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PLUMAGE COLORATION AND DOMINANCE BEHAVIOR IN THREE
SPECIES OF SPARROWS OF THE GENUS ZONOTRICHIA

The University of Oklahoma

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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

PLUMAGE COLORATION AND DOMINANCE BEHAVIOR IN

THREE SPECIES OF SPARROWS OF

THE GENUS ZONOTRICHIA

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

By

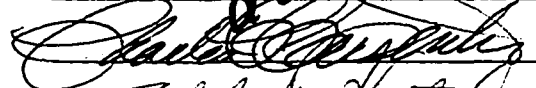
DORIS JANE WATT

Norman, Oklahoma

1983

PLUMAGE COLORATION AND DOMINANCE BEHAVIOR IN
THREE SPECIES OF SPARROWS OF
THE GENUS ZONOTRICHIA
A DISSERTATION
APPROVED FOR THE DEPARTMENT OF ZOOLOGY

By



Paul D. Smith
Douglas Mock
Alan B. Corvick

PREFACE

This dissertation is prepared as four chapters. Each chapter will be submitted to a refereed journal. The first and second chapters will be submitted to Animal Behaviour, the third chapter to the Journal of Field Ornithology, and the fourth chapter to The Wilson Bulletin.

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A COMPARATIVE STUDY OF STATUS SIGNALING¹
IN SPARROWS (GENUS ZONOTRICHIA)

by

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Running head: Watt: Sparrow Status Signaling

Abstract. The evolutionary aspects of status signaling (plumage variability used to signal dominance status), as developed by Rohwer (1975, 1977, 1978), Rohwer & Rohwer (1978), and Rohwer & Ewald (1981), have become increasingly discussed and cited in the ethological literature (Krebs & Davies 1978, Morse 1980, Barash 1982). Detailed evidence that the model species, the Harris' sparrow (Zonotrichia querula), actually does signal status is lacking.

I used an operational definition of "signaling" whereby behaviour of focal birds (potential receivers) were recorded in the presence of birds having specific color types (potential signalers). Then, applying an inter- and intra-specific comparative approach, I assessed groups that were monomorphic (therefore unlikely to be status signalers) and compared their behaviour with groups of birds of more varicolored plumage. In this manner, I investigated Rohwer's general

hypothesis that plumage variability in winter flocking birds acts as a status signal.

I also tested Geist's (1966) prediction that display organs should allow subordinates to avoid even unfamiliar dominant animals. Here, groups of variably-plumaged birds (presumed status signaling groups) exhibited increased avoidance behaviour compared to groups with less variability in plumage. Of the three species compared, both Harris' sparrows and white-crowned sparrows (Z. leucophrys) exhibited increased avoidance of strangers, but only in mixed-age groups, while white-throated sparrows (Z. albicollis) exhibited low levels of avoidance of strangers.

An alternative hypothesis to explain variable plumage, facilitated individual recognition (Shields 1977), was also supported in two species. Both white-throated and Harris' sparrows had high correlations between attack and avoidance levels, a phenomenon hypothesized to be due to individual recognition. None of the white-crowned sparrow groups, monomorphic or mixed-age, exhibited attack-avoidance correlations as high as the more variably-colored species. I suggest that signals functioning in individual recognition, as well as age class recognition, are present in the extremely varicolored Harris' sparrow.

(Introduction)

Evolutionary theories involving status signaling, the correlation of plumage variability to dominance status and the use of such variability to signal potential dominance, have been proposed to explain the widespread occurrence of plumage variability in winter foraging flocks (Rohwer 1975, 1977, 1978; Rohwer & Rohwer 1978; Rohwer & Ewald 1981). The unique features of plumage variability as a status signal would appear to be relatively low cost to the bearer and the ease with which the signal could be assumed by a "cheater." Most other signals associated with dominance appear to be examples of "honest advertisement," having a high reliability component (Zahavi 1977). Examples include horn size in mountain sheep, (Ovis canadensis; Geist 1966) and red deer, (Cervus elaphus; Clutton-Brock & Albon 1979), and croak pitch in toads, (Bufo bufo; Davies & Halliday 1978, Ryan 1980). The possibilities for dishonest advertisement have been discussed by several authors (Krebs & Davies 1978, Morse 1980, Barash 1982) who most commonly cite Rohwer's conclusions for the Harris' sparrow (Zonotrichia querula) as an example. It is surprising that, at this point, evidence of status signaling in the Harris' sparrow is minimal. Rohwer (1975) found that darker birds won 57 of 75 dominance encounters with lighter birds. In a later paper (Rohwer et al. 1981), no difference was found in number of wins between dark and light birds at concentrated food (n=151), but at more diffuse food, darker birds won 18 and lost 5 encounters. These studies contribute data that are correlative at best and do not address whether or not blackness of the bib, throat or chest of Harris' sparrows, in fact, functions as a signal to other members of

a flock. The general purpose of my investigation was to test Rohwer's general hypothesis that plumage variability in winter flocking birds acts as a status signal and, specifically, to test whether or not Harris' sparrows signal status.

Geist (1966) was first to hypothesize that display organs, horns in mountain sheep, were used as dominance-rank signals. He made several predictions from this hypothesis, including the requirement that individuals must be able to recognize a stranger's dominance rank from the organ. Mountain sheep met this requirement in that sheep with smaller horns avoided strangers with larger horns after only seeing them from a distance. I have used the requirement of avoidance of strangers in this study to predict and compare relative degrees of dominance-rank signaling in three species of sparrows.

In the spirit of Rohwer's (1975) original usage, I employ the following definition of a status signal: a characteristic or set of characteristics having a variable range of expression that is correlated to the dominating ability of individual animals. In addition, I have included the requirement proposed by Geist (1966), that such characteristics be used by other individuals to assess the potential outcome of encounters prior to physical interaction.

Three general predictions about status signaling can be derived from Geist's (1966) requirement: (1) Subordinates of status-signaling groups should avoid probable dominants on first encounter. (2) For non-status signaling groups, avoidance behaviour should increase in frequency with the passage of time. Eventually strange birds will have had a chance to interact, determine dominance and learn identities of

other individuals and, thus, could avoid dominants. (3) Status signaling groups should exhibit quantitative differences in avoidance behaviour between groups with differing ranges of plumage variability. I also included a fourth prediction (Rohwer 1975) that the total number of social encounters, especially contest fights, should be reduced in groups that signal status.

In the first part of this paper, I report on my investigation of the above predictions. I compared social interactions of Harris' sparrows, which are likely to be a status signaling species, with those of white-crowned sparrows (Z. leucophrys), which show less intraspecific variability in plumage coloration. In the second section, I present investigations of three alternative hypotheses that could explain differences in behaviour observed between the species. The results of the third section include a comparative analysis of three species: Harris' sparrow, white-crowned sparrow and white-throated sparrow (Z. albicollis). The additional comparison with a third species allows independent assessment of predictions of status signaling theory.

Methods

Harris' and white-crowned sparrows were caught with mist nets in Norman, Cleveland County, Oklahoma during spring migration (12 April to 5 May 1980) and during fall migration (6 November to 14 December), and 0.6 km north of Fort Supply, Woodward County, Oklahoma 6 to 13 December 1981. White-throated sparrows were captured in Norman during November,

1980, with the above two species. Plumage characteristics, age classification, weights and wing lengths were recorded at capture (Appendix). Each bird was banded with colored vinyl leg bands for my use in identification. An experiment demonstrated that white-crowned sparrows do not use the bands for individual recognition themselves (Watt 1982).

Birds were housed in three indoor aviaries (ca. 2 m on a side) at the Animal Behavior Laboratory of the University of Oklahoma. Artificial lights with timers provided a 12:12 L/D light cycle in spring and a 8:16 L/D light cycle in the fall. Birds were fed a mixture of finely ground Purina dog food and commercial wild bird seed mix, with Purina Game Bird Feed as a supplement in the fall.

Fall age classifications for white-crowned sparrows were based on plumage: tan head stripes indicated immatures, black and white head stripes indicated adults (Parsons & Baptista 1980). For Harris' sparrows, tail wear was used to classify birds as immature or adult (Rohwer 1973). Initial sex classification was based on wing lengths for all birds, and when possible was later verified by gonadal examination (see Appendix). Thirty of 87 birds escaped or died, and their sexes were unverified.

Experimental Methods

Test birds were introduced into a fourth aviary (also about 8 m³) and observed through a one-way window. Ground dog food was placed in a finger bowl on a lighted shelf inside the aviary next to the window. A hardware cloth platform approximately 2 cm high, placed under the food

dish, prevented birds from picking up spilled food. A finger bowl with water was placed on the platform next to the food dish. During testing, all other food and water was removed from the aviary floor. These precautions to prevent foraging elsewhere forced the birds to compete and interact with one another on the shelf.

In each test group, five birds formerly housed together were introduced to five other birds ("strangers") that had also been maintained together. I selected the first five birds of a test group based on disparate wing lengths, in order to include both sexes and an array of body sizes in each group. The second set of five birds was chosen with the same wing lengths as the first set to match sexes and body sizes. Observations commenced immediately after the 10 birds were introduced into the test cage.

Observations were continued on day 2 and for some groups, again on day 6 to contrast behaviours during hierarchy formation with those of established groups. Observations began at the start of the lights-on period when birds began to feed. I recorded total numbers of interactions during 8 to 11 continuous 15-min periods each day. Total observation times per day ranged from 120 to 165 min.

Behavioural Interactions

When birds met at the food or water dish, I scored these encounters as an attack, avoidance, face-off or share (see below), and noted identities of the individuals involved. In a few cases, the identities of the participating birds could not be determined; however, I was able to score almost all of the encounters as attacks,

avoidances, face-offs or shares.

An attack was defined as a win-loss encounter where a bird chased or supplanted another bird. Attacks were subclassified as strong attacks when the attacker chased the other bird by flying after it rather than chasing it on foot. Avoidance encounters were those in which a bird left the area quickly as another bird approached but before the second bird attacked it. In some encounters the attacked bird did not leave the food dish and faced the attacker, usually with its mouth open. Most of these "face-offs" were temporary and ended in an escalated attack by the dominant bird. Face-offs appear to be similar to the "head dance" of dark-eyed juncos (Junco hyemalis) described in Balph et al. (1979), and often result in the "jump fights" of Harris' sparrows (Rohwer 1977). In contrast, for other cases, close proximity of two birds did not result in an attack or avoidance behaviour. At the extreme limit of toleration, some birds "shared" the food dish while both ate.

In most analyses, numbers of behavioural events were converted to relative avoidance scores (percent of total interactions that were avoidances), because absolute frequencies are more likely influenced by extrinsic factors such as temperature. However, in one analysis rates were used to correlate avoidance and attack behaviours.

Test Species

Three congeneric species were studied in the previously outlined experiments in order to represent a gradation of plumage variability to test the critical components of the status signal concept. Individual

Harris' sparrows in fall plumage exhibit a wide range of variability with respect to the amount of black feathering present on the head, throat and chest (Rohwer 1973, 1975). Rohwer (1973, 1975) designed an index for scoring such variability and reported that, although some variability can be accounted for by sex (males are generally darker than females) and age (adults are generally darker than first year birds), overlap exists across age/sex classes (Rohwer 1973, Rohwer et al. 1981). In his original study (Rohwer 1975), plumage characteristics were positively associated with dominance rank in a small sample ($n=75$) of interactions. I also have found that darker birds are more often dominant to lighter birds (Watt 1983). However, I did not find the close correlation between increasing dominance and darkness suggested by Rohwer (see Watt 1983 for details).

Assuming that Harris' sparrow plumage characteristics are used as a status signal, I constructed a comparative experimental design in which predictions of status signaling were tested by comparing the social behaviour of Harris' sparrows with that of a species having relatively little plumage variability. I chose the white-crowned sparrow (Z. leucophrys leucophrys) for comparison because of its close taxonomic relationship to the Harris' sparrow (Zink 1982), availability, and low degree of variability in adult plumage.

The two model groups used for testing status signaling predictions--Harris' sparrows in variable fall plumage and monomorphic adult white-crowned sparrows--represent extremes of avian plumage variability, and thus hypothetically represent status signalers and non-status signalers, respectively. Within and between these two

species, intermediate plumage conditions exist. Four of these sets were also used to test status signaling predictions: (1) immature white-crowned sparrows, whose plumage is more variable than conspecific adults but less than Harris' sparrows (a few immature white-crowned sparrows had some black and white feathers on the crown, see Appendix); (2) mixed groups of adult and immature white-crowned sparrows (essentially dimorphic); (3) groups of light-throated (usually immature, Rohwer et al. 1981) Harris' sparrows; and (4) groups of Harris' sparrows in alternate plumage, which were similar to one another in the amount of black on the throat but displayed considerable individual variation in breast patterns.

The third species, the white-throated sparrow, was used because it has considerable plumage variability (Vardy 1971, Atkinson & Ralph 1980) that is not consistently age- or sex-related (Lowther 1961; Atkinson & Ralph 1980). One group of nine white-throated sparrows was used for these comparisons in Part III.

Statistical Treatment

I used Sokal & Rohlf's (1969) test of the equality of two percentages to contrast relative avoidance levels in experiments using monomorphic white-crowned sparrows with those in experiments using other birds. This test was also used to investigate changes in percent avoidance from day 1 to day 2.

To test for seasonal effects I used a one-way analysis of variance over the 11 experiments. Total encounters, avoidance rates, attack rates and percent avoidances did not deviate significantly from normal

distributions, therefore, no transformation was used on the data. Attack rates were the only variable with unequal variance; the ANOVA test for unequal variances (Sokal & Rohlf 1981) was used on these data.

Chi-square was used to test goodness of fit between observed encounter rates between sexes and the expected values based on sex ratios in the group. Observed attack and avoidance rates were also compared for each sex using this test.

Part I: STATUS SIGNALING

Predictions

Four specific predictions follow from the general predictions in the Introduction: (I) Harris' sparrows in variable (fall) plumage should be able to avoid probable dominants better than adult white-crowned sparrows, which are assumed to be non-status signaling. (II) If avoidance behaviour in the non-status signaling white-crowned sparrow depends on development of individual recognition, relative avoidance levels should increase over time after introduction of strangers for that species. (III) The relative amount of avoidance within species should be highest for groups of birds with the greatest plumage variability. Specifically, in order of decreasing plumage diversity: Harris' sparrows in "mixed" groups (containing both white-throated and dark-throated forms) should avoid one another more than those in groups of all light-throated birds, which, in turn, should avoid more than individuals in groups of adults in alternate (dark) plumage. Similarly, for white-crowned sparrows, adults and

immatures in mixed-age groups should avoid one another more than immatures, which should avoid more than individuals in groups composed entirely of adults. (IV) If status signaling results in fewer fights over rank, Harris' sparrows should have fewer aggressive encounters overall than white-crowned sparrows.

Group Compositions

All groups used to test the above predictions are described below. Test groups represented different ranges of plumage variability within each species. Seven groups of Harris' sparrows were assembled, representing three conditions: (1) minimal plumage variation (two groups of all adult birds with black throats in alternate plumage); (2) intermediate plumage variation (one group of all light-throated birds, one group with one light-throated plus nine dark-throated birds, and one group with one dark-throated plus nine light-throated birds); and (3) maximal plumage variation (two groups of similar proportions of mixed light-throated plus dark-throated birds). Similarly, four white-crowned sparrow groups were assembled to represent the same three conditions: (1) minimal plumage variation (two all-adult groups in spring alternate plumage); (2) intermediate plumage variation (a group of all immatures); and (3) maximal plumage variation (a group of five immature plus five adult birds). A summary of experimental treatments of group composition, seasons and dates of observations is given in Table 1. Comparisons of results of observations of these test groups were used to test the predictions outlined above, and are described in the following sections.

Results

Data on interactions recorded on the first day of hierarchy formation for all 11 experimental groups are shown in Table II. Below, the results are above presented for the tests of each of the four predictions.

Groups of variable Harris' sparrows did avoid one another more than monomorphic white-crowned sparrows (cf. prediction I). On the first day of introduction of strange birds, all seven groups of Harris' sparrows (experiments 1-7) averaged 51.2% avoidances (out of total interactions). This was significantly higher than the two groups of adult white-crowned sparrows (experiments 10 & 11) with 30.2% avoidances ($t=9.4$, $P<0.01$). These higher avoidance levels for Harris' sparrows could be due to increased avoidance of strange birds possible in the status signaling groups but not possible in the adult white-crowned sparrows. To test this hypothesis, percent avoidance values were compared for interactions between familiar birds versus those between strangers. Because the experimental design had involved adding strangers to groups, the results of each experiment were divided into interactions between strangers and those between familiars (Table III). Again, comparisons between Harris' sparrows and the presumed non-status signaling adult white-crowned sparrows were made in terms of percent avoidances. All Harris' sparrow groups avoided familiars more than did the white-crowned sparrow adults. However, only in experiments 1-4 (mixed-age groups of Harris' sparrows) did birds have higher percent avoidances of strangers than in the two adult

white-crowned sparrow experiments (Table III). Groups of all dark-throated and all light-throated Harris' sparrows (experiments 5 & 6, same-age groups) did not avoid strangers significantly more than the monomorphic adult white-crowned sparrows, and therefore, do not support "Prediction I."

In addition, experiment 9, containing a mixture of adult and immature plumaged white-crowned sparrows, also had significantly higher percent avoidance between strangers than did the groups of adult white-crowned sparrows (Table III). In fact, there was no difference between their relative avoidance behaviour of strangers (63.8%) and that of the mixed-age fall Harris' sparrows (63.7%).

Monomorphic white-crowned sparrows did increase relative avoidance behaviour after the first day of hierarchy formation (cf. Prediction II). On the second day after introduction of strangers, adult white-crowned sparrows (experiments 10 & 11) averaged 44.9% avoidances, a significant increase ($t=3.36$, $P<0.01$) over the 30.2% avoidances on the first day. By the sixth day, they had 49.7% avoidances. In contrast, Harris' sparrow avoidance levels in mixed-age groups (average of percentages in experiments 1-4) did not increase significantly from the first to the second day (54.5% to 54.6%; no sixth day recorded). Moreover, there was no statistical difference between these initial avoidance values for Harris' sparrows and the monomorphic white-crowned sparrow percent avoidance levels on day 6 (49.7%). There appeared to be an upper limit to the percentages of avoidance behaviour in the groups I tested; most values on day 2 or day 6 were about 50% (Table IV). In this study a 40-60% range appears to be maximal relative

avoidance for groups of birds housed together in captivity for more than one day.

Intraspecific groups with greater plumage variation did exhibit greater levels of relative avoidances than groups with less variability (cf. Prediction III). On the first day of hierarchy formation and within both species, groups of birds having greater ranges of plumage variability, compared to groups having lower ranges, exhibited higher relative avoidance behaviour (Fig. 1). Again, the mixture of adult and immature plumaged white-crowned sparrows had avoidances as high as the fall Harris' sparrows.

Total aggressive encounter rate was not lowered in Harris' sparrows (contra Prediction IV). Rohwer's (1975) suggestion that status signalers should have fewer encounters was not supported. Overall encounter frequency for Harris' sparrows (1.30/min) was not less than that for white-crowned sparrows (0.91/min). Because the mixture of adult and immature plumaged white-crowned sparrows exhibited properties of status signaling seen in examples of Harris' sparrows in previous tests (above), experiment 9 was omitted from this comparison.

Harris' sparrows also had higher initial avoidance and attack frequencies than did the monomorphic white-crowned sparrows (Fig. 2). Other evidence that Harris' sparrows did not exhibit reduced aggression levels relative to white-crowned sparrows included: strong attacks were not lower for Harris' sparrows relative to white-crowned sparrows (Table II), and spring white-crowned sparrows were more tolerant of other individuals as demonstrated by the relatively high number of shares compared to Harris' sparrows (Table II).

Summary of Prediction Tests

Harris' sparrows did display higher avoidance levels at introduction of strangers than adult, monomorphic white-crowned sparrows did (Prediction I). However, these differences in avoidance levels were due to avoidance of strange birds only for groups of mixed ages. Therefore, mixed-age Harris' sparrow groups met Geist's (1966) requirement for status signaling. Groups of all light- and all dark-throated Harris' sparrows did not avoid strangers any better than the monomorphic white-crowned sparrows, and do not meet Geist's requirement. The mixed-age white-crowned sparrows avoided strangers as well as Harris' sparrows did and therefore also met Geist's requirement.

After the first day of hierarchy formation the adult white-crowned sparrows increased relative avoidance levels significantly (Prediction II). They were apparently able to learn the dominance rank of other birds, possibly through behaviour (e.g. face-offs), and could avoid dominants more efficiently after a day of interactions.

Differences between groups having different ranges of plumage variability, for both species, agreed with Prediction III (that increased plumage variability among individuals in the group results in higher avoidance levels). And finally, in contrast to Prediction IV, Harris' sparrows did not experience a reduction in numbers of total encounters, avoidances, attacks, or strong attacks, compared to the adult white-crowned sparrows.

Part II: ALTERNATIVE HYPOTHESES

Three alternative explanations of the observed differences in avoidance behaviours between the two species are that differences could: (1) result from seasonal influences because some experiments were conducted in the spring and some in the fall; (2) be due to different sex ratios within the groups, possibly with males avoiding less than females and being more abundant in the white-crowned sparrow groups; and (3) be due to facilitated individual recognition (Shields 1977), where plumage variation is used by individuals to recognize previous winners in encounters and, thereafter, to avoid them. Each alternative is discussed in the following sections.

Seasonal Differences

An analysis of variance performed on percentages of avoidances (the measurement used to compare species in previous analyses) for two seasons showed no seasonal effect ($F=1.86$, $P>0.05$, $df=20$), while an analysis for species effect on percentages of avoidances was significant ($F=10.18$, $P<0.01$, $df=20$). Further, analysis of variance within each species showed no seasonal effects for percent avoidances (white-crowned sparrows, $F=0.42$, $P>0.05$, $df=8$; Harris' sparrows, $F=0.87$, $P>0.05$, $df=11$). Therefore, differences in percentages of avoidances are due to species effects, not seasonal ones.

Total supplants, attacks and avoidances (Table II), converted to rates, did show seasonal effects for the first day of hierarchy formation in each of the 11 experiments. These results were obtained using a one-way analysis of variance for total supplants per min

($F=6.28$, $P<0.05$, $df=20$), avoidances per min ($F=6.09$, $P<0.05$, $df=20$) and attacks per min ($F=5.23$, $P<0.05$, $df=20$). These effects can be seen in Fig. 2 where Harris' sparrows in the fall (experiments 1-5) tended to have more encounters than other groups. The seasonal effects for the above measures do not affect the conclusion that differences in percent avoidances is due to differences between species, not seasons.

Sex

The distribution of sexes within each species (Table I & Appendix) indicated that, in spite of my attempts to equalize their numbers in groups by selecting individuals with extreme wing lengths, unequal numbers of males and females were represented. White-crowned sparrow groups had more males than females while those of Harris' sparrows had more females than males. If females avoid other birds more than males do, this difference might explain my observed differences between the species. However, several sets of results, discussed below, support a non-sexual explanation.

(1) If white-crowned sparrow groups avoided less because they were disproportionally male, the group of mixed-age white-crowned sparrows (experiment 9) should not have exhibited such high avoidance values (Table III).

(2) Avoidance levels would not be expected to change with different ranges of plumage variability in groups (Fig. 1).

(3) Analysis of spring Harris' sparrows (experiments 6 & 7) showed that female and male birds did not act differently with regard to avoidance, attack or encounter frequencies. Both experimental groups

had three males and seven females. Expected encounter frequencies of sexes based on a 3:7 ratio are: 9% male-male encounters, 42% male-female encounters and 49% female-female encounters. For total supplants ($n=242$) of experiments 6 & 7 combined, male-male encounters were 24, male-female encounters were 116, and female-female encounters were 102 ($\chi^2=4.54$, NS). Also, for both groups, female and male attack or avoidance of the same and opposite sexed birds were not different from expected.

(4) In experiment 3, fall Harris' males ($n=5$) had 46.4% of the total avoidances, while females ($n=5$) had 53.6% ($n=166$, $t=0.93$, NS).

I conclude from these four points that Harris' sparrow avoidance levels are not likely due to higher avoidance rates by females. A similar analysis for adult white-crowned sparrows was not possible due to unknown sex of some of the birds (experiment 10) and low numbers of females (experiment 11). However, in the mixed-age group (experiment 9; 6 males, 4 females) females neither attacked nor avoided other birds more frequently than expected based on sex ratios. Males attacked 66 times (57%) and females 49 (43%; expected = 40% for females, $t=0.46$, NS). Males avoided other birds 66 times (49%) and females avoided 68 times (51%; expected=40% for females, $t=1.81$, NS).

All lines of evidence for both species indicate that behavioural differences between the two species were not due to differences between sexes. Specific tests, where possible, indicated that males and females attacked, avoided and encountered other birds as expected based on the frequency of sexes in the group. Also, differential behaviour

among experimental groups (e.g. experiment 9) were inconsistent with a sexual hypothesis.

Individual Recognition Facilitation

The data showing that increased plumage variability was correlated to increased relative avoidance levels (Fig. 1) are also consistent with the individual recognition facilitation hypothesis proposed by Shields (1977). The comparisons of relative avoidances between familiar birds, in which all groups of Harris' sparrows had higher values than adult white-crowned sparrow groups (Table III), are also suggestive of a individual recognition explanation. It is possible that Harris' sparrows avoid strangers faster than white-crowned sparrows due to an ability to distinguish individuals more rapidly. If recognition is enhanced and avoidances increase in frequency (as seen in Fig. 2), attack frequencies might be expected to decrease. However, a strategy of total avoidances is unlikely to be evolutionarily stable (Maynard Smith 1976), and it is expected that an intermediate proportion of attack and avoidance strategies would occur (cf. Rushen 1982). For instance, as dominant individuals become more aggressive, subordinates should avoid them at higher rates.

If such a system is based on individual recognition (rather than on a broad "class recognition" like status signals), it should exhibit higher concordance between attack and avoidance behaviour over time. Such concordance is expected simply because of a more immediate response of birds to others that increase or decrease attack rates. I designed the following comparisons to separate the resulting

behavioural differences among experimental groups into those components supposedly caused by status signaling and those more likely due to differences in facilitated recognition. The separation is based on the assumption that recognition facilitation can be attributed to those groups that exhibited a high correlation between attack and avoidance frequencies, while groups exhibiting low levels of correlation indicate lack of, or lesser amounts of individual recognition. Harris' sparrows were found to display high correlations between these behaviours, as shown below.

Attack-Avoidance Concordance

Because all observations were recorded consecutively over 15-min periods, changes between these periods could be analysed within a given day. Thus graphed, the same data (cf. Table IV) show short-term changes in frequencies of attack and avoidance behaviour. On the first day of hierarchy formation there was a sustained close relationship between avoidances and attacks for fall Harris' sparrows from one period to the next (Fig. 3A). Adult white-crowned sparrows did not exhibit such a close relationship (Fig. 3B); nor did the mixture of adult and immature white-crowned sparrows (Fig. 3C), which had previously exhibited relative avoidance levels as high as Harris' sparrows (from Part I). A product-moment correlation was calculated in order to compare attack and avoidance frequencies of each experimental group on the first day of hierarchy formation (Table V). The spring Harris' sparrows were more similar to the fall Harris' sparrows than to the monomorphic groups of white-crowned sparrows.

Even after six days of interactions within their group, adult white-crowned sparrows did not exhibit the strong correspondence between avoidances and attacks (Fig. 4B) exhibited by Harris' sparrows (Fig. 4A; this time represented by all-adult groups). Because avoidance levels (percent avoidances) even reach maximal observed values by day 6 in adult white-crowned sparrows, I suggest that white-crowned sparrows are not capable of such finely-tuned responses as Harris' sparrows.

Summary of Alternative Hypothesis Tests

Two alternative hypotheses for explaining observed differences in behaviours of experimental groups of sparrows with differing amounts of plumage variability (season and sex) were not supported by the data. The third alternative, facilitated individual recognition, was supported in all groups of Harris' sparrows, including the all-dark and all-white throated groups, but not by tests of white-crowned sparrows, including the "polymorphic" group of mixed ages.

The facilitated individual recognition hypothesis cannot explain all the findings presented in Part I of this paper supporting the status signaling hypothesis. Status signaling effects were not found for groups of a single age class and individual recognition effects were not found in any white-crowned sparrow groups. For example, avoidance of strangers on the first day of hierarchy formation was accomplished as well for mixed-age white-crowned sparrows as it was for mixed-age Harris' sparrows. I suggest that Harris' sparrows possess an individual variation factor (possibly the spot patterning on the

breast) as well as a status signaling system (the blackness of the throat). Fall Harris' sparrows were no better at avoiding strangers (mean=64%) than mixed-age white-crowned sparrows (64%), but they more closely tracked changes in individual aggression levels and responded with increased avoidance behaviour more quickly than the white-crowned sparrows.

Part III: COMPARISON OF A THIRD SPECIES

In the first two parts of this paper, the comparative approach facilitated the separation of behavioural effects due to subtle differences in plumage variation both within groups of a species and between groups of two species. This approach was extended to test the generality of my hypothesis that variability in individual plumages enhances individual recognition and, therefore, closely related attack and avoidance frequencies over relatively short time periods, but is not used as a status signal among strange birds. The white-throated sparrow is a good test species because it has considerable plumage variability, but that variability is not consistently age or sex related (Lowther 1961; Lowther & Falls 1968; Atkinson & Ralph 1980).

From the results in Parts I and II, it was predicted that variable-plumaged white-throated sparrows should have low initial avoidance levels but that finely-tuned avoidance/attack relationships would develop. On day 1 of hierarchy formation, white-throated sparrows had 21% avoidances ($n=264$ encounters), the lowest of any group. On day 2 the value increased to 53% ($n=350$ encounters), results that agree with the facilitated recognition hypothesis and resemble the

results found for monomorphic groups of white-crowned sparrows. Also, as predicted, the white-throated sparrows developed a close relationship between attacks and avoidances on day 2 (Fig. 5b), although no such association existed on day 1 (Fig. 5a). In sum, they were able to attain the close association of attack and avoidance frequencies found in the highly variable Harris' sparrows, although they did not reach these levels as quickly as did Harris' sparrows, and they did not avoid at the high rates found in the same Harris' sparrows.

Discussion

A summary of the results relating to the tested hypotheses on plumage variability in three species of Zonotrichia, given in Table VI, shows that: (1) Harris' sparrows seem to signal status, as predicted by Rohwer, but only in mixed-age groups; (2) mixed-age groups of white-crowned sparrows also appear to signal status; (3) white-throated sparrows do not appear to signal status; and (4) both Harris' and white-throated sparrows exhibit individual recognition facilitation effects due to plumage variability. The comparative approach involving three species strengthens the interpretations from the results obtained for each species singly.

Rohwer (1975) suggested that the wide range of plumage variability in the Harris' sparrow and other species is used as a status signal. However, finding variation in a species does not necessarily justify its assumed signaling purpose (Green 1976, Ketterson 1979). By use of an operational definition of communication, focusing on behaviour of the receiver (Klopfer & Hatch 1968, Scott 1968), I have documented the

use of differences in plumage as a signal in two species of sparrows. Other studies (e.g. Guhl & Ortman 1953; Johnston 1976; Rohwer 1977; Parsons & Baptista 1980) have shown that alteration of visual traits resulted in behaviour differences of other individuals in a group, thus the traits were considered signals. Although plumage is evidently being assessed as a status signal in some groups of Harris' and white-crowned sparrows, other groups appear to lack such plumage variability or signals. In this study, all these latter groups (for both species) were single age-class groups.

Shields (1977) and Rohwer (1978) have discussed the problem of whether or not a dichromatic species should be considered "variable" and, therefore, a possible status signaler. At this point, no consensus exists in the literature; however, Parsons & Baptista (1980) have considered the two-signal system in white-crowned sparrows as a status signal. I propose that the term "status signal" be defined broadly to include signals of all types of status, cf. Barnard & Burk's (1979) "assessment unit." In contrast, Geist (1966) more narrowly defined the requirements for "dominance displays" as signals that predict dominance status independent of age or sex class.

In general, "status" may describe any of several conditions, including: breeding versus non-breeding, older versus younger, territorial versus non-territorial, male versus female, larger versus smaller, superior fighter versus inferior, or socially dominant versus subordinate. Therefore, as a subset of general status signaling, we might designate "rank-", "age-", "sex-", etc. signals. By this system, Geist's (1966) "dominance display" would be termed a "rank-signal."

Many of these types of status are likely to be correlated such that, for example, a socially dominant individual may be a breeding, territorial, older, and more fit male. Thus, a signal conveying information about one condition could also serve as a signal of other highly correlated conditions. Dominance rank may often be inferred from features associated with age or sex, simply because these are usually good predictors of rank.

The results presented in this paper suggest that the signaled status in Harris' sparrows may be of a "two-state" nature: adult versus immature rather than a graded series of specific dominance ranks. The only groups of this species that seemed to exhibit status signaling behaviour were combinations of adult and immature birds, exhibiting a possibly dichotomous color signal because adult Harris' sparrows are generally black-throated and immatures usually have white throats (Rohwer et al. 1981). In contrast, my groups composed of a single age class of Harris' sparrows were no better at avoiding strangers than monochromatic white-crowned sparrows (Table III), i.e. plumage variability within both of these groups apparently did not serve a status signaling function. At this point the question of signal function of plumage variability in Harris' and white-crowned sparrows seems to be most parsimoniously answered as an age-signal associated with gross differences in plumage. This conflicts with recent textbook interpretations (e.g. Morse 1980, Dawkins & Krebs 1978, Barash 1982) of Rohwer's (1975) hypothesis being one in which variability in plumages evolved as a "rank-signal," regardless of age class. Rohwer's own manipulations do not distinguish between

age-signals or within-age signals: he bleached or coloured birds only in ways that resulted in changes between major rank classes, equivalent to age-class changes (Rohwer 1977; Rohwer & Rohwer 1978).

Elsewhere (Watt 1983), I develop this question further: is the continuous variability in Harris' sparrows a predictor of status within age classes? If darkness of the throat can be shown to be predictive of dominance status within age classes then the status signal demonstrated in this paper may be more than simply an "age signal" for Harris' sparrows. Otherwise, at this time, an assumption of a more complex status signaling system for the Harris' sparrow is unwarranted.

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Table I. Experimental Groups Used to Test Status Signaling Predictions (See Text for Explanation).

Species & experiment number	Sex composition*	Group composition**	Dates tested	Duration of observations (min)
Harris' sparrow				
1	2 M, 6 F, 2 U	6 L, 4 D	8 & 9 December 1980 (fall)	150, 150
2	2 M, 6 F, 2 U	4 L, 6 D	11 & 12 December 1980 (fall)	150, 150
3	5 M, 5 F	1 L, 9 D	15 & 16 December 1981 (fall)	150, 150
4	1 M, 9 F	9 L, 1 D	17 & 18 December 1980 (fall)	165, 135
5	9 F, 1 U	10 L	17 & 18 December 1981 (fall)	150, 150
6	3 M, 7 F	10 D	21, 22 & 27 May 1980 (spring)	120, 150, 120
7	3 M, 7 F	10 D	11, 12 & 17 June 1980 (spring)	150, 165, 165
White-crowned sparrow				
8	5 M, 5 F	10 I	13 & 14 December 1980 (fall)	150, 135
9	6 M, 4 F	5 I, 5 A	15 December 1980 (fall)	150
10	5 M, 2 F, 3 U	10 A	23, 24 & 28 May 1980 (spring)	120, 150, 120
11	9 M, 1 F	10 A	3, 4 & 9 June 1980 (spring)	135, 150, 150
White-throated sparrow				
12	5 M, 4 F	9	16 & 17 December 1980 (fall)	150, 150

* M=male, F=female, U=unknown

** L=light-throated, D=dark-throated, I=immature, A=adult

Table II. Frequencies of Behaviours Recorded on the First Day of Hierarchy Formation for Eleven Experimental Groups (Defined in Table I) of Harris' and White-crowned Sparrows (See Text for Explanation of Behavioural Categories).

Species & experiment number	Shares	Face-offs	Attacks	Strong attacks	Avoidances	Total supplants*
Harris' sparrow						
1	0	0	72	10	89	161
2	1	1	104	11	141	246
3	6	14	150	9	204	363
4	0	4	151	19	148	303
5	0	4	176	3	166	345
6	0	0	54	7	43	97
7	6	4	78	11	75	157
White-crowned sparrow						
8	2	4	113	8	72	189
9	5	2	118	1	151	271
10	21	5	18	0	10	33
11	16	12	106	14	51	169

*Total supplants=attacks, strong attacks & avoidances

Table III. Relative Avoidance Levels (Percent Avoidances of Total Supplants) Recorded on the First Day of Hierarchy Formation as Encounters Between Strangers and Between Familiars.

Species & experiment number	Familiars			Strangers		
	% avoidances	<u>n</u>	<u>t</u>	% avoidances	<u>n</u>	<u>t</u>
Harris' sparrow						
1	63.83	47	3.71**	66.67	69	2.72**
2	64.04	89	4.42**	66.33	98	2.91**
3	54.55	154	3.54**	64.84	128	2.84**
4	52.67	131	3.20**	66.18	68	2.65**
5	56.03	116	3.57**	54.70	117	1.41 NS
6	58.82	34	2.85**	48.83	43	0.48 NS
7	66.04	53	4.10**	51.43	70	0.87 NS
White-crowned sparrow						
8	52.56	78	2.86**	48.44	64	0.50 NS
9	47.76	134	2.54*	63.77	138	2.73**
10	28.57	14		37.50	16	
11	31.03	58		50.88	57	

The t-statistic is computed from comparison of percent avoidances for experiments 1 through 9 with the average percent avoidance in experiments 10 & 11 following Sokal & Rohlf's (1969) test for equality of two percentages. *, $\underline{p} < 0.05$; **, $\underline{p} < 0.01$; NS, $\underline{p} \geq 0.05$.

Table IV. Relative Avoidance Levels on the First, Second and Sixth Days of Hierarchy Formation.

Species & experiment number	Day 1		Day 2		Day 6	
	% avoidances	<u>n</u>	% avoidances	<u>n</u>	% avoidances	<u>n</u>
Harris' sparrow						
1	55.3	161	62.9	380		
2	57.6	246	53.8	396		
3	56.2	363	51.3	456		
4	48.8	303	50.3	537		
5	48.1	345	43.2	380		
6	44.3	97	59.3	226	54.7	172
7	47.8	157	55.5	330	49.8	319
White-crowned sparrow						
8	38.1	189	45.0	211		
9	55.7	271				
10	30.3	33	43.3	120	43.9	114
11	30.2	169	46.4	194	55.6	277

Table V. Product-moment Correlations between Attack and Avoidance Behaviour Frequencies over Sequential 15-min Time Periods during the First Day of Hierarchy Formation for Harris' and White-crowned Sparrows in Two Seasons.

Species & experiment				
number*	Season	<u>r</u>	<u>P</u>	<u>n</u>
Harris' sparrow				
1, 2, 3, 4, 5	Fall	0.90	0.01	10
6 & 7	Spring	0.91	0.01	8
White-crowned sparrow				
8	Fall	0.65	0.05	10
9	Fall	0.71	0.05	10
10 & 11	Spring	0.59	NS	8

*Where more than one experiment is listed, the behaviours were summed for that number of experiments.

Table VI. Summary of Results Relating to the Two Hypotheses Proposed
to Explain Plumage Variability in Winter Foraging Flocks.

Species groups	Hypothesis supported	
	Status signaling	Facilitated individual recognition
Harris' sparrow		
Mixed ages	yes	yes
All adults	no	yes
All immatures	no	yes
White-crowned sparrows		
Mixed ages	yes	no
All adults	no	no
All immatures	no	no
White-throated sparrows		
No age dimorphism	no	yes

Figures

Fig. 1. Relationship between relative avoidance levels (percentage of win-loss encounters that were avoidances) and degree of plumage variability within the 11 experimental groups for two species. Each group was made up of 10 birds and was observed on the first day of hierarchy formation (see Table I for details of experiment composition). Bar graphs for the experiments are arranged from left to right in order of increasing within-group plumage variability for each species.

Fig. 2. Attack frequencies (squares) and avoidance frequencies (circles) for day 1 (closed symbols) and day 2 (open symbols) of hierarchy formation in 11 experiments for two species. Lines are drawn between days to highlight changes in frequencies over a day's time.

Fig. 3. Comparison of frequencies of attack (dashed line) and avoidance (solid line) behaviours during consecutive 15-min periods of observation for (A) three groups (summed) of Harris' sparrows, (B) two groups of adult white-crowned sparrows, and (C) one group of immature white-crowned sparrows on the first day of hierarchy formation.

Fig. 4. Comparisons of frequencies of attack (dashed line) and avoidance (solid line) behaviours during consecutive 15-min periods of observation for two summed groups of adult Harris' sparrows and two groups of adult white-crowned sparrows six days after introduction.

Fig. 5. Comparisons of frequencies of attack (dashed line) and avoidance (solid line) behaviours during consecutive 15-min periods of observation on (A) day 1 and on (B) day 2 of hierarchy formation for the test group of white-throated sparrows.

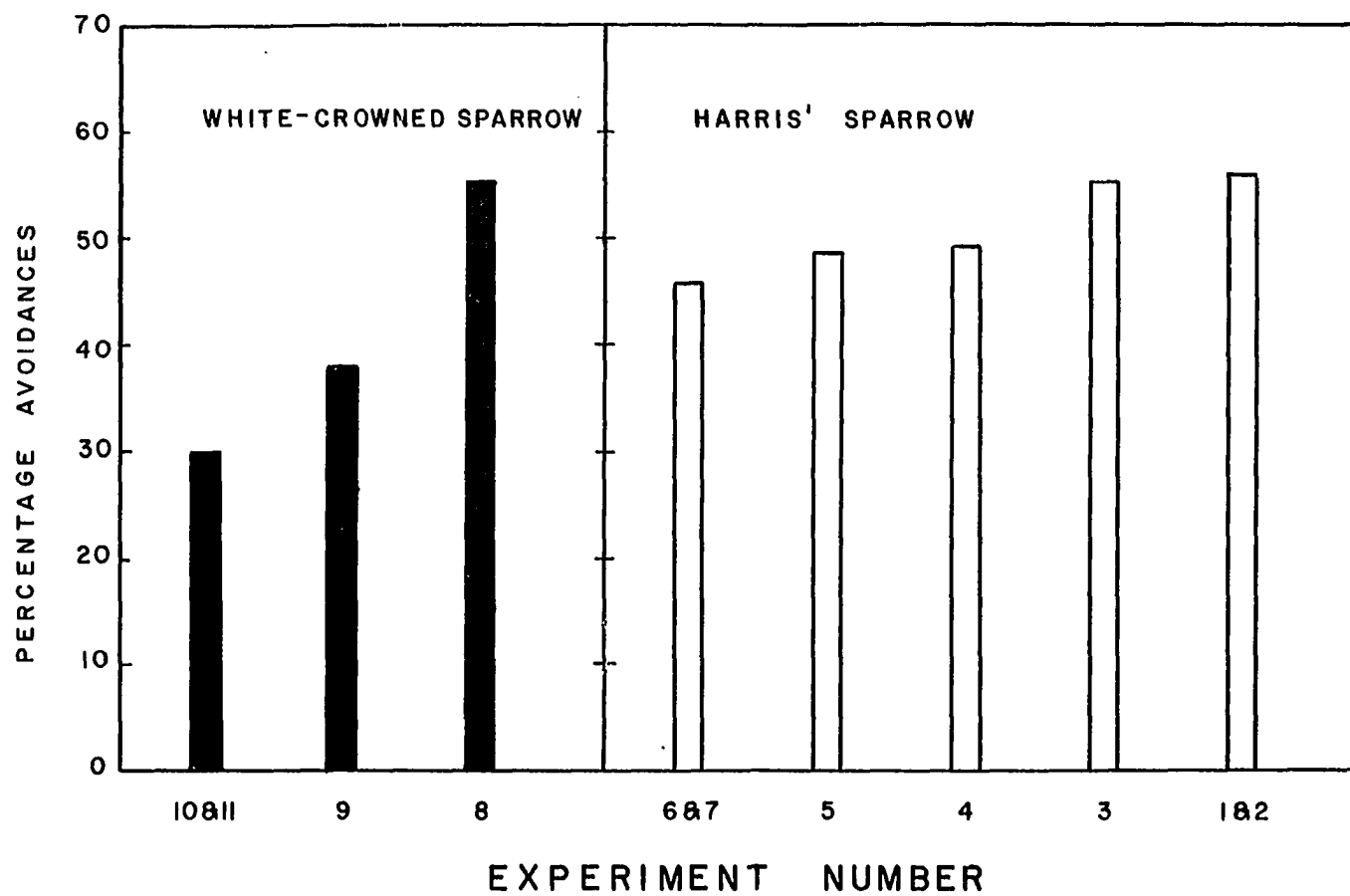


Fig. 1

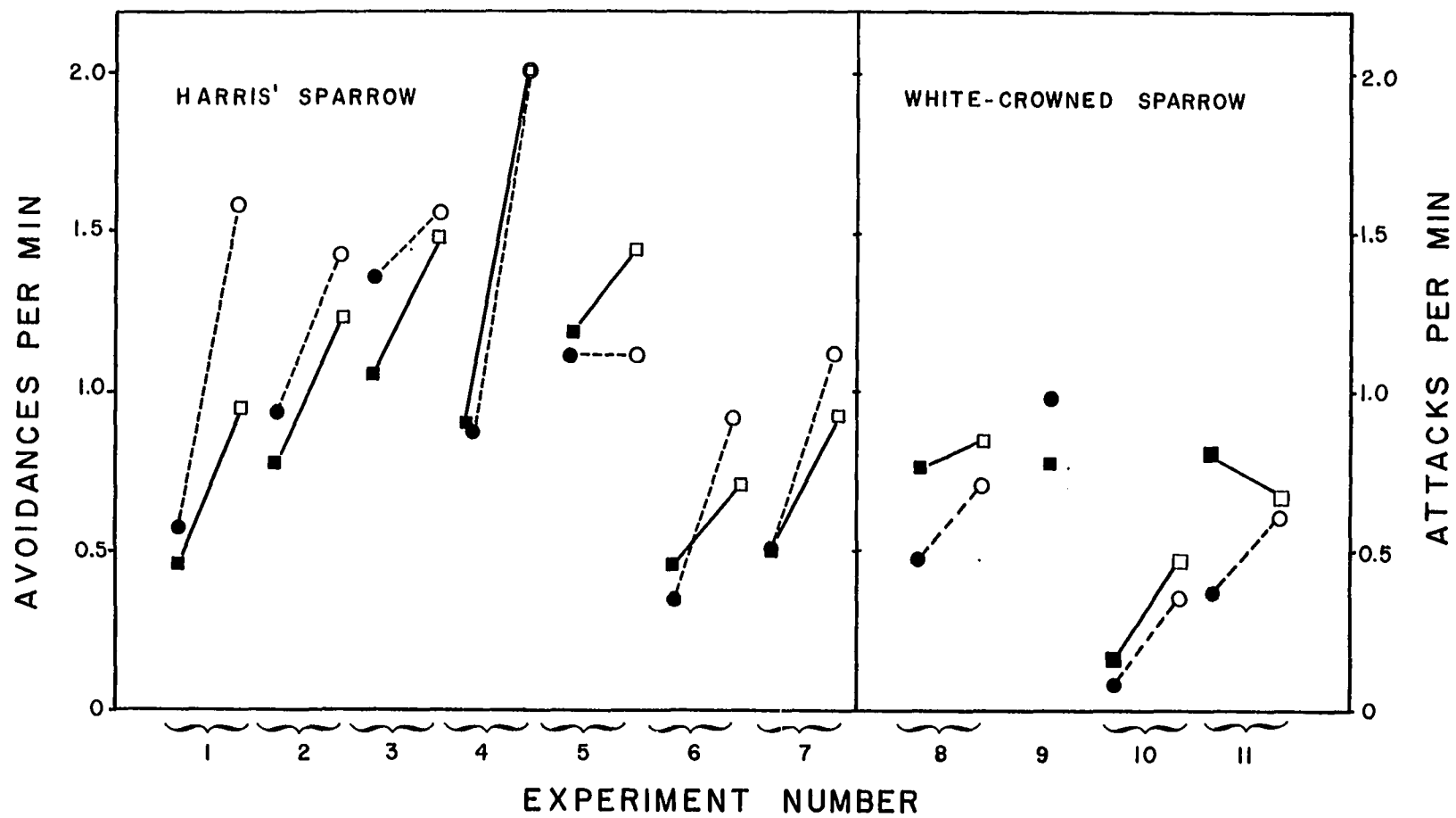


Fig. 2

Fig. 3

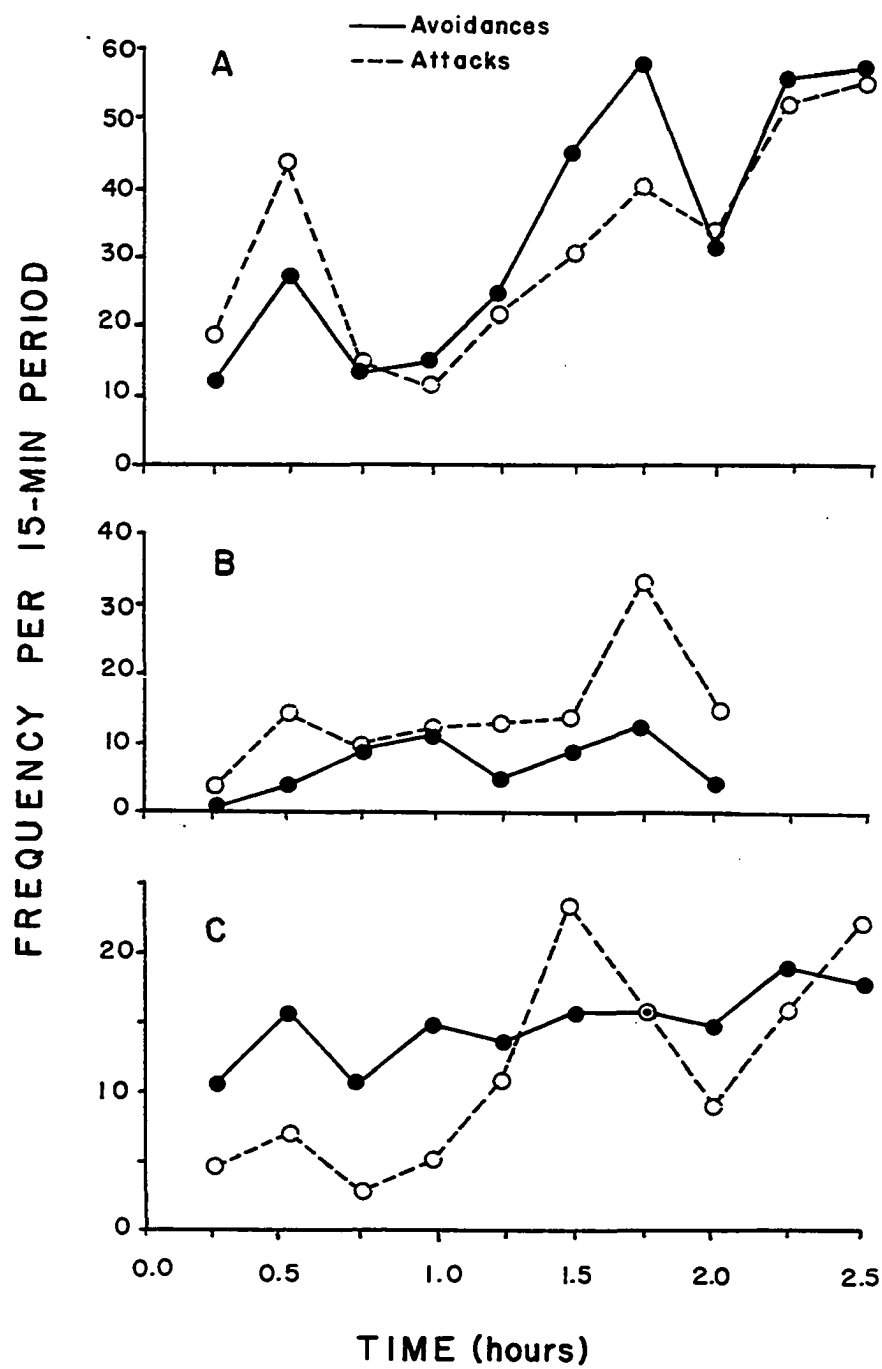


Fig. 4

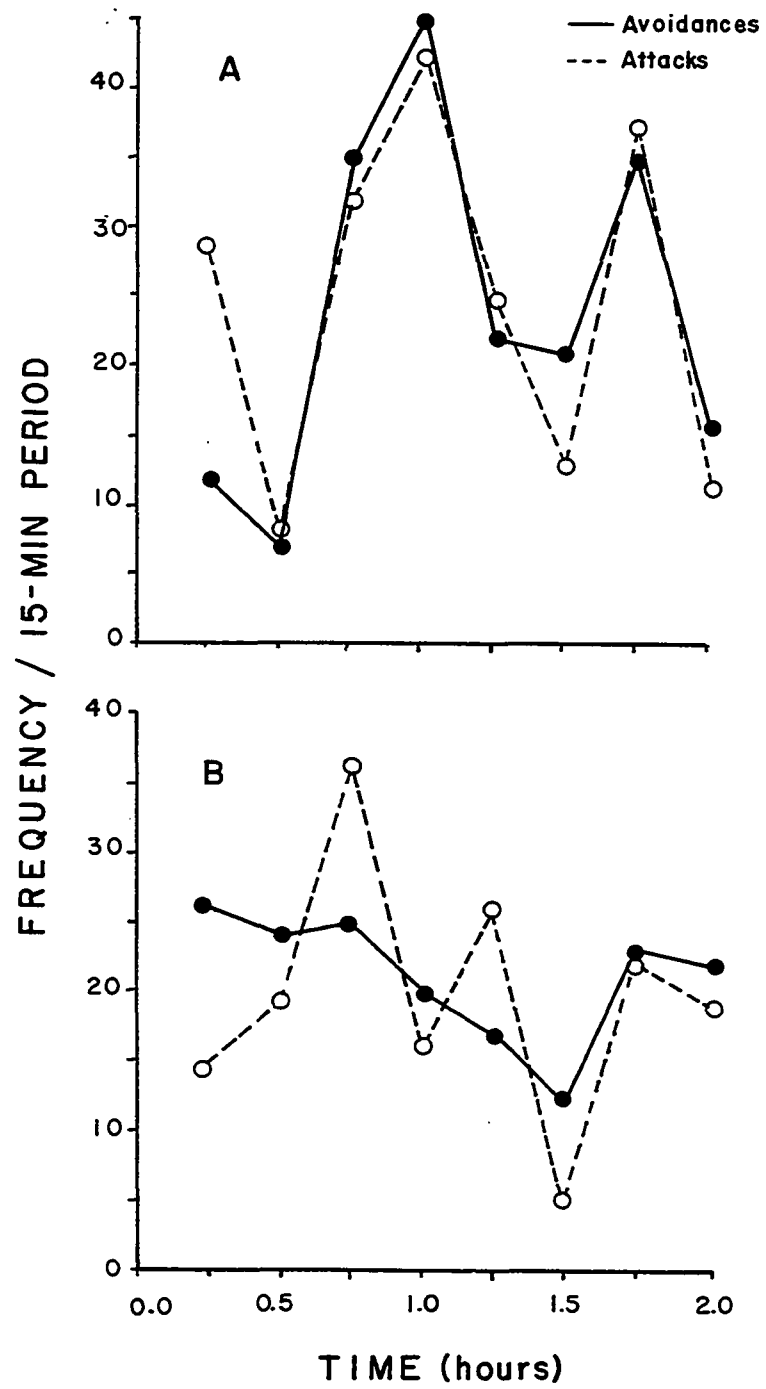
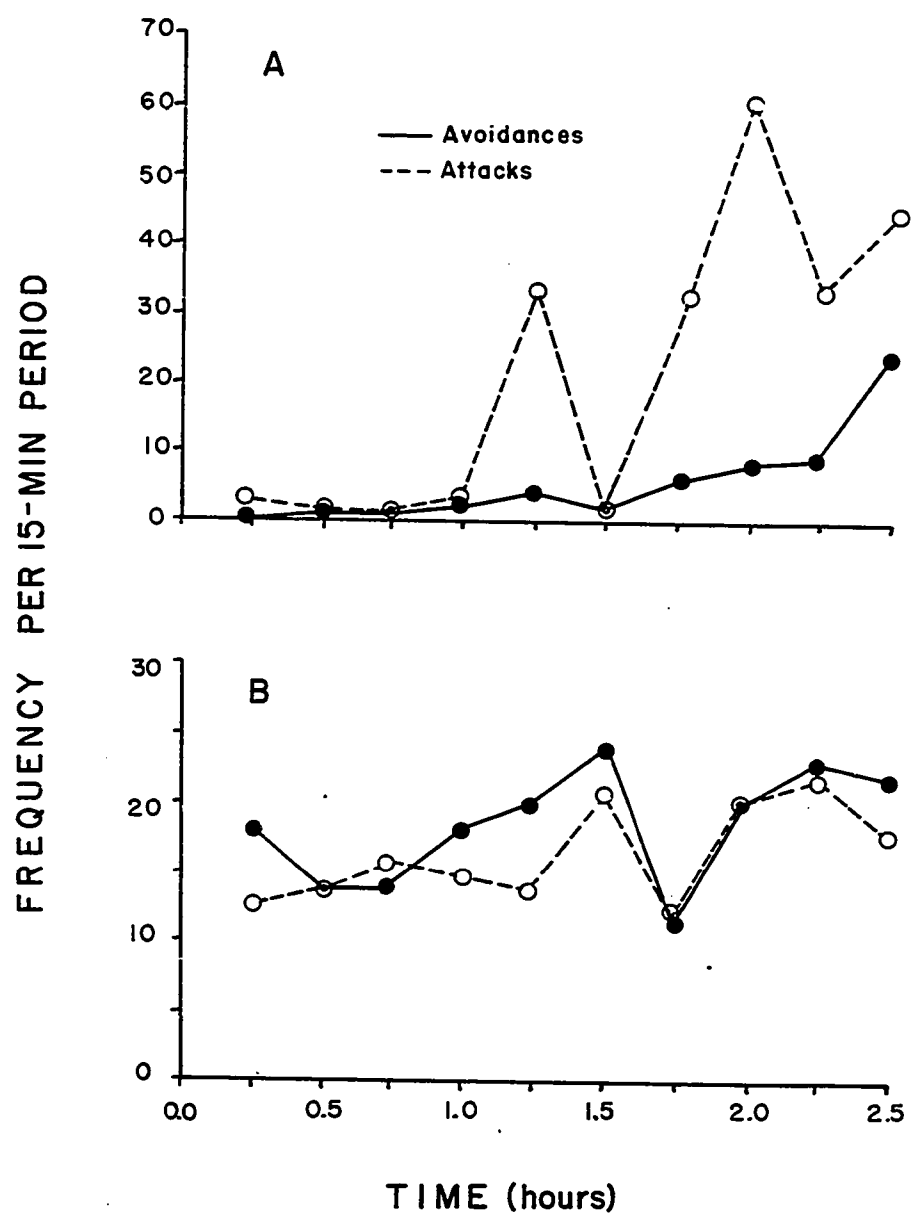


Fig. 5



Appendix: Capture Data for Birds Used in Experiments

Capture date	Plumage*	Age	Wing length (mm)	Sex	Weight (g)
<u>Harris' sparrow</u>					
5 May 1980	14	Adult	80	F	36.1
5 May	14	Adult	83	M	39.4
3 May	14	Adult	85	F	38.8
5 May	14	Adult	82	F	33.2
3 May	14	Adult	78	F	30.9
1 May	14	Adult	79	F	33.2
30 April	14	Adult	84	M	37.6
29 April	14	Adult	84		35.8
30 April	14	Adult	78	F	31.6
29 April	14	Adult	78	F	30.7
12 April	14	Adult	89	M	36.5
12 April	14	Adult	79	F	33.8
29 April	14	Adult	86	M	41.3
30 April	14	Adult	78	F	32.3
23 April	14	Adult	83	F	32.9
21 November 1980	2	Immature	79	F	28.4
21 November	2	Immature	78		28.8
21 November	13	Adult	86		31.5
15 November	11	Adult	85		32.9
19 November	10	Adult	81		31.9
20 November	1.5	Immature	79	F	30.0

Appendix (continued)

Capture date	Plumage	Age	Wing length (mm)	Sex	Weight (g)
21 November	1	Immature	78	F	29.1
20 November	2	Immature	87		36.6
20 November	8.5	Adult	84		32.0
20 November	2	Immature	80		30.0
20 November	4	Immature	79	F	31.8
20 November	2	Immature	80	F	35.4
20 November	9	Immature	83	F	33.8
12 November	11	Adult	85	F	29.2
19 November	13	Adult	90	M	--
14 December	1.5	Immature	81		24.5
14 December	3	Immature	79		27.6
20 November	2	Immature	79	F	32.3
13 December 1981	13	Adult	89	M	32.3
13 December	11	Adult	84		27.2
13 December	14	Adult	90	M	32.5
13 December	11	Adult	85		29.4
13 December	13	Adult	83	F	29.9
20 November	13.5	Adult	84		29.5
20 November	12	Adult	90	M	33.3
6 December	13.5	Adult	91	M	36.1
6 December	1	Immature	88	M	36.7
20 November	13	Adult	82	F	30.7
13 December	1.5	Immature	80		25.0
13 December	1	Immature	80		29.2
13 December	2	Immature	80		30.2

Appendix (continued)

Capture date	Plumage	Age	Wing length (mm)	Sex	Weight (g)
13 December	1	Immature	83		26.6
13 December	7	Immature	79		29.8
6 December	1	Immature	79		29.6
6 December	1	Immature	84		34.6
6 December	1.5	Immature	78		32.7
6 December	1	Immature	78		29.6
6 December	2	Immature	79		27.2
<u>White-crowned sparrow</u>					
3 May 1980	Black & white	Adult	76	M	28.9
3 May	Black & white	Adult	80	M	33.6
3 May	Black & white	Adult	76	M	30.0
5 May	Black & white	Adult	71		25.8
3 May	Black & white	Adult	71		27.7
30 April	Black & white	Adult	80	M	29.6
2 May	Black & white	Adult	73	M	28.9
30 April	Black & white	Adult	77		26.5
29 April	Black & white	Adult	78		30.7
28 April	Black & white	Adult	75		29.7
29 April	Black & white	Adult	80	M	30.0
28 April	Black & white	Adult	80	F	36.9
2 May	Black & white	Adult	78	M	31.6
29 April	Black & white	Adult	75	M	25.5
30 April	Black & white	Adult	77	M	30.7

Appendix (continued)

Capture date	Plumage	Age	Wing length (mm)	Sex	Weight (g)
12 November	Brown & tan	Immature	76	F	24.2
15 November	Brown & tan	Immature	79	M	30.5
12 November	Brown & tan	Immature	77	F	24.7
11 November	Brown & tan	Immature	75	F	24.8
11 November	Some black & white	Immature	77	M	23.6
20 November	Brown & tan	Immature	80	M	26.5
20 November	Brown & tan	Immature	78	M	29.3
20 November	Some black	Immature	76	F	24.0
20 November	Brown & tan	Immature	75	F	24.8
20 November	Brown & tan	Immature	80		28.3

White-throated sparrow

13 November 1980	3		73		22.7
13 November	5		75	M	24.8
15 November	3		74	M	26.8
15 November	4		73	F	24.0
13 November	3		70	F	25.4
6 November	2		70	F	23.9
6 November	3		76	M	25.8
11 November	5		69	F	24.5
6 November	2		75	M	24.9

*Plumage characteristics for Harris' sparrows are given as Rohwer's index values (Rohwer 1973, 1975). Plumage index values for white-throated sparrows are given as in Watt (1983).

RELATIONSHIP OF PLUMAGE VARIABILITY, SIZE AND SEX

TO SOCIAL DOMINANCE IN HARRIS' SPARROWS

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Running head: Harris' sparrow dominance

Abstract. Harris' sparrows (*Zonotrichia querula*) have been used to demonstrate status signaling, the use of plumage variability to signal status (Rohwer 1973, 1975, 1977, Rohwer & Ewald 1981, and Rohwer & Rohwer 1978). In a previous paper (Watt 1983), I suggested that the plumage variability associated with signaling properties might be of a two-state nature and reflect age-signaling. To test this idea, I investigated the degree to which the signal might be correlated with dominance status in captive flocks. Rohwer's (1975) plumage index was estimated and 15 other variables were measured (7 morphological and 8 plumage characteristics) to evaluate measures that could be associated with dominance rank. In general, dark-throated birds dominated light-throated birds as expected but, within these broad classes,

throat color was not a good predictor of dominance status. The best overall predictor of dominance was wing length. These findings support the conclusions of Watt (1983) and indicate that the Harris' sparrow plumage variability is not well correlated to dominance within age classes and is probably not used to signal dominance within these age classes.

(Introduction)

The concept of status signaling in birds was first developed by Rohwer (1975). He proposed that variable plumage is common in winter-flocking species and that this variability is correlated with dominance and is used by individual birds to signal rank. The Harris' sparrow (Zonotrichia querula), used as Rohwer's central example, exhibits variability in the relative amount of black versus white plumage on the head, throat and chest, with individual birds ranging from very light to very dark (see fig. 3 of Rohwer 1975). In his first study (Rohwer 1975), darker birds won 57 and lost 18 dominance interactions. Later, Rohwer et al. (1981) reported that at highly localized food sources, no significant differences were found in number of wins of dark- and light-bibbed birds (n=151), whereas, at diffuse food, birds with blacker bibs won 18 and lost 5 encounters. These three sets of data constitute the only published information concerning dominance behaviour and its relation to colour in Harris' sparrows. They do not confirm that plumage is used as a status signal (dealt with in Watt 1983) or that darker Harris' sparrows are dominant to lighter ones.

The development of the status signaling theory and testing of predictions (Rohwer 1975, 1977, Rohwer & Rohwer 1978) have been based on the assumption that darker Harris' sparrows are dominant to light ones regardless of age, and that continuous variation in plumage is associated with specific ranks, i.e. darkest birds are most dominant, lightest birds have lowest dominance ranks, and intermediate-plumaged birds are mid-ranking. However, Rohwer & Ewald (1981) showed that most dark-throated Harris' sparrows are adults and light-throated birds are

immatures. In addition, Watt (1983) found evidence supporting a status signaling function of variable plumage only in mixed-age groups of Harris' sparrows. Therefore, a two-state plumage condition associated with two age classes (adult versus immature) is sufficient to explain previous results.

The problem of determining what level of plumage variability, whether between or within age classes, is important in status signaling was acknowledged by Rohwer (1975) and discussed by Shields (1977) and Rohwer (1978), but has not been resolved. Rohwer's treatment of status signaling in Harris' sparrows clearly implies that it has been demonstrated within age classes. For instance, a composite photograph used to score individual birds into 14 descriptive ("studliness") categories was cited as the reference for the statement (in Rohwer 1977) that "individuals with more black are dominant to those with less black." In addition, Rohwer & Rohwer (1978) stated that "intraspecific variations in appearance are closely correlated with individual fighting prowess," citing only the earlier papers (Rohwer 1975, 1977). This statement (and others) seems to have been interpreted by readers and reviewers (e.g. Morse 1980) to mean that the actual rank in dominance can be inferred from the studliness score. Insufficient data have been published to warrant the assumption of such a close relationship between plumage and dominance rank, especially within age classes.

The purpose of my study was to investigate how closely the differences in plumage actually do predict dominance rank in captive Harris' sparrows. In this paper, I present (1) analyses involving

quantitative measurements of plumage variables that demonstrate which aspects of darkness (on the chest, head, bib, etc.) are interrelated, and (2) a comparison of various morphometric and plumage measurements related to dominance rank to determine their relative importance in predicting status.

Methods

General methods of capture and maintenance of birds are given elsewhere (Watt 1983). By using the experimental methods, also described there, I made observations of 135 to 165 min per day for one to three days for each of five groups of 10 Harris' sparrows in fall plumage. Following Brown (1975, p. 86), the numbers of dominance encounters (attacks and avoidances) recorded on these days were incorporated into a dominance matrix, representing a hierarchy, for each of the five groups (see Appendix). From these dominance hierarchies, I assigned a relative dominance rank (1-10) to each bird in each group. These five groups represented different combinations of ages and colours of birds (see Table I).

In addition to these small groups, a large group of 26 birds caught from 6 through 13 December 1981 was assembled and observed on 19, 20 & 22 December. The agonistic encounters within this large group are presented in a dominance matrix (Fig. 1), representing a hierarchy. The hierarchy is linear except for one set of three individuals that formed a close triangular relationship (Fig. 1; i.e. $F > G$, $G > H$, and $H > F$). Dominance ranks were assigned to each of the 26 birds (F, G, and H were all given the tied rank of "7"). A 27th bird, "II", was

included in subsequent analyses to represent the only immature male in the group. This bird's dominance rank relative to the others was determined in separate sets of interactions on 15, 16 and 23 December. The total 27 birds are referred to throughout the rest of this paper by letters A-I, II, and J-Z, reflecting their relative dominance ranks (e.g. the most dominant bird is referred to as "A").

Birds were scored according to Rohwer's (1975) plumage index values (1-14, from lightest to darkest) by comparing them to his composite picture. Individuals with plumages intermediate between those in the pictures were given integer values half-way between his values.

Wing length (to the nearest mm) was measured on live birds at capture as the flattened wing chord, and body weight (to the nearest 0.1 g) was taken on 23 December 1981 at the end of my behavioural observations. Next, 26 of the 27 birds were prepared as study specimens (one bird, "C", was not in good enough condition), and an additional 13 physical characteristics were measured as follows:

(1) Culmen length (nearest 0.1 mm), measured with dial calipers, was taken from the bill tip to the base of the culmen at the point where it disappears into the feathered forehead. (2) Bill width (nearest 0.1 mm) was recorded at the widest part of the bill (at the commissure base where the base meets the feathers). (3) Tarsus length (nearest 0.1 mm). (4) Skin length (nearest mm) was measured from the tip of the bill to the tip of the tail. (5) Length of coloured breast plumage (nearest 0.1 mm) was the distance from the middle and base of the lower mandible to the most caudal spot of black on the belly. (6)

Forehead black (nearest percent) was the relative amount of black colour in an area between the eyes and ranging from the base of the bill, caudal to a line parallel to the upper edge of the eyes (when the bird was facing me). (7) Throat black (nearest percent) was an estimate of black feathering relative to total colour on the throat patch area (defined by two malar lines descending from the base of the bill, the lower mandibular edge and a line perpendicular to the malar lines across the lower edge of the throat). (8) Lores black (nearest percent) was the estimated percentage of black between the base of the bill and the eye, delineated by a line from the top of the eye to the culmen and a similar line from the eye's lower edge to the base of the lower mandible. (9) Breast colour amount was measured by placing a 5x5 (2-cm²) grid over the breast and tallying the number of grid intersections where black or dark brown colour occurred (number of "hits" out of 25). The grid was oriented with the central vertical line at the base of the bill and the top horizontal line across the bottom of the throat patch. Also, the spatial pattern of hits was recorded for each bird (Fig. 2). (10) Breast colour hue was measured using the Munsell Soil Color Charts (Macbeth Co., Munsell Color, Baltimore; see Wood & Wood 1972 for details) to evaluate spot colour (redness, greenness, etc.) on the breast. Hue values for the 26 specimens ranged from 2.5 to 7.5, all yellow-red hues (increasing in yellowness with increasing size). (11) Breast colour value, also a Munsell measure, indicates relative lightness and darkness of the breast spots. Values measured were 2.0, 2.5 and 3.0, in order of increasing darkness. (12) Breast colour chroma, the third colour

measurement using the Munsell system, measured colour intensity (values for the 26 specimens ranged from 0 to 4), indicating increasing importance of browns (lower saturation of black) as numbers increase.

(13) Sex of the specimens was noted after examination of the gonads except for three specimens where gonads could not be seen. Because extreme wing lengths are good predictors of sex in Harris' sparrows (Rohwer et al. 1981), sex was assigned to these three individuals based on their wing lengths (79, 83, 84 mm; all less than the smallest male recorded in Rohwer et al. 1981).

Rohwer et al. (1981) have shown that light-throated birds are usually immatures and dark-throated birds adults. Therefore, ages of these 26 birds were initially estimated by throat colour. Records of tail wear (following Rohwer 1973) and skull ossification at the time of skin preparation agreed with estimates made from throat colour. Because age was directly related to plumage characteristics, it was not included as a variable in plumage analyses.

Statistical Methods

Several multivariate techniques were employed to investigate relationships among physical characteristics and between these and dominance rank for the large group of 26 birds. The measurements of the 15 characters were standardized with mean of 0.0 and standard deviation of 1.0. Principal components analyses, Pearson's product-moment correlations and cluster analyses (unweighted pair-group method using arithmetic averages) were performed using NT-SYS programs (Numerical Taxonomy System; a series of multivariate computer programs

developed by F. J. Rohlf, J. Kishpaugh, and D. Kirk). Clustering procedures were used on both the distance and correlation matrices for individual birds. Stepwise multiple regression was used to find characters that, in combination, best predicted dominance rank within the group (program from Bio-Medical Programs, Health Sciences Computing Facility, University of California, Los Angeles, 1979).

Results

In the five groups of 10 birds each, dark-throated birds (adults, with Rohwer's plumage index values of 8.0 or more) were always dominant to light-throated birds (immatures, with index values less than 8.0) (Table I). Within the two age classes, however, index values were not predictive of dominance rank.

Dark-throated birds usually were dominant to light-throated birds in the larger group (n=27) of Harris' sparrows as well (Table II). I further analysed physical aspects of 26 birds of this latter group to determine similarities and differences of the birds with respect to physical measures, both plumage and other morphological characteristics. I also found those physical characteristics that best predicted dominance among the 26 birds. The following sections detail those analyses.

Physical comparisons of individual birds

Birds most similar in terms of physical characteristics were also similar in dominance rank, as demonstrated by clustering of individuals based on pair-wise correlation values of physical characteristics

(Fig. 3A). One large cluster included birds A through J (except for C which was not included in these analyses), and the second large cluster included a group of II, K, L, and N through Z. The two groups can be described, respectively, as black dominants, and light- and medium-coloured subordinates. "II" was relatively dominant, but light-throated (the only immature male in the group).

While groupings based on correlations emphasized plumage similarities, clustering of birds using the average distance values stressed differences in the size of individuals (Fig. 3B). Two clusters (Groups 3 & 4, Fig. 3B) were composed of males; the remaining two groups contained only females.

Correlates to dominance

Both plumage and other morphological characters, such as size, appear to be important in determining dominance ranks of the large group of Harris' sparrows. The correlation matrix (Table III) for 16 characteristics (omitting Rohwer's index) measured for the 26 birds shows that dominance rank was highly correlated to wing length, forehead black, throat black, lores black, culmen length and breast colour chroma. Dominance rank has a negative correlation since rank numbers are lowest for highest ranking birds (e.g. #1 is the highest rank). In addition, blackness measures were correlated to one another, wing length with sex, and breast colour hue with bill width.

Principal components analysis confirmed the close relationship between dominance rank, wing length, and forehead, throat and lores black found in the previous correlation analyses (PC I in Table IV).

Most of the remaining variance (represented by PC II, III and IV) was correlated to breast colour hue, bill width, and tarsus length, respectively, and these were not highly correlated to dominance rank. Because I was most interested in relations of physical characters to dominance rank, I plotted individual birds along the first principal component (Fig. 4). In general, darker, larger and more dominant birds had positive scores, while the smaller, lighter, and subordinate birds had negative scores. The positions of individuals along the gradient from dark to light revealed that birds at the bottom were more similar to one another (appear closer) with regard to this axis than birds at the top (Fig. 4); dominants were more variable in plumage characters than were subordinates.

Stepwise regression of the 15 physical variables on dominance rank provided wing length as the best single predictor. The best combination of characters for predicting dominance rank included wing length, breast colour chroma and breast colour amount (Table V). No additional characters contributed significantly ($F = NS$ in further stepdowns, $P > 0.05$) to predicting dominance rank.

Discussion

My data show that, within age classes, differences in Rohwer's index for close values do not predict dominance rank in captive Harris' sparrows. Correlations of plumage with dominance rank were found only between age classes: adults (dark-throated birds) dominated immatures (light-throated birds). This result supports an age-signaling system suggested by data gathered previously (Watt 1983). In five small

groups and one large group, adult birds dominated immatures. However, within the two age classes, Rohwer's plumage index of individual birds did not predict their dominance rank (Tables I & II). Within the large group, adult birds with plumage index values greater than 10 did dominate adult birds with values between 8 and 9; however, in two small groups, one relatively light-throated female (index=8.5) dominated several birds that were much darker (indices=10 to 13). It is possible that correlation between plumage coloration and dominance rank is stronger in larger groups of birds.

Studdiness Characteristics

Assessing Rohwer's index for Harris' sparrows involves comparing the bird to a composite picture of example plumages. There is probably some observer error involved in such comparisons and the criteria for choosing between indices are not clear. By quantifying plumage characteristics in a large group of birds, I was able to assess how various characteristics contributed to the darkness ranking of individuals. In terms of plumage, blackness measures for the throat, forehead and lores were highly correlated to one another (Table III) and appear to be the basis of Rohwer's index values.

Correlates to Dominance

Within a large group of Harris' sparrows, wing length was the best predictor of dominance rank of individual birds. I also found a high correlation between wing length and plumage blackness measures, possibly due to the low representation of immature males in my samples. Immature males, with lighter plumage, are larger than adult females

(with darker plumage). The lack of immature males in my study is unfortunate because they might be key in explaining whether size (as indexed by wing length) is as useful in predicting dominance between age and sex classes as is blackness of throat and head plumage. For example, if immature males typically dominate adult females, then wing length is more important, whereas the reverse--adult females dominating immature males--would support plumage differences as the best predictor of dominance. The data of Rohwer et al. (1981) for this point are equivocal since immature males won 14 times and lost nine times to adult females. Clearly, if immature males consistently win over adult females, the concept of status signaling, even between age classes, would be questionable. At best, if adult females dominate immature males, there is still no evidence that status signaling is occurring within age classes.

Status of Current Knowledge and the Theory

Shields (1977) proposed that variability in Harris' sparrows evolved to facilitate individual recognition, an explanation that Rohwer (1978) dismissed because of the "difficulty in justifying the apparent correlation between signal and status under that interpretation." Even if a strong correlation between dominance rank and plumage darkness exists in Harris' sparrows (and in my study it did not), a status signaling function would have to be demonstrated in behavioural tests (see Watt 1983).

Considering results from the present study and those of Watt (1983), I propose that both Shields' and Rohwer's explanations may be

partially correct: a basic age-signal (dark throats and heads versus light throats and heads) reflects potential dominance ranks of adults versus immatures. In addition, considerable individual variability, especially in the breast spot patterns (Fig. 2), is available for use in facilitating individual recognition.

The advantages to individuals, of both types of signaling systems might be as follows: Rohwer & Ewald (1981) suggested that subordinate birds ("sheep") benefit from association with dominants ("shepherds"). Increased variation in plumage of dominant adults, might make the adult birds easier to recognize and follow. Selective forces of adult competition for "shepherd" position in foraging groups may be enhanced by immatures recognizing and following particular dominants in daily foraging flocks. In such a system one might expect to find aggressive interactions highest among dominants when individual competition for food is low (e.g. diffuse food) as a mechanism to decrease numbers of dominants in the group. In fact, this is what Rohwer & Ewald (1981) found. On the other hand, if dominants attract and use subordinates for selfish purposes, one would also expect direct competition between dominants and subordinates at concentrated food. Again, this is what Rohwer & Ewald found.

Within such a system as detailed above, one would also predict that individual plumage variability of dominant adult birds would be greater than that within the immature age class. Adults reveal individual identity to followers (i.e. immatures) but the reverse does not occur. The ordination of 26 birds along the first principal component reflects this greater variability among adults (Fig. 4), as

do index values for the same group of birds (Table II; most plumage index values for immature birds are 1-3). A frequency distribution of plumage types (Rohwer et al. 1981) also shows that immatures are less variable in plumage type than are adult birds.

Several questions regarding status signaling remain unanswered: (1) Rohwer & Ewald's (1980) and my findings suggest that daily foraging flocks should contain both black dominant adults and light subordinate immatures; age-signaling or shepherd-sheep relationships require the presence of both classes within the foraging flock. These observations have not been made.

(2) Are plumage characteristics more highly correlated with dominance in very large groups? It is possible that in very large groups dominance interactions no longer depend on individual recognition between birds, but may instead be based on plumage differences. I generally found foraging groups to contain small numbers of individuals (10-15); however, roosting congregations are usually larger (40-75 birds in the three that I observed). Functions of status signaling in a roosting context would be an interesting topic for further research.

(3) Selective pressures resulting in plumage patterns are not clear. Prehistorically, Harris' sparrow roosting sites may have been rare in the prairie regions of their range due to lack of small trees. Dense local populations of birds might have resulted from attraction to the few suitable roost sites available. Competition for daily foraging areas might have been strong, resulting in patterns seen today. Study of composition of daily foraging groups, flock stability, and

preference tests of birds proposed to be "shepherds" or "sheep" in the laboratory should shed light on these hypotheses.

In an analogous situation (high local densities), dominant male ruffs (Philomachus pugnax) allow satellite males on mating territories (Hogan-Warburg 1966, Rhijn 1973). Plumage differences enhance individual variability among ruffs, as well as a general "status signal" of territory owner versus satellite male. Perhaps there are similar advantages for both Harris' sparrows and ruffs to signal subordinate status and to display a large degree of individual variation. Comparative studies of several species (as done in Watt 1983 for white-throated, white-crowned and Harris' sparrows) would reveal the degree to which other species use plumage to signal status or to aid individual recognition in their interactions within social groups.

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Table I. Rohwer's Plumage Index Score and Sex for Individual Harris' Sparrows in Five Groups of 10 Birds Each in Order of Their Dominance Rank. Adults (Index $\geq$ 8.0) Were Always Dominant to Immatures (Index $<$ 8.0). Some Individuals Were Used in More Than One Group.

Dominance rank	Plumage scores and sexes				
	4 Ad/6 Imm [*]	6 Ad/4 Imm	1 Ad/9 Imm	9 Ad/1 Imm	10 Imm
1	8.5 (F ^{**})	13.0 (M)	9.0 (F)	12.0 (M)	1.0 (F)
2	11.0 (F)	8.5 (F)	2.0 (M)	13.5 (M)	1.5 (F)
3	10.0 (F)	11.0 (F)	2.0 (F)	14.0 (M)	1.0 (F)
4	13.0 (F)	10.0 (F)	2.0 (F)	11.0 (F)	1.0 (F)
5	2.0 (M)	11.0 (F)	2.0 (F)	13.0 (M)	2.0 (F)
6	1.5 (F)	9.0 (F)	2.0 (F)	11.0 (F)	1.5 (F)
7	2.0 (F)	2.0 (M)	4.0 (F)	13.0 (F)	2.0 (F)
8	2.0 (F)	2.0 (F)	2.0 (F)	13.0 (F)	1.0 (F)
9	2.0 (F)	4.0 (F)	1.5 (F)	13.5 (F)	1.0 (F)
10	1.0 (F)	2.0 (F)	3.0 (F)	1.0 (M)	7.0 (F)

^{*}Numbers of adult (Ad) and immature (Imm) birds in each of the groups.

^{**}F=female, M=male

Table II. Identities, Rohwer's Plumage Index Score, and Sex for 27 Harris' Sparrows in One Group in Order of Dominance Rank.

Bird	Dominance rank	Plumage score	Sex
A	1	12.0	M
B	2	13.5	M
C	3	14.0	M
D	4	11.0	F
E	5	13.0	M
F	6	13.0	F
G	7	13.0	F
H	8	11.0	F
I	9	13.5	F
II	10	1.0	M
J	11	11.0	F
K	12	9.0	F
L	13	8.0	F
M	14	9.0	F
N	15	8.5	F
O	16	1.0	F
P	17	8.0	F
Q	18	1.5	F
R	19	1.0	F
S	20	1.0	F
T	21	2.0	F
U	22	1.5	F
V	23	2.0	F
W	24	1.0	F
X	25	1.0	F
Y	26	7.5	F
Z	27	7.0	F

Table III. Pairwise Correlations Between Sparrow Characteristics.*

	Dominance rank	Culmen length	Bill width	Tarsus length	Wing length	Forehead black	Throat black	Lores black	Length of coloured breast	Skin length	Breast colour amount	Breast colour hue	Breast colour value	Breast colour chroma	Sex
Body weight	-0.33	0.30	0.31	0.45	0.54	0.39	0.23	0.38	0.30	0.44	0.08	0.17	-0.13	-0.12	<u>0.63</u>
Dominance rank		<u>-0.61</u>	-0.12	-0.03	<u>-0.77</u>	<u>-0.76</u>	<u>-0.75</u>	<u>-0.76</u>	-0.35	-0.39	-0.55	0.09	0.55	<u>0.71</u>	-0.56
Culmen length			0.06	0.33	0.55	0.59	0.55	0.45	0.40	0.25	0.43	-0.10	-0.57	-0.51	0.43
Bill width				0.25	0.12	0.18	-0.03	0.10	0.11	0.19	-0.02	<u>0.65</u>	-0.25	-0.06	0.09
Tarsus length					0.16	0.31	0.09	0.33	0.36	0.03	-0.03	0.04	-0.10	0.00	0.33
Wing length						0.55	0.55	0.54	0.40	<u>0.68</u>	0.19	0.06	-0.30	-0.35	<u>0.83</u>
Forehead black							<u>0.78</u>	<u>0.85</u>	0.33	0.29	0.58	-0.16	-0.56	<u>-0.66</u>	0.42
Throat black								<u>0.78</u>	0.43	0.40	<u>0.65</u>	-0.26	-0.50	<u>-0.67</u>	0.31
Lores black									0.47	0.34	0.53	-0.17	-0.47	<u>-0.63</u>	0.40
Length of coloured breast plumage										0.43	0.11	0.13	-0.38	-0.20	0.33
Skin length											0.02	0.22	-0.20	-0.19	0.54
Breast colour amount												-0.26	-0.26	-0.47	0.03
Breast colour hue													-0.09	0.25	0.09
Breast colour value														<u>0.74</u>	-0.31
Breast colour chroma															-0.24

*Values over 0.60 are italicized for emphasis.

Table IV. Loadings (Correlations) of Sparrow Characteristics on
the First Principal Component

Characteristic	Loading*
Body weight	0.52
Dominance rank	<u>-0.89</u>
Culmen length	<u>0.73</u>
Bill width	0.19
Tarsus length	0.31
Wing length	<u>0.78</u>
Forehead black	<u>0.87</u>
Throat black	<u>0.84</u>
Lores black	<u>0.85</u>
Length of coloured breast plumage	0.54
Skin length	0.53
Breast colour amount	0.54
Breast colour hue	-0.07
Breast colour value	<u>-0.66</u>
Breast colour chroma	<u>-0.72</u>
Sex	0.65

* Values > 0.60 are in italics for emphasis. Component accounts for 42% of total character variance.

Table V. Stepwise Multiple Regression Analysis Using the Best Three Significant Plumage and Morphological Characters to Explain Dominance Rank Among a Group of Harris' Sparrows (N=26).*

Variable	Coefficients		<u>F</u>
	Unstandardized	Standardized	
Wing length	-0.58	-1.264	47.19**
Breast colour chroma	-0.26	-1.056	8.52**
Breast colour amount	0.38	2.611	16.34**
Y-intercept		124.647	
	Mean square	df	<u>F</u>
Regression	433.31	3	45.30
Residual	9.56	22	

* Multiple R=0.93; R-square=0.86; adjusted R-square=0.84; standard error=3.09

** , P < 0.01

Fig. 1. Dominance matrix of total interactions, both attacks and avoidances, among 26 Harris' sparrows identified by letters A-Z over a three-day period (R=reversals).

Fig. 2. Recorded patterns of breast pigmentation for 26 Harris' sparrows demonstrating the high degree of individual variability with respect to this character.

Fig. 3. Phenograms portraying relationships among 26 Harris' sparrows based on physical characteristics; (A) UPGMA clustering of pair-wise correlations, and (B) UPGMA clustering of distance measures.

Fig. 4. Ordination of 26 Harris' sparrows (indicated by letters A-Z and II) along principal component I based on dominance rank and morphological and plumage characteristics. The axis is highly correlated with dominance, size and blackness measures (see Table IV). To the bottom are light coloured, small, subordinate birds; to the top, dark, large dominants. Birds to the bottom are more similar to one another with respect to this axis than are birds to the top.

Fig. 1

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	
A		6	1	7	2	2	3	4	3	3		2	2	7	4	1	1	1	1		3	9	3	5		2	
B			2	3	2	1	3	3	1			4	5	2	2	1		3	2	2	1	2		3	3		
C				5		4	2	5	2	3	1	4	5	3	1	2	5	7	3	7	1	7	3	4	6	5	
D					3	7	6	8		3	1	7	10	1	7	2	8	6	3	7	1	7	3	6		3	
E						9	3	7	4	2		4	4			1	7	4	3			5	4	5	3		
F							7	1 ^R	18	6		7	4	15	8		12	10	4	5	1	15	7	5	12		
G								5	2	3		2	4	3	7	2	7	3	1	11		7	6	1	6	2	
H						3	1 ^R			3	1	10	9	10	3	1	12	3	2	7	2	10	2	10	15	2	
I				4						4	1	10	4	8	10		6	3	3	9	1	13	2	13	7	4	
J											2	3	1	10	2		1	1	3	5		4	3	2	2	1	
K												1	1									1			1		
L													7	4	6		1 ^R	2	3	5		2	5	6	2		
M											1			7	8	6	2 ^R		3	5			3	7	11	7	
N												1 ^R		5	4	5	8	3	7		2	6	1	5	1		
O												1 ^R			1	7	7		8		12	8	3	11	1		
P										2							2		1	3		3	1		3		
Q											2	3						7	2	12		5	7	5	8	2	
R										1			5						1	1	1	2	2	2	4	3	
S															3							4		2	1		
T														1 ^R													
U						1					1	1										3	2	2	5	16	3
V													12		1 ^R									2	14	9	3
W										1						1								1	7	1	
X																				1 ^R					7	2	
Y																					1					1	
Z																											

Fig. 2

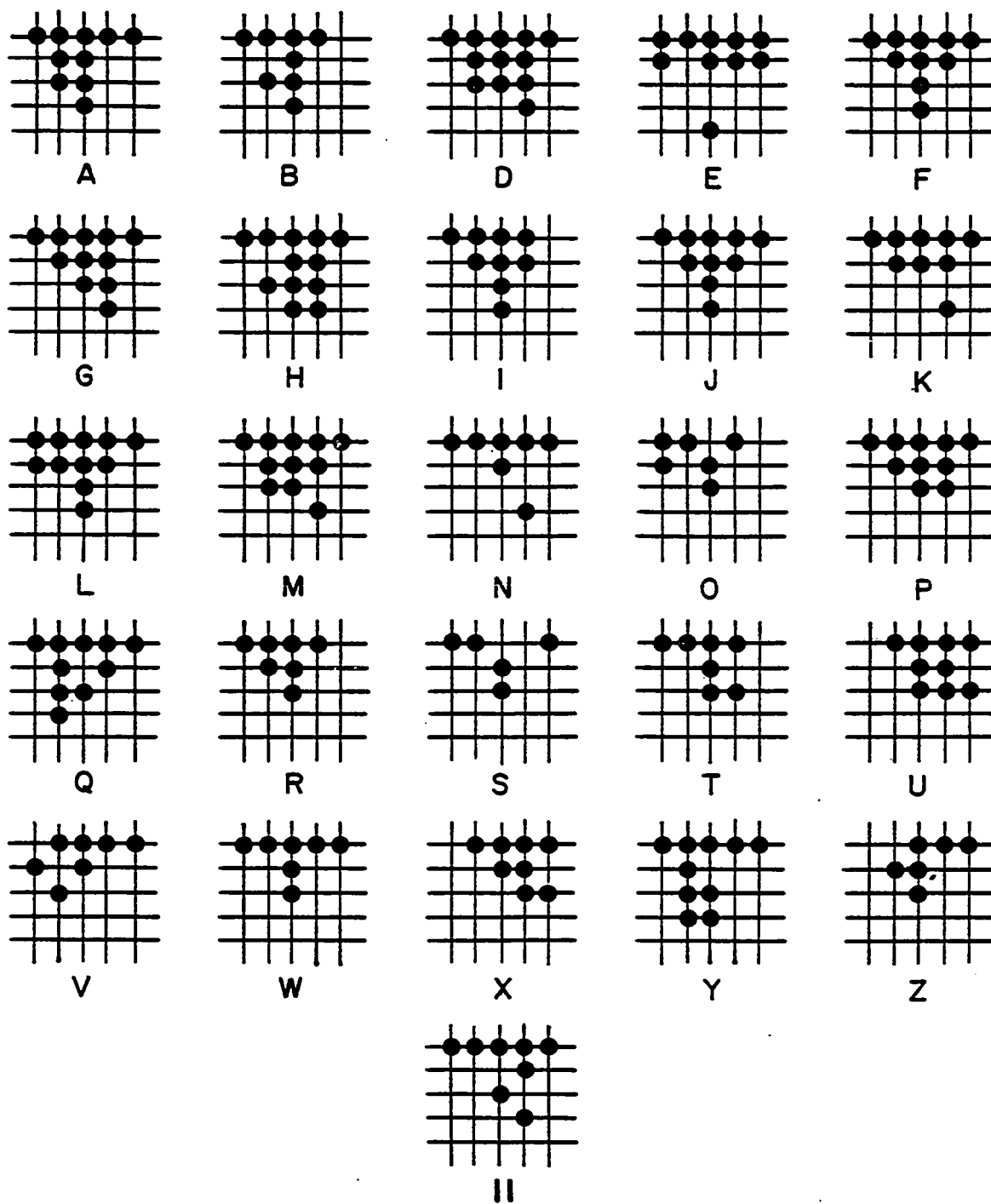


Fig. 3

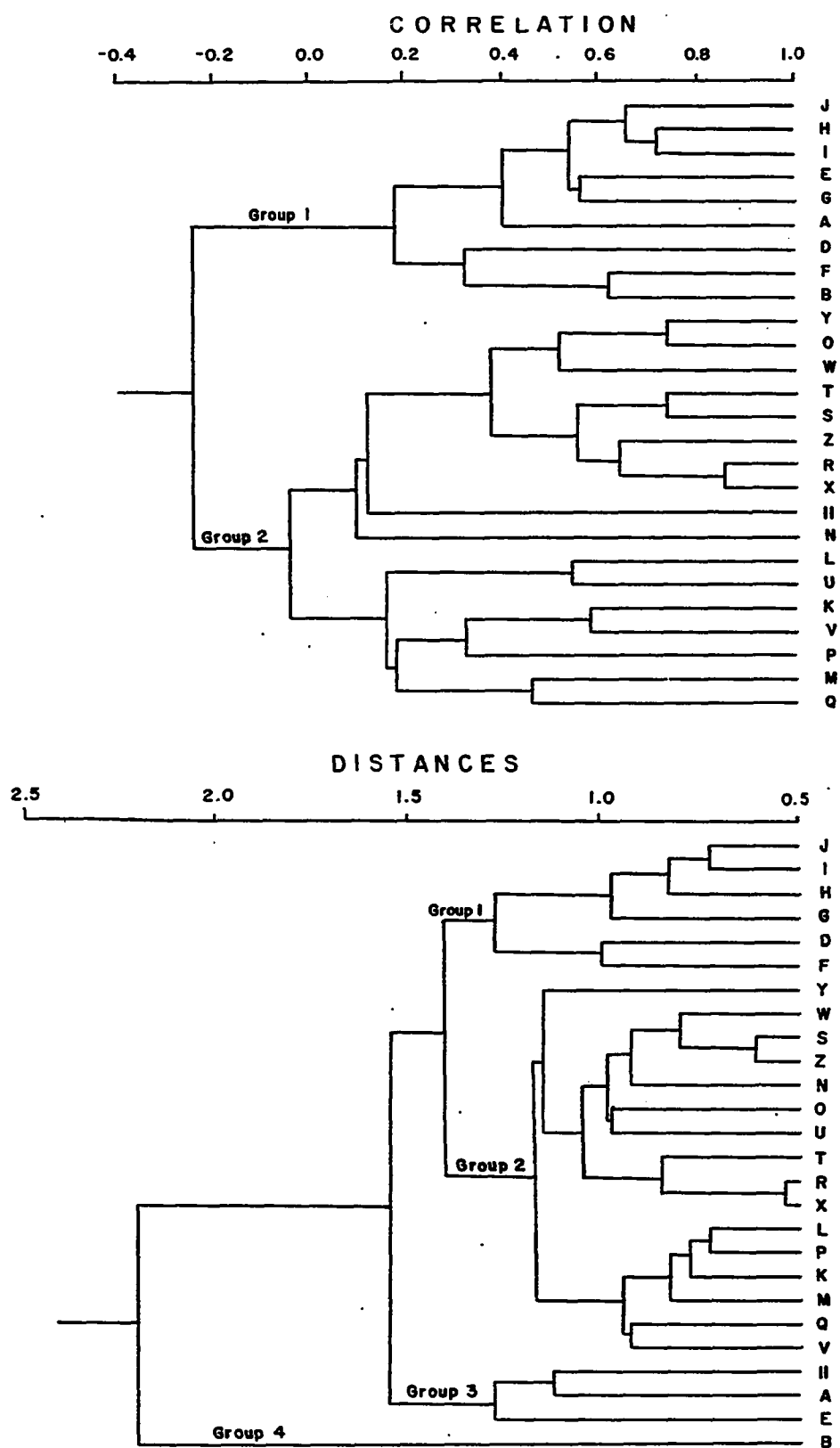
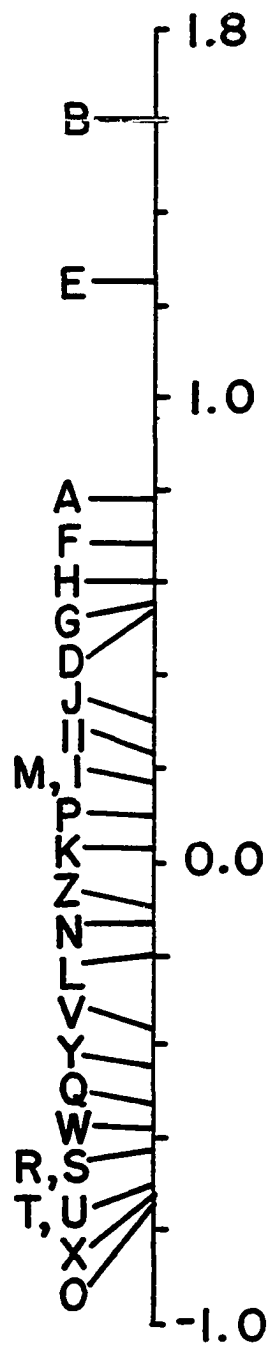


Fig. 4



Appendix. Dominance matrices for five groups of Harris' sparrows observed in the fall season. Values in the matrices are frequencies of behavioural dominance encounters between individuals (A-J refers to the dominance rank of the birds in each group). The winning bird in each encounter is listed from top to bottom; the loser, from left to right. Reversals (R) occurred when a typically subordinate bird supplanted a dominant bird. Each group contained different proportions of adults and immatures, as given at the top of each matrix.

6 ADULTS, 4 IMM.

	A	B	C	D	E	F	G	H	I	J
A		14	10	11		5	7	12	14	22
B			8	7		8	22	10	13	14
C				12	4	6	18	24	26	24
D					2	8	16	17	7	15
E	7					2	6	1	3	9
F			1 ^R				7	4	6	7
G								13	15	18
H									17	16
I										23
J										

4 ADULTS, 6 IMM.

	A	B	C	D	E	F	G	H	I	J
A		8	19	1	23	4	6	4	2	7
B			39	4	13	13	11	1	4	10
C				1	25	37	5	8	1	14
D					16	12	10	3	1	9
E						16	10	7	2	23
F							17	4	1	19
G								1	3	10
H									1	12
I										
J										

9 ADULTS, 1 IMM.

	A	B	C	D	E	F	G	H	I	J
A		10	18	19	12	17	19	12	3	9
B			18	29	18	10	14	3	11	5
C				36	12	20	34	18	13	22
D					20	19	14	7		7
E						8	19	3	1	6
F							1 ^R	9	6	2
G								1 ^R	10	3
H									1 ^R	12
I										8
J										

9 IMM., 1 ADULT

	A	B	C	D	E	F	G	H	I	J
A		9	5	15	2	5	44	31	16	4
B			11	7	6	1	21	4	19	13
C				7		5	32	7	23	11
D					2	5	26	10	6	
E						7	1 ^R	2	10	5
F								23	1	1
G									20	31
H										3
I										25
J										

10 IMMATURES

	A	B	C	D	E	F	G	H	I	J
A		21	12		21	4	22	2	33	4
B			15	10	11	5	20	6	36	13
C				17	11	13	28	4	18	2
D	7	2 ^R			13	9	5	1	7	
E				2 ^R		15	18	2	28	9
F	3 ^R	1 ^R					2	4	8	3
G					2 ^R			8	27	3
H			1 ^R			1 ^R			8	3
I										20
J									1 ^R	

PLUMAGE BRIGHTNESS INDEX FOR WHITE-THROATED SPARROWS

Running head: Sparrow Brightness Index

By Doris J. Watt

Lowther (1961) first described plumage dimorphism, involving white- versus tan-striped forms in the White-throated Sparrow (Zonotrichia albicollis). Using a graded series of museum specimens, all in breeding plumage, he also found that, regardless of sex, white-striped morphs had more black in the lateral crown stripe, less streaking on a wider and grayer chest band, less intense black on the malar markings, and brighter yellow on the superciliary stripe.

However, using live birds and a graded series of specimens, Vardy (1971) concluded that variation in crown color was not bimodal for any given age or sex class of the White-throated Sparrow. She employed two characters, median and lateral coronal stripes, establishing eight categories for the lateral crown stripe and six for the median crown stripe. Her results suggested a greater diversity in plumage types than that described by Lowther (1961).

Thornycroft (1966, 1975) found that an individual's plumage was correlated with its karyotype--all birds in bright alternate plumage (with a white median crown stripe) possessed a single 2m chromosome, those lacking this autosome were dull (tan-striped). White-striped and tan-striped birds are pictured in his 1975 paper and he detailed the following facts concerning the plumage polymorphism in the White-throated Sparrow: (1) all birds with the 2m chromosome were

white-striped in alternate plumage; (2) all males with the 2m chromosome were also white-striped in basic plumage; (3) some females with the 2m chromosome were tan in the basic plumage; (4) all birds without the 2m chromosome were tan in both alternate and basic plumages; and (5) young (of the year) of either type could be tan-striped in their first basic plumage.

Atkinson and Ralph (1980) used quantitative measures of plumage characteristics to examine 105 captive White-throated Sparrows in fall and spring plumage. Some of their characters were color measures involving use of the Munsell system of color notation (for description of the application of this system to bird plumage coloration see Wood and Wood 1972). This method removed much of the subjective interpretation of plumage variability that occurs when using a graded series of specimens (e.g., Lowther 1961, Vardy 1971). Atkinson and Ralph also computed a composite index by summing plumage variables. However, their index is complex, and requires fairly extensive character coding and computations.

The purpose of this paper is to introduce a simple index that provides sufficient detail to be useful in plumage studies by banders and others. Use of this index will facilitate accumulation of data on the distribution and abundance of White-throated Sparrow morphs, as well as provide important data for examining aspects of the species' biology. Several examples of applications are given resulting in new information regarding the color morphs of the White-throated Sparrow.

METHODS

Ninety-nine White-throated Sparrows were netted in Fayetteville, Washington County, Arkansas from 26 November 1978 to 11 March 1979. Plumage scores (as described below) were obtained at capture. These birds were moved to the Animal Behavior Laboratory of the University of Oklahoma, Norman, Oklahoma. Fifty-four of the birds were maintained in captivity until after alternate molt, and on 23 April plumages were scored again. Nineteen of these birds were held through the following basic molt and measured again for plumage values in November 1979. Finally, 12 birds were kept until the following May when they were again scored for alternate plumage values.

All birds were housed in indoor aviaries (approximately 2m on a side) and fed ground dog food, mixed seeds and occasionally lettuce. Colored leg bands were used to identify individuals. Artificial, timed lighting was used to control daylength approximating natural lights (e.g., 8 h light:16 h dark in winter, 12 h light:12 h dark in summer). Birds were sexed according to wing length (Atkinson and Ralph 1980) where: < 69 mm = female; > 71 mm = male; and 69-71 were classified as unknown sex.

PLUMAGE MEASUREMENT

Four plumage characteristics on the heads of the birds were assessed (Fig. 1a) including the median crown strip, lateral crown stripe, throat pattern, and yellow in the superciliary stripe. Values for each character, used to compute a "brightness index," were determined as follows.

Median crown stripe (MCS) values were determined by estimating the

percentage of the stripe that contained white feathers. The bird was held so that I looked directly down on the top of its head. A ruler was placed across the top of the head at the posterior edge of the eyes and perpendicular to the crown stripes (Fig. 1b). Then the percentage of the median crown stripe containing white was estimated from the area between the edge of the ruler and the base of the bill. Similarly, lateral crown stripe (LCS) values were estimates of the percentage of black in the area between the ruler and the base of the bill in the lateral stripe regions (Fig. 1).

Throat patterns (TP) were classified similarly to Lowther's (1961: Fig. 1) method in which five possible throat patterns were represented: plain, dotted, single bar, forked bar, and double bar. Most birds matched one of Lowther's categories (Fig. 2, top row); however, when a specimen had a different pattern combination (Fig. 2, bottom row; e.g., one single bar and one forked bar), the bird was given the throat pattern classification most different from the median value. Intermediate conditions were not common (12 of 99 in fall; 5 of 54 in spring). All conditions that I recorded are given in Fig. 2.

The condition of the yellow in the superciliary stripe (SSY) was scored as very bright, bright, medium, dull, or very dull. I first determined these categories on a set of specimens (OU numbers 4792, 1501, 4531, 6294, and 2892) in the collection of the Stovall Museum, University of Oklahoma. Additionally, quantitative values were determined by using the Munsell system and can be compared to the qualitative categories used in this paper (Table 1). These SSY measures are the extremes found in the museum collection and probably

represent the maximum variation found in wild individuals. Single pages (5Y page) of the Munsell Soil Color books can be ordered from the Macbeth Co., Munsell Color, 2441 North Calvert St., Baltimore, MD 21218. However, the quality of yellow can be estimated without use of the chart. Persons unfamiliar with the species might wish to survey the variation in yellow coloration from a collection of specimens.

After these four measures were recorded for each bird, I assigned a "rank value", from 1 to 5, for each measure (Table 2). For example, a bird might have rank values of: MCS=1, LCS=1, TP=2, and SSY=2. I next calculated a plumage brightness index (BI) as the mean rank for the four characters:

$$\underline{BI} = (\underline{MCS} \text{ value} + \underline{LCS} \text{ value} + \underline{TP} \text{ value} + \underline{SSY} \text{ value}) / 4$$

The index value for the example bird above would be 1.5 (computed from $[1 + 1 + 2 + 2] / 4$). The duller possible bird would have an index value of 5.0 ($[5 + 5 + 5 + 5] / 4$); the brightest, 1.0 ($[1 + 1 + 1 + 1] / 4$).

This index can be easily calculated and measured without any specialized equipment. Two colleagues (D. Scott Wood and Joe Grzybowski) and myself independently obtained nearly identical BI values for the same set of birds, indicating a high degree of reproducibility. It is also a sensitive measure of variability in plumage in the White-throated Sparrow as the examples in the next section demonstrate.

RESULTS AND DISCUSSION

As suggested by Thorneycroft (1975) and documented by Atkinson and

Ralph (1980), fall distribution of plumage is described by a normal curve, while spring distribution is bimodal. These distributions found by Atkinson and Ralph in Pennsylvania also applied to my birds captured in northwestern Arkansas (Fig. 3). Spring birds are more easily separated into bright and dull types, whereas fall birds are more variable and overlapping in plumage characteristics. My index was sensitive enough to reveal these patterns (Fig. 3).

Thornycroft (1966, 1975) and Lowther (1961) reported that examination of the median crown stripe color was sufficient to determine the color morph of White-throated Sparrows in alternate plumage. Fig. 4 shows the MCS measurements I obtained for birds in spring and fall. In alternate plumage, 44% (24/54) of the birds had no white in the median crown stripe, and only 2 of the remaining birds had less than 50% white in the stripe. Thus, there is clearly a bimodal distribution of plumage types based on this one character in the spring, in agreement with Lowther (1961), Thornycroft (1975) and Atkinson and Ralph (1980), but contrary to Vardy (1971). In the fall, birds were more evenly distributed with respect to MCS (Fig. 4). Thornycroft (1975) pointed out that the large number of immature birds (often tan morphs), in fall samples skewed distributions to the tan side, as seen in my fall example (Fig. 4). However, the extreme bimodality of this character (MCS) is not apparent in the distribution of composite BI scores (Fig. 3) due to the effects of other plumage characteristics.

Information available for 19 birds followed through 2 to 3 molts and having 3 to 4 measurements of plumage index values (Table 3)

provided information on color morph stability of individuals across seasons. Of 8 male birds, 2 (Nos. 12 and 14) showed a large increase in index value (darkened) from spring to winter (contra Thorneycroft 1975). Five of the males (Nos. 15-19) stayed bright or dull across seasons and 1 (No. 13) was dark the first winter and bright thereafter. Females, on the other hand, often exhibited reversals of bright plumage in spring to dull plumage in the fall (Nos. 1, 2, 4, and 6). Two females (Nos. 3 and 5) remained dull in all seasons and 1 (No. 9) stayed bright after being dull the first winter. Thorneycroft (1975) documented that immatures in their first winter could be dull and then became brighter in later plumages, which may explain the 2 individuals in my sample (Nos. 9 and 13) that became brighter with time.

Ficken et al. (1978) found that white-morph birds on spring migration were more often aggressors than tan-morph birds. Watt et al. (in press) have shown that birds in fall flocks demonstrated the opposite relationship with respect to females: tans were dominant to whites. Clearly, there are demonstrable differences in aggressive levels for the two morphs, especially when sex and age are known. Further investigations into these behavioral differences are needed, and the brightness index introduced here could be used to quantify plumage differences.

Ketterson and Nolan (1976) have shown that adult sex ratios of Dark-eyed Juncos (Junco hyemalis) differ from north to south in their wintering range. This question, as yet unstudied in White-throated Sparrows, would benefit from banding information where wing length, age and brightness index were recorded. That is, do White-throated

Sparrows of different sex or morph tend to winter at different latitudes? If sexual differences in wintering latitude exist in the White-throated Sparrow, it should be reflected by geographic differences in brightness index frequencies. Such data should be evaluated in light of Thorneycroft's (1975) finding that the frequencies of morphs within each sex are different (more tan females and more white males).

ACKNOWLEDGMENTS

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Table 1.

Values of Munsell system color variables that correspond to the categories of yellow brightness in the superciliary stripe (SSY; see text for explanation).

Category (<u>SSY</u>)	Color variables		
	Chroma	Value	Hue
Very bright	8	8	5
Bright	6	7	5
Medium	8	7	5
Dull	8	6	5
Very dull	6	5	5

Table 2.

Rank values (1-5) assigned to four head plumage variables of White-throated Sparrows reflecting five categories of each.

Median crown stripe	Lateral crown stripe	Throat pattern	Superciliary stripe	Rank value
81-100%	91-100%	Plain	Very bright	1
61-80%	81-90%	Dotted	Bright	2
41-60%	71-80%	Single bar	Medium	3
21-40%	61-70%	Forked bar	Dull	4
0-20%	0-60%	Double bar	Very dull	5

Table 3.

Wing length, sex, and brightness index (BI) values recorded for 19 birds in four seasons. BI for each bird was measured twice in alternate plumage (spring 1979 and 1980) and twice in basic plumage (winter 1979 and 1980, except for 7 birds that died before spring 1980).

Bird No.	Wing length (mm)	Sex ¹	Brightness Index (BI)			
			Winter 79	Spring 79	Winter 80	Spring 80
1	66	F	2.75	2.00	3.75	—
2	67	F	3.00	1.25	2.75	1.25
3	67	F	4.25	4.50	5.00	4.50
4	67	F	3.50	1.75	3.50	1.25
5	68	F	5.00	5.00	4.75	—
6	68	F	4.25	2.25	3.50	1.25
7	69	U	3.50	1.25	3.75	—
8	70	U	bright ²	2.25	3.00	1.50
9	70	F	dull ²	1.25	1.00	1.00
10	70	U	2.00	1.25	2.75	—
11	70	U	2.00	1.75	1.50	1.50
12	72	M	dull ²	2.00	3.25	—
13	72	M	3.50	1.25	2.25	—
14	72	M	3.25	2.00	4.00	3.75
15	72	M	1.50	1.00	1.00	1.00
16	73	M	2.25	1.00	1.00	1.00
17	74	M	1.75	1.50	1.75	—
18	74	M	3.75	4.00	3.75	3.50
19	75	M	4.00	4.50	4.50	5.00

¹Sex was determined from wing lengths where < 69 mm = F (female), > 71 mm = M (male), 69-71 mm = U (unknown) except for bird no. 9, where gonads were examined.

²Qualitative assessments of plumage for three birds were recorded where quantitative measurements were not made and are designated as "bright" and "dull".

Figure 1. Left: head of a White-throated Sparrow showing the 4 characteristics measured. Right: the dotted line indicates the caudal limit of area of estimation for percent black in the lateral head stripes or the percent white in the median crown stripe.

Figure 2. Throat patterns recorded in White-throated Sparrows; patterns and names (above) from Lowther (1961), and intermediate conditions I recorded (below). Rank values (1-5) assigned to both types of patterns are given at the bottom of the figure.

Figure 3. Number of birds occurring in the 17 categories of the brightness index in spring (above) and fall (below).

Figure 4. Number of birds with differing frequencies of white feathers in the median crown stripe in spring (above) and fall (below).

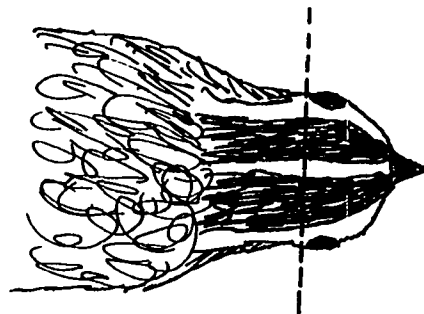
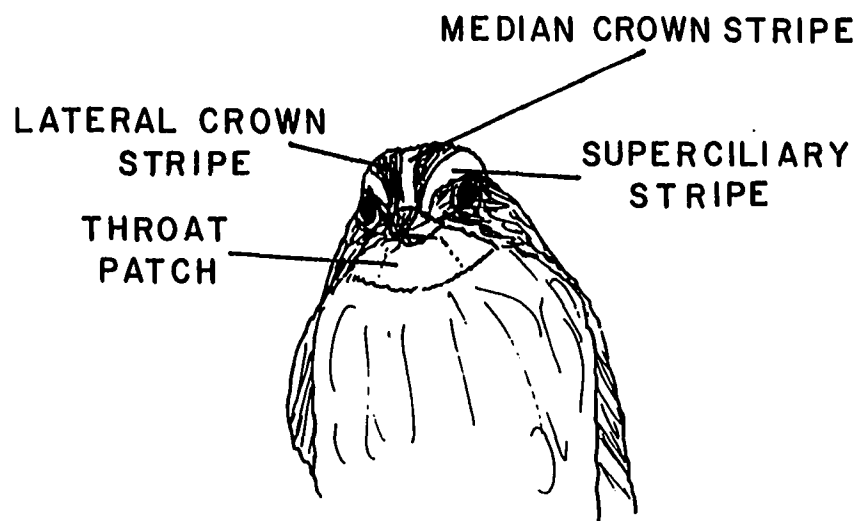


Fig. 1

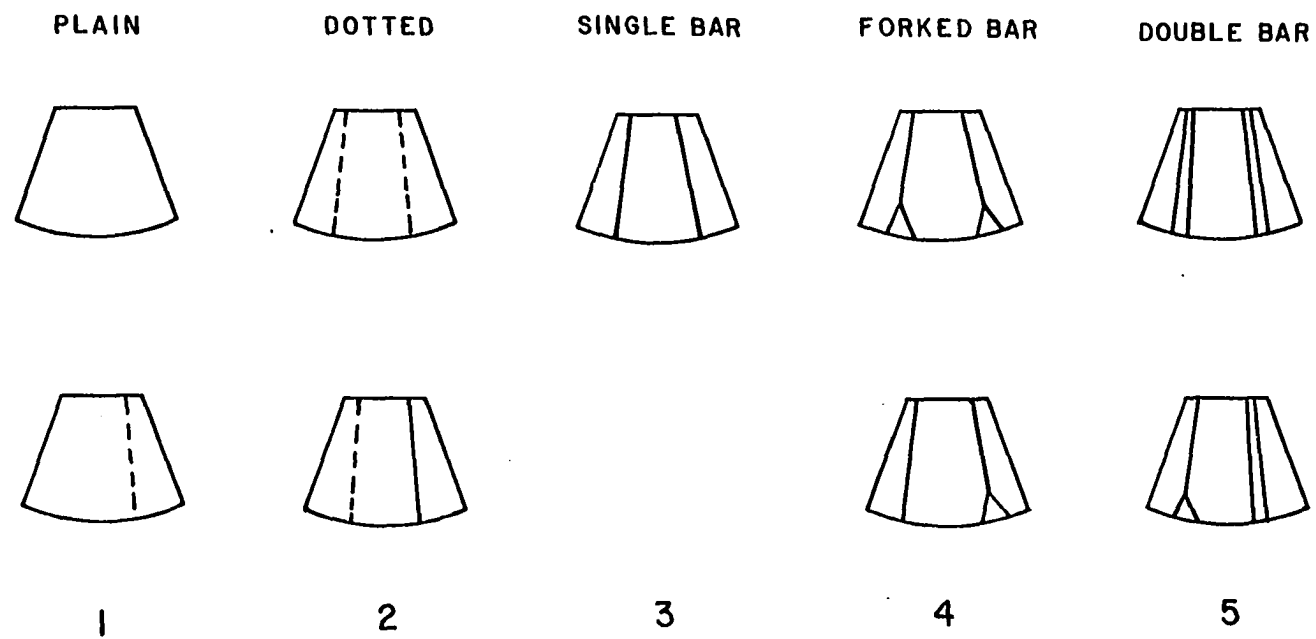


Fig. 2

Fig. 3

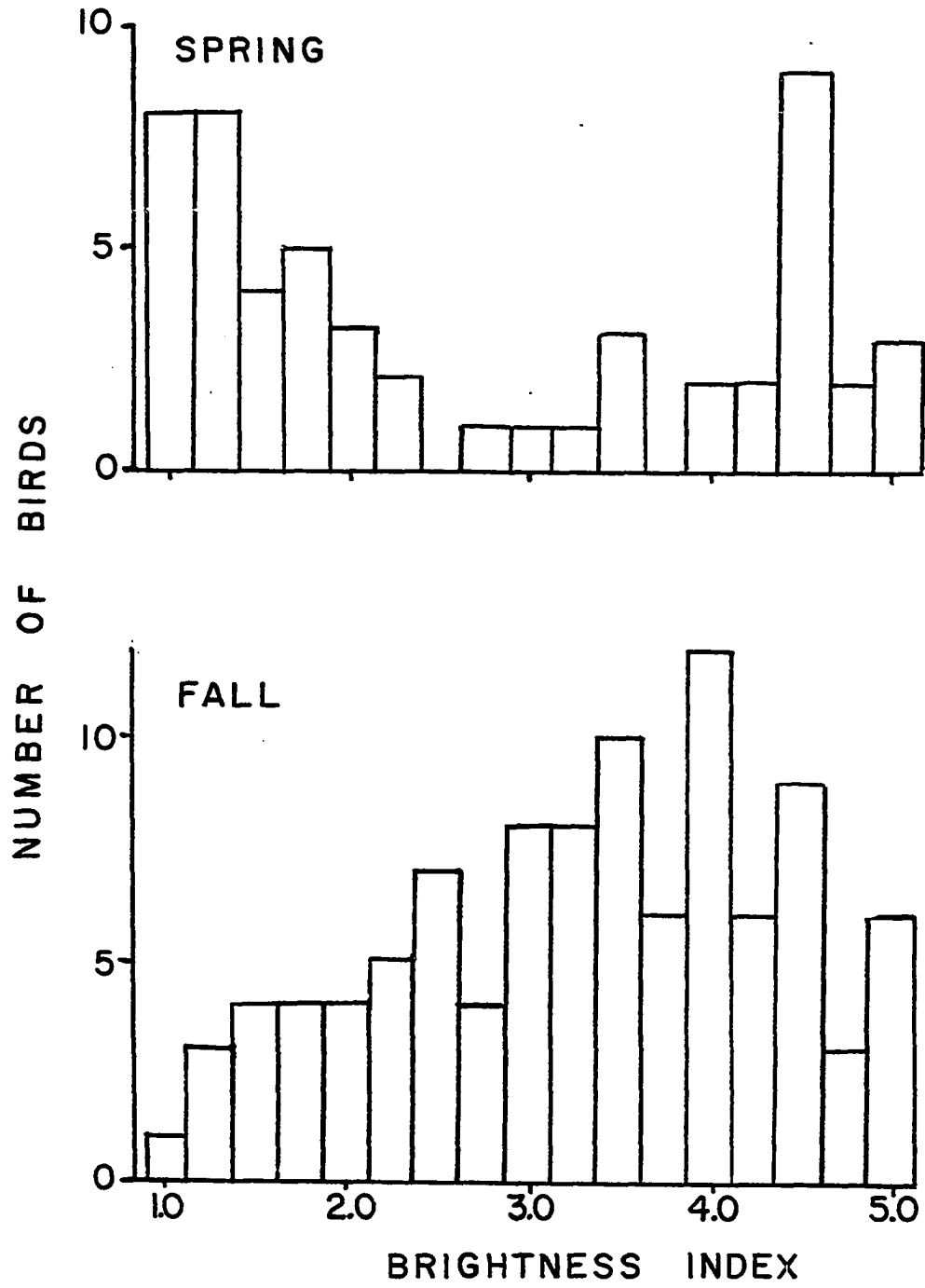
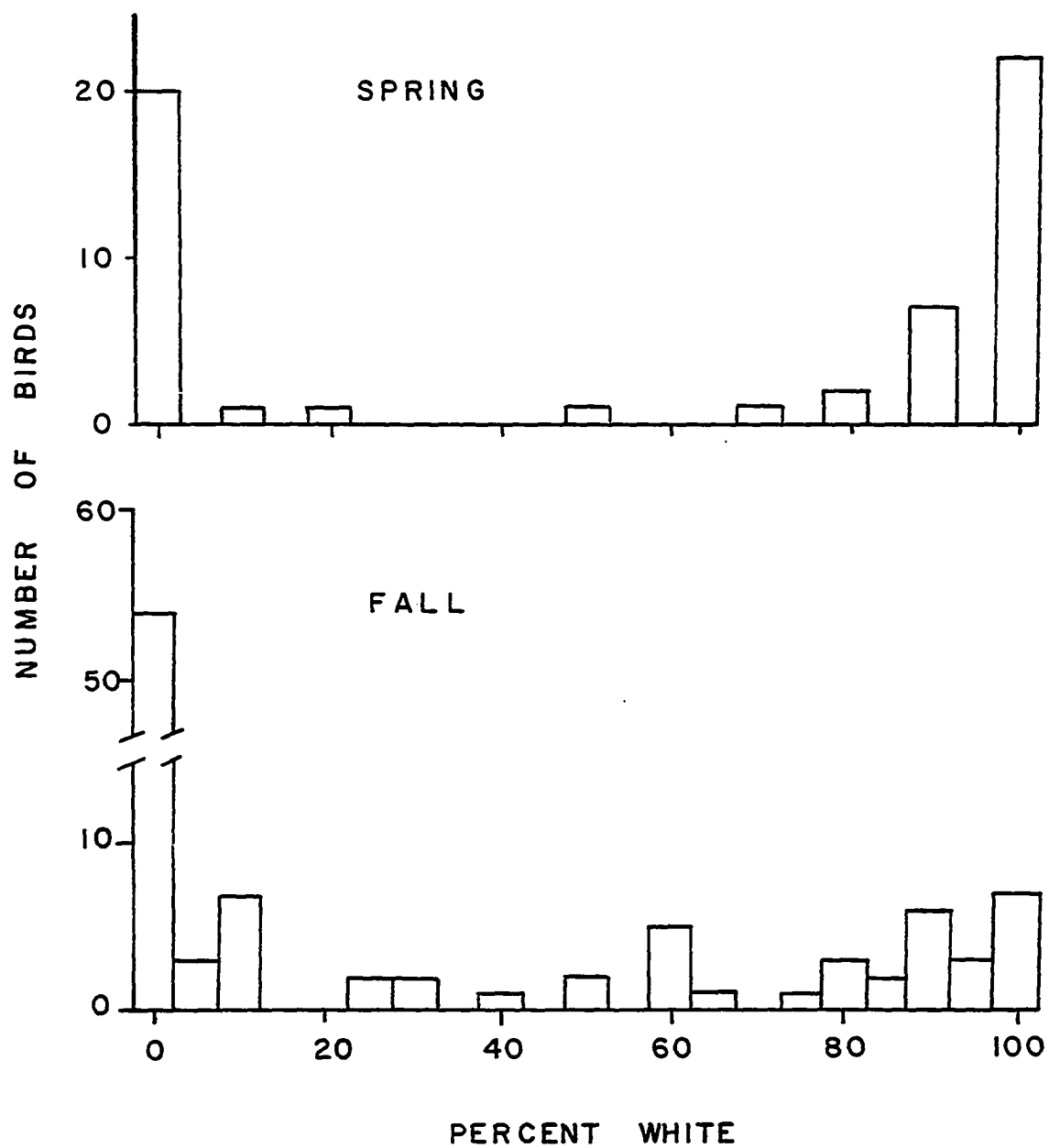


Fig. 4



EFFECTS OF SEX, SIZE AND RESIDENCY STATUS ON
DOMINANCE AND SURVIVAL IN WHITE-THROATED SPARROWS

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Running head: White-throated Sparrow Survival

INTRODUCTION

Several studies have proposed that dominant birds in winter foraging flocks have a higher probability of surviving than subordinates (Fretwell 1969, Murton et al. 1971, Kikkawa 1980a). For many species of birds in such flocks, males dominate females (e.g., European Starlings, Sturnus vulgaris, Van der Mueren 1977; Jackdaws, Corvus monedula, Tamm 1977; and Dark-eyed Juncos, Junco hyemalis, Baker and Fox 1978, Ketterson 1979), suggesting that females of such species are at a competitive disadvantage compared to males, due to their relatively subordinate status. For example, social subordination has been proposed to explain differential migration distances of the sexes for Dark-eyed Juncos (Ketterson and Nolan 1976, Ketterson 1979) and for many species in general (Gauthreaux 1978), with females migrating farther distances.

In this study I investigated relationships between weight loss during periods of food limitation and sex, body size, and dominance rank of White-throated Sparrows (Zonotrichia albicollis). Male White-throated Sparrows are larger than females (Atkinson and Ralph 1980, Rising and Shields 1980) and are generally dominant to females (Watt et al. in press). If females are at a competitive disadvantage in winter foraging flocks, female White-throated Sparrows should lose more weight during competition in captivity than males, assuming that captive situations are similar to the wild. Thus, the primary prediction tested in this study was that female White-throated Sparrows would lose more weight than males during periods of limited food availability.

The second objective of my study was to assess the relative importance of sex and residency in determining dominance ranks of male and female birds. Although males generally dominate females, Ken Yasukawa (pers. comm.) has suggested that juncos in unfamiliar aviaries are less likely to become dominant in a new hierarchy than are birds that are in familiar surroundings. Therefore, differences in residency status (home versus away) might influence relative dominance rank determination between males and females. I tested this hypothesis for White-throated Sparrows; specifically, by manipulating the birds' residency statuses, I sought to produce a group in which females dominated males. If such arbitrary asymmetries (Maynard Smith and Parker 1976, Parker 1974) could be simulated in captivity under conditions where manipulations are relatively easy, it would suggest that in the wild, resident female birds might dominate immigrant males. If so, the impact of the generality that males dominate females might be lessened, and the persistence of females in winter flocks could be explained.

And finally, because Watt et al. (in press) found that differences in dominance ranks of White-throated Sparrows were associated with color type, sex and age of birds, plumage characteristics were also noted in the present study. Findings regarding the relationship between plumage and dominance, especially for males, provide further information on differences between tan and white morphs of the White-throated Sparrow.

METHODS

Birds were captured from November 1978 to February 1979 in Fayetteville, Washington County, Arkansas and transported to the Animal Behavior Laboratory, University of Oklahoma, Norman. Each bird was banded with colored vinyl leg bands. Unflattened wing chord, weight, eye color and plumage characteristics were recorded upon arrival in Norman. Eye color was used to discriminate adult or immature status (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1977). Plumage measurements were also taken after the prenuptial molt in June 1979 to more reliably assess each bird's color morph (Thornycroft 1975). Four plumage characteristics measured in fall and spring included (1) percent black in lateral crown stripes, (2) percent white in median crown stripe, (3) throat pattern, and (4) brightness of yellow in superciliary stripes. These characteristics were used to compute a brightness index (Watt 1983) for each bird. Index values (BI) ranged from 1.0 (very bright) to 5.0 (very dull).

All birds were housed in indoor aviaries (approximately 2 m on a side), fed ground dog food and mixed seeds supplemented with lettuce, and kept under controlled artificial lights simulating natural daylength. Temperatures were maintained above freezing but they rose and dropped with outside weather changes.

During behavioral observations, I removed all food except 1 finger bowl of ground dog food and another of water. These were placed on a feeding shelf near a one-way window through which I observed identities of birds involved in dominance encounters on the shelf. Winners were those birds that chased, supplanted or were avoided by other birds

(losers). Dominance matrices containing frequencies of these interactions (constructed following Brown 1975, p. 86) were used to assess the relative dominance ranks of individual birds in all of my study groups.

In the first series of experiments (relationship of weight loss to sex, dominance rank and body size), 2 groups of birds were used. The first group, composed of 11 birds captured in November 1978, was introduced into an aviary on 26 November, and behavioral observations were made on 27 November, and 1 and 4 December of the same year. The second group, 17 birds captured in December 1978, was introduced into another aviary 4 January 1979 and observed on 10 and 11 January. On 10 January I removed all food from the 2 aviaries except 100 g of ground dog food in 1 small dish per cage to elicit competition among individuals. Birds in the first group were weighed on 10 January before removal of food (pre-competition weights). Weights of the second group were recorded on 11 January and should reflect intragroup competition because these birds had 24 h of limited food before being weighed. Each group was weighed only once to minimize the effects stress during capture and weighing might have on body weights. All weights were recorded in the morning at the end of the lights-off period to minimize variation common during a feeding day (Kontogiannis 1967; also, see Clark 1979 for review of body weight in birds). A cold front passed through Norman on the evening of 12 January and, by the morning of 13 January, 21 of the 28 birds in the two groups had died. These were weighed immediately and are analyzed here for information on the relationship of dominance and body size on survival in

White-throated Sparrows. Presumably, birds that died starved due to lack of food, hastened by cold stress.

In the second series of experiments (relative importance of sex, color, and residency effects), birds were captured in January, 1979 and on 5 February were divided into 2 groups based on differences in wing length. Birds with wing lengths of 72 mm or greater were assumed to be males; those with 68 mm or less were assumed to be females (Atkinson and Ralph 1980). Four birds had intermediate wing lengths; 1 bird with a wing length of 71 mm was classified as male, and three 70-mm and two 69-mm birds were classified as female. Autopsies later confirmed that one 69-mm bird and the 70-mm bird were female, but the sex of the other 4 birds could not be determined. The group assumed to be males was composed of 18 birds, while 14 birds made up the female group. Each group was then introduced into an aviary where behavioral observations were made for determination of the birds' relative dominance ranks. The male group was observed on 8, 10, 11 and 12 February; females, on 17, 18 and 19 February.

On 24 February I switched birds in the aviaries so that 2 new groups were formed. One group contained the 10 most dominant males and 7 females and was returned to the males' home aviary. The other group contained the 6 least dominant males, 5 females, plus 2 females and 2 males from another aviary (to increase the sample size). This combination of birds was returned to the home aviary of the 5 females. Dominance behaviors of these recombined groups were recorded on 3 and 8 March for the first group and on 10 March for the second group, after allowing time for dominance relationships to become well established.

Statistical tests were used to evaluate product-moment correlations and regressions by methods in Sokal and Rohlf (1981).

RESULTS

Weight loss.--Dominance matrices used to determine dominance ranks of birds within each of the 2 groups are given in the Appendix.

"Pre-competition" weights for the 11 birds in Group 1 and "competition" weights for the 17 birds in Group 2 are given in Fig. 1, plotted against the birds' wing lengths. There is positive relationship between weight and wing length for both groups considered together ($r=0.71$, $P<0.01$). Group 2 (competition weights) displayed less variability in weight for a given wing length than Group 1 (Fig. 1).

The correlation between death weight and wing length ($r=0.90$, $P<0.01$, Fig. 2) is even stronger than that between pre-death weight and wing length. Birds of smaller size (shorter wing lengths) died at lower body weights than did larger birds. Regression analysis of death weight on wing length produced the equation, $Y = -14.84 + 0.47X$.

Survivors (points with stars in Fig. 1 represent birds that survived) were characterized by heavier body weights for their wing length during the competitive period (stars are more frequent towards the top of Fig. 1). However, dominance ranks of individual birds within their group (given in Fig. 1 next to each point) could not be used to predict a bird's weight at a given wing length or its survival. Similarly, weight and wing length per se did not predict survivorship. Females (birds with wing lengths less than 68 mm), as well as males, were among the survivors and they were equally likely to survive (3

females and 3 males survived, Fig. 1).

Sex, morph and residency.--In the second series of studies, dominance matrices for males (Fig. 3A) and females (Fig. 3B) were relatively linear with few reversals. Adult males of both dull and bright coloration were dominant to immatures, and brightly plumaged immature males were dominant to dull immatures with 1 exception (Table 1). Adult males that were bright in at least 1 of 2 seasonal plumages dominated the three dull plumaged adults. However, 1 of the top 3 dominant birds was marginally bright ($\underline{BI}=3.00$) in winter and dull ($\underline{BI}=3.75$) in spring plumage (Table 1). These three most dominant birds exhibited a triangular relationship in the dominance matrix (Fig. 3A), indicating the unstable nature of their dominance relationship to one another.

In the female group (Fig. 3B and Table 2), dull females usually dominated bright females as previously documented by Watt et al. (in press). However, the most dominant bird was bright ($\underline{BI}=1.75$) in spring plumage (even though it was dull, $\underline{BI}=3.50$, in the fall), and the least dominant bird was dull in both spring ($\underline{BI}=4.50$) and fall ($\underline{BI}=5.00$) plumages. Contrary to other groups, immature birds had higher dominance ranks than the 2 adults in this group.

The effect of sex and residency in the recombined groups of birds can be seen in Figs. 4A and 4B. The mixed sex group in the males' home aviary developed a quite linear hierarchy, with males usually dominant to females (Fig. 4A). However, the mixed sex group in the females' home aviary exhibited a very non-linear matrix with numerous dominations of males by females (Fig. 4B).

DISCUSSION

Some subordinate female White-throated Sparrows survived severe competition and starvation in mixed sex groups in this study. My results indicate that assuming advantages for being dominant and male in winter foraging flocks require further investigation. While Baker and Fox (1978) found more low-ranking birds lost weight below a critical level (pre-determined average death weight) than high-ranking birds under conditions of food restriction, from my study it is clear that such a criterion biases results against the smaller birds (i.e., females). Baker and Fox's criteria did not allow for smaller birds dying at lower body weights; therefore, in their study, subordinates (females) reached the critical level first and were declared non-survivors. In contrast, the results of my study suggest that survival during periods of food restriction are not related to dominance, body size (wing length) or sex. Rambo (1981) has also found that subordinate Dark-eyed Juncos in a captive flock were under no particular disadvantage with respect to access to food, and Kikkawa (1980b) found no sexual differences in weight change during captive experiments with silvereyes (Zosterops lateralis).

Smith (1980) suggested that male-female dominance relationships in monogamous species change across seasons due to the relative advantages of being dominant. She proposed that in the breeding season there is no particular advantage to the female, to defer to a male and because of this, males often dominate females. I suggest that there also should be no advantage to the female to be dominant in the non-breeding

season; otherwise, there would be more dominant females in wintering flocks. Supposedly, females are capable of dominating males since they do so in the breeding season in many species (Smith 1980).

In species that exhibit different proportions of sexes in different wintering areas (Ketterson 1979, Ketterson and Nolan 1976), there are assumed disadvantages to females, and they have presumably responded by wintering in areas where less competition with males occurs. However, the geographic differences in wintering sex ratios could also be explained by relatively higher advantages to males of wintering closer to breeding territories, or possibly by energetic constraints on birds of smaller body size (females) farther north. At this point, it would appear that selection pressures of competition within flocks between males and females is relatively low; therefore, my finding no large differences in survival between the sexes should not be entirely unexpected.

Smith et al. (1980) found that adult Song Sparrow (Melospiza melodia) survival was not affected by supplemental feeding during the winter, but survival of young was higher than in 6 previous years. Young females were also found to start egg laying at a significantly later date in spring on areas not supplemented by food in the winter than those on supplemented areas. It is possible that first-year birds are at more of a disadvantage in winter foraging flocks than adults. Kikkawa (1980a) found that dominant silvereyes had significantly better chances of survival through the winter than subordinate birds; however, adult classes showed no dominance-dependent survival. Weights and dominance differed between adult and first-year birds and, within the

first-year class, young hatched early in the breeding season contained proportionally more dominants than did later-hatching birds. Even so, winter mortality within each year-group was not related to early winter body weights.

The relationship between body weight and wing length is apparently only close at near-death weights (Figs. 1 and 2). The increase in variability of body weights among birds not in limited food situations may provide a clue to predicting survivorship later: those birds that accumulate larger stores of body fat can survive through periods of lower food availability. In my study and others (e.g., Kikkawa 1980a, 1980b, Smith 1976), body weight and dominance were not highly correlated. However, several studies have found wing length to be predictive of dominance rank (Ketterson 1979, Searcy 1979, Watt 1983). Possibly, the variable nature of body weight decreases its predictive value in this regard. Apparently, a bird's potential body size, as indicated by its wing length, is a better predictor of dominance rank than weight.

The close relationship between death weight and wing length provides a useful criterion for removal of birds during competition before they actually starve (e.g., Baker and Fox 1978). For instance, birds might be removed from the group when their body weight drops to 2 to 3 grams above predicted death weight as based on their individual wing length. Also, the difference between a bird's current body weight during competition and its predicted death weight could be used to assess relative competitive abilities at weights well above critical levels.

The second set of studies also indicated that females might fare well in resident flocks when immigrant birds arrive, even if the new birds are males. The relationships among females that dominated males were apparently stable, since 3 weeks passed between their introduction together and the date of my behavioral observations. Balph (1979) found that foreign members of flocks of Dark-eyed Juncos were usually subordinate to and preferentially attacked by, residents.

Finally, the relationship between bright morph males and dull morphs appears to support the hypothesis that behavioral differences exist between the morphs of the White-throated Sparrow as suggested in Watt et al. (in press), Harrington 1973, and Ficken et al. 1977. In particular, bright-morph males dominated dull-morph males, for both adult and immature age classes, while dull-morph females more often dominated bright-morph females.

SUMMARY

Some subordinate female White-throated Sparrows survived competition and starvation in mixed sex groups in this study. In general, birds surviving starvation had heavier body weights for their wing length during competition for limited food. However, dominance rank, sex or body weight per se could not be used to predict survival. Females in their home aviary were capable of dominating introduced males. These results suggest that females in winter flocks may not be at a severe disadvantage due to their subordinate status compared to males.

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Table 1.

Characteristics of size, age, rank and plumage for 18 large (assumed to be male) White-throated Sparrows. Plumage brightness indices were calculated following Watt (1983), where spring plumages were bimodal with a value of 3.0 separating bright and dull types. Estimates of genetic morph type are given as determined from spring index values.

Dominance rank	Age	Wing length	Winter index	Spring index	Morph
1	Adult	66	3.00	3.75	Dull
2	Adult	72	3.25	2.00	Bright
3	Adult	74	2.50	1.75	Bright
4	Adult	76	3.25	3.75	Dull
5	Adult	72	4.00	5.00	Dull
6	Adult	74	3.75	4.00	Dull
7	Immature	77	1.00	1.25	Bright
8	Immature	72	1.50	1.25	Bright
9	Immature	74	1.75	1.50	Bright
10	Immature	73	2.25	1.00	Bright
11	Immature	74	2.50	1.00	Bright
12	Immature	71	2.00	1.50	Bright
13	Immature	75	4.00	4.50	Dull
14	Immature	77	4.50	3.25	Dull
15	Immature	72	4.25	5.00	Dull
16	Immature	72	3.50	1.25	Bright
17	Immature	74	3.75	--	--
18	Immature	73	3.50	--	--

Table 2.

Characteristics of size, age, rank and plumage for 14 small (assumed to be female) White-throated Sparrows. Plumage brightness indices were calculated following Watt (1983), where spring plumages were bimodal with a value of 3.0 separating bright and dull types. Estimates of genetic morph type are given as determined from spring index values.

Dominance rank	Age	Wing length	Winter index	Spring index	Morph
1	Immature	67	3.50	1.75	Bright
2	Immature	70	4.75	5.00	Dull
3	Immature	67	4.25	4.50	Dull
4	Immature	69	4.00	4.50	Dull
5	Immature	68	4.25	3.00	Dull
6	Immature	70	4.50	5.00	Dull
7	Immature	67	4.50	3.00	Dull
8	Immature	67	4.25	--	--
9	Immature	70	2.00	1.50	Bright
10	Immature	66	4.50	--	--
11	Immature	69	3.50	1.25	Bright
12	Immature	66	2.75	2.00	Bright
13	Adult	67	3.00	1.25	Bright
14	Adult	68	5.00	4.50	Dull

Fig. 1. Individual White-throated Sparrow weights plotted with respect to wing length at capture. Open circles represent birds in Group 1, established in November, weights taken 10 January; closed circles represent birds in Group 2, established 4 January, weights taken 11 January. Dominance rank of each bird within its group is given next to the circle. Stars designate those birds that survived the 12 January cold snap.

Fig. 2. Weights of White-throated Sparrows that died in Group 1 (open circles) and in Group 2 (closed circles) plotted against wing length at capture. Weights were measured near the time of death.

Fig. 3. Dominance matrices of White-throated Sparrows for (A) a group of males and (B) a group of females. Numbers in matrices are frequencies of dominance interactions in which the winner supplanted or chased the loser. Matrices were organized so that minimal numbers of interactions occurred below the diagonal (Brown 1975, R=reversals, T=ties). Dominance ranks of individuals (Tables 1 and 2) were assigned from the matrices.

Fig. 4. Dominance matrices for: (A) a group composed of 10 dominant males (M) from the hierarchy in Fig. 3A and 8 females (F) from the hierarchy in Fig. 3B, and (B) a group of 6 males from the hierarchy in Fig. 3A, 5 females from the hierarchy in Fig. 3B; and 4 birds from a third group (R=reversals, T=ties). In (A) the group was introduced into the males' home aviary; in (B) they were introduced into the

females' home aviary. Group (A) produced a linear hierarchy with males generally dominant to females, while group (B) produced a non-linear hierarchy with many females dominating males.

Scatter plot showing Weight (g) on the Y-axis versus Wing Length (mm) on the X-axis. The data points are numbered 1 through 17, with some points marked with an asterisk (*) indicating specific characteristics. The Y-axis ranges from 20 to 28 g, and the X-axis ranges from 65 to 77 mm.

Point	Wing Length (mm)	Weight (g)	Symbol
1	71.0	23.9	Filled Circle
2	71.0	25.2	Filled Circle
3	71.0	25.3	Open Circle
3*	73.8	27.0	Filled Circle
4	76.0	25.0	Open Circle
4*	73.8	27.2	Filled Circle
5	75.0	26.3	Filled Circle
6	73.8	26.0	Filled Circle
6*	68.0	26.2	Open Circle
7	73.8	24.9	Open Circle
7*	73.0	25.5	Filled Circle
8	70.0	22.3	Open Circle
8*	68.0	24.5	Open Circle
9	68.0	24.5	Open Circle
9*	68.0	22.6	Filled Circle
10	73.0	24.9	Filled Circle
10	70.0	25.2	Open Circle
11	67.0	22.5	Filled Circle
11	70.0	22.8	Open Circle
12	71.0	23.4	Filled Circle
13	66.0	20.3	Filled Circle
14	73.8	26.4	Filled Circle
15	69.0	22.5	Filled Circle
16	73.8	26.5	Open Circle
17	71.0	23.9	Filled Circle

Fig. 2

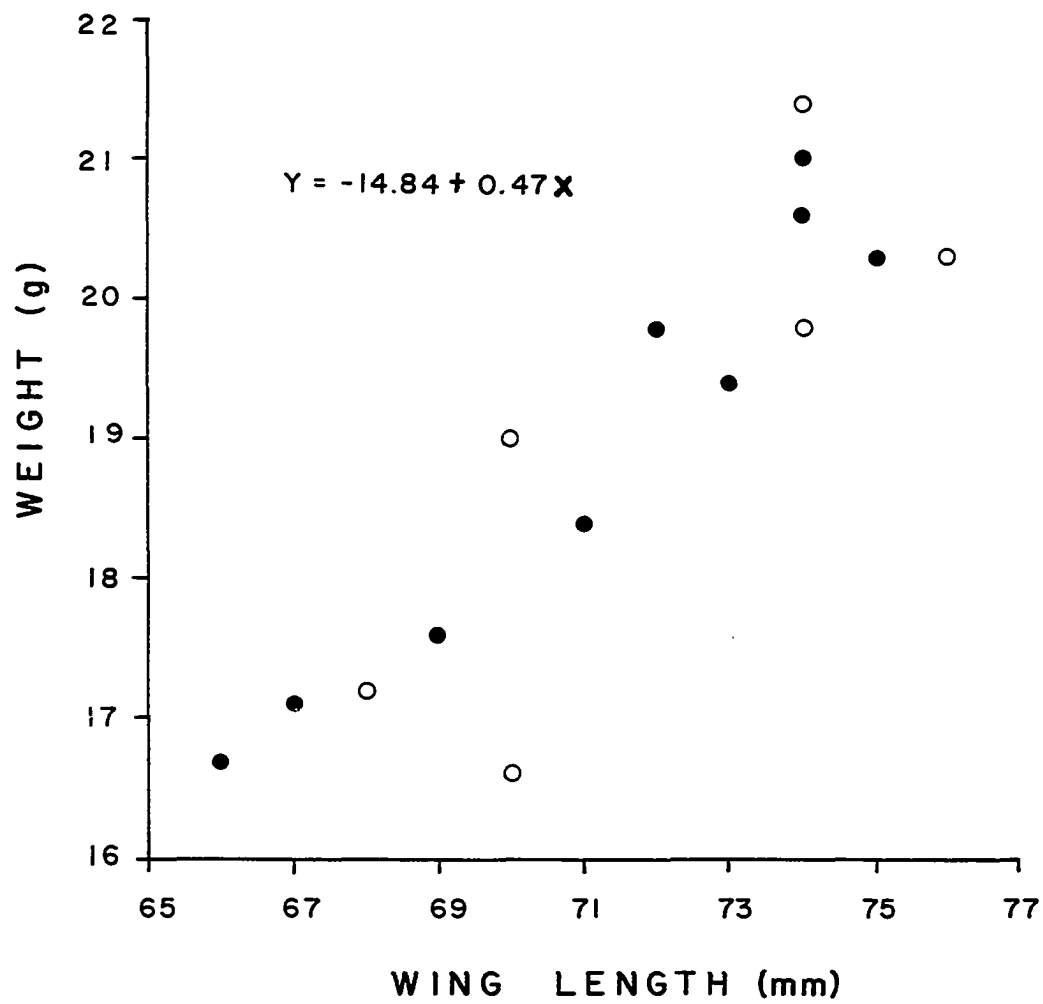


Fig. 3

(A)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1		3		2	3	5	7	3	6	7	3	1	7	3	9	4	1	5
2			6	1	5	4	2	6	2	1	4	2	1	1	5	1	1	
3	2			^T ₁	1		3		3	2	2	4	3	6	2	4	3	1
4			^T ₁		2	2			1	4		2	2			1	1	1
5					2	1			1	4	2	5	2	5		3	5	
6			5				6	^T ₁	7	10	8	8	^R ₁	8	7		9	7
7				1			4	2	5		4	8	4	4	2	2		
8					2	^T ₁	^R ₁		2	2		2		5	5		2	5
9	^R ₁					^R ₁		^R ₁		2	4	2	5	4	6	1	3	2
10			^R ₁							2	3	2	1	5	6	3	2	
11						1					3	1	4	1		2		
12												4	4		4		1	
13					9				^R ₁				6	6		5		
14														17	4	8	10	
15			^R ₁			^R ₁				1					1	4	7	
16																	1	4
17										2								2
18						6					8							

(B)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1		^T ₁	4		2	2	6	5		4		2	2	1
2	^T ₁		2	4		2	2	4	2	7	1		2	
3					5	8	1	6	2	3		3		2
4					2	1	2	2	^T ₁		5		2	1
5		5				3	5	3	1	^R ₁	1			3
6	^R ₁						1	1		3	3	2	2	4
7								14	1	10	2		3	
8					^R ₁				1	10	4		2	
9	4			^T ₁						1	4	8	^R ₁	
10				3	4						4	10		2
11												2	5	3
12		1	^R ₁	3	3		9	1					6	5
13			5	^R ₁					3					5
14		4						4						

Fig. 4

(A)

	M1	M2	M3	M4	M5	M6	M7	M8	M9	F6	M10	F1	F2	F3	F10	F12	F13	F14
M1		2		1	2	11	1	5	5	2	1	1	3			4	2	3
M2			2		1	4		1 ^R	1	1			2					
M3	4				2			2	3	1	3		3				1	2
M4									1				1					
M5						8	3		3		1	1	4	2		2		4
M6			2				6		7	3	1		6	4	1	7	7	
M7		3				1 ^R		9	4		3		3	3			1	4
M8		2		1	2				4	2			2	1 ^T		2		1
M9										1	3		1	1 ^T		3	2	1
F6												1		1		2		1
M10												2				2		
F1														3			1	
F2											1			4		1		
F3								1 ^T	1 ^T						1	3		1
F10																	1	
F12																	1	
F13																		1
F14													3					

(B)

	M	M11	M12	M13	M14	M15	M	M18	M16	F4	F5	F7	F11	F	F
M		2	1		1	2			4	5				2	2
M11			1		1	2 ^T					1				
M12				1	2				6						1
M13		3			3	2	1			2		1			3
M14						3	3	2		2	1	1 ^T			
M15		2 ^T	3					3	2	1	1	1			1
M									2			1 ^T			
M18			1						2	1					2
M16										1					4
F4											1			2	3
F5			1	2					1			1	1	3	
F7					1 ^T		1 ^T			5					
F11			1	1	1	1			2	2				1	1
F			1		1	2			2						3
F							4								

Appendix. Dominance matrices used to determine relative dominance ranks among groups of White-throated Sparrows. Values in the matrices are frequencies of dominance interactions between birds. The matrix is organized by minimizing the numbers of interactions below the diagonal following Brown (1975). The first group (A) was set up in November 1978; the second (B) in January 1979.

(A)

	1	2	3	4	5	6	7	8	9	10	11
1		3	5	3	6	14	2	1	9	8	2
2			5	7	6	8	6	3	7	2	6
3	2 ^R			7	6	18	8	5	7	10	3
4			4 ^R		6	8	11	4	9	9	3
5	1 ^R		4 ^R			17	6	5	4	5	
6	1 ^R		2 ^R		4 ^R		13	11	8	16	10
7				1 ^R		2 ^R		4	8		3
8									3	3	
9						3 ^R	2 ^R			2	4
10						1 ^R	8		1 ^R		2
11			2 ^R			2 ^R	1 ^R			1 ^R	

(B)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1		5		3	4	6		3		3	4	2	7	1	6	12	6
2				2		2	2		3	2		1		1	1	1	
3				2	3	6			1	5		3	1 ^T	2	4		1
4					5	2		1	3	7	2	1	2		12	10	1
5			1 ^R			2	9	2	7	1	2		2		4	11	1
6			2 ^R				2	13	11	1 ^R	8	6	4		4	24	7
7	1			2					2	3 ^T	1	2	1	2	3	6	
8									2	1		5	3	2	2	7	2
9	2									8					1	5	1
10		1 ^R	1 ^R			4	3 ^T				5	4		5	14		1
11									1			1	3		1	4	1
12					2								3	3	1		1
13			1 ^T							3				2	2	5	1 ^R
14						5										2	7
15																4	1 ^T
16			6		1 ^R					9		3			1 ^R		5
17						1 ^R							7		1 ^T		