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STATUS SIGNALING IN DARK-EYED JUNCOS: PERCEIVED STATUS OF OTHER BIRDS AFFECTS DOMINANCE INTERACTIONS[1]

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In a number of avian species, individual members of the species vary considerably in appearance. Differences in plumage coloration may be correlated with social status (Rohwer 1975, Whitfield 1987, Butcher and Rohwer 1989). The status-signaling hypothesis states that variation in plumage has evolved to signal differences in individuals' abilities to win agonistic contests (Rohwer 1975, 1977, Butcher and Rohwer 1989). The fundamental assumption is that coloration is a reliable predictor of rank, so that an individual's color at least partially determines its acquired rank during hierarchy establishment (Rohwer 1985). According to this hypothesis, superior fighters benefit from distinctive color markings ("badges of status") because they reduce either the number or intensity of contests in which they are involved in order to maintain dominant status or priority access to resources (Rohwer 1985).

In addition, plumage variability may facilitate individual recognition (Shields 1977, Whitfield 1986, 1987, Rohwer and Røskaft 1989). Individuals that are superior fighters may benefit from clearly signaling their identity since it will lead to a reduced number of contests repeated with the same individuals (Whitfield 1986, 1987, Rohwer and Røskaft 1989).

Potential badges have been identified in a wide variety of avian species (Rohwer 1975, Whitfield 1987). However, experiments involving the manipulation of plumage have sometimes had mixed results: in some cases the manipulations resulted in changes in rank and in others they did not. For example, in White-crowned Sparrows (*Zonotrichia leucophrys*), the contrast in the crown stripes has been shown experimentally to signal status between age and sex classes, but in the closely related White-throated Sparrow (*Z. albicollis*), there appears to be no relationship between crown pattern and status (Fugle et al. 1984, Watt 1986). Although plumage characteristics were correlated with dominance status in both Harris' Sparrows (*Z. querula*) and Dark-eyed Juncos (*Junco hyemalis),* when subordinates of these species were dyed to mimic dominants, many of these cheaters did not rise in social status because their badge was constantly being checked (detected and persecuted) by already established dominants (Rohwer 1977, Holberton et al. 1989).

Plumage alone may not be sufficient to determine dominance; appropriate behaviors may also be needed (Shields 1977, Rohwer and Rohwer 1978, Cristol 1995a). In most research to date, the plumage of focal birds was manipulated, but the bird being manipulated was still viewing its peers in the same manner, and thus might not be expected to alter its behavior. When subordinate Harris' Sparrows were both dyed and injected with testosterone, the birds became successful

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cheaters (Rohwer and Rohwer 1978). However, this study only suggests that behavior is necessary; it does not directly test the effect of color by itself.

If the plumage of both dominants and subordinates is manipulated and the behaviors of both are observed and recorded, a more reliable test of the value of the badge of status can be obtained because each individual of the pair will be both wearing a different badge and viewing its peer in a different manner. We predict that by altering all individuals in a group, rather than just one or a few, dominance changes will be pronounced and unambiguous in all groups.

Dark-eyed Juncos (*Junco hyemalis*) are relatively small (20 g), migratory sparrows that are slate-gray or gray-brown with a white abdomen. They form relatively stable flocks with a hierarchically organized social system during the winter months and exhibit a considerable amount of plumage variation (Balph et al. 1979, Ketterson 1979, Holberton et al. 1989, Cristol 1992). The darkness of the head and body plumage, the amount of white in the tail, age, sex, size, and aggressiveness have all been shown to be correlated with status (Balph et al. 1979, Holberton et al. 1989). By manipulating both individuals of known relative status in dyads, each individual will perceive the other as different, and we should expect to see a reversal in dominance. In addition, if the variable plumage functions to signal individual identity, changing the plumage should result in an increase in aggression as individuals test each other (Whitfield 1986, 1987).

METHODS

Wild Dark-eyed Juncos were captured via Potter traps at baited sites in Meadville, Crawford County, Pennsylvania, from late November to late December 1994. On the day of capture, sex, age, mass, left wing chord length (to the nearest 1 mm), and capture date were recorded. Sex was determined by head and body plumage and wing chord length (Ketterson and Nolan 1976, Pyle et al. 1987). Only adults (birds greater than one year of age), as determined by skull pneumatization (Ketterson and Nolan 1976, Pyle et al. 1987) were used in this study. Mass was determined to the nearest 0.1 g using an electronic balance. Each bird was fitted with a unique combination of color bands. All birds were visually isolated from one another in 30 × 30 × 60 cm wire cages for at least ten days prior to experimentation to alleviate the stresses of capture and handling (Holberton et al. 1989). While captive they were fed a mixture of cracked corn, hulled and whole sunflower seeds, and a wild bird seed mixture and provided with fresh water ad libitum. Twice a week, an avian vitamin supplement was added to the water supply.

After the transition period, the establishment of dyad relationships began. In order to control for extraneous variables and to focus on plumage variability, juncos were matched as follows: body mass (within 1 g); wing length (within 1 mm); sex (male or female); and capture date (within 10 days) (Cristol 1992). By matching for age and sex, our dyads were also closely matched for plumage color.

After pairing birds into dyads, they were introduced to a 30 × 30 × 60 cm test cage that contained two perches, one at each end of the cage, and single dishes of food and water centrally located in the cage in order to provoke and catalyze disputes between dyad members. The birds were allowed to establish either dominant or subordinate status within their dyad for 90 min. The number of agonistic contests won by both members of each dyad was recorded. An agonistic contest win was defined as a displacement of one bird's position over the other or a successful defense of position after a provoked encounter by the other bird. A subject was classified as dominant if it displaced its partner more often than was expected by chance alone, based on a binomial distribution (Holberton et al. 1989). All observations took place from a behind a blind in order to reduce external distractions.

The sample included five pairs of males and four pairs of females. There were two randomly selected control groups (both a female and a male dyad) and seven experimental groups in the sample. Following the establishment of nine dyads and determination of the initial social status, head and mantle plumage was manipulated. In the experimental group, the dominant birds' plumage was lightened by a non-toxic, water-soluble white shoe polish which was applied with a cotton applicator. The subordinates' plumage was darkened with a dilute solution of India Ink using the same method. The control dyads received the same treatments as the experimentally manipulated dyads, including the same methods for dominance establishment, but only received sham manipulations that consisted of applying hair shampoo and warm water instead of dyes or lighteners. Immediately following the manipulations, the birds' plumage was dried first with a paper towel and finally with a quiet electric hair dryer. After the plumage was dried, the birds were isolated from one another for at least forty-eight hours before further experimentation took place to allow them to recover from the stresses of manipulation.

After all plumage manipulations were completed, the birds were reinstated into their original dyads under the same conditions as the pre-manipulation trials. Birds were permitted to establish a new dominance rank (achieved by the same process as previously indicated for initial dominance rank establishment). All data were recorded in the same manner as in the pre-manipulation trials. Upon completion of the experiment, the dyes were washed from the birds' plumage before the birds were released at their capture site.

Because of small sample sizes and possible deviations from the assumptions of most parametric tests, we used a non-parametric analog of an analysis of variance (ANOVA) by rank transforming our data and then performing a repeated measures ANOVA on the ranks (Conover and Iman 1981).

RESULTS

Matching birds for mass appeared to control the effect of this potentially confounding variable. The heavier bird of each dyad was dominant in five of the eight trials (Sign test, $P = 0.73$). The bird with the larger wing was dominant in six of seven dyads where there was a difference in wing length, but this trend was not significant ($P = 0.12$).

The effect of the dyads' sex and the experimental treatment on the total number of aggressive encounters per dyad before and after manipulation were examined using a nonparametric repeated measures ANOVA (Conover and Iman 1981, Abacus Concepts, 1989). Males had significantly more aggressive encounters than females ($F_{1,4}$ = 63.8, P = 0.0013), but the sex of the dyad did not otherwise influence the results, as there were no significant interactions between sex and any other variables ($P > 0.1$ for all 2 and 3-way interactions). There were significantly fewer encounters following treatment than before ($F_{1,4}$ = 10.6, P = 0.031), perhaps the result of increased familiarity with either the experimental arena or with each other (Fig. 1). There was no significant interaction between treatment (experimental or control) and time (before or after manipulation) ($F_{1,4}$ = 0.49, P = 0.52), suggesting that the manipulations did not affect individual recognition.

In all dyads, there was a clear dominance relationship prior to experimental manipulation of plumage, with the dominant individual winning 82–97% of the encounters in all trials. Following the experimental plumage manipulation, the situation reversed, with the former dominant winning fewer than 40% of the encounters (Fig. 2). Controls, on the other hand, did not exhibit a reversal of dominance; if anything, the relationship became more clear cut, perhaps due to increased familiarity. This is demonstrated by a significant interaction between treatment (experimental manipulation or control) and time (before or after treatment) on the proportion of encounters won by the original dominant (Table 1). Although there was a significant difference between male and female dyads (dominant males won a larger proportion of encounters than did dominant females), the sex of the dyad did not affect the change in aggressiveness, as there were no significant 2- or 3-way interaction terms involving sex (Table 1).

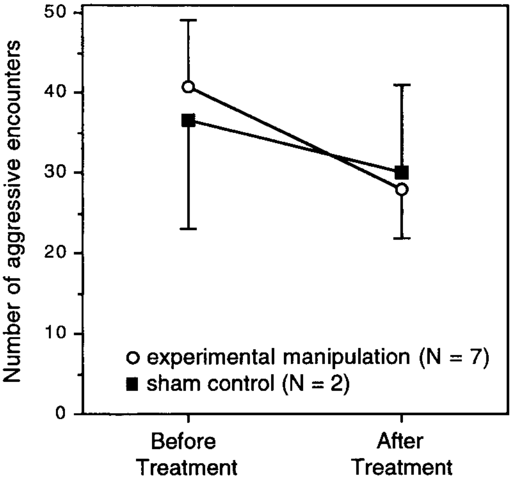

FIGURE 1. The total number of aggressive encounters per 90 min observation period in dyads of Dark-eyed Juncos before and after experimental or sham control plumage manipulations. The sexes are pooled. Only one standard error bar is shown for clarity.

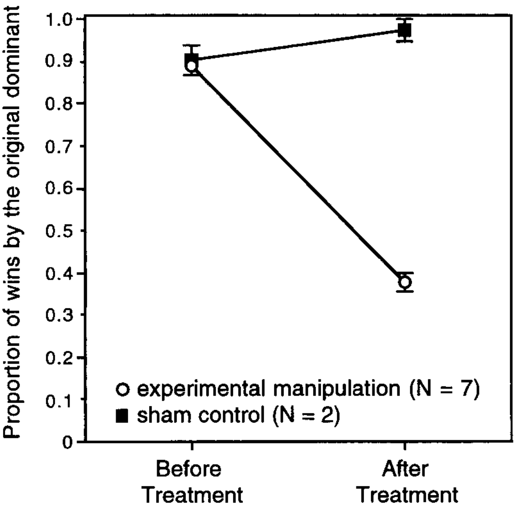

FIGURE 2. The proportion of interactions (mean ± SE) won by the original dominant bird before and after plumage manipulation. The sexes are pooled.

Although we did not subdivide our observations into smaller time periods to quantify this, our impression was that early in the post-manipulation experimental trials, the darkened original subordinate won virtually all of the agonistic contests, but near the end of the experimental time allotment the original dominant began winning more agonistic contests.

DISCUSSION

Despite small sample sizes, we obtained clear, unambiguous results; in all seven experimental dyads, dominance reversals were evident after the plumage of the original subordinate was darkened and that of the original dominant was lightened. There was no such change in our controls, which is consistent with other studies that have found dominance relationships to remain

TABLE 1. Nonparametric repeated measures analysis of variance (see text) of the effects of experimental treatment and sex on the proportion of wins by the original dominant before and after treatment.

Source of variation	*F*	df	*P*-value
Between subjects			
Treatment (experimental or control)	42.9	1,4	0.0028
Sex (male or female)	12.3	1,4	0.0247
Treatment*Sex	0.039	1,4	0.85
Within subjects			
Time (before or after treatment)	1.09	1,4	0.355
Time*Treatment	21.4	1,4	0.0098
Time*Sex	0.418	1,4	0.55
3-way interaction	0.299	1,4	0.61

stable in captive groups or dyads of this species (Holberton et al. 1989, Cristol 1995b). These results are consistent with the hypothesis that variable plumage color in the Dark-eyed Junco serves as a signal of social status. The failure of some previous studies (Rohwer 1977, Watt 1986, Whitfield 1986, Holberton et al. 1989) to get consistent dominance reversals may be due to the fact that the manipulated individuals still perceived their unmanipulated flock mates in the same manner as before and continued to behave subordinately to them. The familiarity between flockmates also can influence the outcome of social interactions with strangers (Cristol 1995a).

If the variable plumage of Dark-eyed Juncos functioned in individual recognition, we would expect that alteration of the plumage would inhibit recognition and lead to an increase in aggressive contacts as individuals try to determine their relationships (e.g., Whitfield 1986, 1987). Since we did not observe such an increase, it seems likely that the head and mantle color play little role in individual recognition in this species.

If plumage darkness signals dominance, subordinates might be expected to cheat by growing darker feathers and rising in social status, since mimicking the dominant plumage should be both energetically and evolutionarily easy (Studd and Robertson, 1985). Although it may be possible for an individual to fake a badge of dominance, there is no advantage for an individual who is not capable of equating its fighting ability and aggressiveness to its faked badge of status, since adoption of a more costly but equally successful behavioral strategy would be necessary to actually increase status level (Studd and Robertson, 1985). In our study the "cheaters" (originally subordinate birds with darkened plumage) achieved at least a short-term rise in social status, but we suspect that this change in status may be temporary since the original dominant of each dyad began to win more contests late in the experimental time allotment. Had the experimental time period been longer, the original dominant may have resumed its dominant status.

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