SOCIAL STATUS SIGNALING IN WINTER FLOCKING BIRDS: AN EXAMINATION OF A CURRENT HYPOTHESIS

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ABSTRACT.—S. Rohwer recently has proposed that intraspecific plumage variability in winter flocking birds represents a polymorphism that functions to signal social status. We test several predictions of Rohwer's status signaling hypothesis for Dark-eyed Juncos (*Junco hyemalis*), explore some theoretical implications of our findings for juncos, and discuss the generality of social status signaling. Both darkness of hood and whiteness of tail were positively, although imperfectly, associated with social rank in captive winter flocks of first-year juncos. If plumage differences function as cues to dominance status in this species, our results suggest that their signal value derives primarily from learned associations between plumage attributes and other variables (such as sex or body size) that might influence fighting ability. Ultimate factors possibly responsible for winter plumage variability in juncos, both within and between age/sex classes, appear to be complex; selective pressure for a system of social status advertisement could (but need not) be one of these factors. Findings for some other winter flocking species reveal both similarities to, and differences from, our results for juncos. We suggest that more information on the behavior and ecology of a variety of winter flocking birds is needed before a satisfactory generalized model of social status signaling can be formulated—if such a model is possible. *Received 28 February 1978, accepted 5 September 1978.*

FLOCKING is a widespread phenomenon among birds that winter in temperate regions. Such behavior affords many benefits; for instance, it may facilitate orientation during migration or refuging, aid in the location and efficient exploitation of food, and assist in the detection and mobbing of predators. However, flocking also may impose costs, not the least of which is the promotion of intraspecific competition for essential resources. The cost of such competition may be reduced by social systems, such as social dominance hierarchies, that function to order individual priorities at resources and to regulate the frequency, form, and intensity of aggressive behavior (discussed by Balph 1977a).

Of considerable interest is a hypothesis stating that dominance hierarchies are predetermined by adaptive variation in the appearance of individuals. Rohwer (1975, 1977) observes that wintering birds differ markedly in the degree to which they vary intraspecifically in appearance and indicates that flocking species tend to exhibit polymorphism in plumage coloration or pattern, whereas non-flocking species show monomorphism. He speculates that in flocking species ". . . plumage variability has evolved to signal the approximate social status of each individual" (Rohwer 1975: 594). According to this hypothesis, position in a dominance hierarchy within variably plumaged species is signaled by the "studliness" (Rohwer 1975: 598) of individuals (defined as the degree to which each exhibits black, brightly colored, or contrastingly patterned plumage, particularly of the head or breast). Rohwer predicts such status advertisement to be especially advantageous if individuals change flocks, as it should enable both an incoming bird and established flock members to assess accurately the newcomer's proper social position without engaging in energetically costly fights. From a series of tests using Harris' Sparrows (*Zonotrichia querula*), he concludes that winter plumage variability does serve a status-

signaling function in this species. He also indicates, on the basis of qualitative observations of some other winter flocking passerines, including Dark-eyed Juncos (*Junco hyemalis*), that the phenomenon may be a general one. However, Shields' (1977) fine critique points out serious problems in Rohwer's (1975) paper. In the present paper we examine Rohwer's status signaling hypothesis both from an empirical and a theoretical standpoint.

METHODS

An investigation of winter social behavior in Dark-eyed Juncos (Balph 1977a) provided data to test several predictions of the status signaling hypothesis. Thirty-six juncos (*J. h. montanus*) were captured in November 1973 at Logan, Utah and 6 birds placed simultaneously in each of 6 large, outdoor flight pens. Abundant resources were identically distributed in all aviaries. Each "flock" contained two or more members of each sex. All but one of the 36 birds were young of the year. Dominance-subordination relationships among all members of each flock (totaling 90 two-bird relationships) were ascertained from over 2,000 agonistic encounters observed in December at various resources in the flight pens. In addition, early in January 1974, 4 males and 2 females from 2 of the flocks were individually transferred, each for 24 h, to another of the flocks and their social positions determined from over 1,500 recorded encounters.

We ranked junco specimens from the above study relative to one another within groups according to darkness of the hood (i.e. plumage of the head and upper breast), which ranged from black to brownish gray (Fig. 1). An independent observer concurred in our order of plumage ranking. We also ranked birds within each group on the basis of tail pattern (from most to least white, ascertained from notations made when the birds were first captured). The range of plumage variation probably was reduced somewhat in the captive sample by the virtual absence of adults, which are darker-hooded and whiter-tailed on the average than immature juncos (e.g. Miller 1941, Grant and Quay 1970). However, several factors counteracted this effect. First, Balph (1977a) selected for extremes of hood coloration in an attempt to assure representation by both sexes in each captive flock. Second, the population from which the captives were taken appeared to be composed largely of first-year birds (89% of 121 individuals banded in December 1973). Third, plumage variability due to sexual dimorphism (Balph 1975) probably was greater among captives than in wild flocks at Logan, as sex ratios more closely approached unity in the captive flocks (1:1 or 2:1 in favor of males) than in the free-living population (4:1 in favor of males). Finally, the average difference in hood darkness or tail pattern between individuals in the captive flocks probably was greater than in most free-living flocks, as each captive flock contained only 6 birds, whereas wild junco flocks may contain as many as 40 birds (e.g. Fretwell 1969). Plumage variability therefore may have been slightly greater in the captive flocks than in free-living flocks at Logan.

A question remains as to the degree to which our sample was representative of Dark-eyed Junco populations generally. Although all races of this species exhibit some plumage variation both within and between age/sex classes, Miller's (1941) findings indicate that plumage variability is greater in some races than in others and that the degree of variability within a race can differ for different plumage characters. As *J. h. montanus* is one of the more variably plumaged races, associations between plumage and social status (if Rohwer's hypothesis is applicable to juncos) might be exaggerated somewhat. A second problem was that we were unable to test for associations between age, age-related plumage differences, and dominance status, as our sample consisted almost entirely of first-year birds. However, unless age is positively associated with social status independently of plumage characteristics, estimates of correspondence between "signaled" and actual social rank within age classes should not differ from those between first-year birds and adults (except insofar as errors of plumage discrimination might be more frequent within than between age classes). If age predicts social status independently of plumage differences, overall correspondence between the "signaled" and actual social order within a flock should increase as the ratio of first-year birds to adults approaches unity. The age composition of our flocks also prevented us from determining whether or not first-year and older juncos are equally likely to respond appropriately to plumage cues hypothetically signaling social status. If such cues have evolved as social releasers in juncos, we should expect younger birds probably to respond as strongly as older birds. Alternatively, if the cues operate as conditioned reinforcers, correspondence between signaled and actual social position might be greater among older, more experienced birds than among younger individuals; however, we doubt that such a difference would be appreciable, as first-year juncos probably have substantial learning opportunities prior to the formation of winter flocks (see Gabrielson and Jewett 1940: 571), and as selection should favor rapid learning if individuals responding inappropriately are at a survival disadvantage.

We analyzed data from the captive juncos with tests of goodness of fit and contingency table tests of independence. We used the Chi-square statistic to perform these tests except where small (<5) expected values dictated the use of exact Chi-square tests (Radlow and Alf 1975, Agresti and Wackerly 1977). We pooled data only after testing for, and failing to find, heterogeneity at $P \leq 0.05$ (e.g. male-male with female-female relationships for same-sex versus opposite-sex comparisons). Our analysis necessitated breaking a small number of dominance-subordination "ties" (see Balph 1977a); in such cases, we considered the bird winning the majority of observed encounters to be dominant. Within agonistic encounter types, dominant members of junco pairs almost always were winners (>97% of interactions recorded in December and January).

A multivariate paired comparisons analysis to determine the relative contributions of hood darkness, tail pattern, sex, and wing length to social status in juncos would have seemed desirable (see review of experimental designs for paired comparisons data by Davidson and Farquhar 1976). However, our data were not suitable for extant designs, most of which impose rigid constraints upon how data may be obtained (e.g. David 1963: 36–43). An alternative approach was to hold certain variables constant and to study the effects of other variables upon social status. Although in principle the simultaneous effect of several variables upon dominance could be studied using log-linear models for multidimensional contingency tables (Haberman 1974), such models seemed inappropriate for analyzing our data (see Haberman 1974: 144–146 and Bishop et al. 1975: 177). We therefore opted for a series of traditional two-way contingency table analyses.

RESULTS AND DISCUSSION

Plumage variability and social status in juncos.—Dark-eyed Juncos form hierarchically organized, relatively stable flocks during the winter (Sabine 1949, 1955, 1956, 1959; Fretwell 1969) and exhibit considerable plumage variability. In an attempt to determine whether or not plumage differences might serve a status-signaling function in this species, we examined our data for possible associations between darkness of the hood (cited by Rohwer as indicative of "studliness" in juncos) and social status. Darker-hooded members of junco pairs were dominant in 62 (69%) of the 90 two-bird combinations within the resident captive flocks, a result that differed significantly from the null hypothesis of equal dominance ($\chi^2 = 12.84$, df = 1, $P <$ 0.001). Hood darkness thus appears to be a predictor of social rank in juncos (at least among first-year birds), although not as strong a predictor as Rohwer (1977: 108) implies for Harris' Sparrows: "Reversals, wherein a studlier bird is dominated by one of lower signaled rank, and disputes over status almost never occur."

Rohwer (1975, 1977) either explicitly or implicitly discounts the importance of such factors as sex, age, body size (as estimated by wing length), and residency status as predictors of social position in several variably plumaged species, including juncos. However, in our captive junco flocks males dominated females significantly more often than the hypothesis of equal dominance would predict (41 of 50 intersexual relationships; $\chi^2 = 20.48$, df = 1, $P < 0.001$) (see also Balph 1977a). In most cases the longer-winged member of a pair was dominant (63 of 81 pairs in which the 2 individuals differed in wing length; $\chi^2 = 25.00$, df = 1, $P < 0.001$). Finally, established flock members were dominant to newly introduced individuals significantly more often than not (25 of 30 relationships; $\chi^2 = 13.33$, df = 1, $P < 0.001$) (see also Balph 1977a). These results agree generally with those of several persons working with free-living flocks of this species (Sabine 1949, 1955, 1959; Fretwell 1969; Ketterson 1974; Ketterson and Nolan 1976). Ketterson's (1974) results additionally indicate that older juncos tend to dominate younger individuals.

Our initial findings demanded further scrutiny, as the factors considered do not vary independently of one another in juncos. Although variability within (and overlap between) age/sex classes often is substantial, males or older birds tend generally

to be darker-hooded and longer-winged than females or younger birds (Balph 1975 and references cited therein; Ketterson and Nolan 1976). Rohwer (1977) states that in Harris' Sparrows the plumage "studliness" of individuals reflects social position much more accurately than does sex. We predicted that, if the same is true for juncos, associations between hood shade and social status should be similar for juncos of the same or opposite sex. However, darker-hooded members of junco pairs were dominant in a significantly greater proportion of intersexual than intrasexual relationships (82% of 50, as opposed to 52% of 40; $\chi^2 = 9.02$, df $= 1$, $P < 0.005$). The figure obtained for intrasexual pairs was very close to 50% chance expectation ($\chi^2 = 0.10$, df $= 1$, $P > 0.5$). Hood darkness thus appeared to be a poor indicator of social status in our juncos apart from its association with sex.

Rohwer (1975) indicates that plumage "studliness" in Harris' Sparrows is a significantly better predictor of dominance than is body size as estimated by wing length. We reasoned that, if plumage variability functions similarly in juncos, associations between hood darkness and social status should not differ between junco pairs with members of like and unlike wing length. We distinguished between three wing-chord categories in our analysis: short (71–74 mm), medium (75–78 mm), and long (79–82 mm). Darker-hooded members of junco pairs were dominant in 75% of 64 relationships involving birds that differed in wing length, as opposed to 54% of 26 relationships between individuals of similar wing length ($\chi^2 = 3.86$, df $= 1$, $P < 0.05$). Among birds of similar wing length, the tendency for darker-hooded members of pairs to be dominant did not differ significantly from the 50% expected by chance ($\chi^2 = 0.15$, df $= 1$, $P > 0.5$). Of 9 relationships involving birds with identical wing measurements, the darker-hooded individual was dominant in 3 cases and the lighter-hooded in 6. Once again, hood shade appeared to be only a weak indicator of social status apart from its association with another variable—in this instance, wing length. Although our sample consisted of first-year birds, whereas Rohwer's (1975) sample contained birds of various ages, the difference should be relatively unimportant in view of Rohwer's (1977) statement that plumage "studliness" is a much more accurate indicator of social status than is age in Harris' Sparrows.

These results led us to ask which, if either, of two related variables—sex or wing length—is a better predictor of dominance status in juncos. The tendency for males to dominate females was no greater when the members of a pair were of different wing length than when they were of similar wing length (exact test, $P > 0.5$). However, the tendency for longer-winged members of pairs to be dominant was significantly greater for intersexual than for intrasexual relationships ($\chi^2 = 4.52$, df $= 1$, $P < 0.05$). Our results suggest that sex may possibly be a better indicator than wing length of social status in juncos (at least among first-year birds), although Ketterson (1974) suggests the reverse to be the case. Complicating this picture is the finding of Helms et al. (1967) that wing length is positively related to dry fat-free weight in female but not in male juncos.

An additional question was whether or not perceptual errors by individual juncos in assessing the plumage of others could account for social relationships in which the darker-hooded of two birds was subordinate. We predicted that, if such were the case, hood-rank differences between the members of junco pairs should be smaller when darker-hooded birds were subordinate than when they were dominant. An analysis of hood-rank differences revealed a trend in the predicted direction when all pairs were considered together (exact test, $P = 0.05$). However, this trend was no longer evident when intersexual and intrasexual relationships were analyzed
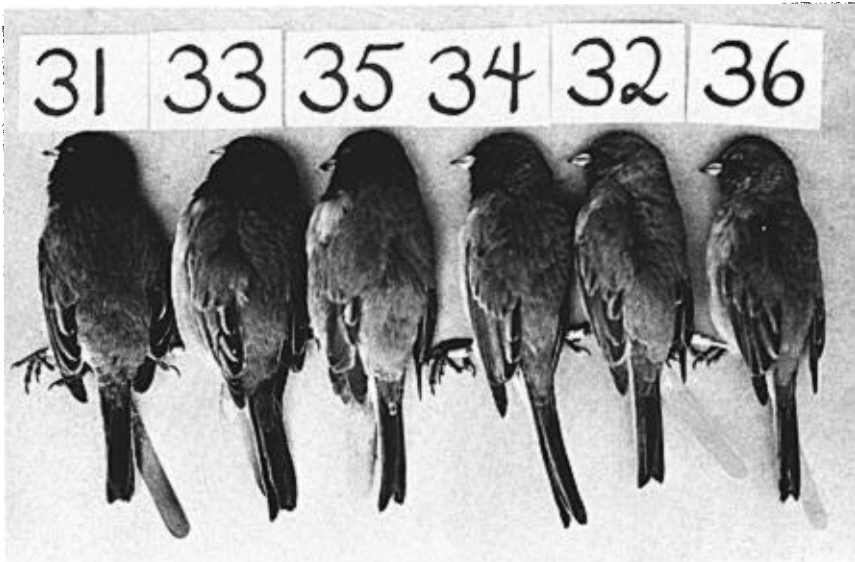
Fig. 1. Variation in darkness of the hood within a representative captive flock of Dark-eyed Juncos. (Numbers symbolize colors of leg tags and bands and are not related to plumage attributes or social status).

separately (exact test, $P > 0.5$ in both cases). The effect observed when all birds were considered together seemed to be due primarily to the disproportionate representation of intersexual relationships (in which females seldom were dominant, whether or not they were close to males in hood coloration) in cells denoting large hood-rank differences. Hence it appeared unlikely that errors of plumage discrimination could account for many of the hood-rank reversals occurring among the captive juncos.

We next examined Rohwer's (1975) proposal that social status signaling permits newcomers to join established flocks and to assume their signaled social positions with little test fighting. We predicted (1) that incoming juncos should assume the social positions predicted by their hoods and (2) that fighting between newcomers and old flock members should be less frequent and intense than if juncos exhibited little or no plumage variability. We tested the first prediction by comparing the "signaled" and actual social positions of newcomers relative to resident flock members in the transfer experiments. Incoming birds were dominant in a significantly smaller proportion of relationships than their hoods predicted they should be (5 of 30, as opposed to 11 of 30 expected; $\chi^2 = 5.17$, df = 1, $P < 0.025$); furthermore, 3 of the 5 cases involved domination of relatively dark-hooded home flock members by a lighter-hooded stranger. Had the strangers remained in the test pen for longer than 24 h, they might have risen in social status as the effect of prior residency waned (Harrington 1973, Rohwer 1977). Three juncos placed in the captive flocks in January 1974 to replace individuals that died (Balph 1977a) did rise slightly in status during the first few weeks following their introduction, although their gains were over birds darker than themselves in two of three instances. These results indicate that resident juncos enjoyed a dominance advantage over introduced birds, particularly at the outset, but that relative darkness of the hood probably was of

little importance. We were unable to test the second prediction; nevertheless, agonistic encounters were markedly more frequent and intense between newly introduced juncos and members of a resident flock than among flockmates of long standing (Balph 1977a). Although aggression between newcomers and residents may have been less than if juncos were alike in appearance, the cost of such behavior (as well as the effect of prior residency) still might be sufficient to prevent individuals from joining new flocks readily during the winter. Our results, if applicable to free-living juncos, might partly explain the relative stability of membership often observed in wild junco flocks.

To this point we have considered only one plumage character, hood darkness, as a possible indicator of social status in juncos. Rohwer (1975, 1977) describes "studliness" in juncos solely in terms of this character. However, juncos also vary in several other plumage characters, particularly in tail pattern: the tail is blackish centrally and white peripherally in all birds, but the extent of white relative to dark feathering differs between individuals and tends to be greater in males or older birds than in females or younger birds (Miller 1941, Wood 1951). Tails with much white appear to be more contrastingly patterned (hence more "studly" by Rohwer's criteria) than those with less white. Although white in the tail is largely hidden when juncos are at rest, the pattern is readily visible as the birds move about and thus could be used to signal social status.

An analysis of tail rank in relation to social status showed that whiter-tailed members of junco pairs were dominant in 65 (72%) of all relationships, a result that differed significantly from the null hypothesis of equal dominance ($\chi^2 = 17.78$, df = 1, $P < 0.001$). Whiter-tailed birds were dominant in 74% of intersexual and 70% of intrasexual relationships; this difference was not significant ($\chi^2 = 0.18$, df = 1, $P > 0.5$), suggesting that tail pattern may be associated with social status independently of sex. However, whiter-tailed members of junco pairs were dominant in a significantly greater proportion of relationships between birds differing in wing length (78%) than between birds of similar wing length (58%) ($\chi^2 = 3.85$, df = 1 $P < 0.05$). The figure obtained for pairs of similar wing length was in the predicted direction but did not differ significantly from 50% chance expectation ($\chi^2 = 0.62$, df = 1, $P < 0.5$). Tests for effects of tail-rank distance yielded results roughly comparable to those for hood-rank distance: when all relationships were considered together, whiter-tailed birds possibly were less likely to be dominant when tail ranks were close than when they were farther apart (exact test, $P < 0.3$), but this association disappeared when intersexual and intrasexual relationships were considered separately (exact text, $P > 0.5$ in both cases).

In sum, it appears that tail pattern may be at least as strong a predictor of social status as hood darkness in juncos. This finding seems somewhat surprising, because the hood is located frontally, whereas the tail is not, and because tail pattern is a less stable character through the winter than hood darkness (as rectrices may be lost accidentally and replaced by feathers of the next plumage). If plumage variability in juncos does serve a social status signaling function, the presence of two signal characters might be viewed as an example of signal redundancy functioning to combat confusion in a receiver. Hypothetically, these cues may influence the order of social ranking during hierarchy formation; if they are used after this time, they probably serve to facilitate individual recognition, as winter social relationships (including those in which the duller-plumaged of two birds was dominant) were stable in the captive junco flocks.
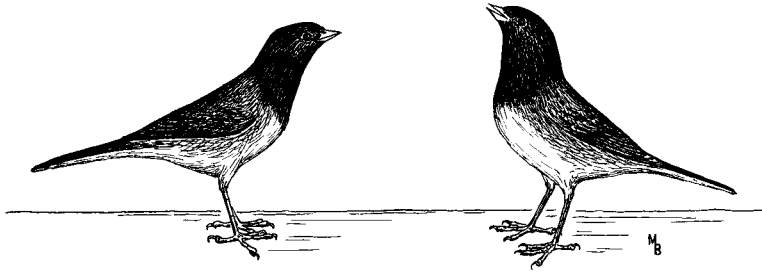
Fig. 2.   The junco head dance (drawn from a photograph by M. H. Balph).

Theoretical considerations in juncos.—Our finding that both hood darkness and tail pattern are associated (albeit imperfectly) with social status in wintering Dark-eyed Juncos leads us to explore several questions concerning the evolution and possible communicative significance of these characters. Our first consideration pertains to the direction of the relationship between dominance status and plumage conspicuousness. Although Rohwer (1975) assumes that non-cryptic plumage is associated with high social status in variably plumaged species, the reverse may sometimes be the case, as in the Cassin's Finch (*Carpodacus cassinii*), in which adult males exhibit reddish plumage but are *subordinate* during the winter to females (Samson 1977), which are grayish brown and thus less "studly" by Rohwer's criteria. The form of some winter agonistic displays of juncos (Balph 1977a) might partly explain why visual conspicuousness of the hood or tail is positively associated with social status in this species. The head dance (Fig. 2) is a mutual agonistic display that accentuates the region of contrast between the dark hood and white belly; in addition, one or both participants may fan the tail laterally, exposing its contrasting pattern. The head dance tends to occur when strangers first meet or when a subordinate flock member fails to yield to a dominant at a scarce resource. The tail-up display (Fig. 3) conspicuously exhibits the tail pattern to an adversary and functions as threat. Use by juncos of the hood and the tail in agonistic displays should result in selection favoring enhancement of the display structures through increases in visual contrast. All else being equal, a relatively dark-hooded or white-tailed junco should present a more effective visual stimulus than a duller-plumaged junco during a head dance or tail-up display.

Our next consideration pertains to the location of plumage characters hypothetically used by juncos to signal social status. The placement of the hood is consistent with Rohwer's (1975) prediction that such a character should be situated frontally and ventrally so as to address competitors rather than predators, although the hood also covers the top of the head, which may render dark-hooded juncos more visible to predators against winter backgrounds than light-hooded individuals. More problematical is the white-and-dark pattern expressed on the rectrices, as it is located posteriorly, is hidden from view part of the time, and when exposed can be quite conspicuous from above. If selection for a social status signaling system has played a role in the evolution of the junco tail pattern, we suspect that the location of the signal represents a compromise between this and other (sometimes conflicting) selective pressures. For example, we believe that juncos may use the tail pattern as a cue to flock location—particularly during flight, when white in the tail is flashed most frequently and when the chances for a bird's becoming separated from its flock
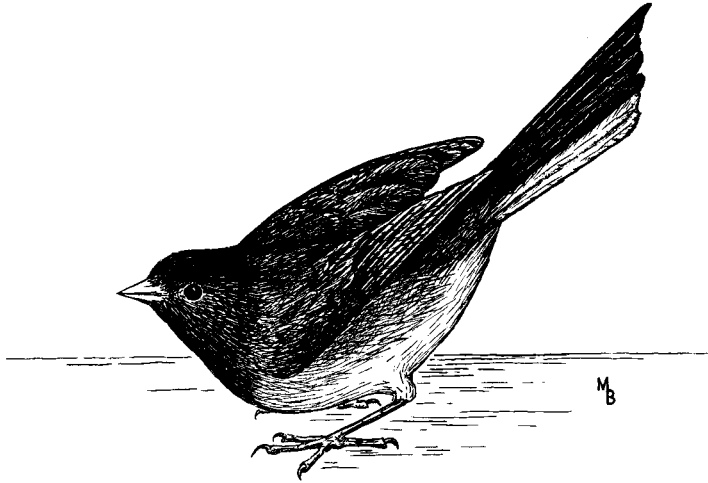
Fig. 3.   The junco tail-up display (drawn from a photograph by M. H. Balph).

presumably are greatest. A junco lacking white outer rectrices might be followed less often than others and thus be more likely to become isolated from conspecifics. Although the contrasting pattern of the rectrices may attract the attention of predators, sudden flashes of white accompanied by shifts in flight direction might serve a startle-deception function; hence we think it possible that the tail pattern decreases the susceptibility of juncos to predation.

Our third question concerns the maintenance of plumage variability in wintering junco flocks. An important prerequisite for the development and continuance of a social status signaling system is that individuals of low signaled status be as likely to survive to reproduce as flockmates of higher signaled status lest selection for certain plumage characteristics eliminate winter plumage variability. However, Fretwell's (1969) results, although based upon a small sample size, suggest that subordinate juncos may die or disperse to marginal habitats more frequently than dominants. Perhaps partly in response to this problem, juncos exhibit some geographic segregation of the sexes during the winter, with females wintering farther to the south on the average than males (Ketterson and Nolan 1976). Although differential migration of the sexes might promote the survival of females as a class by lessening intersexual competition (Balph 1975, Ketterson and Nolan 1976), it also may reduce plumage variability within particular junco flocks. We believe, however, that several factors could act to increase intraflock plumage variability.

First, plumage variation within flocks might be promoted if wintering juncos fight more frequently with individuals of similar than dissimilar appearance to themselves. To test this hypothesis, we analyzed data on 992 pecking attacks, flight pursuits, fights, and head dances recorded at various resources in the flight pens during December and for which both participants were known. We used a method of analysis similar to that employed by Rohwer (1975: 601–602) to test the same hypothesis. We weighted expected values to reflect the relative numbers of two-bird combinations of above-average or below-average distance in plumage rank (i.e. >2.33 or <2.33 intervals apart). Agonistic interactions were significantly more common than expected by chance between juncos whose hood ranks or tail ranks were

closer together than average ($\chi^2 = 28.10$, df $= 1$, $P < 0.001$ for hood; $\chi^2 = 5.38$, df $= 1$, $P < 0.025$ for tail). Our results could reflect heightened aggressiveness between juncos of like appearance, although they also could be produced by differential spacing; for example, Fretwell (1969) and Ketterson (1974) have suggested that low-ranking juncos tend to occupy positions at the periphery of feeding flocks. Ongoing analyses of relationships between social dominance, agonistic behavior, resource use, and spacing in juncos (Balph and Balph in prep.) suggest to us that differential aggression and differential spacing both might be important. To the extent that juncos may be preferentially aggressive toward flockmates of like appearance, it should be advantageous for an individual not to resemble its flockmates closely, as relative dissimilarity could reduce the cost of aggression for that individual. Other considerations being equal, this effect should favor less common plumage characteristics and hence promote intraflock plumage variability. If plumage differences do signal social status in juncos, the cost of agonistic interactions with flockmates of high signaled status possibly could outweigh the advantages of increased social rank for an individual whose advertised status was higher than its underlying abilities warranted, in which case selection might favor correspondence between signaled status and inherent fighting ability.

A second factor that might act to increase intraflock plumage variability could be differential predation. If predators are most likely to take individuals at the periphery of flocks (Hamilton 1971, Vine 1971), and if juncos with black hoods are more conspicuous against winter backgrounds than those with paler hoods, a dark-hooded individual at the periphery of a junco flock should be particularly susceptible to predation. In this case one might expect selection to favor cryptic plumage in peripherally located (i.e. subordinate) juncos.

An additional factor that may increase intraflock plumage variability is suggested by Miller's (1941) finding that juncos exhibit considerable interracial variation in plumage coloration and that more than one race may flock together during the winter in some regions. Characteristics such as wing length, darkness of hood, and whiteness of tail often are not positively associated with one another across races; hence mixing of morphologically dissimilar junco races in some wintering areas could cause confusion as to the meaning of particular plumage cues. Unlike differential aggression or differential predation, which might promote intraflock plumage variability either in the presence or in the absence of a social status signaling system, racial mixing should tend to hinder the development in juncos of a signaling system such as Rohwer proposes.

Our fourth question concerns influences other than those operating in winter flocks that might promote winter plumage variability in juncos. One such factor may be sexual differences in breeding plumage requirements. Because juncos undergo a complete postnuptial but no regular prenuptial molt (Dwight 1900), winter appearances are likely to be affected by summer selective pressures. Male juncos fan the tail laterally during courtship displays (Hostetter 1961, Eaton 1968), and territorial males threaten rivals by raising the breast feathers and alternately elevating and depressing the widely spread tail (Nero 1963). Epigamic or agonistic sexual selection therefore might favor darkness of hood or whiteness of tail in males. Conversely, plumage dullness in females should decrease the likelihood of nest detection by predators (as females apparently perform all incubation and brooding; Greulach 1934, Hostetter 1961) and might facilitate sexual recognition. The potential advantages of cryptic plumage characteristics in the breeding season could outweigh the

disadvantages, if any, of such characteristics during the winter for females. A second factor operating during the breeding season to increase plumage variability is hybridization between junco races (Miller 1941), although it exerts an effect only in particular geographic areas. Third, plumage variation within (and overlap between) the sexes conceivably might represent an intermediate stage in the evolution of sexual dimorphism in hood coloration, considered by Miller (1941) to be advanced for the genus. Finally, we think it possible that individual plumage variability in Dark-eyed Juncos is at least partly a byproduct of relatively weak selective pressure for plumage uniformity. For example, variation in the details of hood coloration or tail pattern should not prevent species recognition, as sympatrically breeding emberizines (other than the Gray-headed Junco, *Junco caniceps,* with which *J. hyemalis* interbreeds and may eventually be considered conspecific) do not exhibit the combination of a black or gray hood and white outer rectrices.

Our next consideration pertains to the evolution and hypothetical social significance of individual plumage differences as opposed to sex- or age-related plumage dimorphism. Rohwer emphasizes in general the importance of individual variability and states that, in Harris' Sparrows, "Differences in studliness among individuals much more accurately represent differences in dominance status than do differences in size, or in sex or age class" (Rohwer 1977: 108). Conversely, associations between darkness of hood or whiteness of tail and dominance status in our juncos usually were insignificant within sex or wing-length classes, suggesting that individual plumage variability in this species probably has arisen independently of selective pressure for a social status signaling system. Plumage differences between sex or age classes of juncos might reflect such pressure, although in this case other factors (such as breeding season requirements) also may have played an important role.

We think it unlikely that juncos are strongly predisposed at this stage of their evolution to respond during the winter to plumage cues to sexual dominance status. Relatively dull-plumaged birds were dominant in 18–26% of intersexual relationships among our captives—a much higher proportion than should be expected if plumage cues function as social releasers. We do not know the extent to which age-related plumage variation may be associated with social status in juncos; however, because plumage overlap between ages (like that between the sexes) appears quite extensive, our guess is that such associations may be imperfect and that plumage cues to age-related dominance status are not social releasers. However, plumage differences still might function as conditioned reinforcers. Because male juncos tend to be more aggressive than, and dominant to, females during the winter (Balph 1977a), females may learn to associate male characteristics (such as a dark hood or white tail) with a reduced probability for establishing social dominance. Acquiescence by females should cause males, in turn, to associate female characteristics with an increased likelihood of success. These responses might be generalized to relationships between individuals of like sex but of dissimilar signaled sex; such a secondary effect could be suggested by the weak (for hood darkness) to moderately strong (for tail pattern) positive associations we noted between male-like plumage characteristics and social dominance among members of the same sex in the captive junco flocks. A comparable system of communication might be expected to function between juncos differing in age.

A social status signaling system hypothetically maintained through learned associations might be enhanced in juncos by the form of winter agonistic displays such as the head dance and the tail-up display (Figs. 2 and 3). One could speculate that

selection for a status signaling system has produced displays serving expressly to draw attention to variably plumaged structures. However, we do not favor this explanation, as plumage differences apparently are not releasers in wintering juncos, and as the displays themselves denote threat and quite often can be initiated by the duller-plumaged member of a junco pair. We think it likely that the head dance and the tail-up display have evolved under selective pressures primarily or wholly unrelated to social status signaling, but that juncos nevertheless may respond to plumage information provided by conspecifics during the displays.

Although our evidence is indirect, we believe that Dark-eyed Juncos probably are attentive to plumage cues and that a system of social status signaling might operate in winter flocks. However, the roughness of the associations we observed suggests that plumage attributes probably are not the only cues used by juncos to assess their chances for establishing social dominance. This finding perhaps is not surprising, as factors hypothetically influencing plumage variability in this species appear to be complex, and as work by various investigators suggests that many factors (genetic, maturational, and experiential) may be related to social dominance in juncos. We suspect that juncos might benefit from a capacity to form learned associations between a variety of stimuli (morphological, behavioral, and contextual) and probabilities for competing successfully with conspecifics for essential resources during the winter.

Generality of social status signaling.—If social status signaling occurs in Dark-eyed Juncos, it apparently differs in several respects from the model proposed by Rohwer (1975, 1977). As Rohwer developed his ideas primarily from his work on Harris' Sparrows, a comparison of the status signaling system of Harris' Sparrows with that of juncos, as well as an examination of social status advertisement in some other winter flocking species, may reveal something of the general applicability of Rohwer's model.

Harris' Sparrows, like juncos, exhibit considerable plumage variability during the winter. Rohwer notes that the extent of black relative to white (or brown) feathering on the throat, breast, and crown tends to be greatest in adult males and least in first-year females, with substantial variation within, and overlap between, age/sex classes. Winter plumage characteristics are not influenced by requirements of the subsequent breeding season, as Harris' Sparrows, unlike juncos, undergo a regular prenuptial molt (Baumgartner 1968, Jones and Rohwer 1974). However, plumage patterns of the throat and crown apparently are unstable in certain respects through the winter (Baumgartner 1968), which potentially could complicate the relationship between plumage "studliness" and social rank. In addition, although overlap between age classes is extensive for some plumage characters, wintering first-year Harris' Sparrows exhibit a broad, buffy superciliary stripe almost never found in adults (Baumgartner 1968).

Overall correspondence between "signaled" and actual dominance status may be fairly similar for Harris' Sparrows and juncos. Rohwer (1977: 108) notes that ". . . Harris Sparrows somehow achieve a matching of uncanny accuracy between signaled and actual social status." However, his data (Rohwer 1975: 600) indicate that "studlier" (i.e. blacker) Harris' Sparrows won 76% and 70% of 75 and 44 agonistic chases, respectively. Rohwer (1977) later adds that reversals in the first sample were due primarily to the activity of a single bird, although he does not specify the number of individuals involved in encounters that conformed to prediction. Nevertheless,

his second result (70%) does agree closely with our results for juncos (69% for hood; 72% for tail). Our figures should be conservative as overall estimates, however, as we studied only one age class of juncos. The results for Harris' Sparrows also may be conservative; Rohwer (1975: 600) notes that avoidance interactions (as opposed to chases) ". . . almost never involve reversals where the studlier loses."

Parallels also might exist between Harris' Sparrows and juncos with respect to sources of correspondence between "signaled" and actual social status. Rohwer (1975, 1977) presents no data to support his conclusion that individual plumage differences among wintering Harris' Sparrows predict social position more accurately than do age or sex differences. More recently, he indicates that plumage "studliness" in this species is a good predictor of dominance status *only* when age and sex classes are pooled (S. Rohwer pers. comm.). Hence the extensive plumage variability occurring within age/sex classes of Harris' Sparrows may remain to be explained, although selection for a status signaling system still might have promoted age- or sex-related plumage differences.

If winter plumage variability in Harris' Sparrows is partly a product of selective pressure for a system of status advertisement, mechanisms for the social control of deception seem as yet unclear. Harris' Sparrows, unlike the juncos we observed, apparently fight most frequently with flockmates of dissimilar rather than similar plumage appearance (Rohwer 1975), which should place individuals of low signaled status at a particular disadvantage during the winter and thereby result in selection for "studly" plumage characteristics. However, pale individuals whose throats and crowns were dyed black experienced a sharp *increase* in attacks by dark flockmates (Rohwer 1977). The results of Rohwer's deception experiments, although suggestive, are nevertheless difficult for us to interpret, as the experiments appear to have lacked stimulus control. For example, flockmates might have perceived a dyed or bleached bird (1) as a changed, but familiar, conspecific; (2) as an unfamiliar conspecific; (3) as a different species; or (4) as a bird exhibiting plumage attributes that were incongruous with other cues (whether visual, vocal, morphological, or behavioral). We therefore do not know to what extent parallels may exist between Harris' Sparrows and juncos with respect to behavioral mechanisms possibly serving to maintain intraflock plumage variability.

In sum, it appears that the social status signaling system of Harris' Sparrows might correspond more closely to what we have hypothesized for Dark-eyed Juncos than to the model proposed by Rohwer. In Harris' Sparrows, as in juncos, associations between plumage attributes and social position appear to be imperfect and may depend primarily upon differences of age or sex. Factors responsible for the origin and maintenance of winter plumage variability probably differ for Harris' Sparrows and juncos but could, we suspect, be complex for both. To date, we believe there is no strong evidence to support Rohwer's (1975: 601) statement that "Apparently, such plumage differences serve exclusively to signal social status . . .," as other (sometimes conflicting) requirements quite probably are important among juncos, and as there seems to be little information available on the form or function of visual displays in Harris' Sparrows.

Winter plumage variability in Dark-eyed Juncos and Harris' Sparrows is largely of a continuous nature. However, some other winter flocking species exhibit a bimodal distribution of plumages. Rohwer (1975: 607) raises the important question: "How does status signaling apply to species . . . exhibiting extreme dichromatism,

sexual or otherwise, or non-overlapping age variation?" Our ongoing studies of winter social behavior in the Evening Grosbeak (*Hesperiphona vespertina*), a cardueline finch that shows strong sexual dichromatism, may be relevant to this problem.

Evening Grosbeaks winter in northern Utah in bisexual flocks of medium to very large size. The stability of flock composition and location is considerably less than in Dark-eyed Juncos but possibly varies inversely with the size of a given winter's invasion (Balph and Balph in prep.). We have found that Evening Grosbeaks form stable intrasexual dominance-subordination relationships—based, we believe, upon individual recognition—when winter populations are relatively small, but we suspect that this system tends to break down when flocks are large and unstable. However, a second social system—one that appears to be based upon sexual status advertisement—operates regardless of population size. Male grosbeaks almost always are dominant to females during agonistic encounters (>97% of several thousand recorded interactions). We suspect that the strength of this association may be reinforced by plumage cues to sexual dominance status. Among juncos, by comparison, sexual dimorphism in plumage coloration is incomplete, males are less often dominant to females (82% of relationships in our captive flocks), and conspicuousness of plumage is less strongly associated with actual social position.

Intersexual social status signaling among Evening Grosbeaks might be expected to benefit males to the detriment of females. However, the potential cost to females of lowered social status may be offset by a reduction in intersexual aggression. An analysis of 1,000 1-min samples of agonistic behavior by individual grosbeaks (500 male, 500 female) feeding in flocks at a 0.74 m² provisioned platform indicated that grosbeaks were significantly more likely to engage in agonistic encounters with available conspecifics of the same sex than with those of the opposite sex (Balph and Balph in prep.). Females were as likely to fight with other females as males with other males. Differential spacing of the sexes appeared not to be a factor influencing these results, as sex ratios at the feeding platform were similar to those observed in the crowns of trees (Balph and Balph 1976) and as sexual segregation was not evident upon the platform itself. An analysis of the form of 1,500 agonistic encounters revealed a further difference between intra- and intersexual aggression: the tendency for physical contact or for "bree" threat calls to occur during encounters was significantly greater when birds were of like than of unlike sex but did not differ between male-male and female-female interactions (Balph and Balph in prep.). Hence intersexual aggression among wintering Evening Grosbeaks may be reduced not only in frequency, but also in intensity.

Although we do not yet have direct evidence, we strongly suspect that Evening Grosbeaks are attentive to plumage cues to sexual social status. In particular, we believe that the birds may respond to plumage features of the head and perhaps the wings, both of which figure importantly in this species' agonistic displays and which are much more contrastingly patterned in males than in females. Such cues might operate as conditioned reinforcers in grosbeaks, similarly to what we have hypothesized for juncos but with a quantitative difference: because the signals are a more reliable indicator of a bird's ability to win agonistic encounters in grosbeaks than in juncos, grosbeaks should learn to depend more extensively upon them. Alternatively, one or more plumage cues to sexual social status may be social releasers, in which case selection for a predisposition to respond appropriately might have followed (or perhaps accompanied) the evolution of complete sexual dichromatism.

The intersexual social status signaling system that we have hypothesized for Evening Grosbeaks should benefit birds of both plumage types by reducing the cost of intraspecific aggression. Under most conditions, the advantages of such a system may outweigh the disadvantages of subordinacy for females. Only when crowding at a food patch became quite extreme (86 birds/m² at a 0.07 m² platform) did we find a significant tendency for males to exclude females from positions at the resource (Balph and Balph 1976). A system of intersexual social status advertisement should be particularly advantageous when grosbeak flocks are too large or too unstable in membership to permit individual recognition, as such advertisement could help to control aggression in up to half of all two-bird combinations within a flock.

Factors possibly responsible for the origin and maintenance of winter plumage variability in Evening Grosbeaks may in some respects parallel those hypothesized for Dark-eyed Juncos. In Evening Grosbeaks, as perhaps in juncos, the potential disadvantages of subordinacy among birds of low signaled status may be at least partly neutralized by a reduction of fighting with birds of high signaled status. Evening Grosbeaks, like juncos, exhibit similar breeding and winter plumages and undergo only a slight prenuptial molt, if any (Speirs 1968); hence breeding season requirements may influence winter plumage characteristics. Finally, dominant classes of juncos and (to a much greater degree) Evening Grosbeaks exhibit plumage attributes which, although socially advantageous, may render them more visible than subordinates to predators. Evening Grosbeaks show sexual differences in alarm responses (Balph 1977b) that might function to reduce predation losses and thus promote the continuance of plumage differences signaling social status.

The system of status advertisement we have proposed for Evening Grosbeaks may in some ways resemble those of certain other dichromatic flocking species. For example, Chaffinches (*Fringilla coelebs*), like Evening Grosbeaks, exhibit strong sexual dimorphism and appear to signal sexual social status. Marler (1955a, 1956) found that male Chaffinches were dominant to females in captive winter flocks; however, measurements of individual distance revealed that males were more tolerant of females than of other males. Through a series of experiments, Marler (1955b) demonstrated that the red breast of males is a social releaser evoking aggression. Females dyed to mimic males enjoyed a rise in social status, particularly in relation to other females, but were no longer treated with tolerance by dominant males.

Some other dichromatic species may exhibit quite different systems of social status advertisement. For example, White-throated Sparrows (*Zonotrichia albicollis*) occur in two color morphs that differ both genetically and in aggressiveness. Individuals with white head stripes are more aggressive and socially dominant than those with tan head stripes (Harrington 1973, Ficken et al. 1978). Plumage differences in this species might be expected to signal social status, through learned associations if not through preprogrammed responses. Unlike male Chaffinches or Evening Grosbeaks, white morphs in spring flocks of White-throated Sparrows are equally likely to attack individuals of either morph (Ficken et al. 1978). Plumage dimorphism appears to be maintained through negative assortative mating; white-striped males may monopolize tan-striped females and leave white-striped females to mate with tan-striped males (Lowther and Falls 1968).

In the light of our assessment, we believe that more information on the behavior and ecology of a variety of winter flocking bird species is needed before a satisfactory generalized model of social status signaling can be formulated—if such a model is

possible. Comparative investigations are needed at three levels: (1) studies to ascertain whether or not plumage attributes are associated with social status (in those flocking species exhibiting winter plumage variability); (2) experiments to determine whether or not such associations reflect causal relationships, and if so, the extent to which particular visual cues serve as releasers or conditioned reinforcers; and (3) inquiries into factors possibly responsible for the origin and maintenance of various kinds of winter plumage variability. Comparable studies of vocalizations also could prove of value, as social status signaling might occur in more than one modality. Above all, we think it important to recognize the implications for research in this area of Hailman's (1977: 108) observation that the morphology and behavior of animals are shaped by numerous competing selective pressures and that it is therefore inappropriate to search for a single adaptive function for each trait.

LITERATURE CITED

AGRESTI, A., & D. WACKERLY. 1977. Some exact conditional tests of independence for R × C cross-classification tables. Psychometrika 42: 111–125.

BALPH, M. H. 1975. Wing length, hood coloration, and sex ratio in Dark-eyed Juncos wintering in northern Utah. Bird-Banding 46: 126–130.

———. 1977a. Winter social behaviour of dark-eyed juncos: communication, social organization, and ecological implications. Anim. Behav. 25: 859–884.

———. 1977b. Sex differences in alarm responses of wintering Evening Grosbeaks. Wilson Bull. 89: 325–327.

———, & D. F. BALPH. 1976. Some factors influencing observed sex ratios in a population of Evening Grosbeaks. Bird-Banding 47: 340–344.

BAUMGARTNER, A. M. 1968. *Zonotrichia querula* (Nuttall), Harris' Sparrow. Pp. 1249–1273 *in* Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies (A. C. Bent and collaborators, O. L. Austin, Jr., Ed.). U.S. Natl. Mus. Bull. 237.

BISHOP, Y. M. M., S. E. FEINBERG, & P. W. HOLLAND. 1975. Discrete multivariate analysis: theory and practice. Cambridge, Massachusetts, M. I. T. Press.

DAVID, H. A. 1963. The method of paired comparisons. New York, Hafner Publishing Co.

DAVIDSON, R. R., & P. H. FARQUHAR. 1976. A bibliography on the method of paired comparisons. Biometrics 32: 241–252.

DWIGHT, J., JR. 1900. The sequence of plumages and moults of the passerine birds of New York. Ann. N. Y. Acad. Sci. 13: 73–360.

EATON, S. W. 1968. *Junco hyemalis hyemalis* (Linnaeus), Northern Slate-colored Junco. Pp. 1029–1043 *in* Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies (A. C. Bent and collaborators, O. L. Austin, Jr., Ed.). U.S. Natl. Mus. Bull. 237.

FICKEN, R. W., M. S. FICKEN, & J. P. HAILMAN. 1978. Differential aggression in genetically different morphs of the White-throated Sparrow (*Zonotrichia albicollis*). Z. Tierpsychol. 46: 43–57.

FRETWELL, S. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). Bird-Banding 40: 1–25.

GABRIELSON, I. N., & S. G. JEWETT. 1940. Birds of Oregon. Corvallis, Oregon, Oregon State College.

GRANT, G. S., & T. L. QUAY. 1970. Sex and age criteria in the Slate-colored Junco. Bird-Banding 41: 274–278.

GREULACH, V. A. 1934. Notes on the nesting of the Slate-colored Junco. Auk 51: 389–390.

HABERMAN, S. J. 1974. The analysis of frequency data. Chicago, Illinois, Univ. Chicago Press.

HAILMAN, J. P. 1977. Optical signals: animal communication and light. Bloomington, Indiana, Indiana Univ. Press.

HAMILTON, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31: 295–311.

HARRINGTON, B. A. 1973. Aggression in winter resident and spring migrant White-throated Sparrows in Massachusetts. Bird-Banding 44: 314–315.

HELMS, C. W., W. H. AUSSIKER, E. B. BOWER, & S. D. FRETWELL. 1967. A biometric study of major body components of the Slate-colored Junco, *Junco hyemalis*. Condor 69: 560–578.

HOSTETTER, D. R. 1961. Life history of the Carolina Junco, *Junco hyemalis carolinensis* Brewster. Raven 32: 97–170.

JONES, E., & S. ROHWER. 1974. Spring molt and dominance. Bird Watch 2(9).

KETTERSON, E. D. 1974. Geographic variation in sex ratio among wintering Dark-eyed Juncos (*Junco hyemalis*). Unpublished Ph.D. dissertation, Bloomington, Indiana, Indiana Univ.

———, & V. NOLAN, JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). Ecology 57: 679–693.

LOWTHER, J. K., & J. B. FALLS. 1968. *Zonotrichia albicollis* (Gmelin), White-throated Sparrow. Pp. 1364–1392 *in* Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies (A. C. Bent and collaborators, O. L. Austin, Jr., Ed.). U.S. Natl. Mus. Bull. 237.

MARLER, P. 1955a. Studies of fighting in Chaffinches. (1) Behaviour in relation to the social hierarchy. Brit. J. Anim. Behav. 3: 111–117.

———. 1955b. Studies of fighting in Chaffinches. (2) The effect on dominance relations of disguising females as males. Brit. J. Anim. Behav. 3: 137–146.

———. 1956. Studies of fighting in Chaffinches. (3) Proximity as a cause of aggression. Brit. J. Anim. Behav. 4: 23–30.

MILLER, A. H. 1941. Speciation in the avian genus *Junco*. Univ. Calif. Publ. Zool. 44: 173–434.

NERO, R. W. 1963. Birds of the Lake Athabasca region, Saskatchewan. Saskatchewan Nat. Hist. Soc., Spec. Publ. No. 5.

RADLOW, R., & E. F. ALF, JR. 1975. An alternate multinomial assessment of the chi-square test of goodness of fit. J. Amer. Stat. Assoc. 70: 811–813.

ROHWER, S. 1975. The social significance of avian winter plumage variability. Evolution 29: 593–610.

———. 1977. Status signaling in Harris Sparrows: some experiments in deception. Behaviour 61: 107–129.

SABINE, W. S. 1949. Dominance in winter flocks of juncos and tree sparrows. Physiol. Zool. 22: 64–85.

———. 1955. The winter society of the Oregon Junco: the flock. Condor 57: 88–111.

———. 1956. Integrating mechanisms of winter flocks of juncos. Condor 58: 338–341.

———. 1959. The winter society of the Oregon Junco: intolerance, dominance and the pecking order. Condor 61: 110–135.

SAMSON, F. B. 1977. Social dominance in winter flocks of Cassin's Finch. Wilson Bull. 89: 57–66.

SHIELDS, W. M. 1977. The social significance of avian winter plumage variability: a comment. Evolution 31: 905–907.

SPEIRS, D. H. 1968. *Hesperiphona vespertina vespertina* (Cooper), Eastern Evening Grosbeak. Pp. 206–237 *in* Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies (A. C. Bent and collaborators, O. L. Austin, Jr., Ed.). U.S. Natl. Mus. Bull. 237.

VINE, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. J. Theor. Biol. 30: 405–422.

WOOD, H. B. 1951. Development of white in tails of juncos, *Junco hyemalis*. Auk 68: 522–523.