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The effects of elevated testosterone on plumage hue in male House Finches

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The majority of studies examining the role of hormones in the proximate mechanisms of plumage coloration in birds have focused on intersexual differences (plumage dichromatism) and on structural- or melanin-based plumage coloration. The relationship between hormones and carotenoid-based plumage color, and in particular intrasexual plumage color variation, has received little attention. We manipulated testosterone levels of both captive and wild male House Finches to determine whether testosterone influences the expression of male plumage color in this species. We found that in captive male House Finches elevated testosterone delayed molt and resulted in drabber, less red plumage, even when birds were supplemented with dietary carotenoids. Elevated testosterone also resulted in drab plumage color in wild males, and appeared to delay molt in wild birds as well. Wild males implanted with testosterone showed wide variation in expression of plumage coloration. Those implanted early in the year molted plumage similar in color to their pre-treatment plumage, but those implanted later molted substantially duller plumage, possibly because delayed molt resulting from elevated testosterone caused these males to molt when carotenoid pigments were not available in sufficient amounts. These observations have the potential to explain previously reported relationships between plumage color and behavior in male House Finches, and highlight the importance of considering the proximate mechanisms of plumage coloration in avian sexual selection.

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In birds, the hormonal mechanisms that control sexual plumage dimorphism are still largely unexplored. The few studies that have been conducted, however, have revealed that the hormonal control of plumage coloration may vary widely among species. Male breeding plumage in some species is related to elevated levels of testosterone while in other species it is the absence of estrogen that is responsible for the showy plumage of the male (Owens and Short 1995). In still other cases, plumage dimorphism is under direct genetic control with no hormonal dependency (Witschi 1961, Owens and Short 1995). In many cases the precise mechanisms are unknown but what is clear is that among birds the proximate mechanisms of plumage dichromatism vary widely (Kimball and Ligon 1999).

To date, virtually all studies examining the hormonal control of plumage color have addressed the presence or absence of showy plumage; that is, the differences between the sexes. Largely unexplored, however, is the influence of hormones on intrasexual plumage color variation. This is puzzling given the attention that plumage color variation has received in the context of sexual selection, especially in light of recent hypotheses examining the possible role of hormones in sexual selection (Folstad and Karter 1992). Furthermore, most studies have examined the hormonal control of plumage coloration in structural- or melanin-based plumage coloration (Kimball and Ligon 1999, Evans et al. 2000, Peters et al. 2000). Thus, the relationship between carotenoid-based intrasexual plumage color

variation and hormones has not received the attention that it deserves.

Here we report the effects of elevated testosterone on male plumage coloration in the House Finch *Carpodacus mexicanus*, in both wild and captive birds. Males display bright, carotenoid-dependent breeding plumage which may vary from yellow to orange to red (Hill 1992, 1993a). Plumage color has been shown to be an important criterion in female mate choice, with females preferring redder males (Hill 1990, 1991, 1994a, Hill et al. 1999).

Methods

We conducted this study on male House Finches captured on the campus of Auburn University, located in east-central Alabama, USA. We conducted the experiment on wild birds in 1997 and 1998, and on captive birds in 1998 only.

Wild birds

Following capture, we scored the hue of the breast plumage of all males using a Colortron hand-held reflectance spectrophotometer (Hill 1998). We then assigned birds to treatment groups randomly, anesthetized the birds using methoxyflurane (Metofane, Pitman-Moore) and gave each bird two subcutaneous implants. The implants were 10 mm lengths of Silastic tubing (Fisher Scientific) sealed on the ends with silicone glue. We filled the implants for experimental birds (T-males: $n = 30$ in 1997, 53 in 1998) with crystalline testosterone (approximately 7.5 mm per implant; Sigma Chemical), and left the implants for control males (C-males: $n = 19$ in 1997, 38 in 1998) empty. We inserted the implants just under the skin on each bird's left side, above the hip and below the wing. Following surgery and recovery, we banded each bird with a unique color combination of three plastic leg bands and one aluminum U.S. Fish and Wildlife Service band and then released the birds. We implanted birds from late February to early April in 1997 and from mid-January to mid-April in 1998.

House Finches molt once each year, just after breeding (molt occurs July–October for C-males, later for T-males). In the spring (February–April) following treatment, after all birds had completed molt, we captured as many birds as we could and scored their plumage again using the spectrophotometer. (Newly molted feathers have a very different appearance from feathers retained from the previous year's molt; thus, determining whether male House Finches had completed molt was simple and unambiguous.) We estimated plumage hue visually in the field for birds we were unable to capture ($n = 3$), with no knowledge of the birds' previous treatments. Although very subtle differences in hue are not easy to detect visually, gross differences (i.e. yellow vs orange vs red) are easily detected. For a number of birds, we had both visual estimates and spectrophotometric measurements of hue, and the relationship between the estimates for birds in the field and their true hues as measured by the spectrophotometer suggest that visual estimates were adequate for detecting true hue differences ($r^2 = 0.87$, $n = 34$, $P < 0.001$).

Most House Finches captured on our site in early spring are not residents and are never seen again. Thus, we scored plumage for only a portion of the total birds banded (12 T-males and 13 C-males); nonetheless, these proportions did not differ from that expected given the number of birds assigned to each treatment group ($\chi^2_1 = 1.30$, $P > 0.05$).

Captive birds

We housed hatch-year male House Finches in large outdoor flight cages (3.7 m long × 1.5 m wide × 2.4 m high) on campus. On 1 June 1998 we implanted three males with two testosterone implants each, using the same procedure for implanting these birds as described above for wild birds.

Following implanting, the birds were returned to the outdoor flight cages and maintained on a diet of sunflower seeds and millet. In addition to food, we provided all birds with drugs to prevent infections by coccidia and *Mycoplasma gallisepticum* (Brawner et al. 2000). We also provided all birds with carotenoid pigments in their water (Roxanthin Red 10 WS canthaxanthin beadlets at 125 mg/l, Roche Vitamins, Inc.). We observed the progress of molt for all birds from 4 September to 14 December 1998. Because testosterone delays molt in male birds (e.g. Hahn et al. 1992) we removed the implants from these males on 2 October. Each time the birds were observed, we noted whether or not they were molting or had completed molt, and whether or not the new feathers coming in were pigmented. On 14 December, we scored the plumage hue of the T-males and a group of ten unmanipulated control birds kept on identical food and carotenoid treatments but that had not been given implants. Although the experimental birds had not completed molt (see Results), all had patches of newly grown breast feathers that were large enough to score with the spectrophotometer.

Effectiveness of hormone implants

We determined circulating testosterone levels of wild birds using radioimmunoassay following the protocol detailed in Mendonça et al. (1996), with minor modifications described elsewhere (Stoehr and Hill 2000).

Results

Testosterone levels

Testosterone-filled implants raised circulating testosterone levels of wild birds to a seasonal mean of 14.2 ng/ml (± 0.63 SEM), and levels generally decreased over the course of the season. Consistent with the results of the assays, the implants of birds caught repeatedly showed a visible decrease in testosterone. (The implants, and the volume of testosterone in them, can be seen in birds in the hand.) During the study, no wild bird captured had lost its implants, and T-males captured the following spring (one year after implanting) always had empty implants. Testosterone levels from wild unimplanted or empty-implanted birds averaged 0.98 ± 0.45 ng/ml and the highest testosterone level recorded from a C-male during this study was 6.6 ng/ml. However, testosterone levels over 15 ng/ml have been recorded from unmanipulated birds in this population (Duckworth 2000); thus, testosterone levels in T-males were comparable to the high levels from wild males. We did not determine testosterone levels of captive birds.

Wild birds

On average, T-males molted into plumage that was substantially duller (less red) than their pre-treatment plumage, while C-males molted into plumage that was virtually the same color as their pre-treatment plumage. We tested this by comparing the change in plumage hue (the difference between before-treatment hue and post-treatment hue) between treatment groups. Because the Colortron arbitrarily assigns lower values to redder hues, positive difference scores indicate an increase in brightness, while negative difference scores indicate a decrease in plumage redness. There were no significant year ($F_{1,21} = 1.66$, $P = 0.21$) or year by treatment interactions ($F_{1,21} = 0.39$, $P = 0.54$), so the data we present are pooled for both years of the study.

Implanting caused little change in plumage hue for all C-males, but the effects varied widely for T-males. Consequently, the variances of the difference scores differed significantly (Levene's test, $F_{1,23} = 9.11$, $P = 0.006$). For this reason, we used a t-test that did not assume equal variances (equivalent to a two-sample Welch ANOVA; JMP Statistical Package, SAS Institute 1995). The mean change in plumage hue in T-males was negative and of greater magnitude (-10.67 ± 2.40) than the mean change in plumage hue of C-males (1.04 ± 0.73) ($t_{23} = 4.67$, $P < 0.001$; Fig. 1).

To determine if the timing of implanting might explain the variation in response to treatment among T-males, we examined the relationship between implanting date and change in plumage hue in these birds.

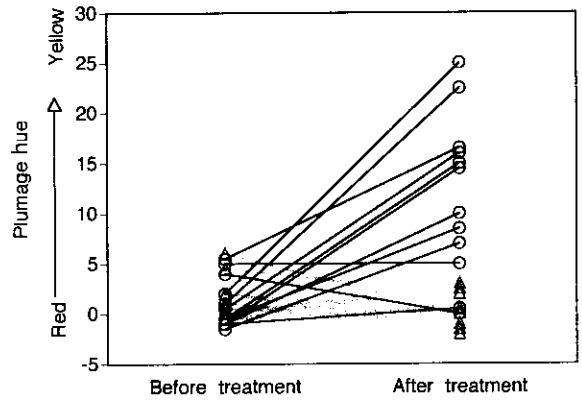

Fig. 1. A comparison of the change in plumage hue of control (C-males) and testosterone-treated (T-males) male House Finches showing plumage hue before and after treatment. T-males (n = 12) are shown as open circles connected by solid black lines and C-males (n = 13) are shown as open triangles connected by gray lines. The mean change in plumage hue (pre-treatment hue minus post-treatment hue) for T-males was negative (indicating a change to drabber, or less red, plumage) and of significantly greater magnitude than the mean change in plumage hue of C-males. Note also the greater variation in post-treatment plumage hues of T-males.

We found that T-males implanted later in the year were more likely to molt into plumage that was duller than their previous plumage hue than were T-males implanted earlier in the year ($r^2 = 0.51$, $n = 12$, $P = 0.006$; Fig. 2).

Testosterone also appeared to delay molt in wild birds; none of three T-males captured in late fall, well after the normal molt period, had completed molt.

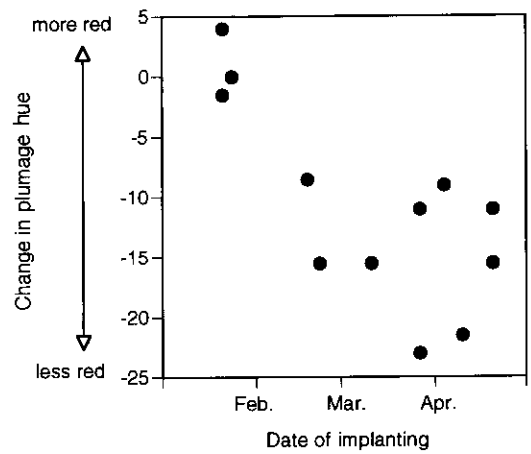

Fig. 2. The relationship between the magnitude of change in plumage hue (pre- vs post-treatment hue) and date of implanting in testosterone-treated males only (n = 12). The figure indicates that male implanted early in the season changed plumage hue very little, while those implanted later in the season molted substantially drabber (less red) plumage. A value of zero would indicate identical pre- and post-treatment plumage colors.

Captive birds

All unmanipulated control birds molted in synchrony with wild male House Finches: they had begun molting by 4 September and were finished molting by 2 October. T-males had begun molting their primary feathers by 4 September, but had not progressed much further by 2 October. By 19 November (several weeks after the removal of the implants) the T-males had still not completed molting their primary feathers and had not yet begun molting their body plumage. By 14 December the T-males had molted some body feathers, but many body feathers had still not been replaced. The body feathers of T-males that had been replaced were clearly not the drab yellow observed in some of the wild T-males, but were significantly drabber than those of the unimplanted control males held through molt on the same diet (captive T-males: 9.67 ± 1.20; captive control males: 5.80 ± 0.58; $U = 1.5$, $P = 0.02$).

Discussion

We found that elevated testosterone delayed the onset of molt in captive male House Finches (and appeared to do the same in wild birds) and caused a significant difference in plumage hue in both captive and wild birds. Furthermore, the effect of testosterone on plumage coloration was greater for wild male House Finches, particularly those males implanted late in the year. Captive male House Finches given testosterone implants but also supplied with red carotenoid pigments during molt grew feathers that were only modestly drabber than those of captive males without implants. Thus, the levels and/or timing of testosterone secretion may play a role in generating the variation in plumage coloration of wild male House Finches.

We stress that the focus of our study was not the role of hormones in sexual dichromatism of House Finches. Male and female House Finch plumage coloration differs primarily in the extent of carotenoid-pigmented areas, not in the actual hue of these pigmented patches; females may have rump patches as bright as or brighter than the red patches of males (Hill 1993b). This is an important point because it suggests that proximate mechanisms of sexual dichromatism in other species of birds, for example the aromatization of testosterone to estradiol in feather follicles (George et al. 1981), are unlikely to explain the intrasexual variation in plumage coloration that was the focus of our study. Thus, unlike virtually all other studies addressing the role of testosterone in plumage coloration, which have searched for the proximate mechanisms of sexual dichromatism (reviewed in Kimball and Ligon 1999), we documented the effects of elevated testosterone on intrasexual variation in carotenoid-based plumage coloration.

Expression of carotenoids in plumage is a complex process requiring both the acquisition and utilization of the pigments (Olson and Owens 1998). That captive male House Finches treated with testosterone grew drabber plumage than controls despite identical carotenoid treatments suggests that testosterone had some effect on carotenoid utilization. Mechanisms of carotenoid utilization are poorly understood, but it is possible that testosterone somehow affects the absorbtion or transport of carotenoids, perhaps by affecting the proteins involved in such processes (Erdman et al. 1993). Our results suggest that this effect may last for some time after a drop in testosterone levels because testosterone-treated males grew drabber plumage despite the fact that their implants had been removed several weeks earlier. The results of our experiment with wild birds, however, suggest that if such an effect exists it does not last indefinitely.

Among wild birds treated with testosterone, some molted into red plumage very similar to their pre-treatment hues but others molted into plumage that was very yellow, the variation being strongly related to the time of implantation. This effect may be related to lasting effects of testosterone on carotenoid utilization. For example, in addition to possible effects on carotenoid absorbtion and/or transport (Erdman et al. 1993), testosterone may have increased parasite loads in males (Folstad and Karter 1992) which then reduced plumage redness (Thompson et al. 1997, Brawner et al. 2000). These effects, or others affecting the utilization of carotenoids, and thus color, of experimentally-treated males may work in concert with other effects on carotenoid acquisition.

Testosterone could affect carotenoid acquisition by changing the behavior of treated males so that they do not seek carotenoids during molt or, by delaying molt until early winter when carotenoids are presumably less abundant (because of a lack of fruits and flowers – the only significant source of carotenoids for House Finches, which do not eat insects), testosterone could indirectly affect the abundance of carotenoids available to males during molt. The evidence provides more support for the 'delayed molt hypothesis' than the hypothesis of changes in carotenoid-seeking behaviors. In captive male House Finches, experimentally elevated testosterone delayed molt and probably had the same effect in wild birds, an effect observed in other species as well (Hahn et al. 1992, Nolan et al. 1992). If proper timing of molt is crucial to the expression of bright red plumage in male House Finches because of seasonal variation in carotenoid abundance, birds that delay molt past a critical window due to the effects of elevated testosterone will be unable to grow fully pigmented feathers. That House Finches implanted with testosterone early in the season did not molt into substantially duller plumage, as did those implanted later, supports this hypothesis. Most likely, in birds

implanted early in the season the implants ran out of testosterone prior to the normal onset of molt; thus molt was not delayed and normal pigmentation resulted. Males implanted later molted later than normal at a time when sufficient carotenoids were unavailable.

To provide a general explanation of plumage color variation in male House Finches, our hypothesis makes two critical assumptions: that sufficient carotenoids are unavailable to late-molting males and that natural testosterone levels may delay molt. Whether carotenoids are limiting in the environment has been a topic of some controversy (Hudon 1994, Hill 1994b), although evidence from both fish (Grether et al. 1999) and birds suggests they may be (Slagsvold and Lifjeld 1985, Hill 1993a, Linville and Breitwisch 1997). Furthermore, in California House Finches shift from a seed-based diet to a fruit-based diet in June that lasts until October, mirroring almost exactly the period of molt (Beal 1907, Hill 1995). In Alabama, we observe a marked decrease in finches feeding at our seed feeders at this time each year, suggesting these finches have shifted their diet away from seeds as well. Experiments by Shields (1997) showed that House Finches prefer red foods during both molt and non-molt periods. Thus, if sufficient carotenoids had been available later in the season when T-males were molting, we would have expected these birds to seek them out. The drab plumage grown by testosterone-implanted males, particularly those implanted later, suggests that carotenoids were not available to them in sufficient amounts. Hill and Montgomerie (1994) have also shown that males initiating molt earlier grow redder feathers. Evidence that naturally occurring testosterone levels will delay molt is provided by Runfeldt and Wingfield's (1985) study of Song Sparrows *Melospiza melodia*. Males paired to females whose seasonal period of reproductive activity had been extended (by estradiol implantation) had higher testosterone levels and molted later than controls despite no direct experimental manipulations of their hormone levels. This hypothesis could be tested in House Finches by similar indirect manipulations of male testosterone levels, combined with analyses of changes in environmental carotenoid abundance.

The relationship between testosterone and plumage color that we observed has the potential to link together several interesting aspects of House Finch biology. If circulating testosterone levels vary among wild male House Finches and are somehow responsible for producing differences in plumage hue, we would expect to find variation in plumage hue to be associated with variation in behavioral or physiological traits. Several studies have found that drab male House Finches were dominant to redder male House Finches (Brown and Brown 1988, Belthoff and Gauthreaux 1991, McGraw and Hill 2000). Drab males also fed their incubating mates less (Hill 1991), and were less likely to survive an epidemic of *Mycoplasma gallisepticum* (Nolan et al. 1998). These observations are all consistent with the idea that drab male House Finches may have higher levels of circulating testosterone than redder males.

Finally, it is important to consider the results of this experiment in light of other recent studies examining the role of testosterone in male plumage coloration. Peters et al. (2000) showed that increased testosterone induces pre-nuptial molt in Superb Fairy-wrens *Malurus cyanus*. Evans et al. (2000) found a positive relationship between testosterone and badge size in male House Sparrows *Passer domesticus*. Important differences between House Finches and these species, however, mean that comparisons with these studies should be approached with caution. Male Superb Fairy-wrens vary in the timing of pre-nuptial molt, but vary little in the 'extent or intensity' of plumage color (Peters et al. 2000). Furthermore, the color of elaborate plumage in Superb Fairy-wrens is not carotenoid-based. House Finches not only have highly variable, carotenoid-based pigmentation, but they also lack a pre-nuptial molt altogether. The badge of male House Sparrows varies in size, but in the study by Evans et al. (2000) the actual color (hue and/or intensity) of the badge was not measured. Like Superb-fairy Wrens, male House Sparrows lack carotenoid-based plumage ornamentation. The mechanisms of color production in carotenoid-, melanin- and structurally-based plumage are different, and thus the costs and functions of these different plumage types are likely to differ (Gray 1996, Badyaev and Hill 2000, McGraw and Hill 2000). However, it is precisely these differences, and their relationships with testosterone, that highlight the importance of studying the proximate mechanisms of plumage color variation if we are to ultimately understand the evolution of this variation.

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