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VARIATION IN SIZE, APPEARANCE, AND DOMINANCE WITHIN AND AMONG THE SEX AND AGE CLASSES OF HARRIS' SPARROWS

By Sievert Rohwer, Paul W. Ewald, and Frank C. Rohwer

Harris' Sparrows (*Zonotrichia querula*) have been useful in developing and testing the hypothesis that individual variability in the appearance of some wintering birds evolved to signal dominance status (Rohwer 1975). In this paper we (1) present criteria by which wintering Harris' Sparrows may be sexed and aged as first-winter or adult birds, (2) quantify the overlap in appearance of the sex and age classes, (3) examine the relationship between age and appearance of birds older than one year, (4) test for correlations between body size and appearance within sex and age classes, and (5) quantitatively summarize the dominance relationships among and within sex and age classes.

METHODS

Bib scores that provide an index of the amount of black on the lores, throat, and breast were assigned both to museum specimens and to banded birds according to the 14-bird composite photograph published in Rohwer (1975, 1977) and in Rohwer and Rohwer (1978). Bird 1 has the least black and bird 14 the most black; intermediate categories vary in the amount of black and in the mixture of black and white feathering. To reduce ties for computation of the Spearman correlation between wing length and bib score, the museum specimens of each sex and age class were rank ordered by the amount of black in their bibs. Where rank order of the previously assigned bib scores (which incorporated both amount of black and mixture of black and white) did not coincide with the rank order of the specimens by total area of black, the earlier bib scores were adjusted with as few changes as possible to make their order agree with that used for the correlation analyses. Thus the bib scores presented in Fig. 1 emphasize total area of black on the bib somewhat more than scores that might be individually assigned using the 14-bird composite photograph.

Bib scores for all of the birds banded in the winters of 1971–1972 and 1972–1973, and part of the birds banded in the winter of 1974–1975 were assigned from photographs of individual birds. In subsequent winters bib scores were assigned as birds were banded.

Wing chord was measured on museum specimens because dried wings are sufficiently inflexible that attempting to straighten them increases measurement error. On living birds we measured the flattened wing because extending and straightening the manus and primaries to obtain the longest possible measurement reduces error. S. Rohwer measured all of the museum specimens and most of the living birds; the remainder of the living birds were measured by F. C. Rohwer, who could duplicate

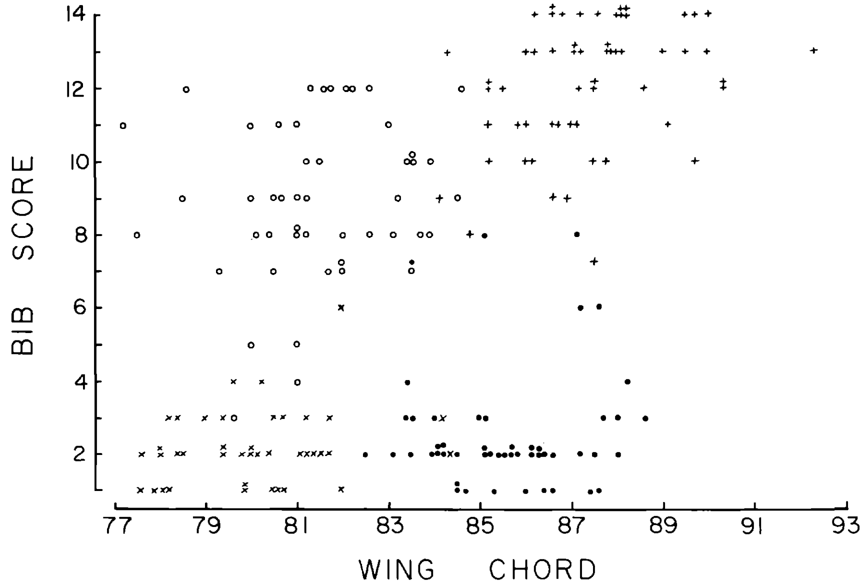

FIGURE 1. Relation between plumage score and wing chord for sex-age classes of Harris' Sparrows. Adult males were the only sex and age class with a significant correlation between wing length and plumage score. + = adult male, O = adult female, ● = first winter male, × = first winter female.

S. Rohwer's measurements accurately. We measured wing length to the nearest .1 mm because our measurements were repeatable to greater accuracy than .5 mm.

Birds scored or collected after 15 March were excluded from this study because of potential effects of the prenuptial molt on appearance (Woolfenden 1955, Baumgartner 1968). Museum specimens were from the Washington State Museum at the University of Washington (UW) and from the Museum of Natural History at the University of Kansas (KU). Most of these specimens were collected in Kansas and all were taken between 1 October and 15 March. Poorly prepared specimens and those missing feathers in the bib or throat were excluded because reliable bib scores could not be assigned to them.

Birds were aged as first-year or adult in a variety of ways, some of which are explained later because the procedure depends on results presented herein. Most UW and a few KU specimens had been aged by skull ossification (Miller 1946). For specimens not aged by skull ossification, age was assigned by condition of the central rectrices (Rohwer 1973). First-year birds may be distinguished from adults by their more worn and pointed central rectrices, a character of use in many birds.

Sex of museum specimens was presumably determined by gonadal inspection as Harris' Sparrows show no obvious sexual dichromatism in

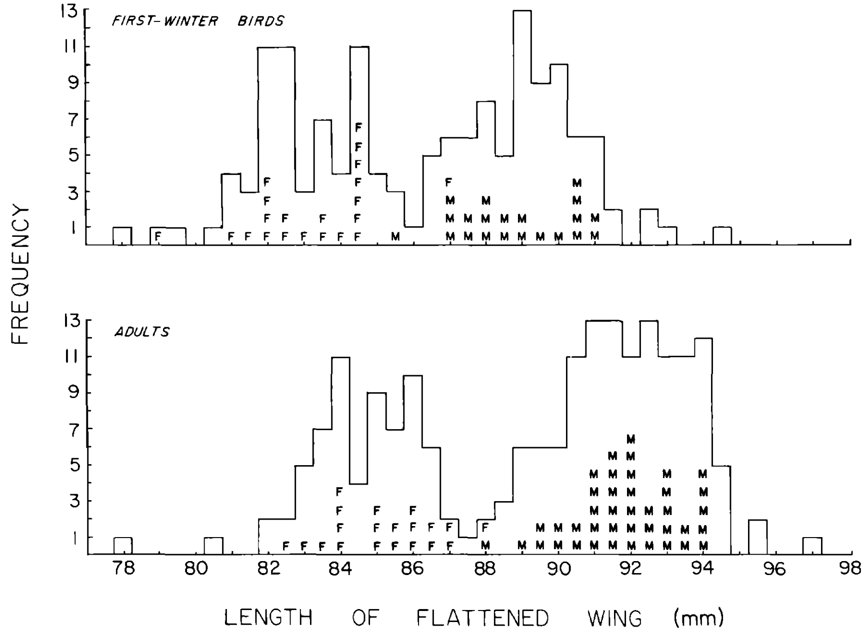

FIGURE 2. Histograms of flattened wing-length for first-winter (top) and adult (bottom) Harris' Sparrows; individuals whose sex was determined by dissection are indicated by M (male) and F (female).

winter. However, some of the museum specimens were undoubtedly missexed. The distribution of wing lengths measured on living birds, whose sex was determined by laparotomy, is strikingly bimodal (Fig. 2). Laparotomy is much more reliable as a sexing technique than dissection of birds being prepared as museum specimens because specimens have often been damaged by shot or decomposition and may have been prepared by inexperienced workers. Though the distributions in Fig. 2 show some overlap, in no case did the wing length of a bird fall beyond the mode for the sex class *other than that* to which it had been assigned. Therefore we excluded as missexed all museum specimens (11 of 207) whose wing lengths fell beyond the expected mode for the sex class other than that to which it had been assigned. For example, specimens of first-winter birds sexed as male were excluded if their wing length was smaller than the expected modal wing length of first-winter females. Expected modal wing lengths were estimated by a normal curve fit to each distribution by eye. This procedure was desirable because it enabled us to provide a better description of the relationship between appearance and wing length within sex and age classes. If these 11 specimens had been left in our analyses, all tests of means would still have been significant.

To assess year-to-year changes in size and bib scores, we used wing length measurements and bib scores provided by a number of cooperating banders (see Acknowledgments). Because each set of measurements for a bird was made by the same observer, no corrections to accommodate potential average difference in measurements among observers were required.

Data on the relative dominance status of individuals within and between the sex and age classes were gathered by observations of color-banded birds in the field. Active and passive supplants were used to assign dominance relationships. Active supplants are characterized by the winning bird overtly rushing toward and supplanting the loser, usually from a distance of 20 to 50 cm. In passive supplants the loser merely moved aside as the winner approached, presumably to avoid an active supplant. Both individuals of every dyad included in this analysis had been color-banded and had had bib scores assigned to them independent of the observed supplants. Multiple interactions between the same pairs of birds were counted only once; interactions between two dyads were excluded because, in each dyad both birds won an encounter.

Our field work was conducted near Manhattan, Kansas in the winters of 1971–1972, 1972–1973, 1974–1975 and 1976–1977. In the first 3 of these winters birds were fed in profusion (seed often >1 cm deep) in circular 1–1.5 m diameter patches on the ground; in 1976–1977 food was distributed much more thinly in a 10 × 3 m patch, the maximum density for any of several dispersion patterns being about 300 seeds/m^2 (see Rohwer and Ewald 1981 for more details).

RESULTS

Appearance versus age class and sex.—Within age classes, the sexes overlapped substantially in plumage scores (Table 1). In each age class, males averaged higher in plumage scores than females, but this difference was statistically significant only for adults (young $\chi^2 = 0$, NS; adults $\chi^2 = 31.1$, $P < .001$; median tests). Plumage scores are useless in determining the sex of first-year birds; for adults, individuals that scored 7–9 were usually females while individuals that scored 13 or 14 were males (Table 1).

The greatest separation in plumage scores is between first-year and older birds (Table 1). Indeed, considering birds with plumage scores ≤ 5 as first year birds and those with scores ≥ 6 as adults results in about 95% of this sample of 196 birds being aged correctly. Some of the high scores for young birds may have been caused by adventitious feather loss, because replacement feathers are likely to be from the next feather generation (Emlen 1938) and will, therefore, be black. Two of the 6 first-year birds scoring 6 or higher showed slightly shinier black feathers than normal, suggesting such loss. Some adult females are simply light-throated in winter, as shown by Rohwer's (1973) figure of one such recaptured individual.

TABLE 1. Frequency of individual Harris' Sparrows in the 14 plumage categories by age and sex; 1 has the least amount of black on the bib, 14 the most black.

	Plumage score[1]													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Juvenile females	10	18	9	2		1								
Juvenile males	9	26	8	2		2	1	2						
Adult females			1	1	2		6	11	8	6	5	8		
Adult males							1	1	3	6	8	9	16	14

[1] Sexes do not differ for juveniles ($\chi^2 = .0$), but do differ for adults ($\chi^2 = 31.1$, $P < .001$.

Adult females are the most variable plumage class (Table 1), and rectrix shape helps distinguish them from first-year birds. However, shape of the central rectrices is difficult to assess without experience, and unreliable if the tail has been damaged. Comparing records of rectrix shape with plumage scores shows that most of the banders who contributed data on Harris' Sparrow plumage scores did not reliably age birds by this character. If birds with bib scores of 1–2 (first-years) or 9–14 (adults) are used to learn the differences in rectrix shape, the character should make possible the reliable aging of birds with intermediate bib scores.

Appearance versus age of adult and first-year birds.—Nice (1929) cautiously suggested, and Swenk and Stevens (1929) flatly asserted, that wintering Harris' Sparrows could be divided into 3 year classes, and Sutton so described the species in Peterson's (1961) eastern field guide. Although Baumgartner (1968) rejected the idea that Harris' Sparrows darken on their bib as they age beyond their second winter, she presented no data. We have quantitatively assessed year-to-year changes in the appearance of wintering adult Harris' Sparrows by using only birds banded in one winter and recaptured and scored for appearance in at least 2 more winters. A few of the assessed changes do not represent consecutive winters as not all birds were recaptured in every winter they were alive. Change in bib score could be assessed for 40 year-to-year comparisons representing 32 adults. (Six birds were scored in 3 winters, producing 2 comparisons each, and one in 4 winters, producing 3 comparisons.)

Bib score changes form year-to-year do not suggest that Harris' Sparrows darken as they age beyond their second winter: 15 individuals decreased in bib score and 18 increased ($P = .30$, 1-tailed sign test; Table 2). Eight of the year-to-year changes were known to be from second to third winters; the mean change of 0.0 for these 8 birds was similar to that for older birds.

Also included in Table 2 are 89 differences between repeat scorings of adults made within winters (adults were defined as having an average bib score ≥ 7). These repeat scorings, made by most, but not all, of the

TABLE 2. Year-to-year change in plumage scores for adults (determined by recapture) compared with measurement error for adults (measured by repeated scoring of the same bird within years).

	Change in plumage score											
	−4	−3	−2	−1	0	+1	+2	+3	+4	+5	+6	+7
Year-to-year change[1]	1	0	2	12	7	11	4	1	1	0	0	1
Measurement error	0	1	4	21	33	19	5	1	0	0	0	0

[1] The approximately equal number and magnitude of positive and negative changes shows that Harris' Sparrows do not blacken as they age beyond their second winter.

banders that contributed the data on the year-to-year changes for known adults, provide an estimate of measurement error. Comparing the 2 distributions suggests that adult Harris' Sparrows vary somewhat in appearance from year to year: The distribution for year-to-year change, which includes both year-to-year changes in feather generation and measurement error, is significantly flatter than that for repeat scorings within years, which represents only measurement error ($\chi^2 = 5.89$, $P \approx .02$). For this 2 × 2 test the categories of change were (1) no change and (2) all more extreme changes, combined. Of course, some of the increased variance in the year-to-year changes could be year-to-year measurement error which could not be estimated.

Can some of the variability in appearance among first-year Harris' Sparrows be attributed to time of hatching? A time of hatching effect seems reasonable both because earlier fledged young of many birds are generally thought to dominate later fledged young in fall and winter (see Dhondt 1970, 1973; Kluyver 1970), and because earlier fledged young of 2 icterids have been shown to have a more adult-like plumage than later fledged young (Selander and Giller 1960). To examine this question we related appearance on the bib to the completeness of skull ossification, hence age (Selander and Giller 1960). Sexes were pooled because first-year males and females do not differ significantly in bib score (Table 1). Neither a sample of 6 first-year birds collected from 2–4 November 1972 ($r_s = -.34$, $P > .40$), nor a sample of 11 first-year birds collected from 2–6 December 1972 ($r_s = -.11$, $P > .35$) showed the expected positive correlation between skull ossification and amount of black on the bib.

Size, age, and sex.—Both males and females show an increase in wing length between their first and later winters (Figs. 1 and 2). Means of wing chords for museum specimens determined to be males (see Methods) were 87.4 mm for adults (n = 58, s = 1.64) and 85.6 mm for first-year birds (n = 50, s = 1.55), giving a mean increase of 1.8 mm ($t = 6.18$, $P < .001$). Among females the means were 81.4 for adults (n = 48, s = 1.73) and 80.0 mm for first-year birds (n = 40, s = 1.65), giving a mean increase of 1.4 mm ($t = 3.87$, $P < .001$). These differences in wing length between adults and immatures could reflect growth between winters or could result from adults and immatures of the same size wintering in different geographic areas. To unequivocally test for growth, we compared birds measured in their first and second winters by the cooperating banders (first-winter age status was assigned by plumage scores). Of the 41 birds measured in both years, 35 increased in wing length, 3 decreased, and 3 did not change ($P < .001$ sign test); the average change for these birds was an increase of 2.6 mm. The wing-length increases for the recaptures proves that Harris' Sparrows do grow between their first and second winters. Interestingly, the increase of 2.6 mm measured directly on recaptured birds was significantly larger than the mean increase of 1.6 mm inferred for the sexes from the museum specimens ($P < .02$; t-test corrected for the correlation between paired measurements). This result suggests either that on average, first-winter birds winter farther south than adults (assuming a Bergman's Rule sort of cline in both age classes) or that smaller first-year birds survive better than larger ones.

Weights of adult and first-year birds were compared to determine whether the increase in wing length reflected an increase in body mass. About two-thirds of the museum specimens for which weights had been recorded had fat reserves estimated on the scale proposed by McCabe (1943:556). Neither sex showed significant differences between the age classes in fat reserves (♂♂, $\chi^2 = .05$, NS; ♀♀, $\chi^2 = 1.5$, NS; median tests); therefore differences in weights between sexes should not be attributable to differences in fat reserves. Adult males averaged 38.3 g ($n = 43$, $s = 2.06$) and young males 36.7 g ($n = 24$, $s = 2.88$), giving a significant weight increase of 1.6 g from first to later winters ($t = 2.4$, $P < .01$). Adult females averaged 33.6 g ($n = 38$, $s = 1.78$) and young females 32.8 g ($n = 15$, $s = 2.13$), giving a non-significant increase in weight of .8 g ($t = 1.29$, $P \approx .20$). The heavier average weight for adults of both sexes suggests the increase in wing length between the first and second winters reflects an increase in body mass.

Figure 1 shows wing chord plotted against bib scores for museum specimens of known age and sex. If age is known, wing length will fairly accurately indicate the sex of Harris' Sparrows. Dividing the first-year birds at 83 mm results in only 3 of 90 birds missexed. The two young birds sexed as female with wing lengths over 84 mm were likely missexed (Fig. 1); both were old specimens from KU without gonadal descriptions to confirm sex determination. Dividing the adults at 84.5 mm results in 4 of 102 individuals missexed.

The sexual difference in wing chord shown by museum specimens demonstrates the utility of wing length in sexing Harris' Sparrows. However, wing chord is difficult to measure accurately on living birds and may be different from the same measurement taken on museum specimens because of the greater flexibility of the manus of living birds. Consequently, we present histograms of the flattened wing for most of the Harris' Sparrows banded in our research between the winters of 1971–1972 and 1977–1978 (Fig. 2). Individuals were included in Fig. 2 if age could be assigned by rectrix shape or bib score, or was known from previous bandings. When bib score was used to assign age, adults were considered to score 8–14 and first-year birds 1–3, unless sex was known by dissection, in which case males scoring 4 or 5 were also considered as first-year birds (see Fig. 1). Unsexed birds of intermediate bib score (4 to 7) were excluded unless they had been aged by shape of the central rectrices. The data in Fig. 2 indicate that first-year birds may be sexed as males if their flattened wing length is greater than 86.0 mm and as females if it is smaller. Similarly, adults are divided at 87.5 mm. With these divisions only 3 individuals were missexed by wing length out of 103 whose sex was known from dissection (Fig. 2). The division point that best separates the sexes is sensitive to measurement technique; therefore, banders would increase the accuracy of their sexing by constructing histograms of large samples of their own measurements and identifying their own dichotomizing wing lengths.

Correlation of bib score with body size.—Figure 1 shows the relationship between bib score and body size, as measured by wing length, for each sex and age class separately. For first-year birds of both sexes there is no correlation between appearance and wing length (♀♀: $r_s = .17$, $P = .27$; ♂♂: $r_s = -.04$, $P = .82$); the same is true for adult females ($r_s = .16$, $P = .26$). Only adult males show a significant correlation between wing length and appearance ($r_s = .40$, $P < .001$). No correlation is apparent for first-year birds when the sexes are considered together ($r_s = .09$, $P \approx .40$); a strong positive correlation exists for adults when the sexes are considered together ($r_s = .67$, $P < .001$; see Fig. 1).

Dominance relations among the sex and age classes.—Table 3 summarizes dominance relationships among the sex and age classes of Harris' Sparrows following the procedure employed by Sabine (1959). Classes are sequenced such that the greatest possible number of interactions lies in the upper right half of the matrix. Five of the 6 pair-wise comparisons are statistically significant (sign test, P's $\leq .05$). With the present sample size of 23 interactions, the dominance of adult females over first-year males is not statistically significant (sign test, $P = .20$). Interestingly, this is the only comparison where body size and bib score asymmetries are in conflict. Adult females are blacker on their bibs (Table 1) but are smaller (Fig. 1) than first-winter males. Since 14 of the 23 supplants were won by adult females, the darker bib of adult females seems more important than the larger size of first-winter males. For these between age and sex class interactions, results were similar on diffuse and concentrated distributions of food.

Dominance relations within the sex and age classes.—On the concentrated food patches used from 1971–1975, neither wing length nor bib score predicted dominance relations among individuals within any of the 4 sex and age classes (Sign tests, NS), and there was no significant interaction between wing length and bib score ($\chi^2 = .04$, NS; Table 4). Balph et al. (1979:89) have already reported this general result from a letter

TABLE 3. Summary of all supplants observed between sex and age classes between the winters 1971–1972 and 1976–1977; totals include active and passive supplants but numbers of passive supplants are given in parentheses.

	Losers			
Winners	Adult male	Adult female	First-year male	First-year female
Adult male		70 (18)	70 (22)	94 (35)
Adult female	19 (6)		14 (1)	9 (1)
First-year male	4 (0)	9 (1)		20 (4)
First-year female	4 (1)	2 (0)	4 (1)	

S. Rohwer wrote to M. Balph concerning a fraction of these observations. On diffuse resources birds with darker bibs won significantly more interactions than those with lighter bibs (dark : light = 18:5, $P = .005$, one-tailed sign test; Table 4). Furthermore, in all 5 cases where an in-

TABLE 4. Bib score versus wing length as a predictor of dominance within sex and age classes[1] on concentrated and diffuse food distributions; totals include both active and passive supplants, but numbers of passive supplants are shown in parentheses.

Concentrated food[1]	Blacker bib wins		Lighter bib wins	Equal bib scores	Totals
Longer-winged wins	27 (6)		26 (4)	11 (3)	64
		NS[2]			NS[3]
Shorter-winged wins	30 (9)		31 (10)	15 (5)	76
Equal wing lengths	6 (2)		5 (2)	0	11
Totals	63	NS[3]	62	26	151

Diffuse food[1]	Blacker bib wins		Lighter bib wins	Equal bib scores	Totals
Longer-winged wins	6 (2)		5 (0)	0	11
		$P < 0.025$[2]			NS[3]
Shorter-winged wins	12 (1)		0 (0)	0	12
Equal wing lengths	0		0	0	0
Totals	18	$P = 0.02$[3]	5	0	23

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[1] On concentrated food (winters of 1971–72 through 74–75) numbers of interactions occurring among individuals in the same sex and age class were adult male—101, young male—33, adult female—3, young female—14; on diffuse food (winter of 1976–1977) the values were 8, 1, 13, and 1, respectively. Data from within each sex and age class are combined in the table; *no* interclass comparisons are included.

[2] Significance level refers to the 2 × 2 interaction of wing length and bib score.

[3] Significance level refers to the binomial test of effect of bib score or wing length, as appropriate.

dividual with a lighter bib displaced an individual with a darker bib, the individual with the lighter bib was larger. This causes the significant interaction between wing length and bib score on diffuse food (one-tailed Fisher's exact $P < .025$; Table 4).

DISCUSSION

The preceding results that pertain primarily to methodology require only a brief summarization. Table 1 shows that Harris' Sparrows may be aged as first-winter or adults with about 5% error by considering bib scores ≤ 5 as first-years and bib scores ≥ 6 as adults. Banders can likely assess age of intermediate ranked birds (especially those with bib scores of 4 to 8) more accurately by shape and wear of the central rectrices (Rohwer 1973). Recall, however, that we have found numerous errors in this procedure when cooperating banders simply tried to apply the technique using the photograph in Rohwer (1973). Therefore, it is essential that banders either use birds aged in early winter by skulling or use birds of extreme bib scores (1–2 or 9–14) to learn how to assess age by condition of the central rectrices. Figures 1 and 2 show that, by treating first-years and adults separately, Harris' Sparrows may be sexed with less than 5% error by wing length.

Year-to-year changes in bib score show the amount of black on the Harris' Sparrow bib does not increase as birds age beyond their second winter (Table 2). This is the first quantitative refutation of earlier suggestions that Harris' Sparrows might be divisible into the 3 age classes: first-winter, second-winter, and older. Comparison of the year-to-year changes with an estimate of measurement error suggests that individuals do not perfectly replicate their appearance from year to year. If this year-to-year variability is not measurement error, then some physiological, social, or environmental cue apparently modifies the appearance of the plumage generated in the fall molt. Such a proximate influence on appearance would be consistent with the supposition that the plumage variability shown by Harris' Sparrows is under a dosage-response type of genetic control. Good year-to-year photographs for adults would facilitate an evaluation both of year-to-year error in the assessment of bib scores and of the possibility that the distribution of black on the bib is constant from winter to winter.

That only adult males show a significant correlation between wing length and bib rank merits explanation. This result, together with the assumption that body size affects fighting ability, leads to the conclusion that fighting among adult males is more important than is fighting within the other sex and age classes. On a 10 × 3 m grid of small caches of seed buried in the snow or ground, Rohwer and Ewald (1981) found that non-feeding high-ranked birds displace other high-ranked birds more frequently than they displace low-ranked birds. The apparent reason for this is that high-ranked Harris' Sparrows compete with each other for the privilege of taking over caches of seed found by subordinates. This grid of resources hidden in caches was designed to provision birds in a way that more nearly mimics natural feeding conditions than does the usual procedure of pouring seeds profusely in a small patch on the ground. Thus we view the discovery of considerable aggression between non-feeding high-ranked birds on hidden caches to be important, because we think the aggression observed approximates that which would occur in an unprovisioned flock.

If high-ranked birds fight among themselves over access to subordinate food-finders (Rohwer and Ewald 1981), then adult males should be subject to more intra-class interference competition than any of the other sex and age classes simply because they are the highest-ranked class (Table 3). This intense competition among adult males should result in them exhibiting the strongest correlation between body size and signaled rank. This logic predicts that the correlations between wing length and bib score should progressively diminish from the most dominant to the most subordinate sex and age class. The prediction is not confirmed: the correlation for adult females was lower than that for first-year males, and the correlation for first-year males was lower than that for first-year females.

Can the preceding interpretation of the strong correlation between size and bib score in adult males still be correct given the failure of this last prediction? The answer may be yes, but only if most flocks of Harris' Sparrows include several adult males that compete among themselves for access to subordinates they use as food finders. Whether or not most natural flocks contain at least a few adult males that so compete is unknown.

That adult females dominate first-year males (which are larger than adult females) suggests that first-winter Harris' Sparrows may profit from an association with adult birds. Their benefit from adults likely relates to the winter philopatry shown by adult Harris' Sparrows and other emberizids (see Rohwer 1978). Wearing a badge of subordination may help first-winter Harris' Sparrows to join flocks of adults (see Rohwer and Ewald, 1981) and, thereby, to profit from the experience adults have accrued in that habitat during the previous winter. This difference in experience likely explains the roughly bimodal distribution of bib scores, wherein most first-winter birds have bib scores of 1–3 and most adults have bib scores of 7–14 (Table 1).

Does the status signaling hypothesis (Rohwer 1975) account for some of the within age and sex class variability shown in Table 1? The data for dominance interactions occurring within age and sex classes on the diffuse resource distribution support this idea because 18 of 23 supplants were won by the darker bird of an interacting dyad (Table 4).

Why should this relationship not hold in the earlier data from concentrated resource distributions? Our guess is that asymmetries between contestants in fighting ability (as signaled by bib score) were overridden by asymmetries in the value of the contested feeding spot. On the concentrated food patches, competition for a space on the patch was often extreme. Consequently, the value of gaining access to the patch for hungry birds off the food patch may have been sufficient to make them dominate more satiated birds on the patch, regardless of slight differences in their fighting abilities. An asymmetry in the value of being on the food patch should not have affected aggressive interactions on the large patch of diffuse resources because there was always enough room on this 3 × 10 m patch for all of the birds present and hungry to search for food. We see no biological reason to invoke potential differences between habitats or years to explain the conflict in results associated with the different feeding methods. However, we cannot rule out such effects because the data for the 2 resource distributions were recorded in different years and at localities separated by about 3 km.

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Department of Zoology and Washington State Museum, University of Washington, Seattle, Washington 98195 (S.R.), *Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109* (P.W.E.), *and Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104* (F.C.R.). Received 25 Nov. 1980; accepted 9 July 1981.