COLOR VARIATION IN THE CROWN OF THE WHITE-THROATED SPARROW, *ZONOTRICHIA ALBICOLLIS*

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Until recently most authors have considered the well-known color variation in the crown and throat plumage of the White-throated Sparrow, *Zonotrichia albicollis*, to be age, sex, and seasonally dependent (Dwight 1900). Studies by Lowther (1961) and Thorneycroft (1966) have renewed interest in the phenomenon by introducing an explanation based upon a theory of polymorphism. The present study analyzes new data derived from banded birds, birds held in aviaries, and museum specimens, and reexamines the basis for this color variation.

Although the regions of the color variation in the plumage of the White-throated Sparrow include the crown, loral spot, breast, and throat, I have restricted my study to the lateral and median coronal stripes because of the ease and consistency with which they can be classified. The lateral coronal stripe varies from chestnut brown, speckled with black, to a homogeneous solid black. The median coronal stripe varies from dull tan to bright white, and is the basis for Lowther's dichotomous classification of individuals as "tan-striped morphs" or "white-striped morphs."

The characters not analyzed in the present study were shown by Lowther (1961) to be correlated with coronal striping. Bright-crowned birds (black and white stripes) exhibited large, bright yellow loral spots, and clear gray breasts, with bright white throat patches. Birds with dull coronal striping had small, dull yellow loral spots, a streaked breast, and little or no evidence of the white throat patch.

The morphological variation of the White-throated Sparrow appears throughout the breeding range. The species is not known to exhibit taxonomically significant geographical variation (Swenk 1930 and AOU 1957).

PROCEDURES

Included among the 618 birds examined for crown plumage characteristics were 349 specimens in the collection of the American Museum of Natural History and 285 live birds processed during a two-year field study at the Kalbfleisch Field Research Station of the American Museum of Natural History.

In order to classify crown stripe coloration in museum specimens and live birds, two graded series of museum skins were prepared. The median stripe series progressed from dull tan through brighter tan and gray to bright white, as illustrated by A.M.N.H. specimens nos. 83628, 404577, 442130, 387570, 404527, and 101789, respectively.

The lateral crown stripe series ranged from dark chestnut brown through specimens with a posteriorly advancing and increasing amount of black to solid black, as illustrated by A.M.N.H. specimens nos. 404539, 404576, 404482, 404538, 404481, 505535, 763165, and 764164, respectively.

Live birds were trapped with seed or mist-netted at the Kalbfleisch Field Station, a 94-acre tract located in Dix Hills, a suburban-rural community in the western section of Suffolk County in central Long Island. The area comprises fields in several stages of succession, secondary growth woodland, several vernal and one permanent pond, and a gently rolling, glaciated topography. The White-throated Sparrow does not breed on Long Island and all birds processed at the field station represent migrants or winter residents.

Sexing of live birds was accomplished by laparotomy, following an intramuscular injection of Equithesin. All birds were retained in holding cages until flight capability returned.

Until late December, aging of live birds was accomplished by examining the extent of skull ossification through a small incision in the thin skin overlying the cranium. Completion of ossification prohibits aging of late winter and spring individuals.

Several birds processed in this manner repeated during the season of capture and returned during subsequent seasons so that their individual histories of crown plumage pattern were available for study. Because of the low percentage of returns, however, groups of white-throats were retained in outdoor flight pens from April 1966 to May 1967. Thus results of both prealternate ("prenuptial") and prebasic ("postnuptial") molts could be observed. (The terminology for molts and plumages used throughout this paper is that recommended by Humphrey and Parkes 1959.) In order to study variation following induced molt, the feathers of the right side of the crown of some individuals were removed; the undisturbed left side served as a control.

Individual birds were identified by numbered Fish and Wildlife Service bands and by unique combinations of colored plastic bands.

RESULTS

BASIC PLUMAGE

Basic-plumaged birds (=birds in "winter plumage") include fall migrants of all ages netted

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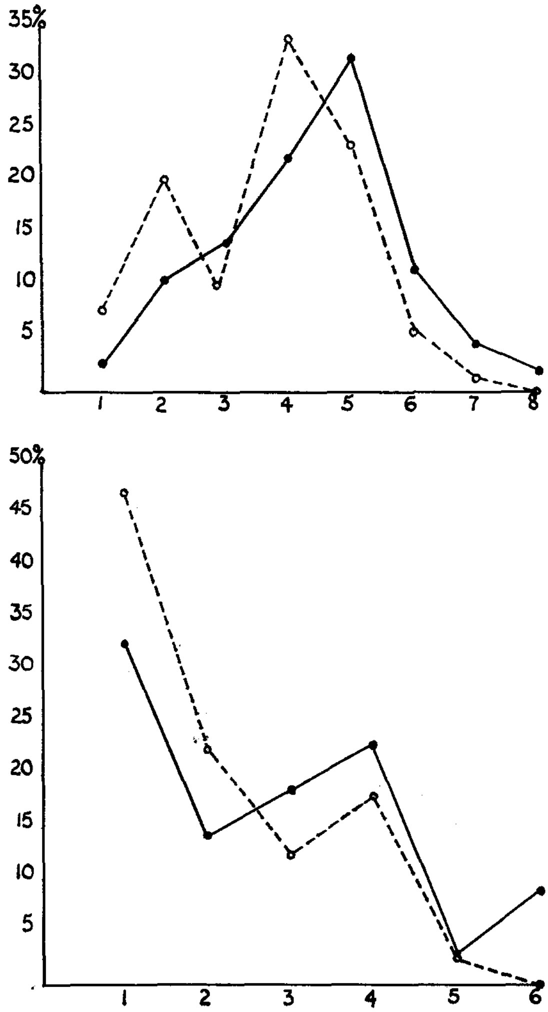

FIGURE 1. Comparison of color of lateral crown stripe (upper) and median crown stripe (lower) of male (●) and female (○) White-throated Sparrows in basic plumage. Ordinate scales are in per cent frequency. Numbers on the abcissae represent categories in graded series of plumage classes (see text for explanation).

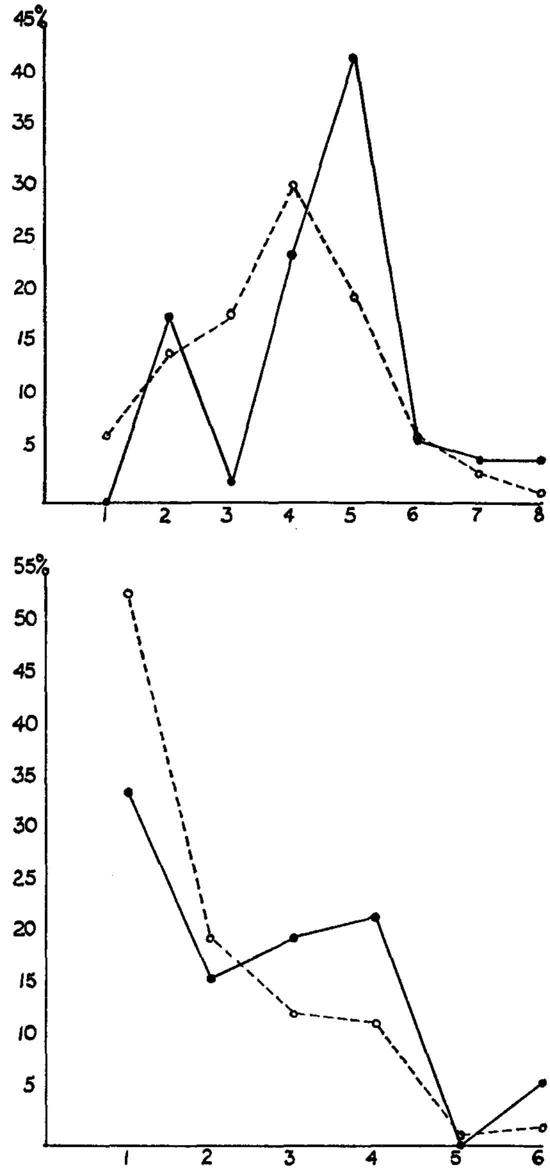

FIGURE 2. Comparison of color of lateral crown stripe (upper) and median crown stripe (lower) of immature (○) and adult (●) white-throats in basic plumage. Ordinate scales are in per cent frequency. Numbers on the abcissae represent categories in graded series of plumage classes (see text for explanation).

in large flocks in the weed-filled fields of Kalbfleisch, and a sparse, roving band of winter residents, trapped only on snowy days when natural food was unavailable. A total of 89 females and 113 males were processed between 1965 and 1967.

Figure 1 gives sexual comparisons of lateral and median coronal striping. All ages are represented so that these graphs may be compared with those of figure 3, their alternate plumage counterparts. Figure 1 reveals that males in basic plumage tend toward blacker lateral stripes than do females. Males exhibit brighter median coronal striping than the generally duller females. Most males were gray-striped but a small number of white-striped individuals were also handled. Most females were of drab tan striping; none was white-striped.

Figure 2, comparing immature and adult birds, regardless of sex, bears a striking resemblance to figure 1. In this case the adults are the brighter group while the immature are browner in lateral striping (fig. 2, upper graph) and duller in median striping (fig. 2, lower graph).

TABLE 1. Analysis of crown stripe coloration with respect to sex in the White-throated Sparrow.

Test	Plumage	Coronal striping	Sex	n	$\bar{x}$	s^2	t
Banded birds							
1	Basic	Lateral	F	89	3.54	2.87	5.00*
			M	113	4.46	0.77	
2	Basic	Median	F	89	2.12	1.43	3.06*
			M	113	2.75	2.55	
3	Alternate	Lateral	F	15	4.78	2.20	2.67*
			M	60	6.20	2.16	
4	Alternate	Median	F	15	2.89	3.50	6.40*
			M	60	5.08	0.48	
Museum birds							
1	Basic	Lateral	F	78	2.97	1.66	4.72*
			M	100	3.81	1.23	
2	Basic	Median	F	78	1.79	1.18	2.48*
			M	100	2.20	1.13	
3	Alternate	Lateral	F	43	4.50	3.25	5.00*
			M	114	5.90	2.11	
4	Alternate	Median	F	43	3.70	2.59	4.13
			M	114	4.80	2.05	

* $P < 0.05$.

The Student t test (Simpson et al. 1960) was employed to test for differences in the means of the above groups. Table 1 indicates that males and females in basic plumage are significantly different in both lateral and median crown striping. Table 2 shows the coronal striping of adult and immature birds to differ significantly. The statistical test confirms graphical analysis of the basic plumaged birds.

ALTERNATE PLUMAGE

Alternate-plumaged males (= males in "breeding plumage") are generally brighter than alternate-plumaged females, the difference between the sexes being more pronounced than in basic-plumaged birds. These differences are borne out by the t test, table 1.

The males exhibited a considerable amount of black in their lateral crown striping. They dominate the blacker end of the lateral crown stripe series (fig. 3, upper graph), while the females tend toward a central distribution.

TABLE 2. Analysis of crown stripe coloration with respect to age in the White-throated Sparrow.

Test	Coronal striping	Age	n	$\bar{x}$	s^2	t
1	Lateral	Imm.	111	3.77	2.14	2.69*
		Ad.	50	4.44	2.25	
2	Median	Imm.	111	1.93	1.44	2.92*
		Ad.	50	2.50	2.69	

* $P < 0.05$.

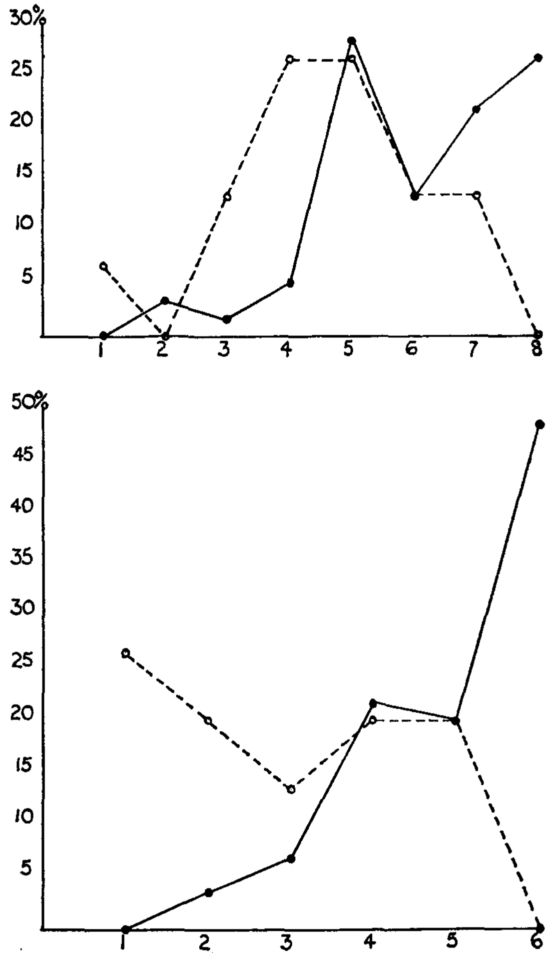

FIGURE 3. Comparison of color of lateral crown stripe (upper) and median crown stripe (lower) of male (●) and female (○) White-throated Sparrows in alternate plumage. Ordinate scales are in per cent frequency. Numbers on the abcissae represent categories in graded series of plumage classes (see text for explanation).

The lower graph of figure 3, where the two curves assume opposing directional tendencies, illustrates dramatic distributional differences between the sexes. While similar proportions of males and females are of intermediate (tan-gray) crown stripe coloration, the greater percentage of females are of drab tan striping, while the majority of males exhibit bright white stripes. Not one female was found with white stripes and not one male with drab tan crown striping.

Upon further examination of figure 3 we find that the alleged bimodality of the spring sample (Lowther 1961) is not in evidence. Rather, the curves form either decreasing or increasing progressions, or assume normal distributions.

TABLE 3. Analysis of crown stripe coloration with respect to plumage in the White-throated Sparrow.

Test	Coronal striping	Plumage	Sex	n	$\bar{x}$	s^2	t
Banded birds							
1	Lateral	Basic	F	89	3.54	2.87	2.12*
		Alternate	F	15	4.78	2.20	
2	Median	Basic	F	89	2.12	1.43	1.75†
		Alternate	F	15	2.89	3.50	
3	Lateral	Basic	M	113	4.46	0.77	9.90*
		Alternate	M	60	6.20	2.16	
4	Median	Basic	M	113	2.75	2.55	9.90*
		Alternate	M	60	5.08	0.48	
Museum birds							
1	Lateral	Basic	F	78	2.97	1.66	5.40*
		Alternate	F	43	4.50	3.25	
2	Median	Basic	F	78	1.79	1.18	7.73*
		Alternate	F	43	3.70	2.59	
3	Lateral	Basic	M	100	3.81	1.23	11.71*
		Alternate	M	114	5.90	2.11	
4	Median	Basic	M	100	2.20	1.13	14.93*
		Alternate	M	114	4.80	2.05	

* $P < 0.05$; † $P < 0.10$.

COMPARISON OF PLUMAGES

Basic-plumaged birds of both sexes were found to be generally duller than their alternate-plumaged counterparts. The *t* test (table 3) revealed significant differences between means of the two groups. The extent of these differences can be seen in graphs figures 4 and 5.

Figure 4 (upper graph) shows that the lateral crown stripes of females in basic plumage contain more brown and fewer black feathers than do those of females in alternate plumage. The lower graph indicates that the median crown stripe of the basic plumaged female is, on the average, duller than that of the brighter alternate-plumaged female.

The differences between samples of males in basic and alternate plumages is even more striking. Figure 5 indicates that alternate-plumaged males tend toward blacker lateral crown stripes, while the basic-plumaged males are not as bright. The widely diverging termini of the two curves in the lower graph of figure 5 emphasize the brightening in crown plumage coloration that occurs with the attainment of the alternate plumage.

MUSEUM SPECIMENS

The data obtained from the specimens examined at the American Museum of Natural History were not combined with those from live birds processed at Kalbfleisch Field Station because the method and reliability of sexual identification of museum specimens are, in many cases, not known. The results obtained from statistical (tables 1 and 3) and graphical analysis (excluded from the present text due to space considerations) of the museum specimens, however, closely parallel those obtained from the live birds, and confirm that males tend to be brighter than females throughout the year, and that birds of both sexes are brighter in alternate ("breeding") plumage than in basic ("non-breeding") plumage. As was true for the live bird samples, there is no evidence of bimodality in the graphical representation of the museum specimens.

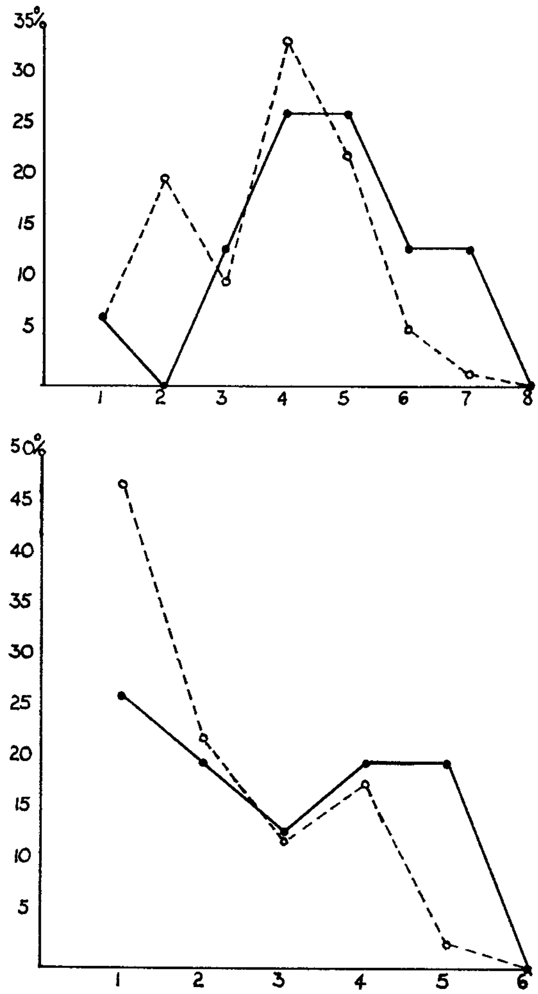

FIGURE 4. Comparison of color of lateral crown stripe (upper) and median crown stripe (lower) in female White-throated Sparrows in basic (○) vs. alternate (●) plumage. Ordinate scales are in per cent frequency. Numbers on the abcissae represent categories in graded series of plumage classes (see text for explanation).

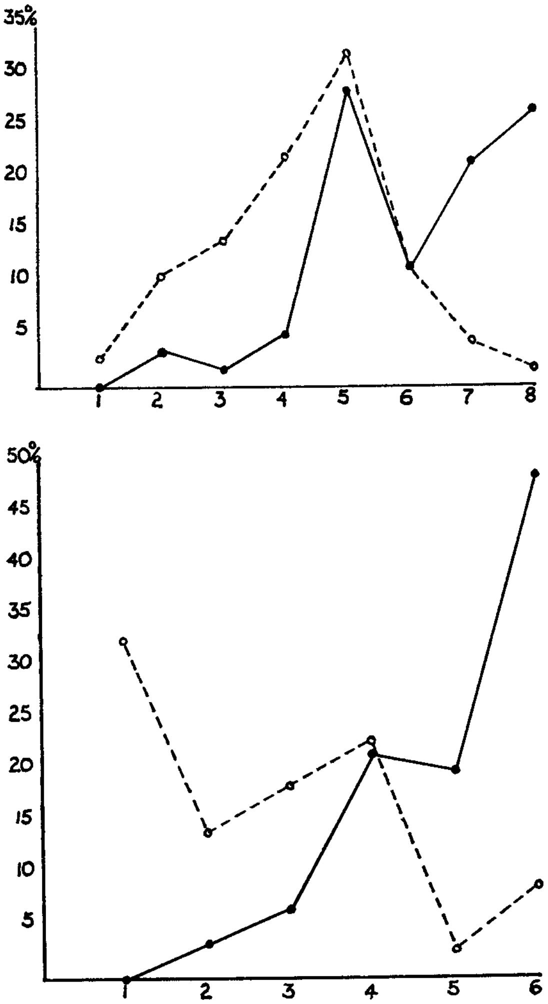

FIGURE 5. Comparison of color of lateral crown stripe (upper) and median stripe (lower) in male White-throated Sparrows in basic (○) vs. alternate (●) plumage. Ordinate scales are in per cent frequency. Numbers on the abcissae represent categories in graded series of plumage classes (see text for explanation).

REPEATS AND RETURNS

Information available via repeat (birds captured two or more times during one season) and return (birds captured and recaptured during subsequent seasons or migrations) data is limited by the low frequency of the events themselves. The probability of an individual returning to the same banding station or being brought to the attention of the bander is particularly low for passerine birds. This problem was encountered in the case of the White-throated Sparrow. As the birds were unavailable during the summer months when breeding and the prebasic molt occur, changes from alternate to basic plumages could not be witnessed unless an individual was handled in the spring and again during the following fall migration. No such event occurred during the present study.

However, several birds were captured during more than one migration or wintered at the field station and appeared in fall and again in late winter. Information could be obtained from these returns as to the constancy or variation of crown plumage coloration.

Examination of table 4 discounts the possibility of random variation. Although not every bird retains a crown classification identical to that of the previous year(s), the change exceeded one crown class category in only one individual. This was an immature male (the last bird on the chart) which increased two classes in the median crown stripe series between the first basic and definitive basic plumages. It was the only return of a bird originally handled as immature. The existing data suggest little annual change after the definitive basic plumage has been attained.

Repeat data are even less informative in terms of annual plumage variation. Fall migrants have already attained their basic plumage and will not change this pattern until the prealternate molt.

Spring repeat data can be useful if a bird is handled either before or during and again after the prealternate molt. Two such individuals, both males, were encountered. Individual 105–126318 was first netted on 26 April 1967, undergoing crown molt, at which time an intermediate 5 lat.-5 med. crown classification was observed. By 30 April 1967 the bird had acquired a bright black and white striped crown and was classified as 8 lat.-6 med. The yellow of the eye spot was also noticeably brighter. The second male, 105–126347, first netted on 30 April 1967, exhibited dull crown plumage with traces of molt. On 7 May 1967, no longer showing signs of molt, the bird was designated as 8 lat.-6 med. Both males had undergone a brightening of crown plumage during the prealternate molt.

THE AVIARY STUDIES

NATURAL MOLT

Because of the low percentage of repeat and return data, I decided to retain a sample of fall and spring migrants in aviaries in order to observe at least one, if not two, molts.

The first birds to be placed in aviaries were those passing through the Kalbfleisch Field Station during the 1966 spring migration. Included were several white-throats that had

TABLE 4. Variation in basic plumage of banded White-throated Sparrows as illustrated by returns.

			Dates		Crown classif.			
					first		second	
Band no.	Age	Sex	first	second	lat.	med.	lat.	med.
102-111013	Adult	♂	8 Dec. 1964–	19 Jan. 1967	5		4	3
33-168273	Adult	♂	20 Dec. 1964–	7 Nov. 1965	6		6	3
102-111029	Adult	♀	21 Nov. 1964–	7 Nov. 1965	5		5	2
105-126403	Adult[a]	♂	23 Jan. 1965–	14 Nov. 1965	5		6	3
				6 Feb. 1967			5	3
105-126404	Adult	♂	22 Nov. 1964–	7 Nov. 1965	7		7	4
32-192066	Adult	♂	22 Nov. 1964–	6 Apr. 1967	5		5	6
105-126405	Adult	♂	7 Nov. 1964–	11 Apr. 1966	5		5	5
				5 Mar. 1967			6	4
105-126406	Adult	♂	31 Jan. 1965–	11 Apr. 1966	5		5	
				2 Feb. 1967			6	2
AMNH#25	Adult	♂	14 Nov. 1964–	31 Jan. 1965	5		5	
				6 Feb. 1967			6	4
AMNH#23	Adult	♀	31 Jan. 1965–	6 Feb. 1967	5		4	4
105-126399	?	♀	7 Apr. 1966–	6 Feb. 1967	5		5	3
105-126400	Imm.	♂	22 Jan. 1966–	6 Feb. 1967	4	1	5	3

[a] All January birds identified as adult had been aged during a previous capture.

wintered in the Huntington vicinity. Because of problems in nutrition, only about one-half the original number were retained for an entire molt cycle. A third group was collected prior to the prealternate molt in the winter and spring of 1967 and retained until May and the completion of the molt. Since the majority of captive individuals were not retained for an entire molt cycle, the molts will first be treated separately.

Table 5 shows the winter and early spring basic plumage and the alternate plumage attained in late April or early May. Four captive females were observed in pre- and postmolt plumages. The first, 103–113014, was assigned the same crown series classification of 2 lat.-3 med. before the molt on 6 April 1967 and at the completion of the molt on 18 May 1967. The other three females did not retain the same classification. No. 105–126395 began as 2 lat.-4 med. in early February of 1967, and brightened after the molt to 4 lat.-

TABLE 5. Variation in crown plumage of captive White-throated Sparrows as a result of the prealternate molt.

			Dates		Crown classif.			
					Basic		Alternate	
Band no.	Age	Sex	Basic	Alternate	lat.	med.	lat.	med.
103-113014	Adult	♀	7 Feb. 1967	18 May 1967	2	3	2	3
105-126395	?	♀	7 Feb. 1967	18 May 1967	2	4	4	5
105-126399	?	♀	6 Feb. 1967	18 May 1967	5	3	5	4
AMNH 16	Adult	♀	7 Nov. 1965	17 Apr. 1967	4	4	4	6
105-126394	?	♂	6 Feb. 1967	18 May 1967	5	4	5	4
105-126396	?	♂	6 Feb. 1967	18 May 1967	6	4	6	4
105-126397	?	♂	6 Feb. 1967	18 May 1967	3	3	8	6
105-126398	Imm.	♂	19 Jan. 1967	18 May 1967	5	4	6	4
105-126400	Imm.	♂	22 Jan. 1966	3 Aug. 1966	4	1	7	6
	Adult	♂	7 Feb. 1967	18 May 1967	5	3	6	6
105-126402	Adult	♂	6 Feb. 1967	18 May 1967	6	6	6	6
105-126403	Adult	♂	23 Jan. 1965	4 Aug. 1966	7		7	6
			15 Nov. 1966	18 May 1967	6	3	7	6
105-126404	Adult	♂	14 Nov. 1965	3 Aug. 1966	6	3	8	6
			6 Feb. 1967	18 May 1967	5	3	6	6
105-126405	Adult	♂	5 Nov. 1966	18 May 1967	5	5	6	5
105-126406	Adult	♂	20 Mar. 1965	3 Aug. 1966	5		7	6
			2 Feb. 1967	18 May 1967	6	3	6	6
104-141911	?	♂	26 Feb. 1966	3 Aug. 1966	7	5	7	6

TABLE 6. Variation in crown plumage of captive White-throated Sparrows as a result of the prebasic molt.

			Dates, 1966		Crown classif.			
					Alternate		Basic	
Band no.	Age	Sex	Alternate	Basic	lat.	med.	lat.	med.
105-126399	?	♀	7 Apr.	15 Oct.	5	5	5	3
B-RY	?	♀	17 Apr.	4 Aug.	7	4	5	4
AMNH 16	Adult	♀	7 Apr.	5 Nov.	4	6	4	4
105-126400	Imm.	♂	11 Apr.	5 Nov.	7	6	5	3
105-126403	Adult	♂	11 Apr.	5 Nov.	8	6	6	3
105-126404	Adult	♂	11 Apr.	5 Nov.	7	6	6	3
105-126405	Adult	♂	11 Apr.	5 Nov.	5	5	5	5
AMNH 19	Adult	♂	23 Apr.	15 Oct.	7	4	7	4
AMNH 18	Adult	♂	30 Apr.	26 Nov.	5	3	3	2
104-141932	?	♂	30 Apr.	15 Oct.	4	4	5	2
104-141911	?	♂	11 Apr.	13 Oct.	7	5	5	4
R-YW	?	♂	17 Apr.	12 Oct.	7	6	5	3
G-RR	?	♂	30 Apr.	6 Oct.	7	6	4	2

5 med. No. 105–126399, classified in full basic plumage as 5 lat.-3 med., brightened after the prealternate molt to 5 lat.-4 med. Similarly, A.M.N.H. 16 showed evidence of brighter post-molt crown plumage. When observed in early November 1965, she was classified as 4 lat.-4 med. On 7 April 1966, still undergoing the spring molt, she was reclassified as 4 lat.-6 med. It is possible that, had the complete alternate plumage been observed, the lateral stripe may also have darkened.

Twelve captive males were handled before and after the prealternate molt. Although not shown, 105–126337 was handled toward the end of its prealternate molt when it exhibited a 5 lat.-5 med. crown coloration. Three weeks later, no longer showing any signs of molt, its median stripe had brightened to the 6 category (white). The first two males did not undergo any change in crown stripe coloration as a result of the spring molt. Unfortunately, the age of these birds was not known.

The third individual, 105–126397, also of unknown age, underwent marked alteration during the course of the prealternate molt. It changed from the drab, brown and tan 3 lat.-3 med. category to the bright, black and white 8 lat.-6 med. classification. The majority of males exhibited a similar or lesser trend toward brightening of plumage as a result of the prealternate molt.

The only two known immature males evidenced a brightening of crown plumage during the molt. No. 105–126398, captured early enough in the year so that a slight "window" was still visible in the rapidly closing skull, exhibited a dull 5 lat.- 3 med. classification prior to the molt. A slight brightening to 6 lat.-4 med. occurred as a result of the molt.

A most interesting and critical individual is 105–126400. This male, first captured in January of 1966 as an immature bird, was observed for two consecutive years. An obvious brightening of the crown plumage occurred during the first prealternate molt, with an accompanying change in classification from 4 lat.-1 med. to 7 lat.-6 med. The subsequent definitive basic plumage of 5 lat.-3 med. was brighter than that of the previous year and brightened still further to 6 lat.-6 med. as a result of the second prealternate molt.

The change from alternate plumage to basic plumage is shown in table 6, in which three females and ten males are listed. Inspection of the table reveals a reversal of the direction observed in the spring; i.e., a dulling of the crown plumage occurs during the prebasic molt, as opposed to the brightening observed during the prealternate molt.

The three females, entering the prebasic molt with crown classifications 5 lat.- 5 med., 7 lat.- 4 med. and 4 lat.-6 med., respectively, emerge with basic crown plumage classified at 5 lat.-3 med., 5 lat.-4 med. and 4 lat.-4 med. The second individual might have become even duller as the data were recorded during heavy molt.

The males exhibited similar trends. Taking the first two males as examples, we note that they decreased in crown series classifications from 7 lat.-6 med. to 5 lat.-3 med., and from 8 lat.-6 med. to 6 lat.-3 med. The remainder of the males exhibited similar or lesser reductions in brightness of the crown striping. Not one individual emerged from the prebasic molt with a crown plumage brighter than that shed with the alternate plumage.

TABLE 7. Variation in crown plumage of captive White-throated Sparrows as a result of two molt cycles.

			Basic (Fall 1965)		Alternate (Spring 1966)		Basic (Fall 1966)		Alternate (Spring 1967)	
Band no.	Age	Sex	lat.	med.	lat.	med.	lat.	med.	lat.	med.
AMNH 16	Adult	♀	4	4	4	6	4	4		
105-126399	?	♀			5	5	5	3	5	4
AMNH 6	Adult	♂	4	4	5	3	5	3		
AMNH 9	?	♂	2	2			5	3		
104-141911	?	♂	7	5	7	6	5	4		
105-126400	Imm.	♂	4	1	7	6	5	3	6	5
103-126403	Adult	♂	6	3	8	6	6	3	6	6
105-126404	Adult	♂	7	4	7	6	6	3	7	6
105-126405	Adult	♂	5		5	5	5	5	6	5
105-126406	Adult	♂	5		7	6	6	3	6	6

Table 7, extending from the fall of 1965 through the spring of 1967 includes information obtained during the entire two-year study. Two females and seven males returned to the station and were held in captivity often enough to provide the necessary information.

One of the longer and more interesting plumage sequences is that of individual 105–126403. Prior to the present study the bird had wintered at the field station during the 1963–1964 season. It was classified in basic plumage as 5 lat. by Dr. Wesley Lanyon in January of 1965. First encountered by the author in November of 1965, it was assigned a basic plumage classification of 6 lat.-3 med. Recaptured on 2 April 1966 at the beginning of the prealternate molt, it was designated as 6 lat.-5 med. One week later, still in molt, it was trapped, given an 8 lat.-5 med. classification and placed in the indoor aviary. Mist-netted in the aviary on 3 August 1966, it possessed the bright black and white plumage, 8 lat.-6 med. Observed in the midst of the prebasic molt on 18 August 1966, it was mist-netted in the aviary on 15 October 1966 and 5 November 1966, both of which times it exhibited a 6 lat.-3 med. crown classification. Released on 26 November 1966, it was once again trapped on 6 February 1967. At this time, the crown plumage seemed worn and duller than it had been in the fall. The bird was returned to the aviary. Finally, having undergone the prealternate molt during mid-April, the bird was released in May, wearing 6 lat.-6 med. alternate plumage.

Although equally complete records do not exist for every individual on table 7, similar trends of brightening and dulling of crown plumage appear to correlated with the molt cycle.

SIMULATED MOLT

Crown molt was simulated by plucking the feathers of the right side of the crown with forceps, while the left side remained as a control. Table 8 contains data collected by Dr.

TABLE 8. Variation in crown plumage of banded White-throated Sparrows as a result of simulated molt.

			Dates		Crown classif. Plucking		Crown classif. Recovery	
Band no.	Age	Sex	Plucking	Recovery	lat.	med.	lat.	med.
32-192027	Adult	♀	23 Jan. 1966	21 Mar. 1965	4		6	
32-192066	Adult	♂	11 Jan. 1965	20 Mar. 1965	5		6	
32-168197	Imm.	♂	23 Jan. 1965	20 Mar. 1965	4		6	
33-168247	Imm.	♂	24 Jan. 1965	20 Mar. 1965	5		7	
33-168258	Imm.	♂	3 Jan. 1965	20 Mar. 1965	4		6	
102-111588	Imm.	♀	3 Jan. 1965	13 Feb. 1965	4		6	
102-111597	Imm.	♀	24 Jan. 1965	20 Mar. 1965	1		1	
103-113002	Imm.	♀	24 Jan. 1965	31 Jan. 1965	1		6	
103-113006	Imm.	♀	4 Jan. 1965	24 Jan. 1965	5		7	
103-113009	Imm.	♂	3 Jan. 1965	6 Feb. 1965	6		7	
103-113012	Imm.	♂	3 Jan. 1965	24 Jan. 1965	5		7	
103-113013	Imm.	♂	24 Jan. 1965	20 Mar. 1965	4		4	
AMNH 26	?	♂	6 Feb. 1967	17 Mar. 1967	2	1	4	4
105-126398	Imm.	♂	19 Jan. 1967	17 Mar. 1967	5	4	7	5

Wesley Lanyon on a wintering population of white-throats. Each individual was plucked during January of 1965, and examined and photographed (the record exists on 35mm color slides) when recovered later that winter or spring. Table 8 indicates that the fully replaced feathers of the right lateral stripe (the median stripe was not plucked) became appreciably darker in most cases and remained the same in two other instances. The undisturbed left lateral stripe retained its original coloration.

The second experiment occurred during the fall of 1966. Seven birds were plucked on 15 October and two on 5 November. The results did not duplicate the late winter experiment. The five birds that achieved total replacement showed no difference in pigmentation between the experimental and control halves of the crown.

A third set of plucking experiments was attempted in late winter and early spring of 1967. Once again, inability to complete regrowth was the major problem. Two birds died and four failed to replace the missing plumage until the prealternate molt. The two males (refer to table 8) that were able to complete regrowth showed results similar to those of the original experiment in that the replacement plumage was brighter than the control plumage. No. 105–126398 was the only bird to complete the prealternate molt in captivity. It lost the induced feathers during the molt, and plumage of the classification 6 lat.-6 med. covered both sides of the crown.

Emlen (1938) and Morton (1962) conducted plucking experiments on young White-crowned Sparrows (*Zonotrichia leucophrys*) and concluded that an undetermined genetic or physiological factor was necessary in order to produce brighter replacement feathers. Morton found this factor to be present in three-month-old birds and Emlen in five-month-old birds, four months before the first prealternate molt would normally "exteriorize" it.

Since hormonal activity is at a maximum during the months leading up to the breeding season (based upon my own unpublished cytological studies of prenuptial neurosecretory activity, and colleagues' work on annual thyroidal and gonadal development), it is possible that increased hormonal levels effect the observed spring replacement with brighter feathers. Further investigation is required, however, to clarify this area of molt, plumage, and hormonal activity.

DISCUSSION

Dwight (1900) found immature white-throats in first winter plumage to be similar to adults, but generally browner with duller crown stripes. He further noted that while some young birds in first breeding plumage are indistinguishable from adults, others are dull, a phenomenon which seemed to be caused by suppression of the spring molt.

Nichols (1957) discovered a very dull bird in its seventh winter. Further investigation revealed third- and fourth-winter birds with dull crown plumage. Others, known to be second-year birds, were bright. He "began to doubt the old-young criteria for brown and black crown stripes."

Incongruities similar to those reported by Nichols had been encountered in the banding studies at Kalbfleisch Field Station and were among the contributing factors in the initiation of the present study.

With the exception of individual histories, the bulk of the age data is contained within the fall migratory sample. That crown coloration is not a reliable age criterion is obvious upon review of figure 2 and the extensive overlap between immature and adult distributions. The graphs, in fact, illustrate that a bright black and white bird or a drab tan and brown one could be adult or immature in either case. The curve for adult birds, however, tends to peak at a brighter crown class category than does that of the immatures, indicating that a percentage of adults are brighter than their immature counterparts.

The frequency distributions imply that a number of white-throats undergo a brightening of crown plumage between the first and definitive basic plumages. The one continuous record of molt sequences in an immature bird is that of 105–126400. This young male was observed to brighten between its first and second years.

There is no evidence to indicate that white-throats continue to brighten with age. Banding records suggest that the definitive basic plumage, once attained, tends to remain at approximately the same classification year after year, with little or no variation in crown stripe pigmentation (see table 4).

THE SEX FACTOR

Sexual dimorphism is non-existent in the plumage of the White-throated Sparrow. Hence, other methods are required for sex identification. Laparotomy was used in the present study. Several workers have attempted sex determination by the cloacal protuberance.

Lowther (1961) used this method after Salt (1954) and Wolfson (1952). Although useful only during the breeding season, the method is fairly accurate when carried out by an experienced worker. The fact that it is not 100 per cent reliable, however, has often been shown by subsequent dissection.

Lowther concluded that sex did not influence crown plumage coloration. The results obtained during the present study suggest otherwise. Figure 2 indicates that males in basic plumage are slightly darker and brighter, on the average, than females.

The limited sexual differences found in basic plumage samples are magnified by the change to alternate plumage (see fig. 3). The majority of males netted, trapped, or observed in aviaries at the Kalbfleisch Field Station became obviously brighter after the prealternate molt. Not one male was of the dull 1 lat.-1 med. crown classification. Conversely, no females were included in the 24 birds assigned the bright black and white 8 lat.-6 med. classification. The majority of males exceeded categories 5 lat.-3 med. while most females exhibited crown classes of 5 lat.-3 med. or below.

Although the females tend to dominate the lower half and males the upper half of the crown class series, a substantial percentage of both sexes share the central area. It is this large area of overlap, plus the possibility of exceptional birds, that prevents the use of crown plumage coloration as a diagnostic character in sex determination.

Consequently, while crown coloration in general is not a reliable indicator of sex, it is highly probable that the bright black and white individual is a male and the drab tan and brown one, a female. Increased use of the laparotomy would be necessary to clarify this problem of sex and alternate plumage.

THE SEASONAL FACTOR

Dwight (1900) described the prealternate molt in the White-throated Sparrow as involving head, throat, and breast, resulting in black and white crown striping in males and in many females and young birds as well. Those birds exhibiting dull spring plumage, he theorized, had suppressed the prealternate molt and were breeding in basic plumage.

A banding report by Fischer and Gill (1946) contains the following passage. "Birds wintering at a bander's station, and repeating in his traps, begin to exhibit gradual changes toward breeding plumage, especially about the head, in early April. At the same time, unbanded birds in full breeding plumage appear in the traps. These may be migrants newly arrived from the south." Although seemingly taking the "breeding plumage" as a well-known fact, Fischer and Gill's study represents the only reference to an identifiable spring plumage in the White-throated Sparrow, since Dwight, which I have been able to locate.

That some sort of plumage change occurs between the fall and spring migrations is undeniable. The vast, drab brown horde that foraged the autumnal fields and hillsides suddenly pops up, one by one, in spring bottomlands and woodlands, with a fresh, bright black and white headdress. Birdwatchers have noted this, and probably taken it for granted. Banders, however, find that not all their spring migrants are of the black and white variety. Several dull and medium-dull birds are also captured.

Examining the fall banding data we find that it corroborates field observation. The fall migrants are mainly of dull crown plumage. No bright birds have slipped through unnoticed. And while the immatures are very drab, the adults are not a great deal brighter. Furthermore, a change in plumage does occur during the spring molt. Most migrating wild birds and captive aviary birds exhibit a brighter alternate crown plumage. That the greater percentage of these black-and-white-crowned birds are males has already been discussed. It has also been suggested that age, once the first basic plumage is shed, appears irrelevant to plumage coloration.

Finally, it was observed that whatever the resultant crown classification, all aviary birds experienced the prealternate molt. Contrary to the theory of Dwight (1900), dull crown plumage was not caused by suppression of the molt but by replacement with plumage of dull coloration.

The overall annual plumage picture can best be illustrated graphically. Returning to figures 4 and 5, the effect of season upon crown plumage classification can be seen. The basic plumage distributions for both sexes are similar and tend to clump at the lower categories of the crown class series. The alternate plumage distributions partially overlap those of the basic plumage but extend beyond them to raise the spring mean above that for fall and winter. These differences are particularly exaggerated in the male samples.

The data suggest a "statistical breeding plumage" in the White-throated Sparrow. White-throats as a whole, regardless of age or sex, appear to brighten with respect to crown plumage as a result of the prealternate molt. As in the case of age and sex variables, the striking breeding plumage is a matter of percentages. Not every bird, not even every male, brightens during the prealternate molt and becomes dull once again as a result of the prebasic molt. A sufficient number of birds do undergo these changes, however, to raise or lower the mean crown classification to a statistically significant new level with each molt. Therefore, season, or more specifically, molt cycles, as well as age and sex, affect the crown plumage coloration of the species.

FIELD OBSERVATIONS

Field observation gives an overwhelming impression of bright-crowned birds among the spring migrants. The frequency distributions, however (fig. 3), indicate that most females and some males possess duller crown plumage.

The resolution of this apparent inconsistency lies in the banding data, and a disproportionate spring sex ratio. A total of 60 males but only 15 females were processed during the spring migrations of 1966, 1967, and 1969, resulting in the observed preponderance of bright crowned birds. Wintering birds of both sexes, usually beginning or in the midst of the prealternate molt, were trapped early in April. The latter part of the month brought the spring migrants in full alternate plumage. Of these, only two of 28 in 1966 and two of 30 in 1967 were females.

In 1967, netting was extended into May. After a brief lull in white-throat activity, a flock of approximately 15 white-throats was observed one evening in the wood-lot adjacent to the permanent pond. Very few, if any, of these birds exhibited the bright black and white crown striping that was so obvious in feeding flocks of the earlier migrants. Netting was resumed the following morning but no sign of the flock could be found. The clear night skies had apparently urged them northward.

Several days later, another surge of white-throat activity occurred. Once again the distinctive song and high-pitched feeding calls arose from the brushy area surrounding the permanent pond. On 11 May five females, all of dull crown plumage, and one bright-striped male entered the traps. Another drab female was netted three days later. Except for several repeats, she was the last white-throat of the season. Two other large flocks of dull-plumaged white-throats were observed, but unfortunately favorable weather spurred them onward before they could be captured.

The spring of 1969 followed a similar pattern with males appearing in April and five new females being processed toward the end of the migration in late April and May.

The observation of late-migrating females is not unique to the present study. Odum (1958) reported residual groups of white-throats stopping over in the vicinity of the University of Georgia, Athens, campus after the bulk of late-April migrants had departed for the north. He found these to be "nearly all female, mostly immature." He suggested that first-year females "tend to winter further south than adults in general and males in particular."

The later migrants encountered in Huntington, Long Island, differed in several ways from earlier arrivals. April birds were easily netted; several could be captured at once if some brush-beating were attempted. May birds proved difficult to net. They tended to huddle in low branches and foraged within small areas on the leaf litter, rarely flying through the open expanses and net lanes as had the earlier birds. Even brush-beating fared poorly, often causing the birds to freeze in place rather than driving them into the nets.

Traps, which had not been particularly effective with the April birds, fared better with these later arrivals. They were wary of the Potter ground traps, but entered readily into Government Sparrow traps placed near a thicket or similar protective covering. Although most observations of the large flocks occurred in the early evening, not one bird was trapped at that time. Early morning captures were the rule. It is probable that the large, tight flocks were collecting for a take-off, and thus would not disperse widely in search of food where they might also have encountered the nets or traps.

THE NATURE OF THE VARIATION

The White-throated Sparrow has been shown to exhibit considerable variation in crown plumage. Although partially influenced by sex, age (before the first prealternate molt), and season, the effect of these variables is not an absolute one. Several degrees of crown plumage melanism can be seen within a single sex, age, or seasonal group.

That the variation is genetically determined is highly probable. The repetitious nature of corresponding annual plumages within an individual plumage history is indicative of at least partial genic control.

Lowther (1961) hypothesized that the variation constituted a polymorphism and cited the existence of tan- and white-striped morphs (referring to the median stripe). He stated that "if the plumage differences are not a matter of age as the data reported herein suggest, then it can be concluded that the White-throated Sparrow is a polymorphic species." Offering Ford's (1964) definition of polymorphism as "the occurrence together in the same habitat of two or more distinct forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation," he strengthens his cause by observing that his morphs do in fact exist within a single habitat; furthermore, they mate with each other, selectively.

The data supporting his hypothesis were collected by means of comparing museum skins and live birds against graded series and percentage ratings. The percentage ratings (to the nearest 10 per cent) served to classify lateral crown striping. Median crown stripe coloration was categorized by comparison against a graded series comprised of six museum specimens.

The need for a type series and a range of percentages immediately discounts similarity between the alleged white-throat polymorphism and the majority of cases of polymorphism reported in the literature. (The interested reader is referred to Mayr, 1965:150 ff.)

Discontinuous is a key word in almost every case of avian plumage polymorphism; phases (morphs) either constitute a dimorphic variation or comprise several unmistakably distinct colors or patterns. This is not so in the case of the White-throated Sparrow. Its lateral crown striping is not a clearly definable brown or black but contains varying percentages of both. The median coronal stripe is not simply either tan or white, but it exhibits a progression of shades between the two extremes.

The one study to which Lowther's work on *Zonotrichia albicollis* may be compared is that of Martin (1950) on *Otus asio*, the Screech Owl, which involved a graded series of type specimens in the investigation of the red and grey "phases" of this species. Lowther (1961) constructed a type series similar to the one used by Martin. Having observed that "the live birds of both sexes examined in Algonquin Park could be readily separated into two groups by the color of the median crown stripe" which he designated arbitrarily as "white" and "tan", he chose his type specimens so that "the first three specimens were 'tan' and the last three were 'white' " and "there was an obvious gap of at least one grade (grade four in the series) between the two groups." Thus Lowther arranged a bimodal curve by choice of specimens. He further claimed that none of the birds examined from nature belonged to this "missing" class. It might be pointed out however, that a tendency exists to restrict comparisons to visually available objects, rather than imagined ones. It is suggested that the resultant bimodal curve indicative of polymorphism may have been a synthetic rather than an actual one.

A series of type specimens representing a progression from tan to white was also constructed for the present study. It, however, did not contain the gap described by Lowther. The type specimens ranged from drab tan (#1) through tan (#2, #3), tannish-gray (#4), grayish-white (#5) and bright white (#6). The birds examined from nature belonged to all crown classes. Many individuals were classified as #3 and #4, the so-called intermediate or "gap" categories. Consequently none of the plotted frequency distributions was bimodal. Rather they tended to approximate normal curves or decreasing or increasing progressions from category #1 to #6, inclusive.

It is interesting that, although we disagree on the interpretation, there exists a great similarity between the data collected by Lowther and the alternate-plumage data that I collected for the present study. My spring data point strongly toward the predominance of brightly striped males. In a table presented by Lowther (1961), the females obviously cluster at the lower end of the median crown stripe series while many males fall in the upper end of it. Similarly, the females tended to have browner, and the males blacker, lateral crown stripes. Lowther allowed, in the case of the breeding females, that "a similar bimodal distribution (i.e., similar to that of the males) would be expected to occur if the sample of white-striped morphs was larger." He did not draw any further conclusions as to the significance of this imbalance.

Lowther (1961) concluded that the polymorphism was a balanced one, since the proportion of morphs collected in the central regions of Canada has remained approximately the same for the last 100 years (conclusion based upon museum specimens).

Several theories concerning the development of balanced polymorphism have been advanced. Perhaps one of the best known is that proposed by Dobzhansky and followers (1954) in which the heterozygote is superior to either homozygote (through heterotic and specific effects such as reduced viability of homozygotes). Continuous selection for heterozygotes results in an equilibrium in which both alleles would be retained in the population in near constant proportion and would necessitate the appearance of homozygotes due to simple Mendelian segregation and consequent reassortment of genetic traits.

Natural selection in white-throat populations does not appear constantly to favor the heterozygote in terms of crown plumage (if the intermediate stages in the median crown stripe series can be assumed heterozygous). Although a central tendency is often present in the lateral crown stripe data, the median crown stripe distributions tend toward the extremes.

I agree with Lowther that the median crown stripe data appear to be more strongly affected by disruptive (Mather 1955) or centrifugal selection (Simpson 1953) than the stabilizing or centripetal selection discussed above. Two general forms of disruptive selection have been studied. The first, favored by Lowther, concerns habitat variation with selection in the different environments for "alternate pathways of development" (Thoday 1959) accompanied by migration between the habitats, so that polymorphism, rather than speciation, may arise.

Lowther theorized that selection would favor white-striped females in the lichen-covered grounds surrounding Hudson Bay, and cryptically marked, tan-striped females in the remainder of the breeding grounds. He solved the migration problem by a selective mating theory (preference for mates of the alternate morphic type). The proportion of male morphs would be influenced by the females' morphic predominance, which in turn is determined by nesting cover. As to the implications and controlling factors of such a complex system, Lowther admits that "further study will be necessary before any conclusion on the factors governing the morphic types can be made."

The results of the present study do not justify the proposal of polymorphism as an explanation of the crown plumage variation of the White-throated Sparrow. It is agreed that the frequency distribution of an entire population, without regard to sex or age data, might produce a bimodal curve. It would be the differing means of the sex and age groups, however, which would be causing this apparent bimodality. For instance, if all adults were analyzed, sexual differences would effect two different modes; if one sex were graphed, the gap between first-year and older birds (true only for basic plumage) would cause a divergence; if one sex and age group were analyzed over an entire year, seasonal or molting cycle changes would produce different modes. However, seasonal, sexual, and age differences do not constitute polymorphism in the classic sense of Ford or Dobzhansky. The White-throated Sparrow appears to be characterized by sex, age, and seasonally correlated variations, rather than strict polymorphism. In addition, the frequency distributions within these differently varying groups are either skewed to one end of the series or tend toward a normal distribution. In either case, the variation approximates a continuous variation, rather than a bimodal polymorphism. And as to Lowther's (1961) observation that "white-striped individuals mate selectively with tan-striped," it would, based upon the spring sex data reported herein, be unique to encounter two bright black and white birds on the same nest, rather than the situation presently observed.

Perhaps the most pertinent recent study has been that of chromosomal polymorphism in the White-throated Sparrow by Thorneycroft (1966). He found three pairs of autosomes that occur in varying proportions in different individuals. A total of four #2, #3, or m chromosomes were found in each individual examined. The second chromosome could occur as a monosomic or trisomic in addition to the normal condition. The third chromsome was found as a pair, or a single chromosome, or was entirely absent. The m chromosome was characterized by monosomy or nullisomy.

Thorneycroft attributed the polymorphism of these equal-length, constant-numbered chromosomes to "rearrangements, including pericentric inversions." Although he found no obvious correlation between sex and chromosomal constitution, Thorneycroft did observe that all bright birds (black- and white-striped) examined appeared to possess the m chromosome. Dull birds lacked this autosome. Other than this, the relationship between phenotype and the chromosomal constitution is unknown.

That the variation is at least partially genetically based is undoubtable. On an individual level it would appear that alleles controlling melanin synthesis and deposition, accompanied by modifiers (possibly in the form of hormones) to cause the observed age and seasonal variations, might be operative. The one experiment with internal environmental controls (a thyroxine experiment) attempted in the presented study was unsuccessful because of procedural difficulties. Had it proven informative, further experiments with sex steroids were planned. I maintain, however, that work of this nature is necessary in order to identify the causes of the white-throat plumage variation.

While Thorneycroft could not detect direct correlation between chromosomal polymorphism, sex, and plumage variation, it is conceivable that the variously combined chromosomes, bearing melanin-differentiating alleles and modifiers in the sense of hormone-producing control areas, could, when active, account for the age, sex, and seasonally influenced continuous variation in the coronal plumage of the White-throated Sparrow.

SUMMARY

The White-throated Sparrow exhibits a non-bimodal variation in the coloration of the crown for any given age or sex group. This variation is in turn affected by age, sex, and plumage.

Most immatures in first basic plumage appear duller than adult birds in definitive basic plumage; plumage histories indicate that second-year birds in basic plumage are brighter than they were in their first basic plumage. The proportion of dull females is greater than that of dull males. Although some females are brighter than some males, males are, on the average, the brighter sex. Most white-throats appear duller in basic plumage than in alternate plumage; individual plumage histories indicate that birds of both sexes brighten as a result of the prealternate molt, but males brighten to a greater extent than females.

A genetic-physiologic control, involving melanin-differentiating alleles and modifiers (possibly hormone-controlling areas), is hypothesized, but has not been proven, to cause the observed variation. Further research into the genetics and physiology of the species will be required in order to clarify the problem of coronal plumage variation in the White-throated Sparrow.

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