

Carotenoid-based ornamentation and status signaling in the house finch

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The status signaling hypothesis (SSH) was devised primarily to explain the adaptive significance of avian ornamental coloration during the nonbreeding season. It proposes that conspicuous male plumage serves as an honest signal of social status within a population of birds. However, to date this hypothesis has been well tested and supported for only one type of plumage coloration, melanin-based coloration. Carotenoid-based pigmentation is known to positively reveal male health and condition during molt in a variety of species, but it is poorly understood whether this ornament type can also function as a status signal during the winter. We tested the SSH in male house finches (*Carpodacus mexicanus*) by manipulating the carotenoid-based plumage brightness of first-year males and then pairing unfamiliar birds of differing coloration in a series of dominance trials in captivity. Manipulated plumage color was unrelated to win/loss outcome in these trials. Similarly, the natural pigmentation of males was a poor predictor of winter dominance; as in other studies with this species, we found only a weak tendency for naturally drab males to dominate naturally bright males. These results suggest that carotenoid-based coloration is not a reliable indicator of social status in male house finches during the nonbreeding season. In fact, carotenoid-based coloration may function only in mate choice in this species, and it may be retained throughout the year either because time constraints preclude a second plumage molt or because it aids in pair formation that begins in late winter. *Key words:* aggression, dominance, *Carpodacus mexicanus*, carotenoids, house finches, plumage coloration. [*Behav Ecol* 11:520–527 (2000)]

The evolutionary significance of plumage variability in male birds is a topic of widespread interest to behavioral ecologists. In species in which males complete two annual molts and exhibit ornamental plumage only in the breeding season, it is clear that the ornament is maintained by sexual selection (reviewed in Andersson, 1994; Hill, 1999). However, in species that molt only once annually, with males displaying ornamental plumage throughout the year, it is possible that ornamental plumage has a function during the nonbreeding season, and this nonbreeding-season function may or may not be the same as that during the breeding season (reviewed in Butcher and Rohwer, 1989; Senar, 1999).

Rohwer (1975) proposed the status signaling hypothesis (SSH) to explain the function of avian plumage ornamentation during the nonbreeding season. For species that form unstable social flocks during the winter in which birds regularly interact with new individuals, Rohwer suggested that aggressive encounters between unfamiliar individuals over limited food resources could be mediated by ornamental traits that signal the competitive ability of individuals. As with sexually selected traits, the honesty of the trait is maintained by a condition-dependent signaling system, where only the individuals that can afford to pay the high costs associated with the trait can also bear the most exaggerated ornament (Rohwer, 1982). Thus, males displaying the most extravagant form of the ornamental trait are expected to be more aggressive and win significantly more contests than poorly ornamented individuals.

Since its inception, the SSH has been tested on a variety of species that retain their ornamental plumage throughout the winter. To conduct an appropriate test of the SSH, one must

ensure that male ornaments function directly as signals of social status rather than merely being correlated with aggression (Slotow et al., 1993; Whitfield, 1987). As a result, emphasis has been placed on experimental tests that employ plumage manipulations, control for extraneous variables such as age and body size, and allow unfamiliar birds to compete in short-term encounters. Even under such strict conditions, it has been shown in a number of species that males with experimentally enhanced ornamentation dominate poorly ornamented males over access to winter food resources (studies reviewed in Senar, 1999).

However, such tests have focused almost exclusively on one type of plumage ornament, melanin-based coloration. Largely ignored in tests of the SSH are carotenoid-based ornaments. Melanin- and carotenoid-based colors in birds respond differently to environmental stress (Hill and Brawnner, 1998; McGraw and Hill, in press), and as a result these two signal types may have completely different information content (Badyaev and Hill, 2000; Gray, 1996). To our knowledge, the SSH has been tested only once for a carotenoid-based plumage ornament—the red coloration of the northern cardinal (*Cardinalis cardinalis*) (Wolfenbarger, 1999). Despite the fact that the natural plumage color of male cardinals was significantly related to aggressive outcomes in this study, the manipulated plumage brightness of males was not a reliable predictor of social dominance. Thus, carotenoid pigmentation in cardinals was apparently not used as a visual signal of competitive ability but simply was a correlate of social dominance.

The aim of our study was to test the SSH in another species in which males display a carotenoid-based plumage ornament. We chose the house finch (*Carpodacus mexicanus*) as our study species because males acquire their ornamental plumage in the late summer/early fall through a complete prebasic molt and display bright coloration throughout the year (Hill, 1993b). Additionally, this ornament has been well studied within a breeding context (Hill et al., 1999). Carotenoid pigmentation in male house finches varies in color from red to orange to yellow, and sexual selection by female mate choice

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maintains the trait during the breeding season (Hill, 1990, 1991, 1994; Hill et al., 1999). Bright red males pair more often (Hill, 1991; Hill et al., 1999) and earlier in the season (Hill et al., 1994, 1999) than do drab orange and yellow males, which allows the more brightly colored males to fledge more offspring in a season (McGraw et al., in press). However, the significance of ornamental plumage coloration during the nonbreeding season remains poorly understood in this species. Three studies of house finches in the nonbreeding season suggest a potential relationship between male ornamentation and social dominance (Belthoff and Gauthreaux, 1991; Belthoff et al., 1994; Brown and Brown, 1988), but to date no study has performed an experimental test of the SSH in this species.

To test this hypothesis in male house finches, we conducted two experiments using captive birds. We manipulated the plumage color of first-year males and conducted paired trials that pitted two unfamiliar birds of contrasting plumage brightness in competitions over access to food. We also conducted an experiment in which we paired unfamiliar males of the same age and of contrasting natural plumage brightness. Belthoff et al. (1994) performed a similar study and detected a trend in which naturally drab male house finches were dominant to more brightly colored males. However, they did not control for the competitive ability of males in their staged contests. Recent work suggests that ornamental plumage may have little impact on the aggressive interactions of birds in stable flocks and that previous social interactions may affect the behavior of birds in subsequent dominance trials (Senar, 1999). Thus, in both experiments, we observed dominance among males in the flocks in which they were housed and subsequently matched unfamiliar males by dominance rank in the paired trials.

METHODS

Manipulated-plumage experiment

On 22 July 1998, we captured 40 male house finches at feeders from two sites in Lee County, Alabama, USA. These sites were separated by approximately 5 km, and we assumed that males from the two sites had little prior experience with one another. As age-related dominance is common among birds (Enoksson, 1988; Hogstad, 1989), we included only hatch-year males in this study. Age was easily determined at the time of capture because hatch-year males had not yet molted their juvenal plumage. Birds were fitted with an aluminum U.S. Fish and Wildlife Service band and a unique combination of three colored bands to allow for individual identification.

At capture, we took standard measurements of flattened wing chord length, bill length (exposed culmen), and tail length (after Pyle et al., 1987). We measured male body mass just before each experimental trial (see below for details). From these four measures, we used a principal component analysis (PCA) to calculate a single body size index. The first principal component (PC1) accounted for 50% of the variation in body size measurements, and eigenvectors for PC1 ranged from 0.31 to 0.62, indicating positive correlations among the four body size measures. At this time, we also visually estimated ectoparasite loads (feather mites) on the right wing using an integer scale from 0 (no mites) to 5 (hundreds of mites on every feather; after Thompson et al., 1997). Birds that were afflicted with avian pox or mycoplasmal conjunctivitis were excluded from this study.

We held males in captivity in four separate outdoor cages of 10 birds each. The cage arrangement visually isolated the flocks to maintain unfamiliarity between males caught from separate sites. Birds were fed *ad libitum* diets of sunflower

seeds, millet, water, and vitamins. We minimized the potential for dominant males to control food resources in flocks by placing multiple food and water dishes in each cage. Diets were supplemented with a small quantity of the carotenoid pigment canthaxanthin (125 mg/l of water; Roxanthin Red 10 WS canthaxanthin beadlets, Roche Vitamins Inc., Parsippany, New Jersey) during molt to give all males a drab orange plumage. Males did not have identical postmolt plumage colors, however, so we quantified plumage brightness using a Colortron™ reflectance spectrophotometer (LightSource Inc., San Rafael, California; Hill, 1998). We used mean hue as our plumage brightness index (Hill et al., 1999), which we calculated as the arithmetic average of three hue scores for each of the regions of plumage pigmentation in males (crown, breast, and rump). The Colortron assigns unitless hue values based on a 360° color wheel with values increasing from red to orange to yellow.

We allowed birds to acclimate to their new social environment for a minimum of 7 days before making observations of dominance behavior. After this time, we accumulated 4 h of morning observations for each of the four flocks to determine the dominance status of each bird from aggressive and submissive interactions. For each interaction, winners and losers were determined based on success in supplanting other males at perches and food sources. We summed the wins and losses for each bird to construct dominance hierarchies for each flock. Those birds having more wins over others were assigned higher dominance ranks, with a rank of 1 being the most dominant. The resulting hierarchies were linear with no reversals, and this allowed us to assign each bird a relative dominance position in his flock.

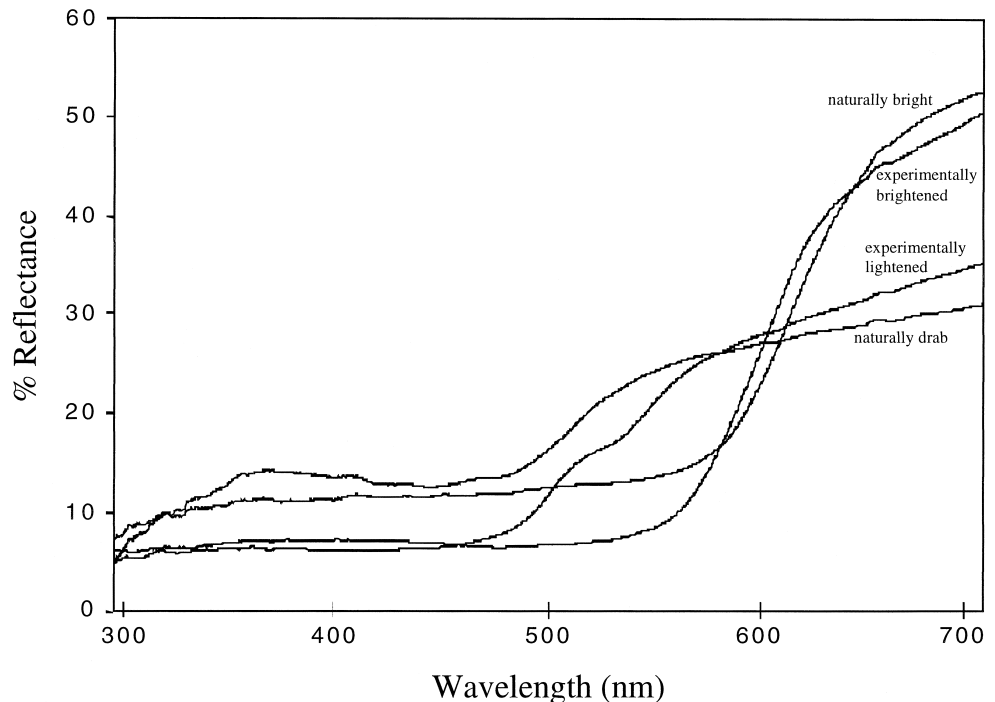
We conducted 20 dominance trials from 21 November–10 December 1998. All trials were conducted in the first 2 h of morning daylight. Each male participated in only one trial, and each trial consisted of two unfamiliar males. To prevent previous social interactions with familiar birds in the housing flocks from impacting the performance of individuals during the dominance trials, males were matched for dominance ability. Thus, we pitted the top-ranked male from one cage against the top-ranked male from another, and so forth.

Each trial also pitted males of contrasting manipulated plumage brightness. We used Berol Prismacolor™ non-toxic art markers to color over the pigmented feather patches and in each trial colored one male red and the other yellow. We selected those marker colors that provided the best visual match with the natural variation of house finch plumage pigmentation (red = PM-6 Carmine Red; yellow = PM-17 Sunburst Yellow). Red markers successfully covered the orange plumage of males, and yellow markers gave males an orange/yellow appearance. We collected spectral reflectance data for these males and found that our color manipulations created close matches with the natural variation in male house finch plumage coloration (Figure 1).

We also noted that coloring feathers with a marker had a small effect on feather reflectance in the ultraviolet (UV; Figure 1). However, our plumage manipulations altered UV reflectance equally for the two experimental groups. Furthermore, the carotenoid-based pigment patches of male house finches reflect minimally in the UV (Figure 1), and house finches possess the poorest UV vision among songbirds tested to date (Chen et al., 1984). Thus, we assume that UV plumage reflectance plays a minimal role in the social interactions of male house finches.

Premanipulated plumage hues did not differ significantly between treatment groups, but after being colored with art markers brightened males had significantly redder plumage than did lightened males, with no overlap between the two groups (Table 1). Males for this experiment were all captured

Figure 1
Representative reflectance spectra for the natural and manipulated plumage of male house finches used in this study. See McGraw et al. (1999) for details on the methods used to collect reflectance data. Note the close match between natural and manipulated plumage colors for both drab and bright males.



on the same day, so the amount of time spent in captivity did not affect trial outcomes. Plumage manipulations were alternated among males in a cage according to dominance rank (e.g., cage 1 = top-ranked colored red, second-ranked yellow, etc., versus cage 2 = top-ranked yellow, second-ranked red, etc.) to prevent one cage from receiving more of one type of manipulation and thus to avoid potential flock/cage/capture-site effects. Brightened and lightened males that were paired in trials did not differ significantly in body size (paired *t* test, $t = 0.91$, $n = 17$, $p = .38$) or wing mite load (Wilcoxon signed-rank test, $Z = -1.60$, $n = 17$, $p = .11$).

The day before males participated in a trial, we removed them from their housing flocks and colored their plumage, giving their feathers time to dry and resume a natural appearance before the trial. Males were then isolated in separate indoor cages and held overnight without access to either food or water. Short-term food deprivation both standardized and maximized the motivation of individuals to compete for food resources during dominance trials (see Andersson and Åhlund, 1991; Lemel and Wallin, 1993). Males were weighed to the nearest 0.1 g on the evening before and on the morning of the trial in which they participated, and these two measures were tightly correlated ($r = .97$, $n = 34$, $p < .0001$), so we used only the morning weights in our statistical analyses.

In the morning, colored bands were removed from males and birds were separately transferred to the experimental test cage in which neither of the individuals had been housed previously. This unfamiliar cage was identical in size to the housing units, was visually isolated from all other cages, and contained perches and a central food dish. Males were placed in separate cardboard boxes on the floor of the test cage, where they remained for 5 min, after which we simultaneously released the males into the cage by pulling on ropes to lift the boxes. This technique avoided the possibility of prior residency effects (after Holberton et al., 1990; Senar et al., 1990), and it allowed the birds to interact immediately without human disturbance.

Because we were interested in determining if males were quickly assessing the aggressive ability of competitors solely on the basis of plumage variation, we ran trials for 20 min or

until one male won seven more aggressive interactions than the other. Trials that failed to meet these criteria were not considered in our analyses ($n = 3$ of 20 for this experiment). The 17 successful trials averaged 15.7 ± 4.5 min in length and yielded a total of 127 interactions, only 3% of which ($n = 4$) were won by males not considered to be trial winners. Thus, this short-term format seemed to be a fair representation of immediate dominance ability and assessment. After the trials, we put colored bands back on males and returned the birds to their flocks to maintain a standardized social setting for all other males prior to their trials.

Natural-plumage experiment

Methodology for this experiment generally followed that given above for the manipulated-plumage experiment. We captured 36 males from the two previously mentioned sites between 1 October and 20 November 1998. Because males were not all caught on the same day, we recorded the date of entry into captivity for each bird. Again, to control for age we included only first-year males in this experiment; however, because all males had completed their prebasic molt, age had to be determined by the extent of skull ossification (Pyle et al., 1987). We captured nine drab males and nine bright males from each site. We defined drab males as having mean plumage hue values > 8 and bright males as having mean plumage hue scores < 4 (see "Manipulated-plumage experiment" for details of hue scoring). All bright males appeared red to the human eye, and all drab males orange or yellow. Males with mean hue scores between 4 and 8 were excluded from this experiment. There was a statistically significant difference in plumage color between the two groups (Table 1), and males paired in trials did not differ in body size ($t = -0.39$, $n = 15$, $p = .48$) or mite load ($Z = -0.58$, $n = 15$, $p = .56$). Bright males were captured and placed into captivity sooner than were drab males ($Z = -2.91$, $n = 15$, $p = .004$), but this did not affect trial outcomes, as winners and losers did not differ significantly in their date of entry into captivity (see Results).

With 36 males, we were able to conduct 18 dominance trials between 12 and 23 January 1999. Clear dominance (see cri-

Table 1

Comparisons of male plumage hue scores for the two experimental color categories—bright and drab—used in this study

Experiment	Treatment	Group	Range	Mean ^a
Manipulated plumage	Premanipulation	Bright	5–35	19.2
		Drab	4–34	19.5
	Postmanipulation	Bright	–1–5	2.5
		Drab	12–34	23.1
Natural plumage		Bright	0–4	2.4
		Drab	8–24	11.9

For the manipulated-plumage experiment, premanipulation plumage hue scores were not significantly different for the two groups (Wilcoxon $Z = -0.03$, $p = .98$), but postmanipulation plumage color differed significantly between the two treatment groups ($t = -8.92$, $p < .0001$). In the natural-plumage experiment, males categorized as bright had significantly lower scores than naturally drab birds ($Z = -3.42$, $p = .0006$). In both experiments, there was no overlap in the plumage color scores of males paired in dominance trials. For all groups in the manipulated-plumage experiment, $n = 17$, and $n = 15$ for all groups in the natural-plumage experiment.

^a Colortron™ hues are lower for redder males and higher for yellower males.

teria above) was established in 15 of these trials. Males of naturally contrasting plumage brightness were paired in each trial. As in our previous experiment, we paired birds with similar histories of aggressive interactions in captivity, but because we could not assign plumage color to males as we did in the manipulated-plumage experiment, we had to be more flexible and match birds that were within one dominance rank of each other.

Statistical analyses

We tested for normality of all variables using Shapiro-Wilk W tests and for differences in variance using equality-of-variances F tests. We used nonparametric statistics whenever the data were not normally distributed or when variances differed significantly. All tests were two tailed unless otherwise noted. For each cage in each experiment, we used a Spearman's rank correlation analysis to examine the relationship between dominance rank in the housing flocks and plumage color, body size, date of entry into captivity (natural-plumage experiment only), and ectoparasite load. We used Kruskal-Wallis H tests to explore the effects of plastic leg band color on dominance in all flocks. We used binomial tests to determine if plumage color was a reliable predictor of win/loss outcome in the dominance trials of both experiments. Based on the tendency for drab males to be dominant to bright males in three previous studies (Belthoff and Gauthreaux, 1991; Belthoff et al., 1994; Brown and Brown, 1988), we used a one-tailed test for the results of the trials using naturally pigmented males. We used a two-tailed test in the manipulated-plumage experiment because the results of Wolfenbarger (1999) did not allow us to devise an a priori directional prediction. We used Wilcoxon signed-rank tests or paired t tests to explore alternative correlates of win/loss outcome in the trials, including body size,

ectoparasite load, pre-manipulation plumage color (manipulated-plumage experiment only), date of entry into captivity (natural-plumage experiment only) and dominance rank (natural-plumage experiment only). We used binomial tests to determine if capture site influenced dominance ability in these trials.

RESULTS

Manipulated-plumage experiment

Housing flocks

Neither premanipulated plumage color, feather mite load, nor body size were significantly related to dominance rank in any of the four cages of males (all $n = 10$, all $p > .15$). Plastic leg band color also did not have a significant effect on dominance status (Kruskal-Wallis $H = 15.37$, $p = .11$).

Paired trials

For the 17 trials in which male dominance was established clearly, neither premanipulated plumage color, mite load, nor body size were significant predictors of win/loss outcome (Table 2). Capture site also had no effect on dominance ability (two-tailed binomial test, $p = .33$). In these trials, experimentally brightened males won 11 trials and lightened males won 6. This difference in wins was not statistically significant (two-tailed binomial test, $p = .33$).

We evaluated the statistical power of this test by considering the probability of detecting results similar to those for species in which a significant relationship between manipulated plumage color and dominance had been previously established. Senar (1999) included a table listing effect size (r^2) values for seven such species in his review of the status signaling function of avian plumage variation. Tests for five of

Table 2

Comparison of male traits for winners and losers of dominance trials in the manipulated-plumage experiment

Variable	Winners	Losers	Z	t	p
Premanipulation plumage hue	20.5 ± 12.6	18.4 ± 11.3	–0.24		.81
Mite load	1.44 ± 0.63	1.47 ± 0.62	0		.99
Body size (PC1)	0.47 ± 1.50	–0.17 ± 1.02		1.04	.32

Means ± SDs are presented for each group, and $n = 17$ for all measures and comparisons.

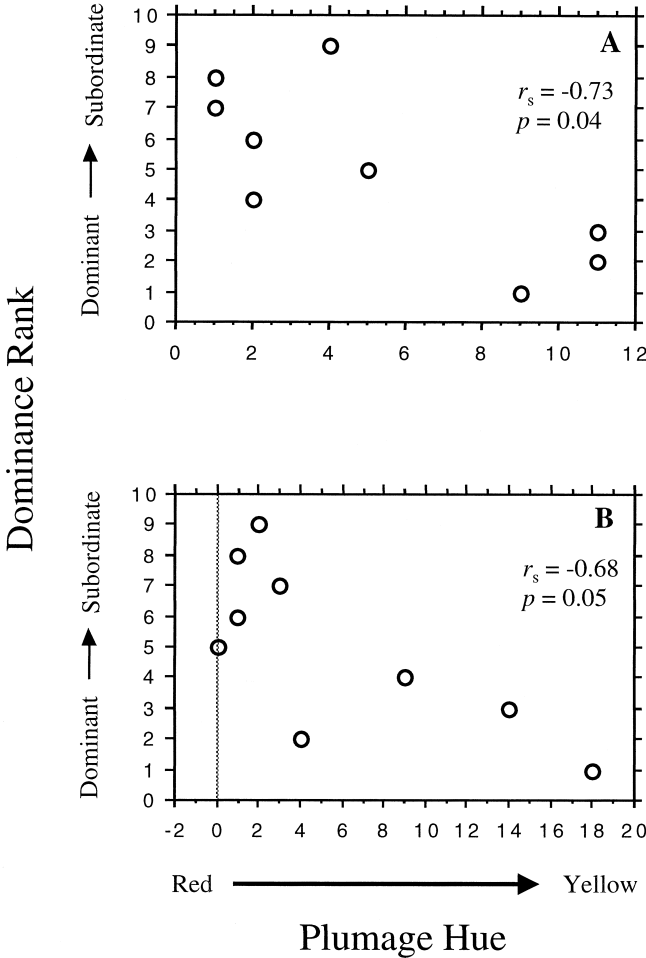


Figure 2
Scatterplots showing the relationship between natural plumage hue and dominance rank among two captive groups of male house finches. Dominant birds were assigned lower ranks than were subordinate males; plumage hue was lower for redder birds and higher for orange and yellow males.

these seven species had sample sizes that were smaller ($n = 7\text{--}15$) than that used in our experiment, yet in all of these studies the effect size was $>.6$ (Fugle et al., 1984; Grasso et al., 1996; Hogstad and Kroglund, 1993; Lemel and Wallin, 1993; Møller, 1987a). With $n = 17$ in this experiment, we had the statistical power to detect an effect size of at least $.6$ at $\alpha = .01$ and effects of at least $.53$ at $\alpha = .05$ (Cohen, 1988). Thus, although we may have failed to detect smaller effects of manipulated plumage color on dominance, we had sufficient

power to reveal effects as large as those shown to be of biological importance in other species.

Natural-plumage experiment

Housing flocks

In none of the four cages of males used in this experiment was dominance rank significantly related to mite load (all $n = 10$, all $p > .15$). We found a significant negative relationship between dominance rank and plumage color in two of the four cages (cages 1 and 3; Figure 2); in the other two cages the trends were in the same direction (both $r_s = -.12$). Dominant males were significantly larger in one of the cages (cage 4; $r_s = -.68$, $p = .05$) and were brought into captivity significantly earlier in one of the cages (cage 3; $r_s = .86$, $p = .02$) than were subordinate males (all other $p > .15$). Plastic band color did not significantly affect dominance among these birds (Kruskal-Wallis $H = 11.81$, $p = .16$).

Paired trials

There were no effects of body size, mite load, dominance rank, or entry date into captivity on win/loss outcome in the 15 trials in which we discerned unequivocal male dominance (Table 3). Capture site also did not influence trial outcomes (two-tailed binomial test, $p = 1.0$). The trend for drab males to dominate bright males was not statistically significant, with naturally drab males winning 10 of the trials and naturally bright males winning 5 (one-tailed binomial test, $p = .15$).

For this test, we also considered the likelihood of detecting results similar to those published for other species. In this case, we found studies of four species in which natural male plumage color was significantly related to winter dominance and in which large effect sizes were obtained ($>.5$) using sample sizes smaller ($n = 7\text{--}13$) than that used in our experiment (Hogstad and Kroglund, 1993; Møller, 1987b; Senar et al., 1993; Wolfenbarger, 1999). Again, we had ample statistical power (with $n = 15$) to detect these biologically significant effects ($r^2 > .5$) at $\alpha = .05$ (Cohen, 1988) and thus feel justified in concluding that, in this species, plumage color is poorly related to a male's success in contests with unfamiliar rivals.

DISCUSSION

We found no conclusive evidence in this study that the carotenoid-based plumage coloration of male house finches acts as a reliable status signal of dominance and aggression in the nonbreeding season. We paired unfamiliar males that differed only in manipulated plumage color (drab versus bright) in dominance trials and detected no significant relationship between aggression and the type of plumage manipulation. Although the number of birds tested was relatively small, we had sufficient power to detect the effect sizes found in those spe-

Table 3
Comparison of male traits for winners and losers of dominance trials in the natural-plumage experiment

Variable	Winners	Losers	Z	p
Body size (PC1)	0.04 ± 1.55	-0.29 ± 1.32	-0.80	.43
Mite load	0.63 ± 0.55	0.53 ± 0.52	-0.58	.56
Dominance rank	5.47 ± 3.09	5.41 ± 3.28	-0.33	.74
Entry date ^a	17.2 ± 25.1	14.6 ± 25.3	-0.24	.81

Means \pm SDs are presented for each group, and $n = 15$ for all measures and comparisons.

^a Number of days after first male was brought into captivity.

cies for which a significant relationship between color and dominance had been established previously. To date, the SSH has been supported only in species in which males display melanin-based ornamentation (e.g., dark-eyed junco, *Junco hyemalis*: Grasso et al., 1996; willow tit, *Parus montanus*: Hogstad and Kroglund, 1993; Eurasian siskin, *Carduelis spinus*: Senar and Camerino, 1998). This study represents the second test of this hypothesis for carotenoid pigmentation, and as of yet there is no indication that this type of plumage coloration functions as a signal of social status during the winter.

Why should melanin pigmentation serve as a badge of status while carotenoid-based ornamentation does not? It appears as though the separate costs associated with producing and/or displaying melanin and carotenoid ornaments generate differences in the information content of these two pigment-based ornament types. Few costs seem to be associated with the production of melanin-based plumage ornaments. Melanin pigments can be synthesized endogenously from basic dietary (amino acid) precursors (Brush, 1978; Fox, 1976), and, although a link between nutritional condition during molt and ornament expression has been suggested (Veiga and Puerta, 1996), three recent studies have demonstrated that the deposition of melanins is unaffected by environmental factors such as food stress or parasitism (Hill and Brawnner, 1998; McGraw and Hill, in press; Senar JC, unpublished data). Furthermore, melanin-based coloration is strongly heritable in some species (Møller, 1989; Norris, 1993; but see Griffith et al., 1999) and is highly canalized during development (Oster and Murray, 1989). Instead of being nutritionally condition-dependent, the honesty of melanin ornaments appears to be maintained by social mediation, where individuals with extreme melanin-based displays are challenged repeatedly, and only males with superior fighting ability can bear the cost of elaborate ornamentation (Rohwer and Rohwer, 1978; Senar, 1999).

Conversely, the expression of carotenoid-based plumage coloration bears high production costs and directly reflects the general condition of males (Hill, 1996, 1999; Hill and Montgomerie, 1994; Olson and Owens, 1998). Carotenoid pigments cannot be synthesized *de novo* by birds (Brush and Power, 1976), so trait exaggeration is directly related to the ability of males to obtain these pigments in their diet and physiologically transport, process, and deposit them in their feathers (Brush, 1990; Goodwin, 1984). During molt, pigment access (Hill, 1992, 1993a), nutritional condition (Hill and Montgomerie, 1994; Hill, in press), and parasite burden (Brawnner et al., in press; McGraw and Hill, in press; Olson, 1996) can all influence carotenoid deposition. Strong sexual selection through female choice maintains these traits, with females preferring to mate with the males in best condition displaying the brightest ornaments (e.g. Hill, 1990; Johnson et al., 1993; Sundberg, 1995). However, depending on the type and value of a resource and seasonal variation in the structure of the social system, male aggressive behavior may vary unpredictably with carotenoid-based plumage brightness and condition. Males differing in condition and mating status may have different motivations and may obtain different benefits for competing for access to either food or mates throughout the year (Enquist and Leimar, 1985; Hammerstein, 1981). Thus, we might expect selective forces driving the evolution of male-male signaling systems to be comparatively weak and less directional in species with carotenoid-based plumage ornaments.

In fact, the relationship between male competitive ability and plumage brightness is not only weak in this species, but if there is a trend at all it appears to be paradoxical. Before our experiments, three separate studies suggested a possible negative relationship between natural plumage brightness and

winter dominance, with drab birds tending to dominate bright birds (Belthoff and Gauthreaux, 1991; Belthoff et al., 1994; Brown and Brown, 1988). Our study represents a fourth case in which there is a nonsignificant tendency in this same direction. We found statistically significant negative relationships between plumage redness and aggression in two of four cages of males displaying natural variation in carotenoid pigmentation, and in trials in which we paired males of contrasting plumage brightness we detected only a marginally significant trend for drab males to be dominant. The accumulation of studies testing the effect of natural plumage coloration on winter dominance among male house finches allows us to meta-analyze the significance of the patterns found to date. Interestingly enough, all 12 of the statistical comparisons in these 4 studies have detected negative relationships between plumage brightness and dominance (sign-test, $p < .001$). If we combine the actual probabilities of these significance tests (Sokal and Rohlf, 1995), the result is also statistically significant ($\chi^2 = 48.26$, $df = 24$, $p < .01$).

So why is the drab plumage of male house finches only weakly associated with social dominance in the nonbreeding season? Although we have no conclusive evidence in support of any particular hypothesis at this time, we offer a few potential explanations. One possibility is that this aggressive male behavior is associated not with a form of intermale communication, but instead represents an aspect of the male-female signaling system in this species. Although redder males enjoy considerable reproductive advantages over less red males (Hill, 1991; Hill et al., 1994, 1999; McGraw et al., in press), drab males are actually dominant to bright males in contests over access to food during the breeding season (McGraw and Hill, 2000). Whereas sexually preferred and healthy bright males may not need to invest heavily in behaviors associated with the acquisition of either food or mates, drab males may allocate more effort to improving their poor condition and competing more for reliable access to either concentrated food sources or females. Such a negatively correlated handicap, where signal intensity is inversely proportional to signaler quality (Lotem, 1998), may occur in the nonbreeding season if ornamental display facilitates early mate acquisition; in fact, house finches begin forming pairs in January (Hill, 1993b).

Brown and Brown (1988) offered an alternative explanation for why drab males tend to be dominant during the nonbreeding season: they suggested that bright males may mistake drab males for females and avoid them because females are dominant to males in this species. However, it seems as though sexual differences in plumage pattern should allow closely interacting birds to discriminate between the sexes. Clearly this idea needs further testing. If this plumage signal does not benefit males in any way during the nonbreeding season, then males may display plumage variation throughout the year simply because there is insufficient time to complete two annual molts and grow separate breeding and nonbreeding plumages in a year. Resident species like the house finch often do not complete their prebasic molt until mid-October and then begin associating with mates as early as January, which leaves them only 10 weeks to fully replace their feathers (Hill, 1993b). On this note, it is interesting that male house finches obscure their colorful winter plumage with buffy feather edges that wear off in about 2 months, which suggests that protecting and/or hiding ornamental plumage in the nonbreeding season may be beneficial.

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