STATUS SIGNALING IN DARK-EYED JUNCOS

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ABSTRACT.—Rohwer (1975, 1977) has proposed that members of certain variably-plumaged avian species may use plumage traits to signal potential dominance status to flockmates. Further, he suggests that plumage variability is maintained because cheaters on the system are detected and persecuted. Data reported herein imply that certain external and noticeable traits of Dark-eyed Juncos (*Junco hyemalis*) are fairly accurate indicators of sex and age class and thus, indirectly, of dominance status. Convergence on signals associated with high status may be prevented by a social system in which dominants are more likely to direct aggressive behavior toward other dominants than toward subordinates. Under such a system, birds whose other traits would lead to subordinate status would suffer a disadvantage if they wore the plumage of dominants. Accurate projection of potential status, whatever that status may be, should prove selectively advantageous. *Received 14 June 1978, accepted 5 September 1978.*

As Rohwer (1975, 1977) has recently noted, some bird species in winter exhibit plumage variability that cannot readily be accounted for by current eco-evolutionary theories such as mimicry, crypsis, or predator/prey-mediated frequency-dependent selection. In these species, certain plumage types seem to be associated with social dominance and other types with subordinance, and he suggests that plumage differences may serve to signal the individual's potential dominance status.

The status-signaling hypothesis produces an apparent paradox: if social dominance is advantageous, then how is plumage variability maintained? Why has not directional selection resulted in monomorphism for the dominant plumage? Rohwer offers two alternative explanations. First, dominant status or correlates thereof may not always be advantageous; traits of subordinates may be favored in some habitats. Secondly, where dominance confers an advantage, convergence on the dominant plumage may be prevented by social regulation of cheating: if subordinate birds were to signal falsely that they were dominant, they would be detected by the true dominants and persecuted.

Consideration of the status-signaling hypothesis will probably be facilitated by separate consideration of the two questions: (1) Does plumage signal potential status? (2) Is plumage variability maintained by social regulation of cheating? Here I describe external cues to potential winter dominance status in the Dark-eyed Junco (*Junco hyemalis*) and offer observations on the maintenance of variability in these cues.

External cues.—Some predictors of dominance in wintering juncos are sex, age, body size as measured by wing length, and arrival date on the wintering grounds as indicated by order of capture (Sabine 1959, Fretwell 1969, Balph 1977, Ketterson 1979, Baker and Fox 1978). Males dominate females, and adults of each sex tend to dominate subadults. Body size is positively correlated with rank, and early arrival confers a dominance advantage. It is not presently possible to determine the mechanisms responsible for the association between these factors and dominance—for example, males may differ physiologically from females in ways that make them more aggressive—but the mechanisms seem irrelevant to the status-signaling hypothesis. The model predicts only that plumage should provide external cues to potential status and that it should be selectively advantageous to heed such cues.

To biologists, juncos provide several external cues to potential status; I shall assume that juncos themselves are at least as able as humans to use those cues. The plumages of the sex and age classes fall into four broadly overlapping categories differing in darkness of color, streaking of the crown, extent of white in the tail, and distribution and number of brown-tipped feathers (Miller 1941, Grant and Quay 1970, Ketterson and Nolan 1976). Additionally, Yunick (1977) has shown that sub-adult juncos have a grayish-brown iris which changes progressively during their first winter to the red-brown or dark-brown that is characteristic of adults.

Some might argue that the status-signaling hypothesis is interesting only if status is signaled by variability in external cues that are independent of sex and age (Shields 1977), but it seems to me that the value of this hypothesis lies in its potential ability to explain why the sex and age classes (or any other class) should be recognizably different during the nonbreeding season. One purpose of this work is to determine the accuracy with which I can assign juncos to sex and age class on the basis of readily perceivable external cues.

Maintenance of variability.—If external cues signal status, then why does not selection favor convergence toward the dominant signals? It does not seem likely that dominant status in a wintering flock of juncos ever causes a net disadvantage. Fretwell (1969) has shown that dominants banded early in winter are more likely than subordinates to be present in a free-ranging flock at winter's end, and Baker and Fox (1978) have demonstrated higher probability of survival of dominant captive juncos when food is restricted. Yet juncos may reveal their sex and youth, hence subordinate status, by plumage and eye color. If it is physiologically possible for the young to alter eye color by spring, and some do so much sooner, then it is arguable that if it were advantageous to do so, adult signals would be assumed earlier in life. Apparently it is adaptive to retain some juvenile and subordinate traits at least until the first breeding season approaches. Perhaps an individual that is likely to be subordinate in winter gains more by signaling its potentially subordinate status than by mimicking dominant individuals.

What may be the pressure that causes probable subordinates to reveal that fact by their appearance? Rohwer observed disproportionate attack upon initially subordinate Harris' Sparrows (*Zonotrichia querula*) whose appearance he had experimentally altered to make them look like dominants. The altered birds were persecuted by the dominants and began to feed alone or at the periphery of the flock. However, Rohwer's work may be criticized because (1) his samples were small (although his results were statistically significant), and (2) he altered birds already belonging to the flock and presumably known to flockmates as subordinate. Even if the altered birds were not individually recognized after the alteration, they themselves had a history of subordinance and might be expected to withdraw from flockmates whose behavior toward them changed (see Shields 1977 for further comment).

Still, social regulation of cheating seems a viable mechanism worth further consideration. If dominants are more frequently aggressive toward (i.e., "test") individuals that signal potential dominance than toward individuals signaling potential subordinance, and if there is some upper limit on the number (or percentage) of dominants tolerated within a flock (e.g., an evolutionarily stable strategy, Maynard Smith and Price 1973, Maynard Smith and Parker 1976), then it would be disadvantageous to look like a dominant if an individual were unable to withstand the

TABLE 1. Utility of plumage traits and eye coloration to determine sex and age class in wintering Dark-eyed Juncos. Determinations based on plumage alone or on plumage and eye color were compared with determinations made on the basis of a combination of plumage, wing length, skull ossification, and occasional laparotomy.

Category	Accuracy			
	Plumage alone[a]		Plumage and eye color[b]	
Adult male[c]	76%	(n = 37)	87%	(n = 31)
Subadult male	88%	(n = 83)	97%	(n = 33)
Adult female	33%	(n = 12)	100%	(n = 9)
Subadult female	100%	(n = 46)	85%	(n = 27)

[a] Determinations were made October–December 1977 near Bloomington, Indiana (n = 157) and Portage, Ohio (n = 20).
[b] Determinations were made October–November 1978 near Bloomington, Indiana.
[c] Subadults are birds hatched during the preceding breeding season; adults were hatched in any prior breeding season.

testing. Thus another purpose of this paper is to determine whether dominants direct a disproportionate amount of their aggressive behavior toward other dominants.

METHODS

External cues.—Judging by plumage traits alone (Ketterson and Nolan 1976), in the fall and early winter of 1977–1978 I quickly sexed and aged 178 juncos in the hand and then checked these determinations by more deliberate methods believed to be completely accurate (plumage, wing length, skull ossification, and laparotomy in doubtful cases of sex). In the fall of 1978 I repeated this exercise on another 100 juncos, but also considered eye coloration.

Maintenance of variability.—To test whether the social system of juncos could serve to maintain plumage variability, I considered the data of Sabine (1959) on junco dominance hierarchies. For each individual belonging to her most intensively studied flocks (Seattle flock and feeding station flock 1959, Figs. 4 and 1), I first determined the number of birds that each individual dominated. Considering then only each individual's subordinates, I counted the number of aggressive actions an individual directed toward the top half of its array of subordinates and compared that result with the number directed toward the bottom half of the same array. If the number of an individual's subordinates was uneven, then interactions involving the middle bird were divided by two, and half was assigned to each half of the array. This process produced Sabine's observed numbers (see Table 2). To obtain expected numbers of aggressive behaviors toward each half of each individual's subordinates, it was necessary to account for possible rank-associated differences in attendance at Sabine's feeders. To do this, for each array of subordinates I counted all the interactions engaged in by members of the top half, then did the same for members of the bottom half. If, for example, members of the top half of an array were involved in a total of twice as many interactions as were members of the bottom half, this might imply that they were present at the feeder twice as often and thus had twice the opportunity to become the focus of aggression by their top dominant.

Finally, for each individual I found the ratio of aggressive behaviors directed toward the top half of its subordinates (T) to aggressive behaviors directed toward the bottom half (B) and compared observed T:B with expected T:B. The null hypothesis was that observed T:B should exceed expected T:B in only half the cases (see Table 2).

RESULTS AND DISCUSSION

External cues.—Results in Table 1 indicate that on the basis of plumage alone, all subadult females and most adult and subadult males, but few adult females, were recognizable by my quick inspection. Consideration of eye color as well as plumage facilitated recognition of all sex and age classes except subadult females and led to recognition of 91% of the individuals inspected.

Perfect projection of potential dominance status during winter by plumage is not to be expected in juncos. Unlike Rohwer's Harris' Sparrows, juncos undergo a very limited prenuptial molt that involves fewer than all feathers of the head. Therefore,

TABLE 2. Analysis of a junco dominance hierarchy (Sabine 1959, Fig. 4, Seattle flock) to determine whether dominants tend to fight among themselves more often than with subordinates.

Bird	Observed[a]			Expected[b]		
	Top half	Bottom half	Ratio	Top half	Bottom half	Ratio[c]
1	119	68	1.75	2,215.5	1,935.5	1.14
2	128	64	2.00	2,066	1,872	1.10
3	61	43	1.42	2,073.5	1,722.5	1.20
4	127	89	1.43	1,950	1,573	1.24
5	27	17	1.59	1,951	1,479	1.32
6	48	35	1.37	1,901	1,383	**1.37**
7	64.5	38.5	1.68	1,823	1,305	1.40
8	57	12	4.75	1,775	1,227	1.45
9	56.5	33.5	1.69	1,602	1,201	1.33
10	43	27	1.59	1,469	1,175	1.25
11	75.5	49.5	1.53	1,393.5	1,035.5	1.35
12	88	67	1.31	1,309	896	**1.46**
13	58.5	38.5	1.52	1,173.5	825.5	1.42
14	24	16	1.50	1,117	755	1.48
15	73	71	1.03	871	702	**1.24**
16	27	25	1.08	734	649	**1.13**
17	32	30	1.07	644.5	582.5	**1.10**
18	8	9	0.89	659	516	**1.28**
19	24.5	8.5	2.88	412.5	483.5	0.85
20	10	7	1.43	304	451	0.67
21	9	7	1.29	277	372	0.74
22	7	8	0.88	223	293	0.76
23	3.5	2.5	1.40	229	222	1.03
24	10	5	2.00	142	151	0.94

[a] Observed indicates number of displacements directed by a bird toward members of the top and bottom halves of its respective array of subordinates.

[b] Expected is based on availability for displacement as indicated by relative total involvement in aggressive interactions by members of top and bottom halves of each array of subordinates. From the original dominance hierarchy matrix (Sabine 1959), I computed row and column totals for each individual, then summed these for members of the top half of an array and compared the sum to that obtained from the bottom half.

[c] Boldface entries indicate results contrary to prediction, i.e. members of bottom half of array were the objects of displacement more often than indicated by the index of their relative availability for displacement.

even if plumage serves to signal status in winter, it obviously may have other functions in the breeding season and thus be subject to counterselective pressures.

Still, juncos may be able to make finer predictions of potential status than indicated by the data in Table 1. Small but significant differences in size (wing, tail, tarsal and bill length, bill depth) distinguish sex and age classes (Ketterson and Nolan unpublished data) and are associated in a probabilistic manner with status; so juncos may also perceive and utilize this information to evaluate a prospective opponent's likely status.

Further, within each sex and age class, variation is found in both plumage coloration and eye color. Subadult males are the most variable in plumage, ranging from light to charcoal gray and differing markedly in the amount of brown on the back and crown. By early November, 3% of subadults (both sexes) exhibit adult eye coloration; yet by mid-April some are still recognizable by eye color (Yunick 1977, personal observation). Whether this last level of variability is associated with social dominance is not known, but it is a possibility. Black-capped Chickadees (*Parus atricapillus*) hatched early in the breeding season (as judged by degree of skull ossification in early winter) tend to be dominant over members of their year class hatched later (Glase 1973).

The data presented here do not, of course, demonstrate that juncos employ status signaling. What they do indicate is that juncos may be readily assigned to sex and age class and, because sex and age are good predictors of dominance status within

a flock, project information that is capable of being used by opponents in evaluating potential status.

Maintenance of variability.—Of the 26 juncos belonging to Sabine's Seattle flock (1959, Fig. 4) only the 24 that dominated at least 2 individuals (i.e., enough to provide a top and bottom half) could be considered (Table 2). Of those, 18 displaced members of the top half of their array of subordinates more often than predicted, and 6 displaced members of the bottom half more often (75%; 95% confidence limits 54.7% to 90.1%). If directing aggression toward another may be considered a kind of "testing," this result may be taken to indicate that dominants test other dominants more often than they test subordinates. However, when the same analysis was performed on the feeding station flock (1959, Fig. 1), the results were ambiguous (data not shown). Only 15 of 25 juncos (60%) displaced members of the top half of their array more often than predicted (95% confidence limits 38.7% to 78.9%). Nevertheless, for both flocks the results clearly differ from those of Rohwer (1977). Whereas he reports that fighting in the Harris' Sparrow is despotic, with dominants focusing a disproportionate number of attacks on the lowest-ranking birds, Sabine's results (as interpreted here) are consistent with the idea that juncos tend to be more aggressive toward stronger rivals.

An obvious criticism of my analysis lies in the method of calculating expected values. The assumption that number of aggressive interactions engaged in can be equated with attendance at a feeder is questionable, as it is well known that subordinates of many species avoid interaction with dominants even when both are present. Still, this tendency to avoid interaction should affect the observed ratio as well as the expected, and may not damage the conclusion. In any case, the analysis is rough and the question of whether dominants tend to be more aggressive toward other dominants should be approached directly. However, other observations of juncos tend to support the conclusion reached on Sabine's data. Ketterson (1979) found male-male interactions to occur more often than expected on the basis of the frequency of males in a flock, and female-female interactions to occur less often.

Infighting among dominants could arise in two ways, only the first of which seems relevant to the hypothesis that such fighting is responsible for the maintenance of variability in external cues to potential status. Dominants might fight more frequently among themselves (1) because dominants recognize stronger rivals by external cues and are more aggressive toward them, or (2) if higher-ranking birds are more persistent in approaching superiors and consequently elicit more attacks by violating individual distance. I cannot add to the discussion of these alternatives at this time.

In summary, juncos vary sufficiently in appearance to justify the prediction that the information thus made available may be used by potential opponents in winter flocks. Convergence toward the complex of dominant signals may be prevented by a net advantage to subordinates in admitting, so to speak, their status. Unwarranted signaling of dominant status may attract the attention of true dominants and result in dissipation of energy, diminished access to resources, or even denial of flock membership for pretenders. While it probably is not advantageous to be subordinate, it may well be advantageous to give the signals of subordinance if that is one's likely status anyway.

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