

Carotenoid-based plumage coloration and aggression during molt in male house finches

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Summary

Birds often use colorful traits to mediate resource competitions, and typically individuals with bright or large patches of color are more competitive than or dominant to those with drab or small color patches. Male House Finches (*Carpodacus mexicanus*) are an exception, however, as drab males tend to be more aggressive than bright males during the breeding season and in winter. One hypothesis for this 'negatively correlated handicap' is that drab male house finches, being comparatively sexually unattractive and in poor health and condition, have more to gain by elevating aggression and increasing access to food and pursuit of (especially extra-pair) mates. It would seem important then to test this hypothesis during the period of molt, when birds are actively acquiring the foods and carotenoid pigments that make them colorful and a time in which there is a clear link between plumage color and nutrition/health in this species. We conducted two captive dominance experiments with male House Finches from the southwestern United States (their native range) to examine the relationship between carotenoid-based plumage coloration and aggression during molt. In the first experiment, where birds exhibited their natural, currently growing plumage color, we found that drab males were significantly more aggressive than bright males. However, when plumage colors were manipulated with art markers in a second experiment, color display was no longer significantly predictive of agonistic outcomes. These results suggest that: (1) drab male dominance is not an artifact in eastern US populations and instead is a conserved property of native and non-native House Finches, (2) like in our previous studies in winter, plumage color is correlated with dominance but does not serve as a visual signal of social status in this species, and (3) drab males should have a competitive advantage over access to important carotenoid-rich foods during molt, but apparently do not become as colorful because they do not adequately locate carotenoid-rich foods or do not use them efficiently for energetic or health reasons, which are perhaps exacerbated by elevated testosterone levels.

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Introduction

The status-signaling role of avian plumage has generated considerable interest among behavioral ecologists for over three decades (Rohwer, 1975; Maynard-Smith & Harper, 2003). In many bird species, rich ornamental colors in males reliably signal fighting ability (Senar, 1999, 2006), but in a few others male plumage variation does not play as clear a role in intrasexual signaling (e.g., Wolfenbarger, 1999; McGraw & Hill, 2000a,b). These cases are informative for understanding the intrinsic costs and benefits and extrinsic selective forces that shape status signal use in animals.

The best-studied of these species in which intense coloration is not positively linked to aggression is the House Finch (*Carpodacus mexicanus*). Male House Finches vary continuously in plumage color from bright red to drab yellow, and females prefer to mate with the reddest males (Hill, 1990, 1991), who are in the best health state and nutritional condition (Hill & Montgomerie, 1994; Thompson et al., 1997; Brawner et al., 2000; Hill, 2000; Hill et al., 2004). However, a series of field and lab and correlational and experimental studies have demonstrated that red males are not more aggressive than or dominant to yellow males (reviewed in Hill, 2002). Instead, this work suggests that yellow males are more aggressive than red males in food contests (Brown & Brown, 1988; Belthoff & Gauthreaux, 1991; Belthoff et al., 1994; Belthoff & Gowaty, 1996; McGraw & Hill, 2000a,b). This is the case during the winter (McGraw & Hill, 2000a) and during the breeding season (McGraw & Hill, 2000b), and the primary hypothesis advanced to explain this example of reversed dominance is that drab males are adopting a compensatory, 'best-of-a-bad-job' competitive strategy because of the nutritional and sexual disadvantages they suffer (McGraw & Hill, 2000b; Hill, 2002; Duckworth et al., 2004). This suggests, however, that drab males may not necessarily experience competitive advantages at the time they are growing their colorful feathers; in fact, because House Finches acquire their color by consuming carotenoid pigments from foods (Hill, 1992; Inouye et al., 2001), we might predict that males growing redder plumage are superior competitors for food than those producing less colorful feathers. To date, very few studies have focused on the potential for status signaling during the molt period (e.g., McGraw et al., 2003), and none have been conducted on species displaying carotenoid-based plumage coloration, where competitions over food can have direct consequences for sexual attractiveness.

Therefore, we investigated the status-signaling role of carotenoid-based plumage color in molting male House Finches. Unlike all previous studies on aggression and color ornamentation in House Finches (Hill, 2002), we studied finches from their native range – the desert southwest of the United States. We captured birds that were growing their carotenoid-based feathers in the early autumn and pitted them in two types of aggression trials in captivity (*sensu* McGraw & Hill, 2000b), one in which males displayed their natural coloration and one in which we experimentally manipulated plumage color with art markers. This allowed us to separately test the intrinsic aggressive tendencies of males of different color as well as the degree to which they use plumage color *per se* to gauge the fighting ability of rivals.

Methods

Capture and housing procedures

On 17-19 August 2005, 24 molting hatch-year male House Finches were captured in basket traps at baited feeding stations on the campus of Arizona State University in Tempe, AZ, USA. As in our previous studies (McGraw & Hill, 2000a,b), only hatch-year birds were used to avoid potential confounding effects of age on dominance (e.g., Senar, 2006). Hatch-year males were distinguished from hatch-year females by the presence of recently grown or growing carotenoid-containing plumage on the forehead, breast, or rump. These feathers are easy to recognize in hatch-year birds because the juvenal plumage of both sexes lacks any carotenoid coloration (all feathers are brown). At capture, we measured tarsus length with digital calipers (to the nearest 0.01 mm) and recently molted breast plumage hue with a handheld reflectance spectrophotometer (Colortron™ II; *sensu* McGraw & Hill, 2000a,b). Males were housed individually in small wire cages, with visual barriers between each, in an indoor IACUC-approved room and fed an *ad libitum* diet of Mesa Feed Wild Bird Seed (Leach Grain and Milling Company, Downey, CA) and water.

General procedures for dominance trials (sensu McGraw and Hill 2000a,b)

Aggression trials were conducted in a large outdoor hardware cloth cage that was equipped with a limited set of perches (a single tree branch) and

a single elevated food dish, which was positioned next to the branch and contained fresh sunflower seeds. On the evening (at 1600 hrs) before a male was to participate in a trial, food and water were removed and were not returned to the cage until after the trial the following morning, so that we could maximize motivation for resource acquisition during the trials.

Trials lasted 30 min each and were always run between 0600 and 0800 hrs. Just after sunrise, males were taken from their housing cage, weighed to the nearest 0.01 g with a scale, and were randomly assigned to receive either a green or blue leg band for individual identification during the trials. Males were then placed into separate cardboard boxes on the floor of the test cage, to which we attached a long rope and pulled from 5 m away to begin the trial so that we could simultaneously release the males into the cage from a distance. From videotapes of each trial, we scored the frequency of several different aggressive and submissive behaviors (Thompson, 1960a,b): (1) *fight*s: when both birds actively directed physical contact (typically beak jousting) at each other; (2) *displacements or chases*: when one bird directed aggression at another on a perch or in the air, inducing that bird to leave its perch or fly away without fighting back; and (3) *avoidance*: when one bird approached another non-aggressively and this induced the other to hop or fly away. We summed these events to determine winners and losers of trials (sensu McGraw & Hill, 2000a,b). We only deemed individuals as winners of a trial when they won at least two more aggressive encounters than their counterpart (see below for more information about rates of aggressive interactions).

To gather additional proxies of dominance, we also determined the amount of time (in s) that bright and drab birds spent on/at: (a) the highest perch in the cage (a site at which birds quickly sought in trials and occasionally competed over), (b) the lowest (least preferred) perch site and (c) the single food source. Moreover, we counted the number of times that birds hopped on perches and flew during the trial, to quantify the general activity patterns of each participant.

Natural plumage experiment

Trials were conducted from 23-31 August 2005. We systematically arranged 12 dyads of males for use in dominance trials by pairing birds that were captured on different days (to minimize the chances of familiarity with each

other) and that differed in hue by at least 5.5 units (mean \pm SE difference = 9.6 ± 0.9 hue units; paired t -test, $t = -10.1$, $p < 0.0001$). Hue range in our captive group of males (2.5-25.5) closely approximated that in our wild population at this time of year (McGraw et al., 2006). In three trials, we could not determine a winner or loser based on our behavioral criteria (birds interacted aggressively/submissively ≤ 3 times), so these trials were excluded from analyses. We observed a total of 107 aggressive/submissive interactions during the nine successful trials (mean \pm SE interactions per dyad = 11.9 ± 2.8), only six of which (5.6%) were won by birds we deemed to be trial losers.

Artificial plumage experiment

Trials were conducted from 6-20 September 2005. The same males used in the natural plumage experiment were used in this experiment, but individuals were pitted against different counterparts; also, two additional birds were captured in the period between the two experiments, bringing our total number of trials in this experiment to 13. The hierarchy of criteria used in pairing birds here was to match them for: (1) natural plumage color (always within 3 hue units), (2) dissimilar capture dates, and (3) win/loss outcome in the natural plumage experiment. Because we obviously could not perfectly match all individuals for such criteria, we still tested statistically whether these variables had significant effects on win/loss outcomes.

We arbitrarily assigned birds to two treatment groups – enhanced v. reduced plumage color – and manipulated plumage hue by coloring the carotenoid-containing feathers red (for enhanced males) or yellow (for reduced males) using Prismacolor™ non-toxic art markers (see McGraw & Hill, 2000b for details of the methods and for spectral measurements of colored feathers). Birds were still growing new carotenoid-containing feathers during this experiment, so to be sure that all feathers on all birds were artificially colored during the behavioral trials we manipulated plumage on the evening before each bird participated in its trial (at the time when food was removed). Males were not given leg bands in this experiment, because manipulated plumage color was different enough for us to individually identify birds competing in a trial. Here, four trials did not meet our criteria for determining a winner and loser (in each case, birds interacted aggressively less than 5 times), so these were omitted from analyses. We observed a total of

114 aggressive interactions during the nine successful trials (mean and SD per dyad = 12.7 ± 3.5), only 2 of which (1.8%) were won by individuals we deemed to be trial losers.

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. When data met the assumptions of parametric statistics, we used paired t -tests to examine morphological and behavioral differences between bright and drab males paired in trials and to investigate the effect of capture date, tarsus length, and body mass on win/loss outcomes in trials; otherwise we used non-parametric Wilcoxon matched-pair signed-rank tests. We also included pre-manipulation (natural) plumage color and win/loss outcome in the natural plumage experiment as potential predictors of dominance in the artificial plumage experiment. Finally, we used one-sample sign tests to examine whether one plumage-class of males (bright v. drab) won more trials than the other, and whether band color (for the natural plumage experiment only) or success in the previous trial (for the artificial plumage experiment only) was biased toward one plumage class or influenced trial outcomes.

Results

Natural plumage experiment

Males paired in trials differed significantly in plumage redness but did not differ in tarsus length, body mass or capture date (Table 1). Drab birds won significantly more trials (eight out of nine) than did bright males (one-sample sign test, $p = 0.04$); on average, they won 6 more aggressive interactions per trial than did bright males (Figure 1A). Drab males did not perform more aerial flights or hops on perches during the trials than did bright males (Figure 1B-C), nor did they spend significantly more time at the food dish (Figure 1D). However, drab males did spend significantly more time on the elevated perch in the cage (Figure 1E) and significantly less time on the lowest perch in the cage (Figure 1F). Date of capture, body mass, tarsus length (Table 1), and leg band color (one-sample sign test, $p = 0.89$) all had no significant effect on win/loss outcome in these trials.

Table 1. Comparison of male characteristics in the ‘natural-plumage’ dominance experiment conducted on molting house finches (*Carpodacus mexicanus*) from Arizona. Results are presented for the two types of relevant comparisons: bright versus drab males, as well as trial winners versus losers. Paired *t*-tests (*t* reported) or Wilcoxon matched-pair signed-rank tests (*z* reported) were used in analyses, depending on whether or not data conformed to assumptions of parametric statistics. Mean difference indicates average trait values for the bright or winner male – average trait values for the drab or loser male in each trial.

Male comparison	Trait	Mean difference	<i>t</i>	<i>z</i>	<i>p</i>
Bright v. drab	Body mass (g)	0.02	0.05		0.96
	Tarsus length (mm)	0.07		0.30	0.77
	Capture date (days)	−0.56	−1.25		0.25
Winner v. loser	Body mass (g)	−0.05	−0.09		0.93
	Tarsus length (mm)	−0.05		−0.06	0.95
	Capture date (days)	0.67		1.62	0.12

Artificial plumage experiment

Males pitted in trials did not differ in pre-manipulated plumage hue, body mass, tarsus length, capture date (Table 2), or in their win/loss outcome during the natural plumage experiment (one-sample sign test, $p = 0.89$). There was no significant difference in the number of trials won by artificially bright versus drab males; bright males won five trials, whereas drab males won four (one-sample sign test, $p = 0.89$; Figure 2A). Number of aerial flights and hops on perches and the amount of time spent at the food dish or on the top or bottom perches also did not differ significantly between artificially bright and drab birds (Figure 2B-F). We found no significant differences in natural plumage hue, body mass, tarsus length, or capture date between trial winners and losers in this experiment (Table 2). Also, individuals that won trials in the natural plumage experiment were not more likely to win trials in this experiment (one-sample sign test, $p = 0.45$).

Discussion

Despite using a relatively small sample size (although comparable to several other published studies of avian plumage and dominance in captivity;

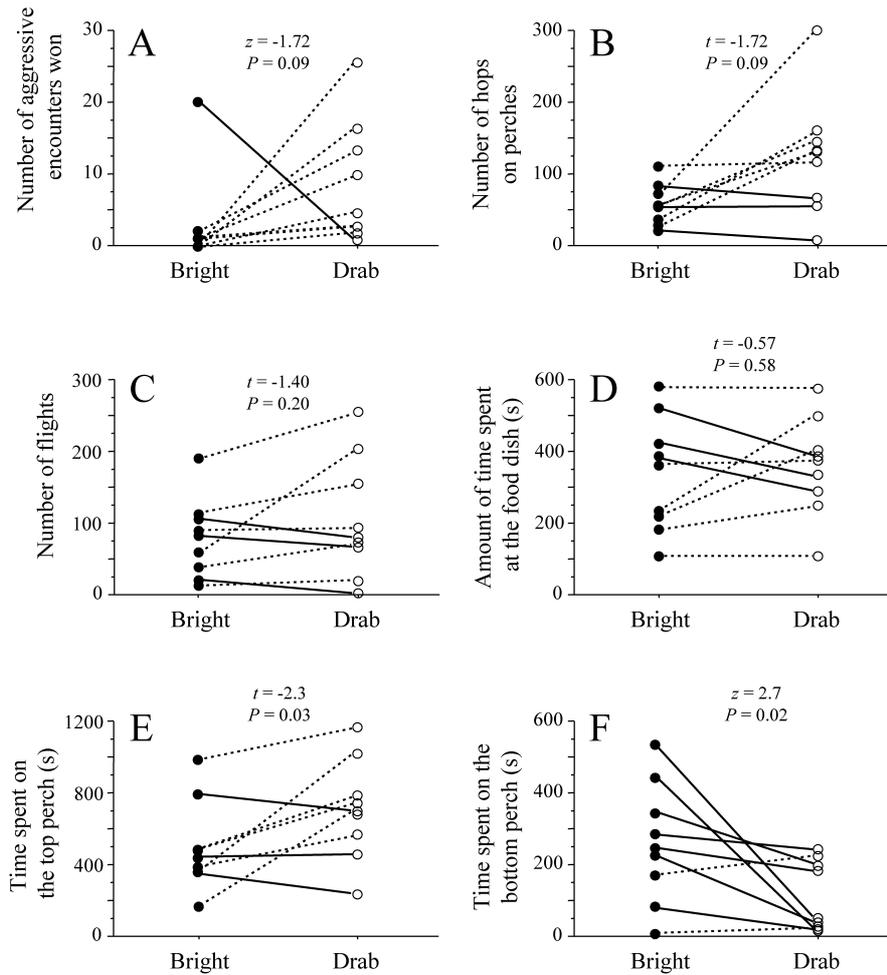


Figure 1. Point plots that compare behavioral performance of bright and drab males in the natural plumage experiment. Points show data for individual birds, and lines connect the points for birds that participated in the same trial. Dashed lines denote trials where drab males had higher values than bright males, and solid lines denote trials where bright males had higher values than drab males.

e.g., Grasso et al., 1996; Wolfenbarger, 1999; Tarof et al., 2005), we found that naturally drab male House Finches were dominant to naturally bright males during molt. This finding is consistent with at least five other behavioral studies of color and aggression in *C. mexicanus*, all of which have been conducted on House Finches from the eastern United States (reviewed in

Table 2. Comparison of male characteristics in the ‘artificial-plumage’ dominance experiment conducted on molting house finches from Arizona. Plumage hue was scored in degrees around a 360° color wheel, with red set at 0° and values increasing as you move toward yellow. See the legend in Table 1 for additional information.

Male Comparison	Trait	Mean difference	<i>t</i>	<i>z</i>	<i>p</i>
Bright v. drab	Pre-manipulated hue (°)	−0.17	−0.29		0.78
	Body mass (g)	−0.22	−0.59		0.57
	Tarsus length (mm)	−0.02		−0.06	0.95
	Capture date (days)	−0.33		−0.72	0.47
Winner v. loser	Pre-manipulated hue (°)	−0.5	−0.89		0.40
	Body mass (g)	0.21	0.54		0.60
	Tarsus length (mm)	−0.02		−0.42	0.68
	Capture date (days)	0.56		1.16	0.25

Hill, 2002), where they were introduced from a small stock of western North American birds ca. a century ago (Hill, 1993). Our study of House Finches from their native range indicates that drab-male dominance is in fact a conserved feature of this species and is not, for example, a product of the different ecological conditions to which House Finches have been exposed in the east (e.g., founder effects, a shift in carotenoid availability, parasite exposure, etc.).

However, when plumage expression was decoupled from the natural coloration of birds using an experimental manipulation, color was no longer predictive of dominance. This result was uncovered using the same number of trials as in our natural plumage experiment, indicating that we had the power to detect the significant effect observed in that experiment. This is consistent with our previous plumage-manipulation study in winter (McGraw & Hill, 2000b) and suggests, at least during fall and winter, that House Finches do not actively use plumage coloration as a visual signal of aggressive ability or social status. Studies have shown that carotenoid-containing feathers can act as status signals in certain species (e.g., Red-winged Blackbird [*Agelaius phoeniceus*], Røskaft & Rohwer, 1987; *Euplectes* widowbirds; reviewed in Pryke & Andersson, 2003), but our work and that of others (e.g., Northern Cardinals, *Cardinalis cardinalis*; Wolfenbarger, 1999) suggests the contrary. In fact, biochemical tests reveal that red feathers from blackbirds and widowbirds also contain high quantities of brown melanin pigments (McGraw et al.,

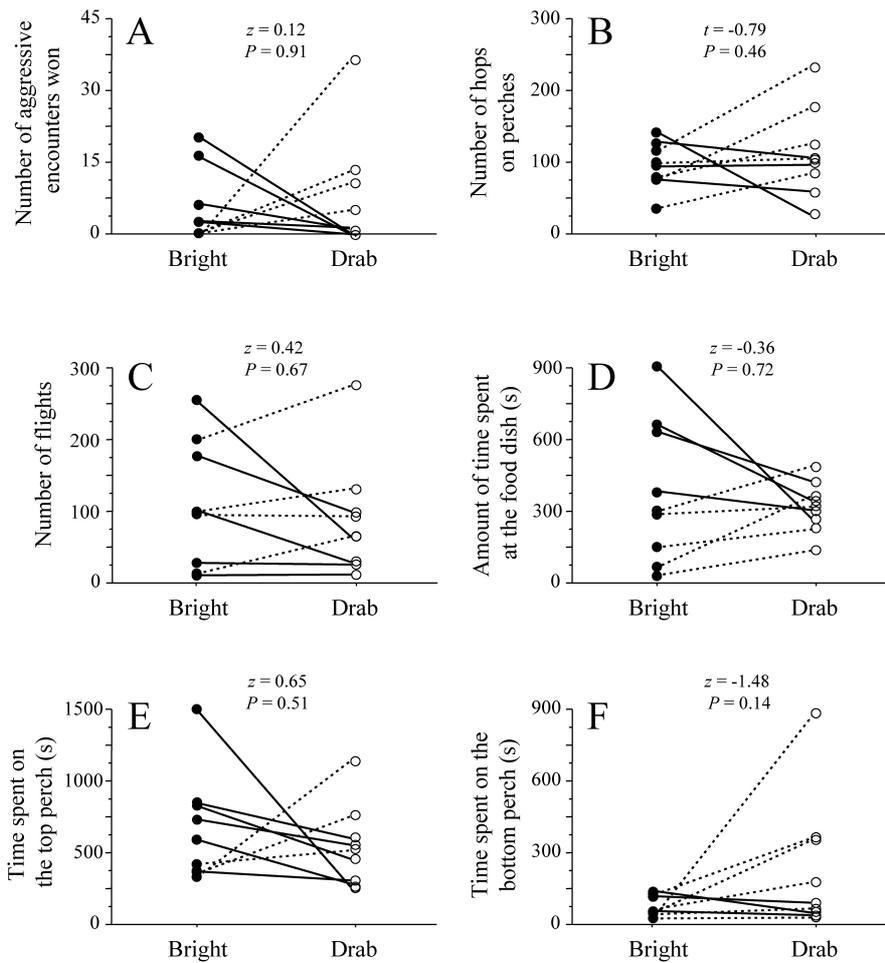


Figure 2. Point plots that compare behavioral performance of bright and drab males in the artificial plumage experiment. See legend for Figure 1 for additional details.

2004; house finch feathers do not, unpubl. data). Because melanic colors are very commonly linked to status signaling in birds (Senar, 2006), carotenoid-pigmented feathers may be more likely to reveal social status when they also are rich in melanin.

Based on previous notions about why drab males may be dominant in this species (McGraw & Hill, 2000a; Hill, 2002; Duckworth et al., 2004), we suspected that redder males might dominate yellower males in this study. Although resources (e.g., food, mates) may be comparatively more valuable

to drab males after the molt period, as they look to compensate for their poor nutrition, health, and appearance suffered during molt, the molt period is the precise time at which bright males are in better nutritional condition (Hill & Montgomerie, 1994; Hill, 2000) and accumulating sufficient carotenoids (Hill et al., 2002) for becoming red. Thus, males that we captured displaying newly molted red plumage should have been more competitive over access to food than naturally drab males. The fact that drab males were still dominant in our study suggests that (a) we did not give them appropriate or limited food to motivate bright males to outcompete drab males, or (b) male-male competition has little bearing on food access, health maintenance, and color development in House Finches. Despite the fact that the carotenoid-coloration system of House Finches is among the most intensively studied sexually selected traits from a proximate perspective (Hill, 2002), we still lack information on the types and limitations of food that finches ingest to become red. Biochemical analyses indicate that there are types of carotenoids (e.g., β -cryptoxanthin) that: (1) are particularly enriched in the blood and livers of red male *C. mexicanus* (McGraw et al., 2006), (2) are important precursors for making red feather pigments (Hill, 2000), and (3) tend to be less common in plant parts and insects than the common yellow (xanthophylls) pigments (Goodwin, 1980, 1984). Identifying important carotenoid-rich food sources (for use in such competitive trials) as well as the social context in which wild birds acquire such foods should also be a priority in future research aimed at resolving the competitive and advertisement strategies of male House Finches and other birds with elaborate carotenoid coloration.

Although we still lack considerable information about why drab male House Finches are dominant to bright males, especially during molt, we may have better insights into how this color-dominance link is controlled physiologically at this time of year. Testosterone (T) predicts aggressive outcomes in House Finches (Duckworth et al., 2004), and treatment with T during molt induces males to develop a drab appearance (Stoehr & Hill, 2001). T is also known to be immunosuppressive in House Finches (Duckworth et al., 2001), and this might be a proximate factor that induces drab males to reallocate carotenoids away from plumage and into health during the molt period (Lozano, 1994). Red males during molt, in contrast, may be superior foragers and/or circulate low T levels, which do not compromise health and require diverting carotenoids away from coloration. The question still remains, however, whether drab males benefit at all from elevating T. We have previously

speculated that drab males may pursue an alternative, 'best-of-a-bad-job' aggressive mating strategy that targets the acquisition of extra-pair mates (e.g., Duckworth et al., 2004). However, no previous study of dominance in House Finches has focused on male-male competitive ability in the presence of potential mates (either intra- or extra-pair), nor in the context of intra-pair, extra-pair, or lifetime fitness. Clearly the costs and benefits of dominance in male House Finches need further attention so that we can better understand the resources over which male House Finches should intensely compete.

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