# THE ROLE OF PLUMAGE POLYMORPHISM IN DOMINANCE RELATIONSHIPS OF THE WHITE-THROATED SPARROW

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ABSTRACT.—We studied dominance behaviors of captive winter flocks of White-throated Sparrows (*Zonotrichia albicollis*) in central Pennsylvania. Preliminary tests with a small group of birds indicated that there might be differences in behaviors between color morphs if age and sexual differences were controlled. Studies of two larger groups produced considerable variation in results between the groups. One group displayed striking correlations between dominance ability and color. In this group white adult males dominated others more than tan adult males did, whereas tan immature males, adult females, and immature females were more often dominant than were white immature and female birds. The second group did not display such striking differences. Tan adult and immature females were more dominant than white females, as in the first group, but not significantly. Immature males displayed the opposite trend from the first group—white morphs were more dominant than tans. Adult males in the second group showed no clear trend. We also found differences in dominance between tan and white females that appeared to depend on season, white birds dominating tan birds in a small group in the spring, a reversal of relationships documented in the fall. Within age-sex classes, dominant females in both large groups tended to be duller in plumage brightness (scaled as an index) than were subordinate females. In one of the two large groups, duller immature males were more dominant than brighter ones, while brighter adult males tended to be more dominant than duller ones. We suggest that the relationships between immature male plumage and dominance may be influenced by the morph of adult males of specific dominance status in the flock. Spring plumage indices were more often correlated with fall dominance differences than were fall plumage conditions, suggesting a genetic or causal relationship between dominance and plumage rather than a proximate (status signaling) function. Recorded morph frequencies from this study and the literature support the hypothesis that selection is balanced between the two morphs and is dependent on the advantages or disadvantages of aggressiveness within a sex. *Received 9 March 1983, accepted 25 July 1983.*

LOWTHER (1961) described two color morphs of the White-throated Sparrow (*Zonotrichia albicollis*), a white-striped and a tan-striped form. He showed that both morphs included males and females. In field observations of 110 mated pairs, he observed negative assortative mating: white-striped males mated with tan-striped females, and tan-striped males mated with white-striped females (Lowther and Falls 1968). Vardy (1971) disagreed that color variation was due to two morphs; she found color types to have a continuous distribution. More recent studies have supported Lowther's interpretation, however: Thorneycroft (1966, 1975) documented a chromosomal dimorphism in the species that was always related to the plumage dimorphism; Atkinson and Ralph (1980) found birds in breeding plumage to be bimodally distributed with regard to quantitative plumage measurements; and Rising and Shields (1980) described other morphological differences between the color morphs. Several of these authors suggested that there might be behavioral differences between the color morphs on the wintering grounds.

We examined differences in dominance behaviors between the two color morphs in winter flocks. Several attempts to find differences in dominance behavior between the morphs

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during the nonbreeding season have been made (Harrington 1973, Hailman 1975, Ficken et al. 1978), but none of these investigators considered the sex or age of the birds. We studied the interrelationships among sex, age, and color morph and found that a combination of characters was a good predictor of dominance rank. The purpose of this paper is to demonstrate the relationships of these variables with social dominance behavior of White-throated Sparrows in captive, nonbreeding flocks.

## METHODS

Birds were caught in mist nets throughout October 1975 at Carlisle, Pennsylvania. Birds were individually marked at capture with colored leg bands and weighed. We determined age by the amount of skull ossification and sex by the unflattened wing chord at capture (Atkinson and Ralph 1980) or by laparotomy the following spring. Birds were kept in three indoor aviaries (2 × 2 × 2 m) under controlled artificial lights, initially on a winter light schedule. The daylength was increased on 1 April to 12 hours light and 12 hours dark to stimulate prenuptial molt. By 16 April the birds were coming into breeding condition, as indicated by molt and singing. We investigated social relationships within four groups of birds: a small group of 16 males and females on 28 November 1975; two large groups of 51 and 54 birds in November and December 1975; and a small group of 17 females on 16 April 1976.

*Determination of color morph.*—Even though White-throated Sparrows in breeding plumage can be divided into two distinct color morphs (Thorneycroft 1975, Atkinson and Ralph 1980), considerable individual variation exists in plumage characteristics (Vardy 1971). Atkinson and Ralph (1980) demonstrated that variation in plumage in the fall ranged from a bright to a dull extreme and that combinations of various plumage characteristics into an index resulted in a normal distribution. In addition, plumage characteristics were correlated with sex, age, and season: males were generally brighter than females, adults brighter than immature birds, and all birds became brighter in the spring (Atkinson and Ralph 1980).

In this study, we calculated an index of plumage brightness similar to Atkinson and Ralph's (1980), using four of their five plumage characteristics: percentage black in lateral crown stripes, throat pattern (as classified by Lowther 1961), median crown-stripe color, and superciliary stripe color. We did not include chest streaking because of its low variability between seasons. The four plumage characteristics were measured at capture in the fall and again in May after prenuptial molt.

We used the median value of the indices to divide birds arbitrarily into "white" or "tan" groups: birds with index values greater than the median were called "white"; those with less were "tan." Because such plumage indices produced a relative comparison of brightness among birds and because we did not prepare karyotypes, our designations of morph may not coincide with Thorneycroft's genetically determined "color morph." Atkinson and Ralph (1980), as well as Thorneycroft (1966, 1975), however, found that, although the two morphs are difficult to distinguish in autumn, they are much more distinct in the spring. Therefore, we used spring-plumage index values to approximate the morph class most similar to Thorneycroft's genetically determined "color morph," and, in fact, only 9 of the 105 birds would have differed in their morph classification between fall and spring plumages.

*Behavioral observations.*—Behavioral interactions were observed through a one-way window overlooking a feeding platform in each of the three aviaries. During observation periods, food was restricted to a small dish on the platform. We recorded winners and losers of dominance encounters at the feeding dish. Winning birds supplanted, pecked, or chased the losing individuals. Using the methods of Sabine (1959) and Brown (1975: 86), we determined dominance hierarchies for the two small groups of birds by constructing dominance matrices of encounters. Large groups did not form clear linear hierarchies, precluding ranking of individual birds. Instead, we tallied dominance dyads for each morph-age-sex class. A dominance dyad between two birds [i.e. A > B: the "pair relations" of Sabine (1959)] was designated when one bird was dominant in more than one-half of the encounters between the pair members, regardless of the number of interactions. The percentage of dyads in which a bird was dominant was defined as its "percentage dominance," or the number of individuals it consistently dominated in known relations. In the two large groups, the numbers of dominant dyads were combined for members of each age-sex-morph class to give the percentage dominance of each class.

*Statistics.*—Because the percentage data were tested and found to be normal, they were not transformed. Statistical tests included a test for differences between two percentages, product-moment correlation, and Mann-Whitney *U*-Tests (Sokal and Rohlf 1969).

## RESULTS

### SMALL GROUP (NOVEMBER)

We conducted a preliminary investigation of a small group (16 birds) in November. The group exhibited an essentially linear and stable hierarchy (Fig. 1). Inspection of physical characteristics correlated with dominance ranks of

LOSER

WINNER

| BIRD RANK | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 |  | 2 | 9 | 4 | 3 | 2 | 5 | 2 | 6 | 3 | 5 | 2 | 1 |  |  | 2 |
| 2 |  |  | 1 |  | 1 | 1 | 3 |  | 2 |  | 1 | 2 |  |  | 1 |  |
| 3 |  |  |  | 7 | 6 | 5 | 5 | 5 | 5 | 4 | 5 | 4 | 4 |  | 6 | 9 |
| 4 |  |  |  |  | 4 | 3 | 3 | 1 | 2 | 1 | 2 | 1 | 3 |  | 1 | 4 |
| 5 |  |  |  |  |  | 2 | 3 | 2 | 6 |  | 3 | 3 | 2 |  | 4 | 4 |
| 6 |  |  |  |  |  |  | 2 | 1 | 1 | 3 | 2 | 3 |  | 1 |  |  |
| 7 |  |  |  |  |  |  |  | 2 |  | 2 | 12 | 3 | 1 |  | 2 |  |
| 8 |  | 3 |  |  |  |  | $1^R$ |  | 2 | 1 |  | 1 | 1 |  | 1 |  |
| 9 |  |  |  |  |  |  | 2 |  |  | 3 | 1 | 2 |  |  | 1 |  |
| 10 |  |  |  |  |  |  |  |  |  |  | 2 |  | 2 |  | 4 | 3 |
| 11 |  |  |  |  |  |  |  |  |  | $1^R$ |  | 5 | 2 | 1 | 3 |  |
| 12 |  |  |  |  |  |  |  |  |  |  |  |  | 2 |  | 4 | 3 |
| 13 |  |  |  |  |  |  |  |  |  |  |  |  |  | 2 |  | 3 |
| 14 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 15 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 14 |
| 16 |  |  |  |  |  | 2 |  |  | 3 |  | 3 |  |  |  |  |  |

Fig. 1. Dominance matrix for 16 White-throated Sparrows in November. The hierarchy is linear except for five instances (bird ranked #8 was dominant to bird ranked #2, etc.). Two reversals (R) occurred where a subordinate bird attacked a dominant bird.

these individuals (Table 1) indicated that sex was the best single predictor of dominance. Other measures, such as morph, age, wing length, or weight, did not explain dominance rank simply. Among females, however, tan birds were more dominant than white birds. The relationship among males with respect to morph was not clear. The results of this preliminary study led us to believe that differences in dominance behaviors between white and tan morphs might be found in larger groups *within* sex and/or age classes.

## LARGE GROUPS

*Appropriateness of encounter-frequency analysis.*—We wished to investigate the role that morph, age, and sex played in determining dominance in the two large groups. Measures involving the percentage of encounters of one class with another class would be a convenient means of analysis. Before we could proceed with this analysis, however, it was necessary to determine how the proportion of birds in each of the two color morphs in a class might affect any measurement of aggression, as Hailman (1975, pers. comm.) has suggested. That is, if birds of one class encountered birds of another class at random, then it would be possible to use encounter frequencies as a measure of dominance. If encounter frequencies were not random, then comparisons of morphs summed over the various age-sex classes would not be valid.

Therefore, we calculated the number of expected encounters from the numbers of individuals in each morph-age-sex class in the two large groups (Table 2) and compared these to observed values (Tables 3 and 4). None of the eight classes, in either of the two groups, encountered the other classes randomly, that is,

TABLE 1. Relationships between dominance rank and physical characteristics of individual White-throated Sparrows represented in Fig. 1.

| Dominance rank | Sex | Morph | Age | Wing length (mm) | Weight[a] (g) | Weight[b] (g) |
|---|---|---|---|---|---|---|
| 1 | M | White | Adult | 74 | 26.8 | 30.4 |
| 2 | M | Tan | Adult | 72 | 23.0 | 26.2 |
| 3 | M | White | Adult | 72 | 25.0 | 27.0 |
| 4 | M | White | Immature | 70 | 24.4 | 23.8 |
| 5 | F | Tan | Immature | 67 | 23.5 | 22.6 |
| 6 | F | Tan | Immature | 65 | 23.6 | 24.5 |
| 7 | F | Tan | Immature | 65 | 22.1 | 20.5 |
| 8 | F | Tan | Adult | 69 | 25.6 | 28.5 |
| 9 | F | Tan | Immature | 68 | 23.5 | 21.7 |
| 10 | F | White | Adult | 65 | 24.0 | 24.8 |
| 11 | M | Tan | Adult | 72 | 23.8 | 29.1 |
| 12 | F | White | Adult | 67 | 23.2 | 25.3 |
| 13 | F | White | Adult | 70 | 23.8 | 25.1 |
| 14 | F | White | Adult | 68 | 22.8 | 23.9 |
| 15 | F | White | Adult | 70 | 26.6 | 26.3 |
| 16 | F | White | Immature | 69 | 22.9 | 24.6 |

[a] Weight at capture.
[b] Weight at testing, 28 November.

in proportion to class size. In general, males were observed in aggressive encounters more frequently, and females less frequently, than expected (row totals in Tables 3 and 4, observed vs. expected). Therefore, encounters were not occurring randomly, and comparisons of morphs summed over classes would not be an appropriate analysis.

Similarly, an analysis of the number of wins (the "attacks" of Hailman 1975) would not be appropriate, because they would be a function of encounter frequency. Also, an analysis of percentage wins or losses, based on total encounters, would be inappropriate, because a particularly aggressive bird might inflate the percentage wins for its class.

*Appropriateness of analysis of dyad formation.*— Another method of comparing dominance relationships of the two morphs within age-sex classes involves the use of *percentage dominance,* the percentage of dyads in which a given class was dominant over another class. The use of percentages alleviates the problem of nonrandom encounter frequencies, because only one dyadic relationship is recorded, regardless of the number of interactions between the two birds. Given that a bird is involved in a set of dyadic relationships, the percentage of those relationships in which it is dominant is independent of encounter frequency. The only remaining problem is the distribution of dyad-formation frequencies: in order to compare percentage dominance values of white adult males with those of tan adult males, the number of dyads they form with other morph-age-sex classes should be equal. We tested these values (Tables 5 and 6) and found that for all eight comparisons of age-sex classes there was no significant difference between white and tan morphs in the probability of forming dyadic relationships with the other classes, with a single exception (significant at slightly greater than the $P < 0.05$ level). Because the assumption of equal probability was met, we summarized percentage dominance values for each morph-age-sex class in each group (Table 7) for testing differences between the morphs within a given age-sex class.

*Dominance as measured by dyad formation.*— Striking differences in dominance between the

TABLE 2. Numbers of birds in each morph-age-sex class for two large groups.

| Class | Group 1 | Group 2 |
|---|---|---|
| Tan adult males (TAM) | 5 | 3 |
| White adult males (WAM) | 7 | 8 |
| Tan immature males (TIM) | 5 | 4 |
| White immature males (WIM) | 9 | 6 |
| Tan adult females (TAF) | 12 | 11 |
| White adult females (WAF) | 3 | 4 |
| Tan immature females (TIF) | 6 | 7 |
| White immature females (WIF) | 7 | 8 |

TABLE 3. Observed and expected (in parentheses) encounter frequencies between a morph-age-sex class with other classes in Group 1. (See Table 2 for class name abbreviations.) Observed values are the same on both halves of the matrix, but expected are different. Observed row totals compared to expected suggest that males encounter other birds more often than expected, while females encounter others less.

| | TAM | WAM | TIM | WIM | TAF | WAF | TIF | WIF | $\chi^{2a}$ | Row total | Expected total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| TAM | 90 (70) | 141 (125) | 94 (90) | 229 (161) | 218 (215) | 7 (54) | 121 (107) | 48 (125) | 127** | 948 | 535 |
| WAM | 141 (83) | 120 (100) | 98 (83) | 197 (150) | 158 (200) | 13 (50) | 91 (100) | 64 (116) | 122** | 882 | 749 |
| TIM | 94 (54) | 98 (75) | 54 (42) | 117 (96) | 109 (129) | 4 (32) | 50 (64) | 43 (75) | 89** | 569 | 535 |
| WIM | 229 (112) | 197 (157) | 117 (112) | 164 (180) | 218 (269) | 12 (67) | 155 (135) | 97 (157) | 215** | 1,189 | 963 |
| TAF | 218 (103) | 158 (144) | 109 (103) | 218 (185) | 180 (227) | 6 (62) | 133 (124) | 70 (144) | 235** | 1,092 | 1,283 |
| WAF | 7 (5) | 13 (6) | 4 (5) | 12 (8) | 6 (11) | 0 (2) | 3 (5) | 3 (6) | 18* | 48 | 321 |
| TIF | 121 (62) | 91 (87) | 50 (62) | 155 (112) | 133 (149) | 3 (37) | 70 (62) | 36 (87) | 139** | 659 | 642 |
| WIF | 48 (37) | 64 (51) | 43 (37) | 97 (66) | 70 (88) | 3 (22) | 36 (44) | 28 (44) | 50** | 389 | 749 |

[a] Comparison of observed encounter frequencies for each class with other classes and expected frequencies based on the numbers of individuals in each class: ** = significant at $\alpha < 0.01$; * = $\alpha < 0.05$.

TABLE 4. Observed and expected (in parentheses) encounter frequencies between a morph-age-sex class with other classes in Group 2. (See Table 2 for class name abbreviations.) Observed values are the same on both halves of the matrix, but expected are different. Observed row totals compared to expected suggest that males encounter other birds more often than expected, while females encounter others less.

| | TAM | WAM | TIM | WIM | TAF | WAF | TIF | WIF | $\chi^{2a}$ | Row total | Expected total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| TAM | 18 (21) | 90 (84) | 82 (42) | 92 (63) | 92 (116) | 24 (42) | 42 (74) | 86 (84) | 80** | 526 | 402 |
| WAM | 90 (65) | 124 (151) | 165 (87) | 200 (130) | 223 (238) | 33 (87) | 106 (151) | 140 (173) | 176** | 1,081 | 1,072 |
| TIM | 82 (61) | 165 (163) | 140 (61) | 164 (122) | 172 (223) | 36 (81) | 119 (142) | 138 (163) | 168** | 1,016 | 535 |
| WIM | 92 (63) | 200 (169) | 164 (84) | 90 (106) | 231 (232) | 23 (84) | 109 (148) | 146 (169) | 155** | 1,055 | 803 |
| TAF | 92 (80) | 223 (213) | 172 (107) | 231 (160) | 218 (267) | 52 (107) | 144 (187) | 201 (213) | 121** | 1,333 | 1,473 |
| WAF | 24 (14) | 33 (38) | 36 (19) | 23 (28) | 52 (52) | 14 (14) | 21 (33) | 33 (38) | 29** | 236 | 535 |
| TIF | 42 (41) | 106 (108) | 119 (54) | 109 (81) | 144 (149) | 21 (54) | 60 (81) | 75 (108) | 124** | 676 | 938 |
| WIF | 86 (54) | 140 (145) | 138 (73) | 146 (109) | 201 (199) | 33 (73) | 75 (127) | 88 (127) | 145** | 907 | 1,072 |

[a] Comparison of observed encounter frequencies for each class with other classes and expected freuqencies based on the numbers of individuals in each class: ** = significant at $\alpha < 0.01$.

TABLE 5. Percentage dominance for 54 birds in eight morph-age-sex classes in Group 1. Numbers in parentheses are the numbers of dominance relationships formed in each class. Data in "total" column were tested for differences between color morphs for each age-sex class. (See text for details.)

| Class | TAM | WAM | TIM | WIM | TAF | WAF | TIF | WIF | Total | $\chi^2$[a] |
|---|---|---|---|---|---|---|---|---|---|---|
| TAM | 50.0 (14) | 46.7 (30) | 88.9 (18) | 84.4 (32) | 85.7 (42) | 100.0 (3) | 90.9 (22) | 86.7 (15) | 176 | 6.06 ns |
| WAM | 53.3 (30) | 50.0 (36) | 80.0 (25) | 75.0 (48) | 75.9 (54) | 72.7 (11) | 75.0 (32) | 91.7 (24) | 260 | |
| TIM | 11.1 (18) | 20.0 (25) | 50.0 (18) | 42.4 (33) | 50.0 (36) | 50.0 (4) | 47.4 (19) | 56.3 (16) | 169 | 1.34 ns |
| WIM | 15.6 (32) | 25.0 (48) | 57.6 (33) | 50.0 (54) | 73.9 (69) | 87.5 (8) | 52.4 (42) | 75.0 (32) | 318 | |
| TAF | 14.3 (42) | 24.1 (54) | 50.0 (36) | 26.1 (69) | 50.0 (66) | 100.0 (5) | 56.9 (51) | 41.9 (31) | 354 | 8.00 ns |
| WAF | 0.0 (3) | 27.3 (11) | 50.0 (4) | 12.5 (8) | 0.0 (5) | — (0) | 33.3 (3) | 66.7 (3) | 37 | |
| TIF | 9.1 (22) | 25.0 (32) | 52.6 (19) | 47.6 (42) | 43.1 (51) | 66.7 (3) | 50.0 (22) | 42.9 (21) | 212 | 5.21 ns |
| WIF | 13.3 (15) | 8.3 (24) | 43.7 (16) | 25.0 (32) | 58.1 (31) | 33.3 (3) | 57.1 (21) | 50.0 (10) | 152 | |

[a] ns = not significant.

TABLE 6. Percentage dominance for 51 birds in eight morph-age-sex classes in Group 2. Numbers in parentheses are the numbers of dominance relationships formed in each class. Data in "total" column were tested for differences between color morphs for each age-sex class. (See text for details.)

| Class | TAM | WAM | TIM | WIM | TAF | WAF | TIF | WIF | Total | $\chi^2$[a] |
|---|---|---|---|---|---|---|---|---|---|---|
| TAM | 50.0 (2) | 43.8 (16) | 33.3 (9) | 75.0 (12) | 27.8 (18) | 75.0 (4) | 26.3 (14) | 100.7 (12) | 176 | 9.93 ns |
| WAM | 56.2 (16) | 50.0 (26) | 40.7 (27) | 84.8 (32) | 54.8 (42) | 66.7 (12) | 76.7 (31) | 94.3 (35) | 221 | |
| TIM | 66.7 (9) | 59.3 (27) | 50.0 (12) | 73.9 (23) | 50.0 (30) | 100.0 (8) | 75.0 (24) | 85.2 (27) | 160 | 5.25 ns |
| WIM | 25.0 (12) | 15.2 (32) | 26.1 (23) | 50.0 (22) | 34.8 (46) | 50.0 (10) | 56.7 (30) | 48.5 (33) | 208 | |
| TAF | 72.2 (18) | 45.2 (42) | 50.0 (30) | 65.2 (46) | 50.0 (60) | 82.4 (17) | 57.5 (40) | 85.7 (42) | 295 | 1.75 ns |
| WAF | 25.0 (4) | 33.3 (12) | 0.0 (8) | 50.0 (10) | 17.6 (17) | 50.0 (4) | 42.9 (7) | 72.7 (11) | 73 | |
| TIF | 73.7 (14) | 23.3 (31) | 25.0 (24) | 43.3 (30) | 42.5 (40) | 57.1 (7) | 50.0 (13) | 66.7 (30) | 194 | 17.5* |
| WIF | 0.0 (12) | 5.7 (35) | 14.8 (27) | 51.5 (33) | 14.3 (42) | 27.3 (11) | 33.3 (30) | 50.0 (24) | 214 | |

[a] ns = not significant; * = $P \leq 0.05$.

TABLE 7. Percentage dominance in two groups of each morph-age-sex class over classes other than its own.

| | Group 1 | | | Group 2 | | |
|---|---|---|---|---|---|---|
| | $n^a$ | % | $t^b$ | $n^a$ | % | $t^b$ |
| Tan adult males | 162 | 79.6 | 1.16 ns | 85 | 51.8 | 2.71** |
| White adult males | 224 | 74.6 | | 196 | 68.9 | |
| Tan immature males | 151 | 39.1 | 2.74** | 148 | 69.6 | 6.16** |
| White immature males | 264 | 53.0 | | 187 | 36.4 | |
| Tan adult females | 288 | 35.4 | 1.39 ns | 237 | 63.3 | 4.23** |
| White adult females | 37 | 24.3 | | 69 | 34.8 | |
| Tan immature females | 190 | 38.4 | 0.60 ns | 176 | 43.75 | 4.29** |
| White immature females | 142 | 35.2 | | 192 | 22.9 | |

[a] $n$ = number of dominance relationships (dyads) considered in the computation of percentage dominance.

[b] Statistical comparisons were made within age-sex class between white and tan birds. ** = $\alpha < 0.01$; ns = not significant.

two morphs, within each age-sex class, were found in Group 2 (Table 7). In encounters between adult males, white morphs were more often dominant. In encounters between immature males, adult females, or immature females, however, tan morphs were more often dominant. Group 1 showed less striking differences. In encounters between adult females or immature females, tan morphs were also more dominant than white morphs, but not significantly. In encounters between adult males or immature males, tan morphs were more dominant, a trend opposite to that shown by Group 2 birds. Only the relationship between immature males was significant, however.

## DIFFERENCES WITHIN AGE-SEX CLASS

Because we found instances of differences in dominance between morphs within each age-sex class, we investigated possible differences involving more continuous plumage variation within Groups 1 and 2. Specifically, we examined whether or not whiter birds were more dominant within each age-sex class (e.g. in adult males) by analyzing correlations of percentage dominance with spring-plumage index values and with fall-plumage index values. If birds were using proximate cues to evaluate probable dominance relationships before interacting, i.e. the status signaling of Rohwer (1975), fall values should have the highest correlations with dominance. If genetic differences in dominance ability were correlated with color morph (apparent only in spring), however, then spring values would be most highly correlated. A third and nonexclusive possibility was that winter dominance behaviors in some way influence the expression of color morph in the spring. We could not distinguish between cause and effect under this last hypothesis. We did assess relationships between fall dominance and degree of change in plumage from fall to spring, however.

We found that spring values of plumage brightness correlated more often with winter dominance behaviors than did fall values (Table 8). To demonstrate the nature of the correlations, we plotted the spring-plumage index of individual birds in each of the two groups against their measured percentage dominance (Fig. 2). A significant *positive* correlation was found for adult males in Group 2 (whiter birds were more dominant). Significant negative relationships were found for immature males in Group 2, adult females in Group 1, and total females (immature females varied in the appropriate direction but were not quite significant when considered alone) (Table 8). While most birds increase in plumage-index value from fall to spring (Atkinson and Ralph 1980), some birds do so more than others. We found that the degree of plumage brightening was negatively correlated with fall dominance behavior of adult females in Group 2 and of all females combined (Table 8). Females that were more dominant in fall had less plumage brightening in spring.

## FEMALE MORPH DIFFERENCES IN TWO SEASONS

Thorneycroft (1975) noted that white females appeared to be more aggressive than tan females on the breeding grounds. We found that tan females usually dominated white females and were more dominant to other birds

TABLE 8. Correlations of percentage dominance measures with plumage measures taken during the fall and spring and degree of plumage brightening from fall to spring. Correlations between plumage and dominance were more often significant in spring than in fall.

| Samples | $n$ | Correlation ($r$) | | |
|---|---|---|---|---|
| | | Fall plumage[a] | Spring plumage[a] | Plumage brightening[a] |
| Adult males | | | | |
| Group 1 | 12 | −0.142 | −0.064 | 0.181 |
| Group 2 | 11 | 0.490 | 0.606 | 0.172 |
| Total | 23 | 0.142 | 0.201 | 0.144 |
| Immature males | | | | |
| Group 1 | 14 | 0.410 | 0.243 | −0.159 |
| Group 2 | 10 | −0.801** | −0.781** | −0.327 |
| Total | 24 | −0.193 | −0.254 | −0.201 |
| Total males | 47 | 0.067 | −0.018 | 0.170 |
| Adult females | | | | |
| Group 1 | 15 | −0.531* | −0.539* | −0.146 |
| Group 2 | 15 | −0.101 | −0.490 | −0.617* |
| Total | 30 | −0.242 | −0.376* | −0.260 |
| Immature females | | | | |
| Group 1 | 13 | −0.062 | 0.210 | −0.281 |
| Group 2 | 15 | −0.202 | −0.347 | −0.368 |
| Total | 28 | −0.143 | −0.286 | −0.305 |
| Total females | 58 | −0.209 | −0.358** | −0.307* |

[a] ** = significant at $\alpha < 0.01$; * = $\alpha < 0.05$.

than were white females. Because our results contradicted previous suggestions, we hypothesized that female dominance relationships might change with season. Tan females could be more dominant than white females in fall but become more subordinate in spring. To test this hypothesis, we assembled a small group of 17 females from the larger hierarchies and observed their dominance behavior in April. Following prenuptial molt, white females were significantly more dominant than tan females (Table 9; Mann-Whitney *U*-Test; $U = 57$, $P < 0.05$). Moreover, a significant positive correlation was found between individual spring-plumage indices and percentage dominance in April ($r = 0.58$, $P < 0.05$). Thus, it appears that behavioral relationships between morphs, at least for females, may change with season. Because male birds were not present in this last test, we cannot rule out the influence males might have had on female dominance.

## DISCUSSION

*Dominance and plumage morph.*—Lowther and Falls (1968) and Falls (1969) found that white White-throated Sparrows are more aggressive and are more persistent and frequent singers than are tan sparrows. Thorneycroft (1975) suggested that white females might be more aggressive than their tan counterparts. Other investigators (Harrington 1973, Hailman 1975, Ficken et al. 1978) have suggested the same for nonbreeding groups—white morphs are more aggressive than tan morphs. Hailman (1975) reanalyzed much of Harrington's data and concluded that the data suggesting that white morphs were more aggressive than tan morphs were inconclusive, because the relative proportions of morphs were not known. Taking into account the proportions of the morphs present during the encounters, Ficken et al. (1978) concluded that white morphs are more frequently the aggressors than are tan morphs. They suggested that there is a behavioral difference between the two morphs. Among the interpretations they discussed was the possibility of a differential sex or age bias in the morph populations present. More important, they also suggested that, like its coloration, the tan morph's relative lack of aggressiveness represents a neotenic condition, in that in both behavior and morphology it retains characteristics of young birds in adulthood: "tan head-

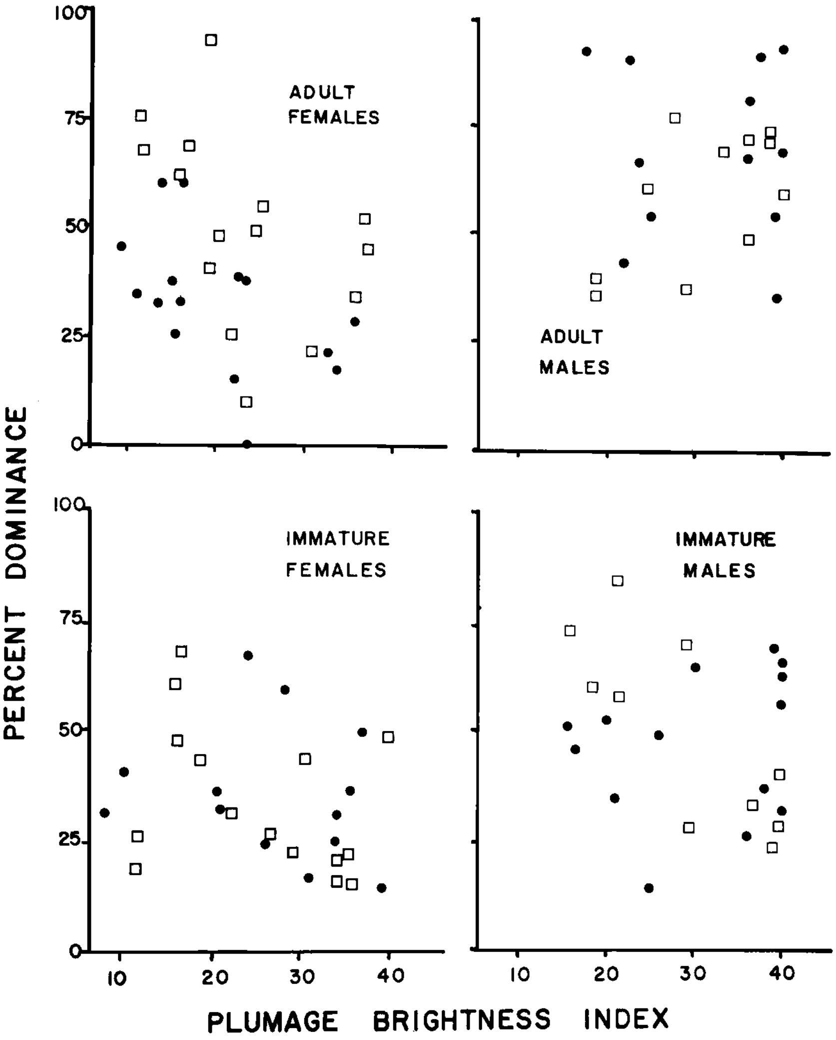

Fig. 2. Plot of percentage dyads in which individuals were dominant in November against their plumage-brightness index as measured after spring molt (see text for explanation). Circles (●) and squares (□) represent birds in Groups 1 and 2, respectively.

stripe and relative unaggressiveness are characteristics of birds in their first fall of life."

Our finding of relatively greater dominance in tan females in the fall is the reverse of the above reports for the spring and breeding seasons, and it disagrees with the neotenic hypothesis of Ficken et al. (1978). We feel that among females, in particular, a reversal in relative dominance occurs between seasons. It is possible that harassment of white females by dominant males could force them to lower levels in the fall hierarchy, and, subsequently in the spring, their levels might rise as males became less aggressive toward potential mates. It is also possible, however, that white female birds actually become more aggressive, relative to tan females, in the spring. This could be due to hormonal changes affecting each morph differently. Future studies should be able to determine whether the presence of males or a change in physiology is responsible for these changes in relative dominance levels.

At this time, we do not know if adult males exhibit such a seasonal change in dominance; in one group we found white adult males were more dominant than tan adult males. Immature males in one group were more dominant when white, in the other group when tan. This obviously requires further testing, especially of all-male groups in both spring and fall. Sexual differences may exist between the color morphs in their relationship to dominance rank, and further studies require assessment of sexual effects in the analysis.

Correlations between fall dominance behavior and the "spring" rather than the "fall" color morph support the hypothesis (Ficken et al. 1978) that behavioral differences between the color morphs are genetic rather than being based on appearances alone (i.e. status signals). We cannot rule out the possibility, however, that behavioral differences in the fall affect the expression of color in spring plumages.

*Sex differences in morph ratios.*—Thorneycroft (1975) found among young females the ratio of tan to white was 1:1, while among males it was 43:57. By breeding season, the ratios were 74:26 in females and 32:68 in males. In our study, 36% of the males were tan, and 64% were white. Among females, 62% were tan, and 38% were white (Table 2). These values are intermediate between Thorneycroft's ratios of young birds and those of his adult breeding birds and probably reflect a normal autumn ratio, at least for central Pennsylvania.

*Body size and dominance.*—Rising and Shields (1980) found that white males were slightly larger than tan males. Although they had small samples of females, they showed that in 8 of 9 measurements, white females were larger than tan females. Based on body size alone, one might have predicted that white birds should dominate tan birds in both sexes. We found in the analysis of the small hierarchy (Table 1), however, that body size was not a good predictor of dominance rank, within either age-sex classes or color morphs.

*Effects of season.*—In the studies of Harrington (1973) and Ficken et al. (1978), data were collected from 22 April to 4 May, when the majority of birds are in nuptial plumage (Lowther and Falls 1968). Therefore, their results can best be compard to those of the breeding studies (Lowther and Falls 1968, Falls 1969). Our results for a group of females in nuptial plumage agree with these previous studies; white birds were more dominant than tan birds in late spring.

Our study is the first to investigate and document dominance differences between color morphs in the fall. [Wessel and Leigh (1941) studied fall birds, but they sexed most of their birds by plumage differences, a method now known to be inappropriate.]

TABLE 9. Relationships between dominance rank, percentage dominance, and color characteristics in a group of 17 female White-throated Sparrows in April.

| Dominance rank | Color morph | Spring-plumage index | Percentage dominance |
|---|---|---|---|
| 1 | White | 36.84 | 93 |
| 2 | White | 26.15 | 69 |
| 3 | White | 35.51 | 67 |
| 4 | Tan | 19.80 | 76 |
| 5 | White | 37.42 | 75 |
| 6 | Tan | 24.15 | 63 |
| 7 | Tan | 23.13 | 69 |
| 8 | White | 36.83 | 69 |
| 9 | White | 34.33 | 44 |
| 10 | Tan | 24.96 | 40 |
| 11 | White | 35.66 | 29 |
| 12 | White | 35.52 | 40 |
| 13 | Tan | 13.63 | 19 |
| 14 | Tan | 8.78 | 29 |
| 15 | Tan | 21.79 | 20 |
| 16 | Tan | 11.26 | 15 |
| 17 | Tan | 16.12 | 13 |

*Plumage brightness within age-sex class.*—We found that, within age-sex classes, spring-plumage brightness was a good indicator of dominance in females, but not in males in two of four groups. The pattern of significance found in one group leads us to hypothesize that dominance in immature males might be influenced by the relations of the adult males in their group. Similarly to a speculation mentioned above regarding female rank, adult males may persecute individuals of their own morph class selectively, so that in groups where white males are strongly dominant, immature white males are strongly submissive. Studies of behaviors in groups with different sex, age, and morph ratios could clarify these questions.

With regard to Rohwer's (1975) hypothesis that plumage variability in birds is used as a status signal, we doubt that it is being used as such by White-throated Sparrows. Plumage itself is not a good predictor of dominance in a mixed-sex group of this species. For example, a tan female in the autumn could not predict the relative status of a white bird without knowledge of its sex—if it were a male, it would be dominant to her; if a female, subordinate. Additionally, changes in signals with season decrease the predictive value of plumages. Plumage variation may be important in facilitating individual recognition, however (Shields 1977).

*Evolution.*—Linkage between color mutations and aggressive levels has been documented in mammals by Keeler et al. (1968, 1970). The interaction between plumage, sex, and hormonal control of aggression may also be a considerable influence on White-throated Sparrows.

As an evolutionary strategy for females, it may be advantageous to be dominant to other females in fall foraging flocks and then to become more subordinate in order to pair more easily with aggressive males. This is the pattern seen in tan females. The same trend (more aggressive in fall but less in the spring), however, would be a disadvantage for tan males when competing with white males for territories in the spring. The apparent selective advantages of being tan, then, could be balanced through opposing pressures on males and females. This hypothesis is supported by the trend of decreasing relative frequencies of tan males from autumn to spring and the increasing relative frequency of tan females (Thorneycroft 1975). White females would appear to be at a disadvantage in both seasons (assuming subordination in winter and aggressiveness in spring are selectively disadvantageous for females), and, in fact, white females are proportionately the least numerous of any sex-morph class by breeding season (Thorneycroft 1975). The white morph, then, could be maintained by its general advantage to adult males at all seasons.

## ACKNOWLEDGMENTS

We thank J. B. Falls, J. P. Hailman, D. James, S. Rohwer, W. Shields, and R. Zink for help during the course of this study and for helpful comments on the manuscript. What forbearance we received from the Reineman Sanctuary was appreciated. Bill Jefferies and Noel Potter provided helpful support for our research at Dickinson College.

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