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PLUMAGE BRIGHTNESS AND BREEDING-SEASON DOMINANCE IN THE HOUSE FINCH: A NEGATIVELY CORRELATED HANDICAP?¹

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Abstract. A variety of observations indicate that the carotenoid-based coloration of male House Finches (*Carpodacus mexicanus*) is an honest signal of quality. Plumage redness in this species positively reveals male

nutritional condition, over-winter survival, and nest attentiveness. As a result, in the breeding season, male House Finches with brighter ornamental plumage are preferred by females as social mates over males with drabber plumage. In the nonbreeding season, however, bright red plumage does not seem to confer an advantage in aggressive interactions, as males with drabber plumage tend to dominate males with brighter plumage. We investigated this apparent paradox by conducting a breeding-season dominance experiment us-

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ing captive males. We paired unfamiliar males of contrasting plumage brightness in a series of dominance trials during the breeding season and found that drabber males were dominant to brighter males in competition for access to food. Furthermore, in two captive flocks of males, plumage brightness was significantly negatively associated with social dominance. Although we have no conclusive evidence to explain why drab male House Finches are dominant to bright males throughout the year, we believe that motivational asymmetry may contribute to the observed negative correlation between signal intensity and signaler quality ("negatively correlated handicap"). Drab males may be more willing to compete for access to food or to females than are bright males because of the nutritional and/or mating disadvantages from which they suffer.

Key words: aggression, *Carpodacus mexicanus*, House Finch, plumage coloration, social dominance.

The House Finch (*Carpodacus mexicanus*) is a sexually dichromatic passerine in which males display carotenoid-based ornamental plumage coloration (Brush and Power 1976). Female House Finches prefer to mate with bright red males over drab orange and yellow males (Hill 1990, 1991, Hill et al. 1999), and bright males seem to provide considerable fitness advantages to their mates. Bright males feed their mates more often during incubation than do drab males (Hill 1991). Redder males are in better nutritional condition during molt than are duller males (Hill and Montgomerie 1994), as they begin molting earlier in the year and grow feathers faster during molt. They also seem to have fewer parasites (Thompson et al. 1997, Brawn et al., in press) and increased access to food (Hill, in press) and to carotenoid pigments (Hill 1992, 1993a). Lastly, male redness is positively associated with both over-winter survival (Hill 1991) and survival during a mycoplasmal conjunctivitis epidemic (Nolan et al. 1998).

However, bright male House Finches do not appear to have the upper hand in all social contexts. A number of captive and wild studies conducted in the nonbreeding season suggest that dull males are dominant to bright males in contests over access to food (Brown and Brown 1988, Belthoff and Gauthreaux 1991, Belthoff et al. 1994). This apparent paradox—where male plumage redness is positively associated with both health and sexual attractiveness during the breeding season but is negatively associated with social dominance during the nonbreeding season—warrants further investigation, particularly because the relationship between male dominance and plumage brightness has not been studied during the breeding season. There may be fundamentally different factors that mediate aggression in the breeding and nonbreeding seasons (e.g., circulating levels of breeding hormones, mating status; Wingfield et al. 1987) and males may have more to gain in the form of mating advantages by displaying bright plumage during the breeding season.

Consequently, we conducted a study of breeding-season dominance among male House Finches in order to consider the relationship between male aggression and plumage brightness. Although male aggression

during the breeding season occurs in two primary contexts in this species—in the presence of food and in the presence of females (Thompson 1960a, 1960b, Hill 1993b)—we focused solely on male agonistic interactions at food sources in our experiments. Aggressive competition over food among male House Finches in the wild is likely to occur at concentrated food sources and, given the nonterritorial and vagile nature of House Finches, it is common for interacting birds to be unfamiliar with one another. Therefore, in this study, we simulated natural conditions in a captive setting by staging short-term encounters between unfamiliar males of contrasting plumage coloration. We subsequently tested for the relationship between male plumage brightness and win/loss outcome in these paired trials. To understand the long-term resource-holding potential of males, we also considered the relationship between plumage coloration and dominance rank in stable flocks of captive birds during the breeding season.

METHODS

We conducted our study of dominance behavior in male House Finches during the breeding seasons (March–August) of 1998 and 1999. In November of 1997 and 1998, we captured male House Finches at feeders from each of two sites in Lee County, Alabama. The sites were separated by approximately 10 km and we assume that birds caught from separate sites had no prior experience with one another. We included only first-year male House Finches in our study; age was determined at capture by the degree of skull ossification (Pyle et al. 1987). Birds were marked with a unique combination of colored leg bands and placed into separate outdoor cages of 7–10 birds each that were visually, but not acoustically, isolated from one another to maintain unfamiliarity between the birds from the two sites. The presence of many captive birds at this site and the spatial separation of individuals minimized the ability of males to become acoustically familiar with one another. Two captive flocks of birds were created in 1998 and four in 1999. All birds were fed a diet of sunflower seeds, millet, water, and vitamins, and the presence of two seed dishes in each cage minimized food resource control by dominant males and presumably allowed all males to feed ad libitum.

Date of entry into the flock was recorded for all birds so we could examine prior residency as a potential correlate of dominance (after Holberton et al. 1990). At capture, we took standard measurements of flattened wing chord length, bill length (exposed culmen), and tail length to the nearest mm (after Pyle et al. 1987). We also determined body mass to the nearest 0.1 g with a scale. Using these four body size measures, we calculated a single body size index for all males using a principle component analysis (PCA). The first principle component (PC1) accounted for 44% of the variation in body size measurements and eigenvectors from PC1 ranged from 0.32 to 0.63, indicating positive correlations among the four body size measures. We calculated body size indices for trial males using body masses that were obtained just be-

fore males participated in a trial instead of those masses obtained at capture.

We estimated degree of infestation with wing feather mites using the five-point scale of Thompson et al. (1997). Males infected with avian pox or *Mycoplasma gallisepticum* were not included in this study. Plumage coloration was quantified as hue, saturation, and brightness using a Colortron reflectance spectrophotometer (Hill 1998). We used mean hue as our measure of plumage ornamentation and calculated mean hue as the arithmetic average of three hue scores for each of the regions of plumage pigmentation in males (crown, breast, rump); by arbitrary convention the Colortron assigns a lower score to redder birds and a higher score to orange and yellow birds.

For each of the six flocks, we accumulated 6 hr of observations (3 observation periods \times 2 hr period⁻¹) and determined the dominance status of each bird from aggressive and submissive interactions. Observations were performed during the week that preceded the beginning of dominance trials in each year. All observations were completed within the first 3 hr of daylight. For each interaction, a winner and loser was recorded based on the success of males in supplanting other males from perches and food sources. In the end, we summed all wins and losses for each bird and assigned each bird a dominance position in his flock; those individuals having a greater proportion of wins over another were assigned higher dominance ranks, with a rank of 1 being the most dominant in the flock. Resulting hierarchies were linear with no reversals, allowing us to assign each bird a unique dominance position in the hierarchy.

A total of 18 dominance trials were conducted—6 in 1998 on 28 and 29 May and 12 in 1999 between 28 April and 3 May. All trials were conducted during the first 3 hr of sunlight each day. Each trial consisted of a pair of birds, one from each capture site, and individuals participated in only one trial. In each trial, we pitted a drab male against a bright male. All drab males had mean plumage hue scores \geq 8 and bright males had scores \leq 4. All bright males appeared red to the human eye and all drab males orange or yellow. As House Finch plumage reflects minimally in the UV (McGraw and Hill, in press), and as House Finches have been shown to have the poorest UV vision among those songbirds tested to date (Chen et al. 1984), we assume that our color categories accurately represent the variation that is both detectable and important to the birds themselves.

There was a statistically significant difference in plumage hue between the groups of males used in the trials; bright males ($\bar{x} = 1.9 \pm 0.4$, $n = 17$) were significantly redder than were drab males ($\bar{x} = 11.2 \pm 1.1$, $n = 17$; $Z = 5.0$, $P < 0.001$). Males paired in trials did not differ in body size ($Z = 0.1$, $P = 0.91$) or mite load ($Z = 0.3$, $P = 0.76$). Because there were far fewer drab males in our local population than there were bright males, there was a tendency for bright males to be brought into captivity sooner than drab males ($Z = 1.9$, $P = 0.06$). However, capture date had no direct effect on trial outcomes (see Results).

Although the goal of our study was to pit two birds against one another that differed in plumage coloration

only, we also were concerned about pairing birds with unequal fighting abilities. To ensure that males paired in trials had similar aggressive histories, we matched them according to dominance rank in their captive flocks (± 2 ranks). We did this in such a way that the dominance ranks of bright males were not significantly different from the ranks of drab males with which they were paired in dominance trials ($Z = 0.2$, $P = 0.87$).

Trial characteristics follow those outlined in McGraw and Hill (in press). Briefly, two birds were simultaneously released into an experimental cage in which neither of the birds had been previously housed. This unfamiliar test cage was identical in size to the housing units, was visually isolated from all other cages to avoid potential distractions from other birds, and contained perches and a central food dish. Plastic leg bands were removed from trial birds to prevent band colors from affecting color signaling and dominance behavior in these trials; we used plumage color differences (drab vs. bright) between the trial birds for individual identification. To mimic the interactions of males in the wild and thus allow unfamiliar males to compete in short-term encounters over access to food, we ran trials for 20 min or until one male won seven more aggressive encounters than his counterpart. A male had to win at least five more interactions than his competitor during the trial to be considered the winner; this occurred in 17 of the 18 trials we ran. These 17 trials yielded totals of 129 aggressive interactions ($\bar{x} = 7.6 \pm 0.3$ interactions trial⁻¹) and 230 min of observation ($\bar{x} = 13.5 \pm 1.4$ min trial⁻¹). Only 10% (13/129) of all interactions were won by males considered to have lost the trial, so it is apparent that this short-term trial format was suitable for assessing competitive ability of unfamiliar individuals.

STATISTICAL ANALYSES

Using Spearman's rank correlations, we compared flock entry dates and morphological variables, including body size, plumage color, and remige mite load, against dominance rank in the stable flocks. We applied sequential Bonferroni adjustments (Rice 1989) to correct for multiple comparisons among the flocks (minimum $\alpha = 0.008$ to correct for 6 tests). We used a Kruskal-Wallis H -test to address the effect of leg band coloration on dominance behavior in these flocks. Using a two-tailed binomial test, we considered the role of plumage brightness in determining win/loss outcome in the dyadic interactions, and we used Wilcoxon matched-pairs signed-rank tests to compare body size, mite load, dominance rank, and capture date between winners and losers. We used a two-tailed binomial test to determine whether capture site predicted win/loss outcomes in the trials. All values are reported as means \pm SE.

RESULTS

STABLE FLOCKS

In two of the six flocks of birds, male plumage brightness was significantly negatively associated with dominance rank (Fig. 1). In a third flock, there was a non-significant trend in the same direction ($r_s = -0.56$, $n = 8$, $P = 0.15$). In the three other flocks, there was no relationship between plumage brightness and domi-

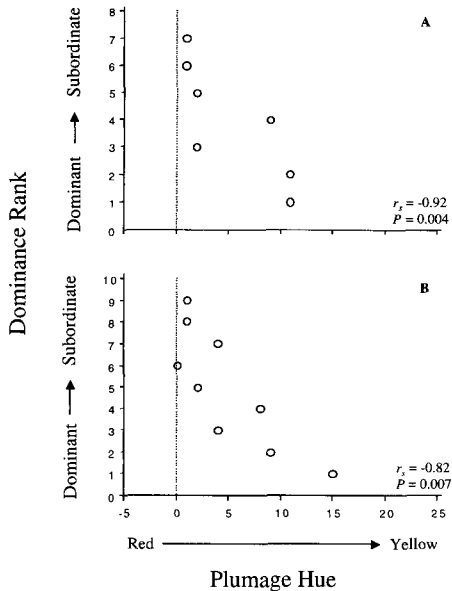


FIGURE 1. Scatterplots showing the relationship between plumage brightness and dominance rank among males in (A) cage 1 ($n = 7$) and (B) cage 2 ($n = 9$). Birds in cages 1 and 2 were captured from separate sites in 1999.

nance rank (all $P > 0.45$). However, in one of these flocks the correlation also was negative ($r_s = -0.30$). Date of entry into captivity was not significantly correlated with dominance rank in any of the six flocks of birds, although in one flock the relationship approached statistical significance ($r_s = -0.88$, $n = 8$, $P = 0.03$; all other $P > 0.15$). Mite load and body size were unrelated to dominance rank in all flocks and leg band coloration also had no cumulative effect on dominance among these birds (all $P > 0.15$).

PAIRED TRIALS

Of the 17 successful trials, 13 were won by drab males and 4 by bright males (two-tailed binomial test, $P = 0.05$). Dominance rank, mite load, body size, and date of entry into captivity did not differ significantly among winners and losers (Table 1). Capture site also was unrelated to win/loss outcome (two-tailed binomial test, $P = 1.0$).

TABLE 1. Comparison of male traits for winners and losers of dominance trials. $n = 17$ for all measures and comparisons.

Variable	Winners	Losers	Z	P
Dominance rank ^a	4.11 ± 0.60	4.35 ± 0.49	0.4	0.68
Mite load	0.50 ± 0.16	0.41 ± 0.12	0.5	0.65
Body size (PC1)	0.22 ± 0.42	-0.24 ± 0.32	0.7	0.49
Entry date ^b	14.41 ± 5.85	8.82 ± 4.31	0.3	0.80

^a Position in flock hierarchy, with 1 being the most dominant, etc.

^b Number of days after the first bird was captured and brought into captivity, calculated separately in each year of the study.

DISCUSSION

In a variety of avian species, ornamental plumage is an honest signal of fighting ability during both the breeding and nonbreeding seasons (reviewed in Senar 1999). Moreover, in those species tested to date for which the male signal is known to be condition-dependent, plumage positively reveals male aggressive behavior as well (Järvi and Bakken 1984, Møller 1987, Pärt and Qvarnström 1997). However, in this study we found that drab male House Finches were dominant to bright males in contests over access to food resources during the breeding season. This was true both when males were housed among familiar individuals and when birds were paired in dyadic trials against unfamiliar counterparts. Because bright carotenoid-based plumage coloration in the House Finch is a reliable indicator of male condition (Hill and Montgomerie 1994; Hill, in press), the fact that drab males are socially dominant to bright males during the breeding season when competing for food complicates our understanding of the signal content of carotenoid-based plumage coloration in this species.

Why might plumage brightness in the House Finch be positively linked to general health, but negatively associated with resource-holding potential? In fact, this phenomenon may represent a "negatively correlated handicap," where differences in the expected benefits of a given behavior may generate a negative correlation between signal intensity and signaler quality (Lotem 1998). In other words, variation in male competitive strategies may reflect an asymmetry in the value of contested resources, with resource-deprived males being more motivated to compete for access to resources than undeprived males (Hammerstein 1981, Enquist and Leimar 1987). In American Goldfinches (*Carduelis tristis*; Popp 1987), House Sparrows (*Passer domesticus*; Andersson and Åhlund 1991), and Dark-eyed Juncos (*Junco hyemalis*; Cristol 1992), nutritionally deprived males win significantly more aggressive encounters at food sources than do their well-fed counterparts.

Thus, aggressive competition for food among male House Finches may depend on the nutritional condition of individuals. With bright male House Finches in better condition, it may be more beneficial for drab males to elevate aggression in order to obtain reliable access to food. Although House Finch males do not maintain feeding territories in either the breeding or nonbreeding season (Hill 1993b), males do compete over access to food at feeders and other concentrated food sources. Thus, by being aggressive, drab males

may receive increased access to food that is both easily accessible and abundant.

Although this study of breeding-season aggression was conducted only in the presence of food, it is possible that we can extend this argument of motivational asymmetry to competition over access to mates as well. Aggression among male House Finches peaks early in the breeding season when individuals seek access to unpaired females as social mates (Thompson 1960a). Thus, the relationship between male plumage color and dominance may represent differences in the mate competition strategies of males in relation to their ability to secure mates. Because female House Finches prefer to mate with bright males (Hill 1990) that are in better condition and are more attentive at the nest (Hill 1991), bright males may have less of a need to behave aggressively and compete for access to mates. At the same time, drab males may be forced into adopting a secondary strategy by elevating aggression and other behaviors (e.g., courtship, song) associated with securing a mate.

Regardless of the resource over which males may be competing, it is interesting to consider the relationship between testosterone, plumage color, and aggression in this species. Testosterone is typically involved in stimulating behaviors associated with mate attraction such as aggression, song, and courtship, and depressing those behaviors involved in parental investment such as nestling provisioning (Wingfield et al. 1987, 1990). In fact, House Finch males with experimentally elevated levels of testosterone feed their nestlings less often and sing more often than do control males (Stoehr 1999). Such behavior also is typical of drab males, who feed their incubating females less often (Hill 1991) and who were the only males observed to sing in our trials (6 out of 6 different males; sign test, $P < 0.02$). Although we have no direct evidence that drab males have higher levels of testosterone than bright males or that testosterone directly mediates aggression, it is curious that experimentally elevated testosterone levels also induce males to molt into a very drab plumage (Stoehr 1999).

Despite the fact that the observed relationship between male plumage coloration and dominance in this study may simply reflect an asymmetry in resource value among males that differ in health and sexual attractiveness, a second explanation remains untested. Brown and Brown (1988) suggested that the reason bright males defer to drab males is because drab males look more like females than rival males and because females are dominant to males in this species. However, even the drabest yellow male is distinct in plumage pattern from all females (Hill 1993c). Thus it seems as though male House Finches interacting in close proximity with other birds should be able to visually discriminate between drab males and females. However, we cannot rule out this idea until it is carefully tested under experimental conditions.

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EFFECTS OF ELECTROMAGNETIC FIELDS ON THE GROWTH OF NESTLING AMERICAN KESTRELS¹

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Abstract. We studied nestling American Kestrels (*Falco sparverius*) in a laboratory setting to determine whether exposure to electromagnetic fields (EMFs) affected their growth. Captive nestlings were raised by their parents under control or EMF conditions similar to those occurring near transmission lines in the wild. Nestlings also were exposed to EMFs as embryos when incubated by their parents. Measurements of

body mass, and lengths of tarsi, antebrachia, and feathers were taken every three days after hatching. EMF exposure affected the growth of female and male nestlings. EMF nestlings and fledglings were heavier and had longer tarsi. The periods of maximal weight gain and antebrachial growth were delayed in EMF males compared to controls, although EMF males were heavier and had similarly long antebrachia to controls by 21 days of age. Growth of ninth primaries and central rectrices of nestlings were unaffected by EMF exposure. Growth patterns of male and female kestrel

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