were given appropriate values.

We quantified the following plumage variables in winter and in spring ranked from bright (10) to dull (0): (1) *Percent Black in Lateral Crown Stripes* (estimated to the nearest 5%) (range: 100% = 10; 15% = 0); (2) *Throat Pattern* (classified by Lowther 1961), with "1" without stripes on the throat (10) and "5" with two lateral double stripes (0); (3) *Chest Streaking* (percentage of the breast below the chest band that is streaked with brown feathers) (range: 0% = 10; 40% = 0); (4) *Chest Band Height* (measured in the center of the breast to the nearest mm (range: 18 mm = 10; 5 mm = 0); (5) *Median Crown Stripe Color* (anterior half of the stripe) [range: value (9), chroma (0) = 10; value (6), chroma (3) = 0]; (6) *Superciliary Stripe Color* [range: value (8), chroma (8) = 10; value (6), chroma (6) = 0]; and (7) *Chest Band Color* [range: value (4), chroma (0) = 10; value (6), chroma (1) = 0].

RESULTS

We computed the intercorrelations of six of the seven plumage variables before and after the prenuptial molt using Pearson *r* (Table 1). We discarded our mea-

TABLE 1. Intercorrelations of six plumage variables. We computed Pearson r and tested the significance of each of the values (Haber and Runyan 1973, significant at the 0.05 level of probability if $z \geq 1.96$).

WINTER						
		% black	Median crown color	Superciliary color	Chest streak	Chest color
Throat pattern	r	0.460	0.545	0.413	0.369	0.149
	z	5.49	6.83	4.82	4.30	1.67
% black in lateral crown	r		0.526	0.403	0.306	0.127
	z		6.52	4.68	3.55	1.45
Median crown stripe color	r			0.423	0.360	0.095
	z			4.95	4.16	1.10
Superciliary stripe color	r				0.343	0.154
	z				3.91	1.67
Chest streaking	r					-0.018
	z					0.22
SPRING						
		% black	Median crown color	Superciliary color	Chest streak	Chest color
Throat pattern	r	0.692	0.649	0.651	0.505	0.254
	z	8.56	7.83	7.83	5.69	2.59
% black in lateral crown	r		0.686	0.581	0.477	0.415
	z		8.56	6.70	5.28	4.52
Median crown stripe color	r			0.738	0.410	0.260
	z			9.59	4.40	2.69
Superciliary stripe color	r				0.338	0.261
	z				3.58	2.69
Chest streaking	r					0.235
	z					2.47

measurements of chest band height, because they were not repeatable, i.e. slight variations in head position resulted in large differences in measurements of width. Throat pattern, percent black in the lateral crown stripes, median crown stripe color, superciliary stripe color, and chest streaking were all significantly correlated with one another in both winter and spring ($P < 0.05$). Chest band color showed the poorest significance of correlation with the other variables in the spring and no significant correlation in the winter.

Next, we compared the six variables to determine whether or not changes occurred in the distribution of each as the birds underwent prenuptial molt (Fig. 3). We tested for significant differences with the Wilcoxon Test for paired observations (Edwards

TABLE 2. Results of the Rank-sum test for differences in composite plumage indices between age and sex classes. Differences are significant at the 0.05 level of probability when $z \geq 1.96$.

	z values	
	Winter	Spring
Adult ♂: Adult ♀	2.518	3.520
Adult ♂: Immature ♂	1.517	-0.033
Adult ♂: Immature ♀	2.414	2.238
Adult ♀: Immature ♂	-1.443	-3.038
Adult ♀: Immature ♀	0.091	-1.245
Immature ♂: Immature ♀	1.276	1.845

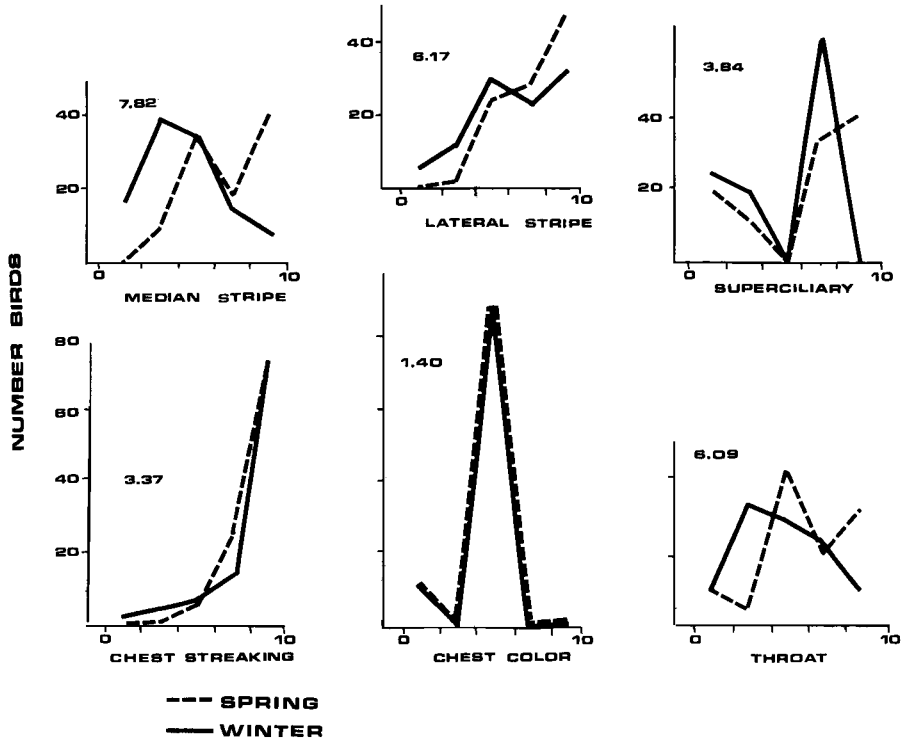


Fig. 3. Plumage variables for all individuals in spring and winter. Seasonal differences were compared with the Wilcoxon test for paired variables and the z value is shown ($P < 0.05$ when $z > 1.96$).

1967). Chest band color was the only variable that did not change between seasons. Because of this, and because it correlated relatively poorly with the other variables, we eliminated it from further analysis.

We computed a composite index for each bird in both winter and spring plumage by finding the sum of the remaining five plumage variables (Fig. 4). This procedure is similar to preparing a hybrid index and should lend itself to the accurate replication of our results (see Corbin and Barrowclough 1978). We tested for significant differences between sex and age classes with the Rank-sum Test (Dixon and Massey 1957) (Table 2). In the winter, only the adult males were significantly different, both from the adult and immature females. In spring plumage, all males were significantly brighter than females, except that immature males were only marginally ($0.10 > P > 0.05$) significantly brighter than immature females. Although these statistical differences exist, it is evident from the bimodal shape of the spring histograms that a large number of males are dull and a large number of females are bright.

We tested the differences between the unimodal winter and the bimodal spring plumages with the Wilcoxon Test for matched pairs and found that they were significant for every age and sex class ($P < 0.01$) (Fig. 4).

Finally, we determined the maximum difference between five plumage characters in each individual to measure the variability of the spring plumage as compared to the winter plumage. The difference in variability was compared with the T-test (Brownlee 1965). Winter plumage had a significantly wider range ($\bar{x} = 6.11$) of vari-

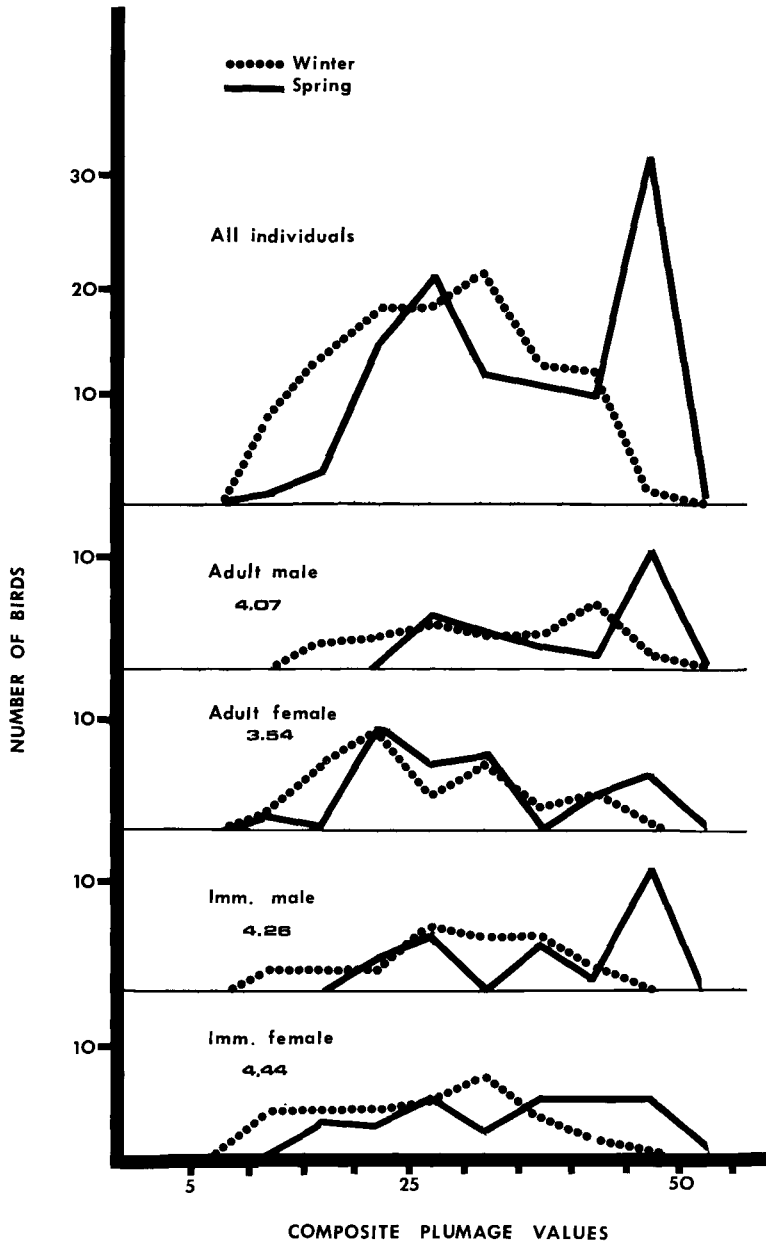


Fig. 4. Composite plumage values of all ages and sexes. Seasonal differences were significant at the 0.05 level if the value shown was greater than 1.96.

ation among individuals than did spring plumage ($\bar{x} = 4.45$, $T = 4.61$, $P < 0.001$). This variation helps to explain why intercorrelations among plumage characters were generally lower in winter than in spring (Table 1). The birds in winter plumage tended to have characteristics of both morphs, resulting in a wider range of plumage variation. In contrast, whitethroats in breeding plumage segregated more readily into two color morphs, as variation within each morph was limited to a smaller range.

DISCUSSION

The results of our study confirm the observations made by Lowther and Thorneycroft that each sex class of White-throated Sparrows is distinctly polymorphic in breeding plumage. During the winter, by contrast, we determined that each sex fails to segregate into two distinct color morphs. This seasonal difference probably occurs because immature birds and some adult birds do not phenotypically express the chromosome determining plumage brightness in winter (Thorneycroft 1975). The relationship that Vardy (1971) found between plumage brightness and sex is present only in breeding plumage. Contrary to what she suggested, sex alone fails to explain the bimodal distributions of composite plumage indices for birds after the prenuptial molt.

Additionally, our study shows that winter plumage is more variable than breeding plumage. This plumage variability may be of adaptive significance to individuals on the wintering grounds. Brown (1975) and others have theorized that wintering birds forming dominance hierarchies must have a means for reducing aggressive interactions within the hierarchy. Otherwise, a tremendous amount of energy that could be used for searching and exploiting food resources would be wasted in repeated aggressive acts between the same birds. Brown believes that after a short period of initial fighting, birds in winter flock are able to recognize and remember one another. Individuals are thus able to avoid a substantial number of fights and a substantial loss of energy by recognizing and avoiding dominant individuals.

White-throated Sparrows typically flock in winter and form well-ordered, linear dominance hierarchies (D. Watt, Atkinson, and Ralph unpubl. data). The wide range of plumage variation in the winter may aid individuals in recognizing one another, thus reducing the number of aggressive interactions in the flock and increasing the overall stability of the flock. In comparison, plumage polymorphism and the segregation of birds into two distinct color morphs could establish the basis for interactions among breeding birds. The two plumage systems are apparently independent of each other yet are linked temporally by migration and molt cycle to maximize the adaptiveness and success of this species.

ACKNOWLEDGMENTS

We thank Doris Watt, Douglas James, Wayne Kuenzel, Carol Pearson Ralph, and Sherry Allhouse for help in conducting this research. Helpful comments on the manuscript were received from M. Balph, L. F. Baptista, J. P. Hailman, C. P. Ralph, and Doris Watt. Our thanks to the Biology Department of Dickinson College for hospitality while the authors were a student and faculty member, respectively, and especially to William F. Jeffries, Chairman of the Department.

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A symposium on **Estimating Populations of Terrestrial Birds** will be held on 26-31 October 1980 at Asilomar, near Monterey, California. Invited papers, given by individuals from the United States, Canada, Europe, New Zealand, and Australia, will cover a wide range of subjects; principal topics will be the problems, methods, and analyses of bird censusing. For further information write **Dr. C. John Ralph and Dr. J. Michael Scott, Bird Census Symposium, P.O. Box 43, Hawaii Volcanoes National Park, Hawaii 96718.**

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