DISTINGUISHING MORPHS OF THE WHITE-THROATED SPARROW IN BASIC PLUMAGE

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Abstract.—The White-throated Sparrow (*Zonotrichia albicollis*) has two genetic morphs, which are clearly distinguishable by color in alternate plumage, but less distinguishable in basic plumage. To determine the accuracy with which the morphs can be identified in basic plumage in a wintering population in North Carolina, we measured the brightness (extent of pure white or black as opposed to tan or brown) in the median, lateral, and superciliary stripes of 279 birds of known age and sex and determined each bird's morph after the prealternate molt in the spring. Age, sex, and plumage all influenced the color of crown stripes in both morphs. However, white morphs were significantly brighter than tan morphs in all age- and sex-classes in basic plumage. A simple formula based on a bird's age, sex, and brightness of its median and lateral stripes identified tan and white morphs in basic plumage with a success rate of 89%. In this wintering population, an estimated 61% of males and 49% of females were white morphs.

LA IDENTIFICACIÓN DE FENOTIPOS PARTICULARES EN INDIVIDUOS DE *ZONOTRICHIA ALBICOLLIS* EN PLUMAJE BÁSICO

Resumen.—En el gorrión *Zonotrichia albicollis* se han descrito dos fenotipos (morphs) particulares que pueden distinguirse fácilmente por su color cuando las aves han mudado a su plumaje alterno. No obstante es difícil diferenciar entre las dos formas, cuando las aves están con su plumaje básico. Para determinar con que exactitud podíamos identificar las dos formas en su plumaje básico, estudiamos por 5 años una población de gorriones que pasan el invierno en Carolina del Norte. De 279 individuos de edad y sexo conocidos, medimos la brillantez (lo extensivo del blanco o negro en contraste con el acanelado o pardo) de las líneas medias, laterales y superciliares durante la primavera cuando las aves ya habían adquirido su plumaje prealterno. Se encontró que la edad, sexo y el plumaje influyen en el color de las bandas de la corona en ambos fenotipos. No obstante en aves con plumaje básico, las formas blancas resultaron más brillantes que las formas acaneladas, sin importar la edad o sexo de los gorriones. Tomando en consideración la edad de las aves, sexo y brillo de las bandas medias y laterales pudimos identificar en gorriones con plumaje básico el 89% de los fenotipos acanelados o blancos. En la población estudiada aproximadamente el 61% de los machos y el 49% de las hembras resultaron ser formas blancas.

Lowther (1961) first described tan- and white-striped morphs in both sexes of the White-throated Sparrow (*Zonotrichia albicollis*) in alternate plumage. He distinguished the two types, which for brevity we shall call tan and white morphs, by the whiteness of the median crown stripe and also noted that they differed in the coloration of the lateral and superciliary crown stripes and in the amount of streaking on the breast. Thorneycroft (1966, 1975) found a chromosomal basis for this difference in that white birds have a distinctive autosome absent in tan birds. The two morphs have subsequently been reported to differ in a number of behavioral and

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ecological aspects, both during the breeding season and during the winter (Ficken et al. 1978; Knapton and Falls 1982, 1983; Lowther 1961; Lowther and Falls 1968; Watt et al. 1984).

The difficulty of distinguishing white and tan morphs in basic plumage was first documented by Vardy (1971). More recently, Atkinson and Ralph (1980) and Watt (1986) measured plumage coloration in groups of White-throated Sparrows held in aviaries during winter and spring. They showed that most measures of coloration are bimodally distributed among birds in alternate plumage, but unimodally distributed in basic plumage. These results suggested that the morphs are not separable in basic plumage.

The present study, part of a 5-yr project to examine the behavior of a wintering population of individually banded White-throated Sparrows, examined differences in plumage coloration in a large sample of resident, free-living birds of known age, sex, and morph. Our results indicate that the morphs can in fact be identified in basic plumage with nearly 90% accuracy.

METHODS

Basic procedures.—White-throated Sparrows were studied at the Mason Farm Biological Reserve in Chapel Hill, North Carolina, where they are abundant from November through April. During the winters of 1983–1984 through 1985–1986, we trapped and color-banded 300–400 White-throated Sparrows a year in 4 ha of thickets and hedgerows at this site. When each bird was first captured, we checked its skull for ossification, sexed it by laparotomy, and measured its unflattened wing chord. Previously unbanded birds captured on or before 15 Dec. with fully ossified skulls were considered to be more than one year old (AHY or after-hatching-year birds), and those with incompletely ossified skulls were considered to be in their first year (HY or hatching-year birds). Birds first captured after 15 Dec. were excluded from this analysis.

Scoring of crown stripes.—Inspection of birds at the outset of the study revealed that the median and superciliary stripes in many birds changed from pure white near the beak to tan or gray posteriorly, whereas the lateral stripes in many birds began as pure black near the beak and became flecked with brown posteriorly. On the brightest birds, these transition points occurred well back on the crown, whereas the stripes of dull birds were often tan, gray, or brown-flecked at their anterior ends. Hence all birds had tan and brown in their crown stripes, but varied in the extent of pure white or black.

Based on these observations, we scored each bird for the extent of pure black or white in its median, lateral, and superciliary crown stripe with a handmade scale (Fig. 1) that measured distance along the midline of the skull from the anterior edge of the nares (score = 0) to a point half-way down the back of the skull (score = 8). All scores were truncated to integer values. Birds with high scores for each stripe had extensive white
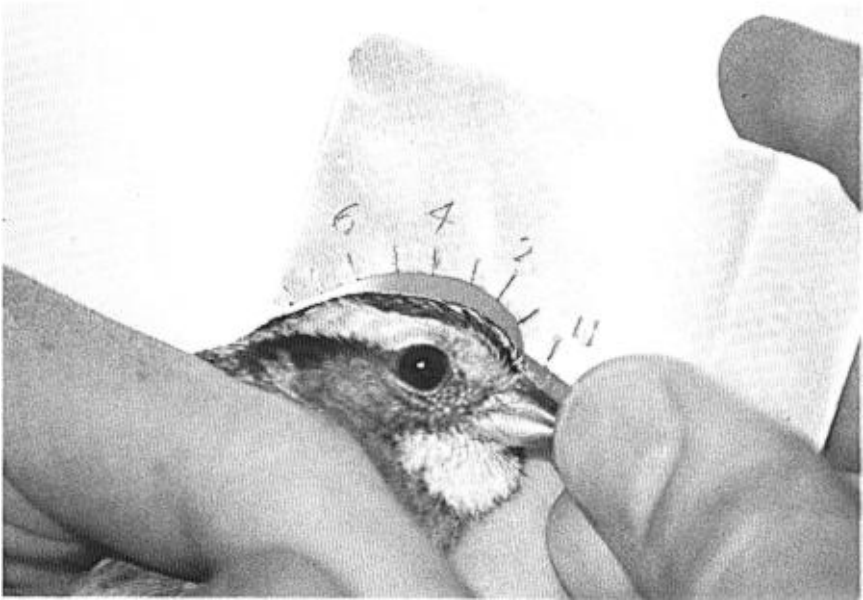
FIGURE 1.   Scale used to measure brightness of stripes on the crowns of White-throated Sparrows. The zero point ("N") is aligned with the anterior edge of the naris.

in the median and superciliary stripes and extensive black in the lateral stripes.

Stripes were scored independently by two observers for every bird. Inter-observer reliability was examined for each stripe in a sample of 389 birds measured by the two authors (for other birds an assistant made one of the two measurements), by determining the proportion of birds in which the scores differed by no more than one unit. The reliability of scores for the median and lateral stripes exceeded 91%, for the superciliary stripe 94%.

Determination of morph in alternate plumage.—Many birds finished the prealternate molt of the crown before leaving the study area in April and May. The earliest date for the onset of molt on the crown (one growing feather) was 17 Mar.; the mean dates of onset were 26 Mar. (SD = 3.9 d, $n = 52$) for males and 29 Mar. (SD = 4.4 d, $n = 69$) for females. On each day from 7 to 25 Apr., more than half of the birds trapped were in heavy molt (at least 20 growing crown feathers and usually many more). Mean dates for the final stage of molt (fewer than 20 growing feathers) were 21 Apr. (SD = 3.2, $n = 26$)and 24 Apr. (SD = 3.2, $n = 36$) for males and females respectively.

From 1984 through 1986, we determined the morph of birds captured between 17 Apr. and 5 May, during or after the final stage of molt, when most birds were in fresh alternate plumage. Individuals were classified as white morphs if the median and superciliary stripes were mostly pure
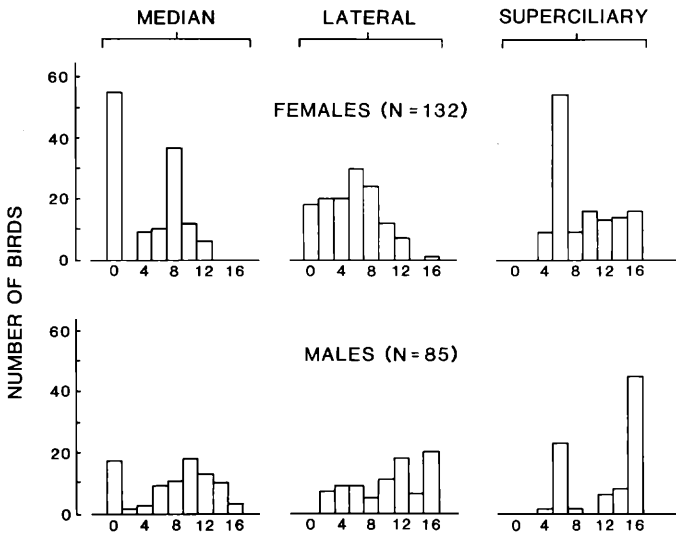
FIGURE 2.   Distributions of scores for median, lateral and superciliary stripes in alternate
    plumage.

white and their lateral stripes mostly black with few or no brown flecks.
They were classified as tan morphs if their median and superciliary stripes
were mostly tan or gray and their median stripes had many brown flecks
(see Knapton and Falls 1982, 1983; Lowther 1961; Lowther and Falls
1968; Thorneycroft 1966, 1975).

Of the 1034 birds captured during the study, 253 (24%) were recaptured
after the prealternate molt. Birds that were captured before and after
prealternate molt in more than one winter ($n = 26$) were treated as
separate observations for each winter, so the total sample size was 279.
Inclusion of these 26 observations did not alter the results.

Predicting morph from basic plumage.—Having classified a sample of
birds as either white or tan morph in alternate plumage, we entered the
scores for each of these birds' crown stripes in basic plumage and its sex,
age, and wing chord into a stepwise discriminant analysis (SYSTAT,
Inc., Evanston, Illinois; Kleinbaum and Kupper 1978), in order to de-
termine which combination of these measures was the best predictor of
morph.

RESULTS

Identification of morphs.—Of the sample of 279 birds captured after
prealternate molt, we could easily identify the morph of 269 (96%) by
their plumage. Both sexes had strongly bimodal distributions of scores
for the median stripe, as described by Lowther (1961), whereas scores
from the superciliary stripe were strongly bimodal among males only
(Fig. 2). The scores for the lateral stripe had a unimodal distribution for
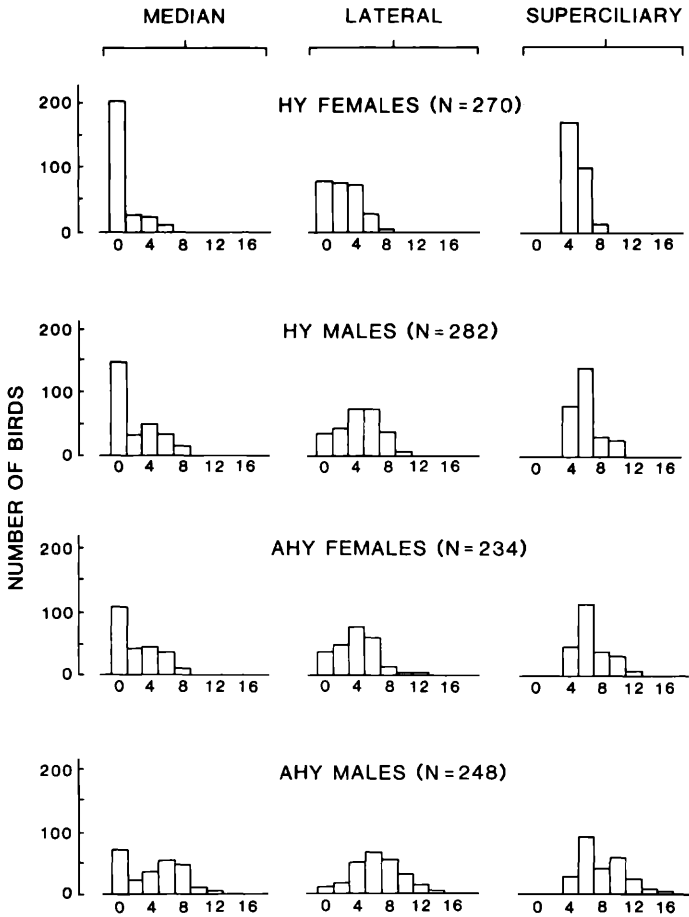females and nearly so for males (Fig. 2). Ten birds (4%) intermediate in

FIGURE 3.   Distributions of scores for median, lateral and superciliary stripes in basic plumage.

coloration could not be assigned to a morph, in some cases because molt was incomplete at the time of examination; these birds were excluded from the discriminant analysis. In basic plumage, scores for the crown stripes were in general distributed unimodally (Fig. 3), although among males scores for the median stripe had slight bimodality.

Since sample sizes were large and the distributions of scores in many cases were close to normal, two-tailed t-tests are used in the following sections to compare differences in scores for each morph in each category of age, sex, and plumage. Because of the large number of tests, we chose $\alpha = 0.01$ as our criterion for statistical significance. See Figure 4 for the means, standard deviations, and sample sizes for all tests. For convenience we use "brightness" to refer to the extent of pure white or black in the crown stripes.
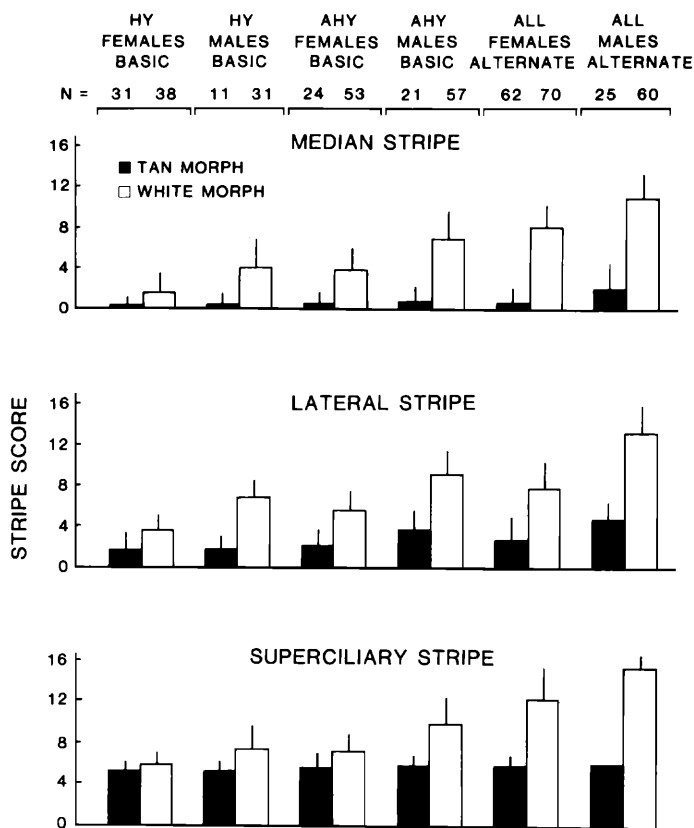
FIGURE 4. Means and standard deviations of scores for crown stripes for each age-sex class in basic and alternate plumages.

Brightness in basic plumage in relation to morph.—Within age- and sex-classes in basic plumage, white morphs averaged brighter than tan morphs. Their median and superciliary stripes were significantly whiter and their lateral stripes significantly blacker in all four age- and sex-classes (12 tests in all).

Brightness in relation to age.—In basic plumage, among white morphs of both sexes, AHY birds had all three stripes significantly brighter than HY birds (6 tests in all). Among tan morphs, although AHY birds had brighter stripes on average than HY birds, the differences were significant only for the lateral stripe in males (6 tests).

In alternate plumage, there were no significant differences in brightness between age-classes for either sex or morph (12 tests). Consequently, we combined age-classes of birds in alternate plumage for the remainder of the analysis.

Brightness in relation to sex.—In basic plumage, among white morphs,

HY FEMALES (N = 69)

■ TAN MORPH
□ WHITE MORPH

25.0 20.0 15.0 10.0 5.0 0 −5.0 −10.0

HY MALES (N = 42)

25.0 20.0 15.0 10.0 5.0 0 −5.0 −10.0

AHY FEMALES (N = 81)

25.0 20.0 15.0 10.0 5.0 0 −5.0 −10.0

AHY MALES (N = 77)

25.0 20.0 15.0 10.0 5.0 0 −5.0 −10.0
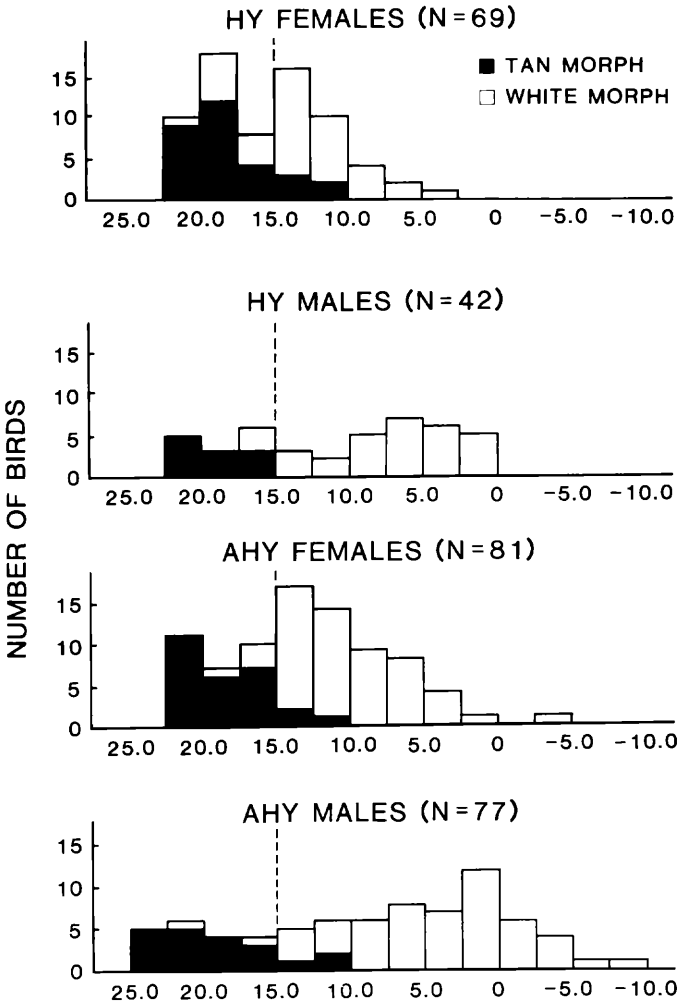
NUMBER OF BIRDS

FIGURE 5.   Distributions of d from the discriminant function for birds of known morph separated by age-sex class. The dashed line indicates the value for best discrimination between morphs.

males of both age-classes were brighter on average than corresponding females (6 tests). Among tan morphs, although males were at least slightly brighter than females on average for all three stripes in both age-classes, males differed significantly from females only for the lateral stripe among AHY birds (6 tests).

In alternate plumage, with age-classes pooled, white males had all three stripes significantly brighter than white females (3 tests). Tan males were significantly brighter than tan females in the median and lateral stripes, but not in the superciliary stripe (3 tests).
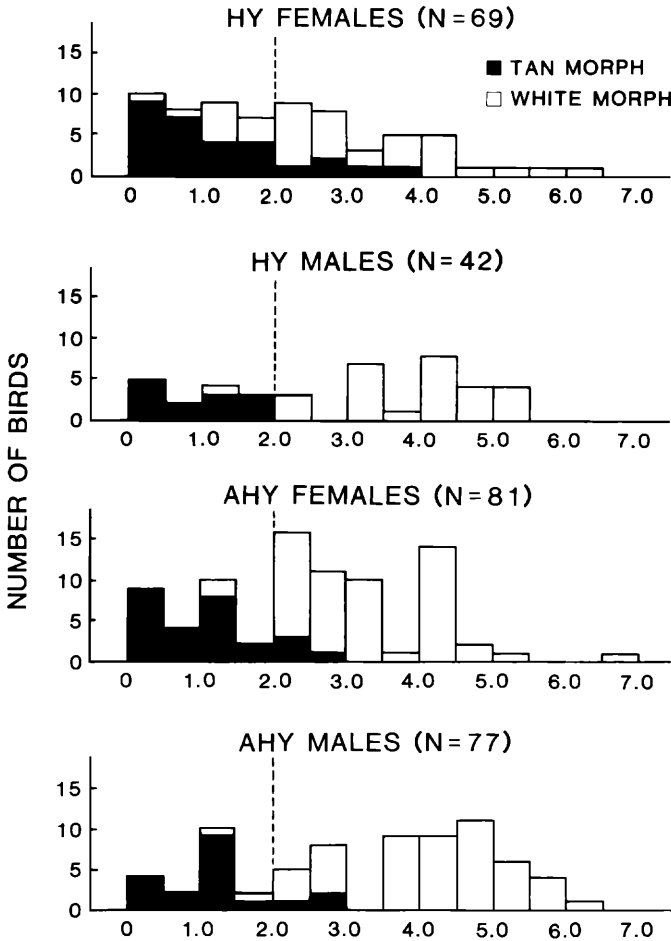
FIGURE 6.   Distributions of X from Formula (1) for birds of known morph separated by
    age-sex class. The dashed line indicates the value for best discrimination between
    morphs.

Brightness in relation to plumage.—White morphs in all age- and sex-classes had all three stripes significantly brighter in alternate plumage than in basic plumage (12 tests in all). Although tan morphs of all age- and sex-classes averaged brighter stripes in alternate plumage than in basic plumage, the differences were significant only for the superciliary stripe of HY females and the lateral and superciliary stripes of HY males (12 tests in all).

Prediction of morph from measurements of basic plumage.—Discriminant analysis showed that brightness of the lateral stripe, brightness of the median stripe, age, and sex were the four best predictors of morph during the winter. Scores for the superciliary stripe did not contribute to the

discriminant function. With $r^2 = 0.536$ and $n = 269$, the discriminant function was:

$$d = 16.9 - 1.25M - 1.41L + 1.87A + 1.80S + 0.185ML - 0.228MA$$

where M is the score for the median stripe, L is the score for the lateral stripe, A is a score indicating age (1 for HY, 2 for AHY), and S is a score indicating sex (1 for female, 2 for male).

The goal of discriminant analysis is to select a value for d that permits classification of observations with the fewest errors (Kleinbaum and Kupper 1978). In our case, $d = 15$ produced the fewest errors in classifying morphs. Although our overall success in predicting morphs was then 87%, the success with which this function predicted morph varied with age- and sex-class. The function correctly assigned the morph of HY females in 77% of cases, but classed HY males, AHY females and AHY males with success rates of 93, 91, and 93% respectively (Fig. 5). Use of different discriminant functions for each age- and sex-class did not improve success.

Several simpler formulas, involving nonlinear combinations of our measures found by trial and error, distinguished morphs as well as or better than the discriminant function. For instance, the following formula classified 89% of the birds in our sample correctly:

$$X = (M + L)/(A + S). \qquad (1)$$

Birds with $X < 2.0$ were classified as tan morphs, those with higher scores as white morphs. As in the case of the discriminant function, the success of this formula in predicting morph varied with age- and sex-class. HY females, HY males, AHY females, and AHY males were correctly classified in 78, 93, 92, and 94% of cases respectively (Fig. 6).

If data on sex are not available, then a modified formula can be used to predict morph with an overall accuracy of 88% when applied to our sample:

$$Y = (M + L)/A. \qquad (2)$$

Birds with $Y < 1.5$ were classified as tan morphs, those with higher scores as white morphs. The success rates of this formula for HY females, HY males, AHY females, and AHY males, respectively, were 77, 90, 94 and 92%.

A third formula can be used when both age and sex are unknown:

$$Z = M + L. \qquad (3)$$

Birds with $Z < 5.0$ were classified as tan morphs, those with higher scores as white morphs. This formula predicted morph in our sample with an overall accuracy of 85% and assigned HY females, HY males, AHY females, and AHY males to morphs with 68, 95, 91, and 88% success.

DISCUSSION

A number of different techniques have been used to measure plumage variation in White-throated Sparrows. Lowther (1961) classified morphs

by comparing birds' median stripes with a graded series of museum specimens. He used a similar procedure to score variation in other features of plumage as well. Vardy (1971) also used a series of museum specimens but based her classification of morphs on both median and lateral stripes. Atkinson and Ralph (1980) and Watt (1986) investigated variation in a number of individual measures and composite indices of plumage coloration. In the present study, for simplicity and repeatability we focused on the crown stripes in classifying morphs, although we recognize that the coloration of the lores, throat, and chest also varies.

Our results in general confirm previous reports that crown coloration is bimodally distributed in alternate plumage and unimodally distributed in basic plumage. Results from our study demonstrate that the shift in the distribution occurs because white morphs—especially first-year birds and older females—tend to increase markedly in brightness following the prealternate molt.

Previous authors have concluded that the white morph is not phenotypically expressed in basic plumage by immature and some adult birds (Atkinson and Ralph 1980, Thorneycroft 1975). However, our data show that HY males differ enough in brightness that they can be assigned to morph with almost the same accuracy as can AHY males and females (see Figs. 5 and 6). Even HY white females are bright enough in relation to their tan counterparts to permit recognition of morph in 78% of cases.

Our results thus show that morphs of both sexes and age-classes can be identified with considerable accuracy in basic plumage. For males and adult females the accuracy exceeds 90%. Even without information about age and sex, we found an overall accuracy of 85% in identifying morphs in basic plumage. Thus a White-throated Sparrow encountering a strange conspecific during the winter could conceivably determine the stranger's morph in about 5 out of 6 cases by its crown stripes alone. If previous experience with a conspecific provided some information about its probable sex or age, or if birds could discriminate other differences between morphs, even greater success would be possible.

By using formula (1), (2) or (3) and scores for plumage stripes, it is possible to estimate the proportion of each morph wintering in our study area. In doing so it is necessary to take into account both correct and incorrect classifications of the formulae. Formula (1), for example, misclassifies 11% of the birds and is biased slightly towards the tan morph (see Fig. 6). This bias must be corrected within each age- and sex-class. For example, changing 3.6% of the HY females (2.5 birds for the sample shown in Fig. 6) from tan to white morphs corrects the bias in this class.

The proportions of white morphs among winter residents (birds with a minimum interval of 60 d between their first and last captures in a winter) at our study site, as estimated by this method, are 0.61 (237/391) among males and 0.49 (165/336) among females. Lowther (1961), based on a survey of museum specimens from breeding populations, concluded that the proportions of white morphs among males and females varied inversely across Canada, with white males and tan females less

frequent in the east. At our study site during winter, the proportion for males corresponds to Lowther's value for breeding males in central Canada, while the proportion for females corresponds to his value for breeding females in Newfoundland. Additional research is needed to check Lowther's figures, especially since the morphs are now known to differ in breeding habitat (Knapton and Falls 1982). In addition, the formulas presented here provide a means for banders to collect information about the geographical distribution of morphs during winter.

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