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EFFECTS OF COLOR MANIPULATIONS ON CAPTIVE FLOCKS OF HOUSE FINCHES

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ABSTRACT: Experimental manipulations of plumage coloration in captive house finches resulted in changes in their dominance interactions that support the hypothesis that sexual dichromatism in this species functions as a simple releaser signal. In May, interaction patterns among groups of males and red-dyed females became random, as if all the birds were perceived as males. The results were similar for familiar and unfamiliar groups, except that unfamiliar males became even more subordinate to the red-dyed females. In autumn, red-dyed brown birds initially dominated familiar brown flock-mates, but, by the sixth day, returned to a random pattern like the control, suggesting that brown birds avoided the red-dyed birds at first but then reestablished prior relationships as in the all-brown flock. In contrast, these same red-dyed brown birds became permanently subordinate when introduced to a new set of brown birds; without individual recognition cues, red color became a subordinate badge. This result was even more compelling because these now-dominant brown birds had previously been subordinate to other brown birds. In other experiments, green-dyed brown birds had fewer dominance interactions with males and with one another in autumn; whereas orange-colored brown birds showed a large increase in interactions with one another in addition to the decrease in dominance interactions with males. Blue-colored males initially increased in dominance encounters with brown flock-mates in autumn, suggesting that covering the red subordinate signal was enough to increase their status. However, coloring males blue had no effect on familiar male cage mates.

KEYWORDS: *Carpodacus mexicanus*, dominance behavior, house finch, plumage coloration.

INTRODUCTION

The function of plumage coloration as a signal for either intrasexual or intersexual communication has been assumed (Butcher and Rohwer, 1989) but rarely tested (Hill, 1996). In a classic experiment, Noble (1936) painted black gular stripes on a female flicker (*Colaptes auratus*), and her mate chased her away as he would have if she had been another male. The male black "mustache" was interpreted as sufficient to identify sex for the male flicker. This concept of a "releaser" signal (Tinbergen, 1948), a simple color stimulus that causes a change in the behavior of the receiver, was equated with sexual recognition in a series of manipulative experiments in the chaffinch (*Fringilla coelebs*). The chaffinch, a small dichromatic European finch, forms winter flocks in which males (having red plumage coloration) generally dominate females (having brown plumage coloration) in social encounters (Marler, 1955a). When Marler colored brown females red (*i.e.*, similar to males), he found that both male and female behaviors changed, and the dyed females were treated as if they were males (Marler, 1955b). Thus, he was able to increase a female's dominance by giving her male coloring.

In this paper, we report the effects of artificial coloration on birds in captive social flocks of house finches (*Carpodacus mexicanus*). The house finch is a dichromatic cardueline finch; females exhibit gray-brown plumage, while males have carotid pigmentation on the head, chest, and rump, ranging from yellowish to dark red (Clement, *et al.*, 1993; Hill, 1993). In contrast to chaffinches, female house finches are typically more dominant than males in social flocks (Thompson, 1960; Kalinoski, 1975; Brown and Brown, 1988; Belthoff and Gauthreaux, 1991).

The purpose of our set of studies was to investigate behavioral changes associated with artificial alterations of plumage color. We wondered how coloring females to resemble males would affect their social status in this species. Would it reduce a female's dominance because she now appeared red like a subordinate male? Would males and females respond differently to such a manipulation on their flock-mates? Would prior familiarity with the dyed females affect the response? We also wondered whether using different colors (green and orange) might have different effects from experiments using red to alter female appearance. Finally, we wondered what effect coloring males rather than females might have. Is it the red or the brown coloration, or both, that acts as the behavioral releaser in this species? For example, if we covered up the red coloration of males, would that cause them to be treated as females even though they were not brown in appearance?

METHODS

This report covers a series of experiments performed in different seasons in different years by the senior author and her students. House finches were captured using mist nets at feeding stations located adjacent to the Science Building at Saint Mary's College, Notre Dame, Indiana, and held in captivity under federal permit #PRT 693151. Birds were captured in April for the May experiments, in August for the September and October experiments, and in late November for the December experiments. Experimental group size was 6 in spring 1991, 8 in fall 1992, and 10 in fall and winter 1993 and fall 1994 (for details, see Table 1). Birds were housed in 3 m x 3 m x 3 m aviaries located in the animal facility of the Science Building at Saint Mary's College. The aviaries were illuminated by artificial timed lighting synchronized with natural day length, and water and finch seed were provided *ad libitum*. Two colored leg bands were placed on each leg for individual identification using combinations of blue, green, purple, orange, pink, black, white, and yellow bands. Birds caught in spring and winter were sexed by plumage color (Hill, 1993) and are referred to as "M" or

Table 1. Summary of color manipulation experiments with house finches over different years and seasons.

Date	Flock Composition	Manipulation
Spring 1991	*n* = 6; 3 males, 3 females; two experiments, one with 6 familiar males and females and a second with 3 new males with 3 dyed females	females (brown) were dyed red
Fall 1992	*n* = 8; all brown birds; two experiments, one with 8 familiar birds and a second with 4 new red-dyed brown birds with undyed brown birds	half the brown birds were dyed red
Fall 1993	*n* = 10; 5 red and 5 brown birds	brown birds were dyed green
Winter 1993	*n* = 10; 5 males and 5 females	females (brown) were colored orange
Fall 1994	*n* = 10; 5 red and 5 brown birds	males (red) were colored blue
Fall 1994	*n* = 10; all red (males)	half the males were colored blue

"F" in the figures. Fall groups of female-plumaged (brown) birds were not aged reliably and may have included adult females and juvenile birds of both sexes. These birds are referred to as "Br" in the figures. Birds were captured a few weeks prior to the experiments and, in most cases, were released immediately following the experiments. In some cases, the birds were released after the artificial colors had either washed out or the birds had molted.

Behavioral observations were made from behind a one-way window in the aviary. Agonistic interactions between birds and the identities of the birds involved were recorded. Each day's observations lasted for 2-3 hours. Agonistic behaviors included dominance chases, supplanting, pecks, and attacks as well as subordinate behaviors like being pecked, being chased, being attacked, and taking subordinate postures. The total number of interactions was computed for each bird, and an average percentage of dominance interactions was computed for the birds in each category (*e.g.*, brown vs. red, male vs. female). The data were also compiled into dominance matrices reflecting the numbers of "wins" and "losses" for each bird, and a value for the percentage of wins was calculated for each bird. Prior to each of the manipulative experiments, we observed behaviors of flock members to establish control values that we could then compare with their behaviors after dyeing or coloring manipulations. Goodness-of-fit tests (Chi-square, InStat 2.03) were used to analyze the data.

Red or green dye was applied on the head, chest, and rump following Hill's (1990) procedure using hair dye. For experiments involving dyed birds, all members of the group were removed from the aviary late in the afternoon and held in the laboratory for the approximate hour needed to apply the dye on half of the birds and sham manipulate the undyed birds. The birds were then released back into the aviary at the time the lights went off. Thus, the experimental flock had a night to settle before observations began when the lights came on the next morning.

Crayola markers were used to alter the color of the plumage on the head, chest, and rump in experiments where birds were colored orange or blue. All birds in the group were caught and placed in holding bags. Individual birds were taken out, manipulated either by coloring with the marker or by rubbing their body with a closed pen, and then released back into the aviary as in the above experiments. Birds did not appear to be adversely affected by any of these manipulations. For experiments using birds of one sex (males) or one color (brown), an "*" was used to distinguish color manipulated birds in the figures.

RESULTS

Spring Mixed-Sex Group, Females Dyed Red. Interactions among six familiar birds that had been housed together for several weeks differed from random expectations during the control period of observation ($\chi^2 = 16.2, p = 0.001$) with male-male interactions being the highest (Figure 1). On the first day after the dyed females were reintroduced to the males, the interaction pattern differed from that of the control ($\chi^2 = 20.34$, $p < 0.001$) but did not differ from random expectations ($\chi^2 = 1.83$, $p = 0.61$). Similar results were obtained on day 5 ($\chi^2 = 13.24$, $p = 0.004$, and $\chi^2 = 3.0$, $p = 0.40$, respectively; Figure 1). The relative number of dominance encounters decreased for same-sex interactions and increased for intersexual interactions. Among these latter encounters, females increasingly dominated males (Figure 1). This pattern was also reflected in the percentage of wins by females (58% for the control, 53% for day 1, and 74% for day 5) compared to males (46%, 40%, and 30%, respectively).

Like the above birds that were caged together and familiar to one another, the set of new unfamiliar control birds (3 females and 3 males) exhibited nonrandom interactions on the first day ($\chi^2 = 52.5$, $p < 0.0001$) with a high proportion of male-male interactions (Figure 2). On the first day after introducing new males to females who had been dyed red, an overall increase in intersexual encounters occurred resulting in a statistically different pattern ($\chi^2 = 9.43$, $p = 0.02$; Figure 2). On days 2 and 5, their interactions were not significantly different from random ($\chi^2 = 0.23$, $p = 0.89$, and $\chi^2 = 4.18$, $p = 0.12$, respectively), but when the male-female class was separated into female > male and male > female classes, day 5 results differed from random expectations ($\chi^2 = 32.11$, $p < 0.0001$) due to the higher rate of females dominating males. As in the previous experiment, dyeing the females resulted in a decrease in male-male interactions, an increase in intersexual interactions, and a more random encounter pattern among males and females. Also, as in the previous experiment, the average percentage of male wins decreased by day 5 (33% on day 1, 44% on day 2,

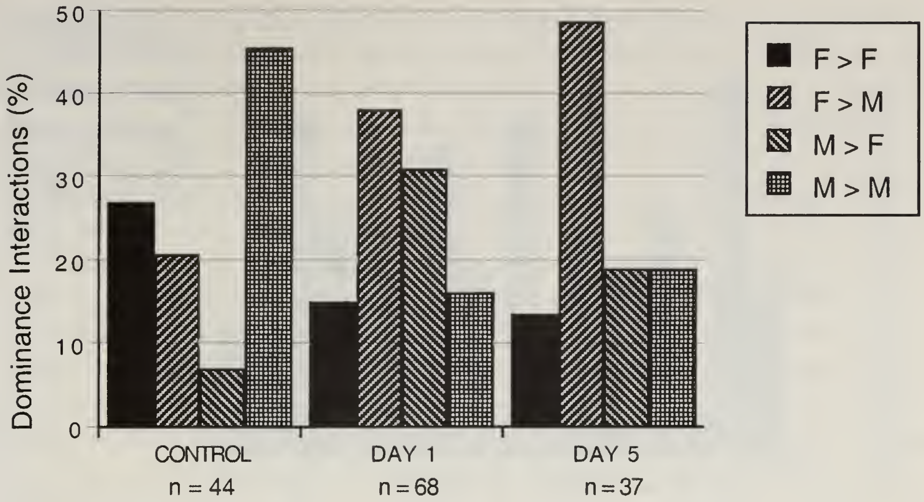

Figure 1. The average percentage of dominance interactions during the spring among familiar male and female house finches before the females were dyed (control) and on the first and fifth days after the females were dyed red to resemble males (female = F, male = M).

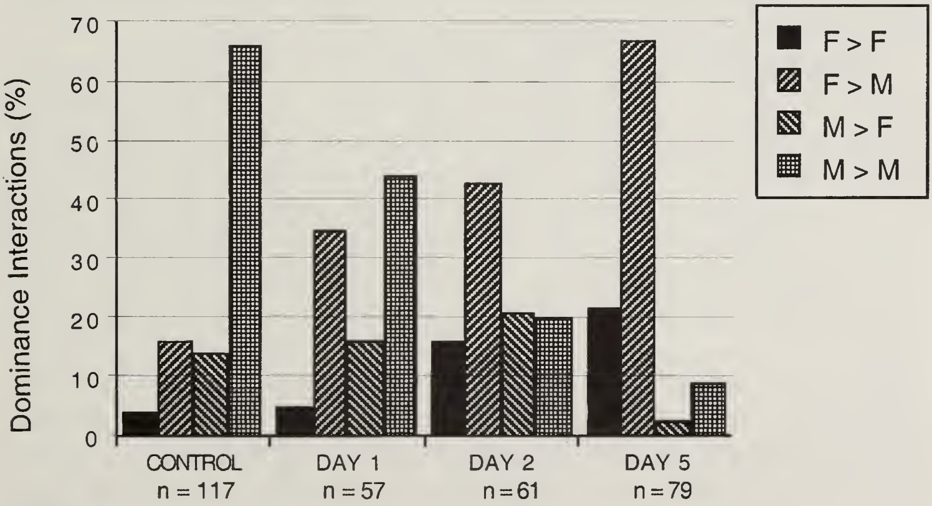

Figure 2. The average percentage of dominance interactions during the spring among unfamiliar male and female house finches before the females were dyed (control) and on the first, second, and fifth days after the females were dyed red and introduced to new males (female = F, male = M).

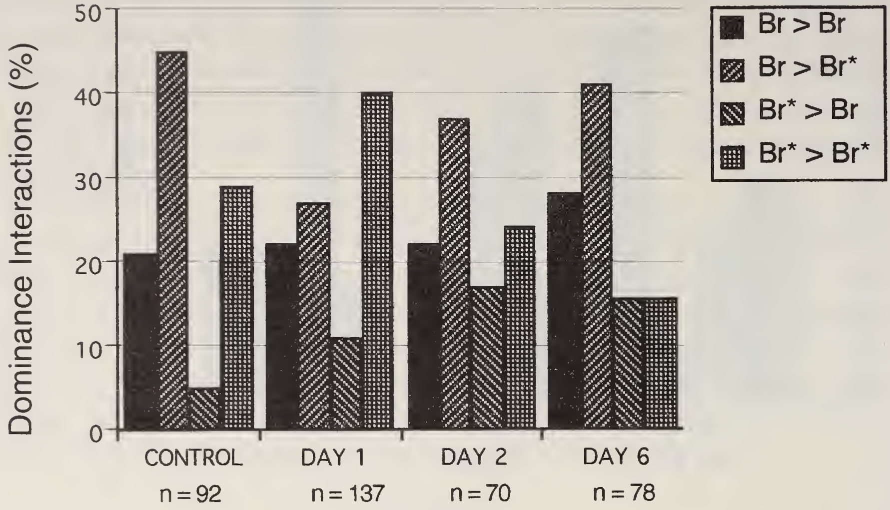

Figure 3. The average percentage of dominance interactions during autumn among familiar brown house finches before the birds were dyed (control) and on the first, second, and sixth days after half of the birds were dyed red (brown undyed birds = Br, brown birds dyed red = Br*).

and 14% on day 5). The average percentage of female wins did not change (61%, 51%, and 59%, respectively) but remained high over the test period.

Fall All-Brown Group, Half Dyed Red. For the set of experiments testing the effects of presenting red-dyed brown birds to familiar brown birds, the interactions differed on the first day of reintroduction when compared to the control ($\chi^2 = 8.73$, $p = 0.03$) with a decrease in the four brown birds dominating the four red birds and an increase in dyed birds interacting with one another (Figure 3). On days 2 and 6, their interactions were not different from random ($p > 0.40$ in each case) or from the control ($p > 0.10$ in each case). Thus, coloring brown birds that had been housed together resulted in an initial decrease in undyed bird dominance over dyed birds followed by a return to control levels (Figure 3). This result was also reflected in the decreased percentage of wins by undyed birds from 73.5% to 57.5% from the control period to day 1. A noticeable increase the number of interactions between dyed birds also occurred on day 1 (Figure 3); however, by day 2 and through day 6, their interactions did not differ from those in the control. Thus, coloring of some of the brown birds did not decrease their dominance rank as predicted and appeared to have little effect on the social order.

Next, the effects of introducing red-dyed brown birds to "unfamiliar" brown birds was tested. The control flock was sampled over six days to provide appropriate comparisons for the 6-day experiment, because the introduction of new birds might result in changes over six days independent of color manipulations. The control birds consisted of the four undyed females from the previous experiment (Br1) and four different brown birds that had been housed separately (Br2). Control group encounter frequencies differed from random on all three days ($p < 0.005$) but not from one another ($\chi^2 = 8.0$, $p = 0.24$). (The non-random aspect of the controls was due to the dominance of Br2 to Br1 birds. Br1 and Br2 interaction patterns were random when Br1 > Br2 and Br2 > Br1. Categories were combined for days 2 and 6 ($p > 0.20$ in each case).) After introducing new red-dyed brown birds (Br3*, Figure 4) to the Br1 birds of the controls, their interactions on the three test days were non-random ($p < 0.0001$ in each case) and differed from their controls due to the significant change in dominance of the Br1 birds. We could not conduct statistical tests of the control vs. the experimental days since different birds were used, but inspection of Figure 4 reveals that the previously subordinate Br1 birds became dominant to the dyed birds (Br3*). In the controls, the four Br1 birds lost 66 encounters and won 15 on the first day; on the first day of the experiment, they lost 4 and won 65 encounters with dyed birds. Thus, while we were unable to lower dominance by dyeing birds and releasing them to their familiar cage-mates, when we introduced dyed unfamiliar birds to relatively subordinate undyed birds, the subordinate birds became dominant, and the dyed birds' dominance was decreased to almost zero (Figure 4).

Fall Mixed-Color Group, Brown Birds Dyed Green. The five red male and five brown birds of this control group exhibited non-random interactions with brown birds dominating red birds more than expected (Figure 5). After reintroduction of the brown birds dyed green, the number of their interactions with red birds decreased, and interactions among red birds increased, resulting in a significant difference in the pattern of interactions ($\chi^2 = 31.3$, $p < 0.0001$) when compared to the control. By the twelfth day, the pattern of interactions did not differ from the control ($\chi^2 = 2.35$, $p = 0.50$; Figure 5). None of the patterns were random. The percentage of wins for the brown birds decreased slightly from 83% to 73% and then increased to 79% by day 12, whereas the percentage of male wins increased from 25% to 42% and then decreased to 24% by day 12. Dyeing brown birds green resulted in an initial decrease in interactions with red males followed by a return to control patterns.

Fall Mixed-Sex Group, Brown Birds Colored Orange. Brown birds captured in late November are reliably sexed by plumage (Hill, 1993); thus, brown birds in this experiment were females, and red birds were males. The pattern of interactions during the control period was non-random ($\chi^2 = 36.9$, $p < 0.0001$) and similar to the pattern in the control period in the previous green experiment with brown birds (females here) dominant to males being the largest category. After reintroduction of the orange-colored females to the five red males, interactions continued to be non-random but were significantly different from the control with an increase in interactions among the orange-colored birds and a decrease in their dominance interactions with males ($\chi^2 = 41.7$, $p < 0.0001$ for days 1-2; $\chi^2 = 19.9$, $p < 0.001$ for days 6-7; Figure 6). The percentage of wins for brown birds initially decreased and then increased again (62%, 40%, 57%),

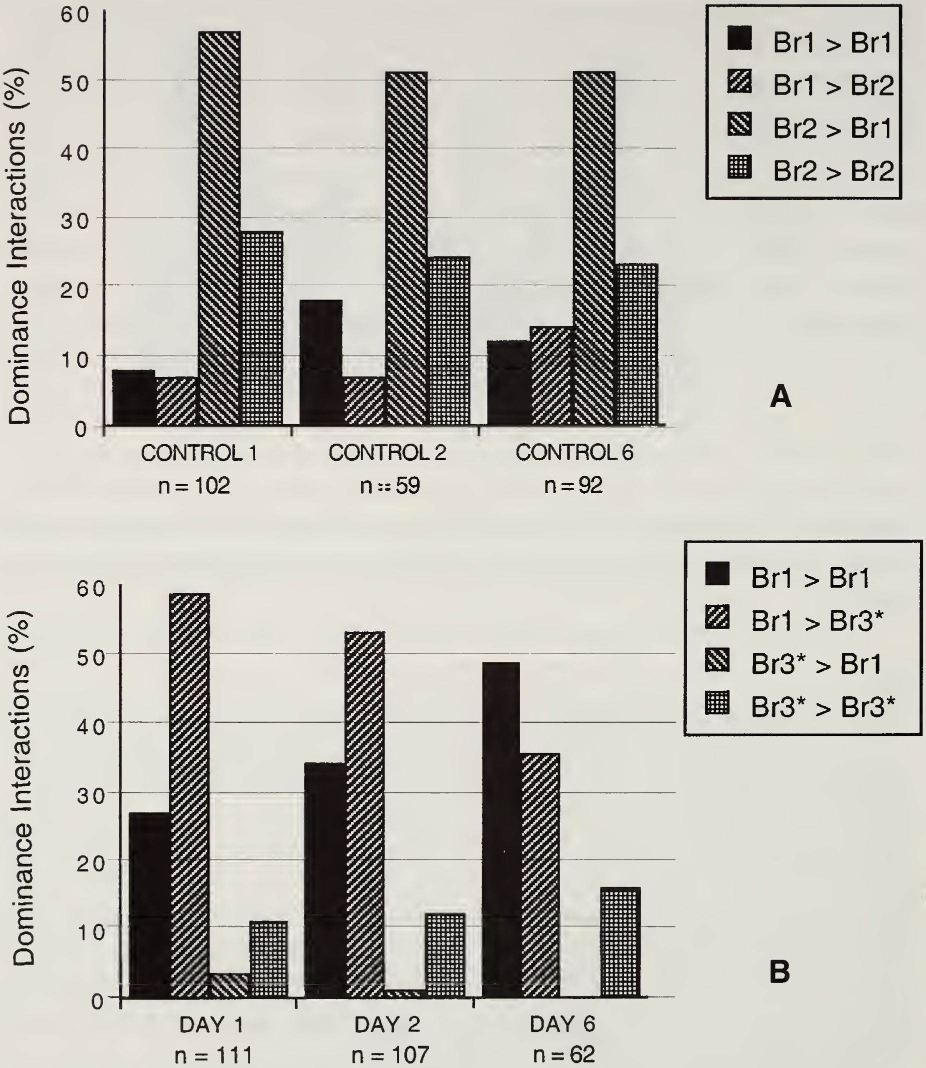

Figure 4. The average percentage of dominance interactions during autumn among unfamiliar brown house finches (A) on the first, second, and sixth days of the control period before the birds were dyed, and (B) on the first, second, and sixth days of the experimental period after half of the control birds were introduced to unfamiliar birds dyed red (focal brown birds = Br1, unfamiliar brown birds used in the control = Br2, and unfamiliar brown birds dyed red = Br3*).

and the percentage of male wins increased throughout the test (30%, 41%, 52%). The most pronounced effect of coloring females orange was the large increase in their interactions with one another.

Fall Mixed-Color Group, Red Males Colored Blue. Interaction patterns for the control group in this experiment were similar to the other mixed-color

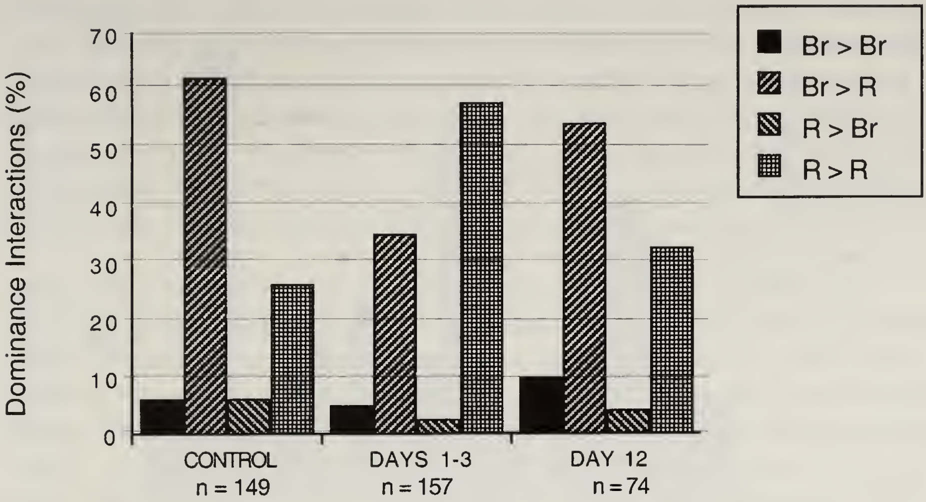

Figure 5. The average percentage of dominance interactions during autumn among familiar brown and red (male) house finches before the birds were dyed (control) and over the first 3 days and on the twelfth day after the brown birds were dyed green (brown birds = Br, red birds = R).

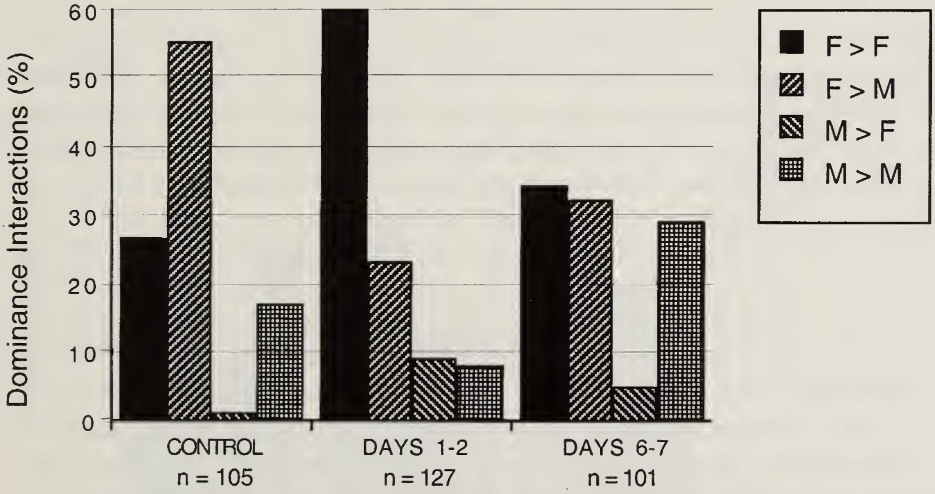

Figure 6. The average percentage of dominance interactions during winter among familiar female and male house finches before the birds were colored (control) and for days 1-2 and 6-7 after females were colored orange (females = F, males = M).

controls with birds interacting non-randomly ($\chi^2 = 30.8$, $p < 0.0001$), and brown birds dominating red males comprised most of the interactions. After the five blue-dyed males were reintroduced to the same five familiar brown birds, the group members interacted non-randomly ($\chi^2 = 12.98$, $p = 0.005$) but differently from the control ($\chi^2 = 66.3$, $p < 0.0001$) with an increase in males dominating brown birds (Figure 7). After a week, interactions were still different from the control ($\chi^2 = 22.9$, $p < 0.0001$) but not from random expectations ($\chi^2 = 5.7$, $p = 0.13$). The change in relative dominance was also reflected in the percentage of wins: brown birds won 73%, 37%, and 50% over the three periods, while males won 24%, 61%, and 49%. Coloring males blue effectively reversed brown-bird/red-male dominance patterns. The effect was not permanent, and the interactions became random by the end of the week, although they still differed from the control values.

Fall All-Male Group, Half Colored Blue. In the last test, ten familiar males, who interacted randomly in the control ($\chi^2 = 6.85$, $p = 0.08$), did not change interaction patterns after half of them were colored blue and reintroduced to their original cage mates (Figure 8). Observations on subsequent days did not differ from random ($p > 0.70$ each period) and were not different from the control ($p > 0.23$ in each period). Coloring males blue had no effect on their dominance interactions. This was the only test that clearly produced no effect from coloring birds.

DISCUSSION

Control Behaviors. Behaviors among control groups during each season were consistent with what is known for house finches from other studies. For our spring mixed-sex groups of control birds, the high level of male-male interactions relative to female interactions was similar to the pattern found by Thompson (1960) and Kalinoski (1975) for western house finches. They attributed the higher male aggressiveness in the breeding season to territory and mate defense. The December control group had similar interaction frequencies to other winter studies (Shedd, 1990; Brown and Brown, 1988; Belthoff and Gauthreaux, 1991) with the highest interaction rates occurring between males and females (56%, with females dominating males) and higher numbers of female-female relative to male-male interactions. Fall controls were similar to the winter control with the highest numbers of interactions occurring between brown and red birds with brown birds dominant to red birds. However, the number of brown-brown interactions was consistently lower than red-red interactions. This result may have been due to the mixture of juveniles with adult females in the brown class, which reflects the situation in wild fall flocks. In addition, our three days of observations on the fall all-brown control produced the same pattern of interactions each day, demonstrating interaction stability. Overall, we feel our controls represented stable, natural interaction patterns for the house finch with which to compare our experimental results.

Experimental Results. Dyeing females red during the breeding season increased the number of encounters between males and females regardless of whether they were newly introduced males or more familiar males. In general, the encounter patterns became more random between the sexes as if males were approaching red-dyed females and red males equally. In both experiments, the proportion of female > male interactions increased as male > female interactions

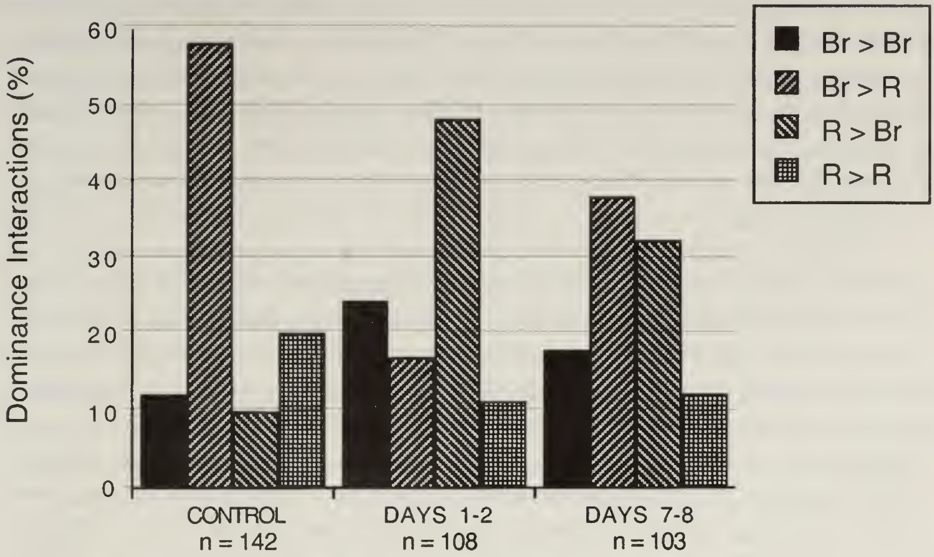

Figure 7. The average percentage of dominance interactions during autumn for familiar brown and red (male) house finches before the birds were colored (control) and for days 1-2 and 7-8 after the males were colored blue (brown birds = Br, red birds = R).

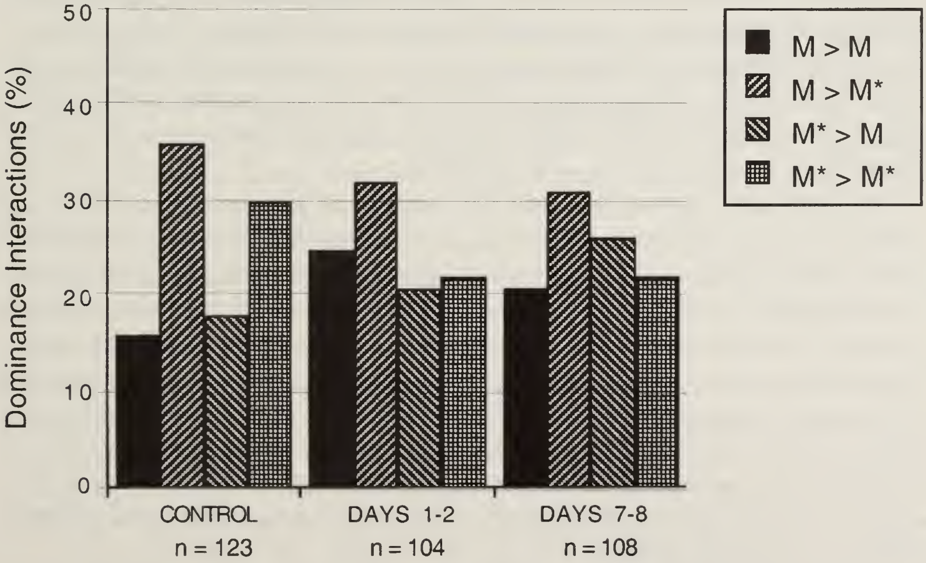

Figure 8. The average percentage of dominance interactions during autumn among familiar males before the birds were colored (control) and on days 1-2 and 7-8 after half the males were colored blue (male = M, male dyed blue = M*).

decreased. We believe these results indicate that females were normally avoided by males during the spring, but when the females were given male appearance, they were approached equally only to have to assert their dominant status. Brown and Brown (1988) and Shedd (1990) suggested that males might "defer" to females even though they were capable of dominance. Our results confirm that females are actually dominant to males in the spring as well as during non-breeding seasons.

As Marler (1955b) found with chaffinches, we were sometimes able to shift the birds' dominance relationships by color manipulations. Compared to Marler's results where subordinate females dyed to resemble males increased in dominance relative to males, our most analogous result occurred after altering subordinate male house finch coloration (covering red with blue) which increased their dominance relative to females. The rise in male house finch dominance was probably due to females avoiding them, as Marler (1955b) found for chaffinch males avoiding females. In addition, we were able to temporarily decrease dominance in a group of red-dyed brown birds when reintroducing them to familiar brown birds and to more permanently decrease their dominance when introducing them to unfamiliar brown birds.

Birds in social flocks probably assess potential dominance visually and then choose to approach subordinates and avoid dominants. By altering dominant brown house finches, we made them appear more subordinate (red), and they were approached more often but were able to defend their status. When Møller (1987) dyed female house sparrows to resemble more dominant males, he found that dyeing the birds had no effect on dominance status but noted that the manipulated birds were challenged more often than undyed control birds. His "social probing of new individuals" may be similar to what we observed as an increase in the number of interactions with dyed birds.

Dyeing females green reduced the frequency of their interactions with one another, while dyeing them red or orange increased their interactions with one another. Why females should respond so aggressively to orange coloration is not clear. Belthoff and Gowaty (1996) found that female house finches were more aggressive towards males with less red and more yellow and orange coloration. Nevertheless, plumage color variation was found to be a poor predictor of social status among wintering male house finches (Belthoff, *et al.*,1994). Therefore, it seems unlikely that females are using red vs. orange coloration to predict the likelihood of a male being relatively more subordinate. Further manipulative studies are needed to compare female response to red vs. orange as a plumage signal of subordinate status.

Dyeing half of a group of randomly interacting red males blue had no effect on the other males, suggesting that red plumage in the non-breeding season elicits a stronger response from females (indicating a potential subordinate that one can supplant at food) than from other males. Coloring males blue in the breeding season might have a greater effect on male-male interactions. On the other hand, brown birds responded quite differently to males that had been colored blue, resulting in a decrease of brown birds dominating them and an increase in their dominance over brown birds. These blue-colored birds did not resemble dominant brown females (a more difficult manipulation), but we think that by blocking the red "honest" signal, we were able to create "cheaters," at least for a couple of days. Perhaps the other group members avoided these strange looking birds, allowing them to win dominance encounters; however, coloring females green did not have that general effect, and they looked even less "normal."

Function of Plumage Coloration. Female dominance of males in the non-breeding season is rare among sexually color-dimorphic species (three species of which are in the genus *Carpodacus*: *C. purpureus*, *C. cassinii,* and *C. mexicanus*), and the absence of a pre-breeding molt suggests that the adaptiveness of coloration may be driven by sexual selection during the breeding season (Butcher and Rohwer, 1989). Our results support the argument that dichromatic plumage may also be advantageous to flock members by reducing intersexual aggressive encounters (Parsons and Baptista, 1980). After manipulating house finches to look more similar (spring groups of males and dyed females), the groups exhibited an increase in frequency of intersexual encounters. If the distinctive red vs. brown signal allows males to normally avoid the dominant females within foraging flocks, the color signal could translate into an energy saving benefit. A benefit to dominants that advertise their status could be a reduction in the time spent defending widely disparate status, such as exists between male and female (red and brown) house finches.

Brown and Brown (1988) suggested that brown juvenile plumage in house finches might be advantageous to birds interacting with potentially dominant adult males. In social groups, all brown birds may be viewed similarly by opponents, and since brown females dominate males in other seasons, juveniles may benefit by resembling dominant females. In studies of species that are dichromatic with regard to age but not sex, Rohwer (1985) showed that dyed immature Harris' sparrows (*Zonotrichia querula*) dominated other immatures, Parsons and Baptista (1980) increased white-crowned sparrow dominance by plucking the immature birds' crowns and reintroducing them with new adult feathers to adults, and Fugle, *et al.* (1984) painted immature white-crowned sparrows to resemble adults. We did not investigate age effects in our studies; however, to complete the understanding of the function of color in dominance relationships in the house finch, further studies need to be conducted that focus on responses of immature and adult brown-plumaged birds and their responses to plumage manipulations. Finally, we suggest that plumage color in house finches probably serves more than one function, functions differently for males, females, and perhaps young birds, and may change in function in different seasons.

Color as a Releaser. The results of our experiments with the house finch demonstrate a "releaser signal" function for dimorphic plumage coloration similar to Marler's (1955b) findings with the chaffinch. Recent trends in studying avian signaling systems have focused on individual variability in plumage rather than dichromatism: sexual selection whereby females select preferred males from among a variety of types has been a popular line of investigation as has the study of status signaling where variation in appearance is interpreted as a signal of relative dominance status among groups of birds. Thus, the emphasis on fine-grained recognition abilities has concentrated researchers' views of signal perception on complex discrimination abilities. For example, sexual selection studies have shown that female house finches are attracted to males with darker, rather than lighter, red coloration (Hill, 1990, 1994), and that this variation is associated with male quality (Hill, 1991). Belthoff and Gowaty (1996) showed that female house finches were less aggressive toward and often less dominant to more brightly colored males relative to drab males during the non-breeding season. These studies demonstrate that females are capable of distinguishing among a variety of color types.

Our data suggest that house finches may also respond to simple cues. We suggest that some behaviors, such as initial dominance encounters in social groups, may still be affected by a simple "releaser" type of stimulus. This response might be advantageous in a group of birds in which color predicts potential dominance (red vs. brown in house finches), and where avoiding dominants and approaching subordinates results in greater energy efficiency (Brown and Brown, 1988).

In support of this hypothesis, we found that simply dyeing females red and reintroducing them to familiar males produced striking results. Every indication would be that these males should "know" the females; however, the pattern of interactions over the next few days after reintroduction indicated to us that they interacted with the dyed females in the same manner they did with other males. Thus, a simple plumage coloration cue appears to act as a releaser for agonistic behaviors in the house finch. Our result is similar to the classic experiments of Noble (1936) and Marler (1955b), where altering females to appear male-like caused males to treat them as if they were males. Another interpretation — that other birds might very well "know" that the colored birds are females and are reacting to them as females that are inappropriately colored — cannot be tested since questions of what is going on in a bird's "mind" are difficult to assess. The simplest explanation is that red coloration serves first as a simple sex-recognition releaser for males (especially in the spring) and females (especially in the fall).

Avian Color Perception. The question of color perception by mates and/or other territorial males has been investigated by a number of researchers using a variety of color manipulations in avian species. A few examples include: placing yellow tape on female mourning dove (*Zenaidura macroura*) heads (Goforth and Baskett, 1965), coloring male epaulets black on red-winged blackbirds (*Agelaius phoeniceus*; Smith, 1972), dyeing the inner wing linings of male village weaverbirds (*Ploceus cucullatus*) black (Collias, *et al.*, 1979), dyeing subadult gray male purple martins (*Progne subis*) black (Stutchbury, 1991), and adding black marks on the heads and chests of territorial male white-crowned sparrows (*Zonotrichia leucophyrys*; Gotmark, 1993). The social dominance hierarchy provides a natural context in which to test the reactions of birds to manipulations by the researcher. As recommended by Bennett, *et al.* (1994), in order to test the effects of color manipulation, we focused on the natural receivers (other flock members) rather than humans to assess the effects of color differences. Our study suggests that orange and red manipulations mimicked male coloration in the house finch, and that blue and green are perceived and reacted to differently. For example, coloring brown birds red increased the frequency of their interactions with one another, while coloring brown birds green did not have the same effect. Coloring red males blue had no effect at all on other males. The discovery of avian perception of ultraviolet colors and studies on the complexity of avian vision systems (Bennett, *et al.*, 1994) remind us that we do not know what the bird is actually perceiving in our color manipulations. Perhaps we are covering up ultraviolet patterns on brown birds, or hair dye and colored pens may look vastly different to the birds compared to natural feather colors. Obviously, avian color perception is a field that needs more investigation, and we should be aware that the results of future research might alter avian color theories (Bennett, *et al.*, 1994). In this study, plumage color manipulations resulted in changes in behavior (except in the case of males exposed to familiar blue-colored males). Our results indicate that house finches perceive the artificial colors and react to the changes, probably due to alteration of the natural plumage coloration that normally functions as a social signal.

Summary. We recognize that there are a number of potential shortcomings in this series of studies, perhaps the most notable being the number of different students who gathered data over the years and seasons using different experimental designs and without replicate studies. However, we believe that several factors in the experiments, such as controls composed of the experimental birds themselves, act to strengthen our findings. We also believe that this series of experiments indicates that further study is warranted on the question of color function in the house finch. For example, we would like to see replicates of the red-dyeing experiments in spring, fall, and winter, follow-up on female responses to orange and red variations in plumage coloration, and studies that analyze the possible effects of age on color perception and behavior. "More is known about the function, evolution, and proximate control of ornamental plumage coloration in the house finch than in any other passerine species" (Hill, 1996, p. 860), and we hope we have stimulated more questions for future research on the interesting question of plumage coloration in this species.

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