

Condition-dependent sexual traits and social dominance in the house finch

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Elaboration of costly sexual traits can reduce investment in other aspects of reproduction, such as parental care or intrasexual competition, which may lead to the evolution of alternative mating tactics. In house finches (*Carpodacus mexicanus*), less elaborately ornamented (dull) males tend to dominate more elaborated (redder) males, but redder males pair earlier and invest more in parental care. This suggests that males may pursue alternative parental or competitive tactics, depending on the elaboration of their sexual trait. Elevation of testosterone, a hormone that is closely associated with condition in male house finches, influences dominance and sexual behaviors but is antagonistic to parental behaviors. We tested the hypothesis that the higher dominance status of dull males reflects an alternative testosterone-dependent mating tactic. First, we experimentally manipulated the testosterone levels of captive males and measured the effect on dominance rank, and second, we measured the association of testosterone elevation and plumage hue in free-living males. We found that, as predicted, testosterone elevation increased dominance rank in captive males. However, in free-living males, testosterone levels were higher in redder males, suggesting that testosterone is dissociated from dominance status under natural circumstances. This may be because the context of social interactions and the higher motivation of dull males to access food resources have a stronger influence on the outcome of dominance interactions than does the physiological effects of testosterone elevation. In turn, the strong positive correlation between testosterone levels and plumage elaboration likely reflects the common condition dependence of these traits. *Key words*: condition-dependent, house finch, sexual ornament, testosterone. [*Behav Ecol* 15:779–784 (2004)]

Theoretical studies suggest that high investment in sexual ornamentation can preclude males from investing in other costly aspects of reproduction (McLain, 1991; Price et al., 1993). This can lead to trade-offs between the elaboration of sexual traits and parental care (Kokko, 1998) or between different components of mating effort (Badyaev and Qvarnström, 2002). These trade-offs can favor alternative mating tactics among males, such that individuals invest in the suite of traits that allows them to maximize their fitness (Gross, 1996). Alternative reproductive tactics can coexist within a single population because variation in the acquisition and allocation of resources among males may favor variability in the ways in which males solve reproductive trade-offs (Gross, 1996; van Noordwijk and de Jong, 1986). For example, in some species with biparental care, males pursue either parental or competitive behaviors, depending on the elaboration of their sexual trait (see Badyaev and Hill, 2002; Studd and Robertson, 1985).

In most species, individual males fall along a spectrum of monogamous parental phenotypes or polygynous competitive phenotypes (Andersson, 1994). These different mating phenotypes are often underlain by distinct hormone profiles. For example, testosterone elevation organizes the expression of male mating behaviors by stimulating courtship displays (Houck et al., 1996) and aggressive behavior, and by influencing dominance behavior (Wingfield et al., 1987)—behaviors that are characteristic of “competitive” tactics. At the same time, testosterone is antagonistic to the expression of parental behaviors, and in experimental studies, males implanted with testosterone often show decreased levels of parental care (for review, see Ketterson and Nolan, 1994; see also Ketterson et al. 1992, Moreno et al. 1999, Ridder et al. 2000). Thus, males pursuing parental versus competitive

tactics should have distinct testosterone profiles. Indeed, Silverin and Wingfield (1982) found that monogamous and polygynous male pied flycatchers differed in testosterone elevation, with polygynous males maintaining elevated testosterone levels for longer periods in order to compete for and attract a second female.

In male house finches (*Carpodacus mexicanus*), plumage coloration is a sexually selected trait that varies from dull yellow to bright red (Hill, 2002). Previous studies of house finches in eastern populations have shown that redder males provide higher levels of parental care than do dull males (Hill, 1991). However, dull males tend to be socially dominant to redder males (Belthoff and Gauthreaux, 1991; McGraw and Hill, 2000a), suggesting that they invest more in competitive behaviors. Moreover, testosterone elevation in male house finches increases investment in mate attraction (e.g., it increases song rate), and at the same time, it decreases investment in parental care (Stoehr and Hill, 2000). These observations suggest that males may pursue alternative parental and competitive tactics based on their plumage coloration.

Elaboration of plumage color in male house finches is limited by nutritional condition and infection by parasites during molt (Hill, 2002). Redder males are preferred by females and usually pair earlier than do dull males, which leads to their higher reproductive success (Hill, 2002). However, investment in testosterone-dependent behaviors, which are also condition dependent in this species (Duckworth et al., 2001), may allow dull males to increase their fitness by either attracting extrapair copulations or attracting late-breeding females as mates. Alternatively, the condition dependence of both plumage color and testosterone elevation may constrain males in poor condition from investing in either of these traits and thus result in the expression of a single reproductive tactic in this population.

In the present study, we used a combination of experimental data from captive house finches and observations from a natural population to test the hypothesis that dull males are

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Received 27 January 2003; revised 5 November 2003; accepted 25 November 2003.

socially dominant to redder males because they pursue an alternative testosterone-dependent reproductive tactic. First, to establish a link between testosterone elevation and competitive behavior, we experimentally test the effects of breeding season levels of testosterone on dominance status in captive male house finches. If testosterone elevation is proximately linked to competitive behavior, then we expected it to increase the dominance rank of males in captive flocks. In the second part of the study, we measure testosterone levels and plumage color of males in a natural population to determine whether testosterone elevation is related to male investment in sexual ornamentation. If males pursue alternative parental and competitive tactics in this population, then dull males should have higher testosterone levels than do redder males. However, if the common condition dependence of testosterone elevation and male plumage hue constrains male investment in testosterone-dependent behaviors, then we predicted a positive relationship between male plumage hue and testosterone elevation.

METHODS

Captive experiment

To form five captive flocks, we captured hatch-year house finches in traps at feeders in Lee County, Alabama, during August and September 1999. Only hatch-year birds were used in the present study to control for the possibility that age may affect dominance ranking. Upon capture, each male received a unique set of two colored plastic bands to allow individual identification during dominance trials. Because the birds had not yet undergone molt into adult plumage, our initial flocks included some female house finches, which were later released. Birds were temporarily held in individual indoor cages that were visually isolated from one another until we had enough individuals to form a flock of 16 birds (we assumed that half would be males), at which time we released them simultaneously into five separate outdoor aviary cages. Thus, all individuals entered a flock at the same time.

Birds were fed a diet of vitamin-enhanced water, sunflower seed, and millet ad lib. We added sulfadimethoxine (1.25 g/l) to the drinking water during the pretreatment period (see details of treatment below) to prevent the spread of coccidia (Brawner et al., 2000), a common endoparasite of house finches. In addition, because all individuals started molting into their adult plumage shortly after we captured them, we added canthaxanthin (Roche chemicals) to the water during molt (approximately October–November) to standardize plumage color among males (Hill, 2002). After the first month in captivity, we clearly identified and released all females from the flocks.

In January 2000, before hormone manipulation, dominance interactions in each flock were observed from a blind for 90 min from 0700–1100 h. An individual was scored as winning a dominance interaction if it displaced another individual from a perch or feeder. All interactions between individuals in a flock were scored, and dominance hierarchies were constructed for each flock. House finches form stable and linear dominance hierarchies with few reversals (McGraw and Hill, 2000), and each male was assigned a rank within the flock.

To modify testosterone levels, we randomly assigned males within each flock to the following three treatment groups: a low testosterone group in which males were gonadectomized (G-males), a high testosterone group in which males were implanted with silastic testosterone-filled implants (T-males), and a sham-treated group (control males). The gonads were removed from G-males during surgery by aspiration. Both controls and T-males received similar surgeries but were left

intact. Each T-male received one subcutaneous silastic implant 8 mm in length (1.95-mm outer diameter and 1.47-mm inner diameter; 6 mm filled with crystalline testosterone). Empty capsules of the same dimensions were implanted in control and G-males. After all surgeries, birds were housed individually in indoor cages that were visually isolated from one another for up to 5 days, and during this time, their health was carefully monitored. Birds from the same flock were released back into the outdoor aviary cages simultaneously to ensure that prior residency did not affect dominance interactions. The post-treatment flocks were comprised of two to three birds from each treatment group. Our pretreatment flocks contained a total of 36 males (12 males/treatment group); however, one T-male and three G-males died early in the experiment and three T-males lost their implants. Thus, our final sample sizes were eight T-males, nine G-males, and 12 control males with five to seven males per flock. The death of some males meant that the final flock size differed from the original size. To calculate the change in dominance rank from the pretreatment to posttreatment flocks, we had to recalculate the initial dominance ranks by deleting the males that had died from the original flocks. We simply removed the males that had died from the initial flocks and moved the remaining males up one position; e.g., a T-male that had died was originally in position 3 in the flock therefore, male 4 in this flock became male 3, and male 5 became male 4 etc.

The birds used in this experiment were part of a concurrent study in which we tested the effects of testosterone on disease resistance. Therefore, after hormone manipulations, all individuals in the present study were inoculated with coccidia (*Isospora* spp.), an endoparasite. Details and results from the concurrent study are reported elsewhere (see Duckworth et al., 2001). During the infection experiment, we monitored the infection status of males by collecting fecal samples once per week for a total of 6 weeks. We scored the intensity of coccidial infection by counting the number of oocysts using a standard sucrose float and slide preparation method (for details, see Brawner et al., 2000). Five weeks after the formation of the treatment groups, we again observed the dominance interactions of males in the flocks and ranked males in a linear hierarchy according to their wins and losses.

To confirm that the hormonal manipulations produced the desired differences in testosterone elevation between the experimental groups, we bled G-males and T-males at the conclusion of the experiment (approximately 2 months after implantation). Approximately 200 μ l blood was collected in capillary tubes from each male by puncturing the brachial vein. Plasma was stored at -20 C for later hormone analysis. Implants produce high and stable plasma testosterone levels for several months after implantation (Duckworth RA, unpublished data; see also Stoehr and Hill, 2001). We did not bleed control males because as they were left intact and not implanted with hormone, their testosterone levels were free to fluctuate, and thus, a single sampling of circulating testosterone levels in these males is unlikely to reflect the range of testosterone levels exhibited throughout the study. However, in a pilot study in which we monitored the hormone levels of captive unmanipulated males (males similar in treatment to our control males) for several weeks, we found that the mean testosterone levels (\pm SE) remained relatively low (0.32 ± 0.64 ng/ml, $n = 23$; Duckworth RA, unpublished data) compared with the testosterone levels of both T-males and free-living males (see Results).

Testosterone elevation in free-living males

This part of the study was conducted on a banded population of house finches breeding on Auburn University campus

located in southeastern USA (east-central Alabama). Breeding birds were monitored closely during the 1999 breeding season, and we recorded the dates for nest initiation, incubation period, and nestling period for all nests. Males were grouped into the following categories according to observations of their breeding behavior: pairing (males captured before the onset of their first nesting attempt for the season), incubation (males whose females were incubating), nestling (males feeding nestlings), and postbreeding (males captured up to 1 month after their most recent nesting attempt). We captured male house finches at feeding stations by using traps that were set approximately twice a week throughout the breeding period from 0600–1100 h and were checked every 45 min. All males were bled from the brachial vein within 10 min of removal from the trap. Individuals remained in traps up to 45 min before being removed; however, testosterone levels do not differ between individuals removed from traps immediately upon entering compared to individuals that remain in the trap for up to 45 min (Duckworth et al., 2001). Whole blood was stored on ice for up to 30 min until it could be transported to the laboratory, where it was centrifuged to separate the plasma from the blood cells. The plasma was stored at -20 degrees C before radioimmunoassay analysis.

We measured male plumage color by using a Colortron reflectance spectrophotometer (Light Source). House finches have distinct carotenoid patches on the crown, breast, and rump. Three hue measurements were taken from each of these areas, and we calculated the overall hue score as the mean of nine hue values. The Colortron arbitrarily assigns lower values to redder hue scores, and to simplify discussion of the data, we transformed hue scores by subtracting the highest hue score from every score so that higher hue values indicate redder plumage color.

Radioimmunoassay techniques

For a detailed description of the radioimmunoassay technique, see Mendonça et al. (1996). We used testosterone antibody from Endocrine Sciences. For captive males, all samples were run in one assay that was sensitive to 13 pg/ml. Intrassay variation was 3.0%, and the average percentage of recovery was 85%. For analysis of testosterone from free-living males, intrassay variation was 3.3% and interassay variation was 15.1%. The average percentage of recovery was 84% and assay sensitivity was 10 pg/ml.

Statistical analyses

All statistical analyses were performed by using SAS. To determine the effect of testosterone manipulation on the dominance ranks of males, we used a repeated measures ANOVA. The relationship between dominance and parasitic infection was analyzed by using a linear least-squares regression.

Some of the males from the natural population were captured multiple times. To ensure independence of data points, we used each male only once in the analysis of plumage hue and testosterone levels. Male testosterone levels can fluctuate over a fairly short time scale according to the context of the current breeding situation (Wingfield et al., 1990). Therefore, we used only the highest testosterone value for each male as a conservative estimate of a male's ability to elevate testosterone levels. Eight males had testosterone levels that were below the detectable levels of our assay (10 pg/ml), and we therefore did not use these males in our analyses. These males did not differ in plumage hue from the males retained in our sample (nonparametric one-way ANOVA $F_{1,47} = 0.02$, $p = .88$), and thus, excluding these males did not bias our sample.

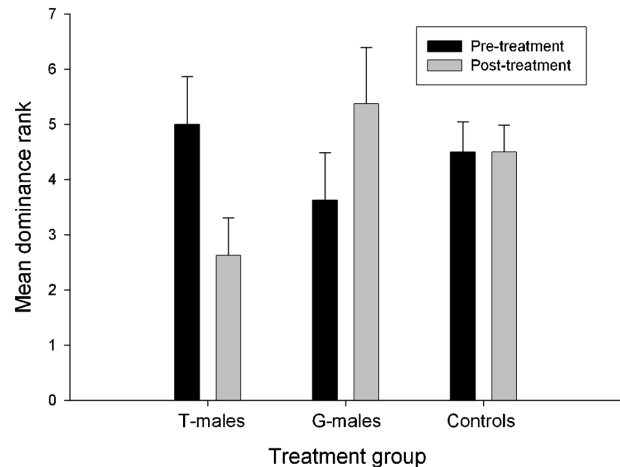


Figure 1

The effect of testosterone treatment on dominance rank in male house finches. Lower numbers indicate a higher dominance rank. After testosterone manipulation, T-males (testosterone-implanted, $N = 8$) significantly increased their dominance rank and G-males (gonadectomized, $N = 9$) significantly decreased their rank, whereas controls ($N = 12$) remained stable in rank. Bars shown are mean and SE.

For the analysis of testosterone levels in relation to breeding stage, we used one-way ANOVA. We also did a separate analysis by using the general linear model, which included capture date as a covariate. The relationship between testosterone elevation and male plumage hue was estimated as the standardized regression coefficient from a linear regression of testosterone on plumage hue. This relationship was also analyzed in all breeding males by using the generalized linear model and included stage of breeding as a class variable. Plumage scores were log transformed, and the reciprocal of testosterone values was used to normalize the data before analysis.

RESULTS

Testosterone treatment significantly affected dominance rank in captive males (repeated-measures ANOVA $F_{2,28} = 3.34$, $p < .03$) (Figure 1). Post hoc analyses revealed that the T-males significantly increased their dominance rank in the flock compared with that of both G-males ($F_{1,16} = 5.72$, $p < .01$) and control males ($F_{1,19} = 3.88$, $p = .02$). G-males did not significantly change their rank compared with control males, although they did decrease in rank ($F_{1,20} = 1.42$, $p = .26$). After treatment with testosterone, T-males increased in rank by (mean \pm SE) 2.4 ± 0.81 positions, and G-males decreased in rank by 1.8 ± 0.76 positions in the flock. The position of control males in the flocks remained stable (mean change \pm SE = 0.17 ± 0.66). Thus, the groups differed significantly in their final ranks (ANOVA $F_{2,28} = 3.21$, $p = .05$). The intensity of coccidial infection had no effect on the change in dominance rank of males ($F_{1,28} = 0.01$, $p = .94$) or on the final dominance rank of males ($F_{1,28} = 0.80$, $p = .38$). Hormone manipulations of T- and G-males produced high testosterone levels in T-males (12.23 ± 2.07 ng/ml) and low levels in G-males (0.18 ± 0.35 ng/ml).

The testosterone levels of breeding males ($N = 35$) captured from January–June was 1.41 ± 0.44 ng/ml, and the maximum level of testosterone recorded was 15.73 ng/ml. Testosterone levels were highest during the pairing stage of breeding (mean during pairing = 2.33 ± 0.96 ng/ml, incubation = 0.47 ± 0.10 ng/ml, nestling = 0.54 ± 0.29

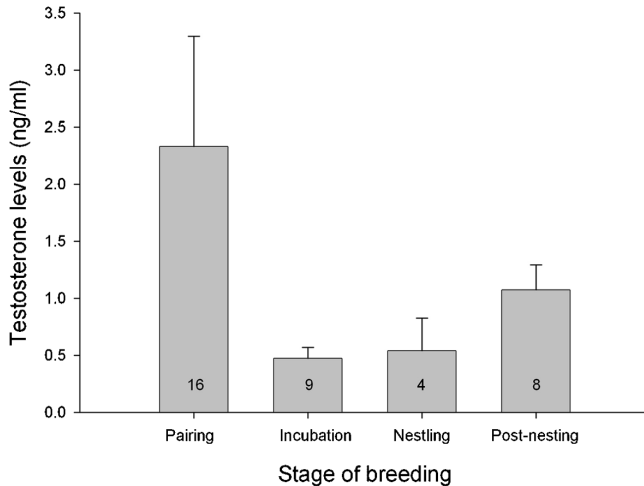


Figure 2

Testosterone levels according to the stage of breeding in which males were captured. Post-nesting refers to males captured up to 4 weeks after a nesting attempt. Sample sizes are indicated on bars. Bars shown are mean and SE.

ng/ml, postnesting = 1.07 ± 0.22 ng/ml) (Figure 2). Although the overall ANOVA for the effects of breeding stage on testosterone elevation was not significant ($F_{3,36} = 1.63$, $p = .20$), including capture date as a covariate improved the model ($F_{4,36} = 2.46$, $p = .08$). In addition, post hoc analyses showed that males captured during pairing had significantly higher testosterone levels than do males captured during the incubation stage ($F_{1,24} = 5.42$, $p = .02$). No other post hoc comparisons were significant. However, males captured during nonparental periods (pairing and postnesting stages combined) had significantly higher testosterone levels than do males captured during parental care periods (incubation and nestling stages combined; $F_{1,36} = 4.22$, $p = .048$).

Redder males had higher testosterone levels than do dull males ($F_{1,34} = 8.10$, $b_{ST} = 0.44$, $p = .007$). Including stage of breeding in the model improved this relationship ($F_{1,34} = 9.37$, $p = .004$). There was a particularly strong relationship between testosterone elevation and plumage hue during the pairing stage of breeding ($F_{1,15} = 16.24$, $b_{ST} = 0.73$, $p = .001$) (Figure 3).

DISCUSSION

Characterizing the suite of traits and behaviors that comprise the male mating phenotype is essential for understanding how selection acts on sexual traits. Negative correlations between sexual traits and reproductive behaviors may indicate trade-offs between investment in different traits. These trade-offs can lead to the evolution of alternative mating tactics of males (Gross, 1996). Alternatively, positive correlations may indicate that two traits are subject to similar constraints (e.g., common condition-dependent expression). Because selection acts on the overall mating phenotype, these correlations are predicted to have important consequences for the evolution of sexual traits (Badyaev and Qvarnström, 2002; Price and Langen, 1992).

In the present study, we found a strong positive correlation between plumage hue and testosterone elevation in male house finches. Thus, we were unable to support the hypothesis that male house finches pursue alternative mating tactics in this population. Redder males had higher testosterone levels despite evidence that elevated testosterone increases domi-

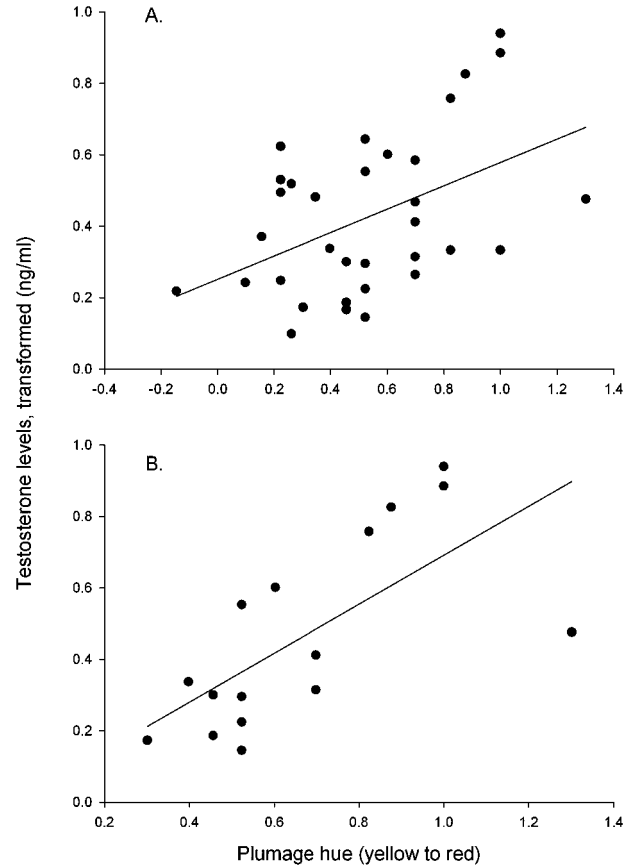


Figure 3

Positive relationship between male plumage hue and testosterone elevation in all males ($N = 35$) (A) and in males in the pairing stage of breeding ($N = 16$) (B). Testosterone levels were transformed by taking the reciprocal of each value, and hue values were log-transformed.

nance status and that dull males tend to dominate elaborately ornamented males in this population. Previous studies have shown that both plumage color and testosterone elevation are dependent on male condition in this population (Duckworth et al., 2001; Hill, 2000). Thus, males in poor condition may be constrained from elaborating plumage coloration and elevating testosterone levels, whereas redder males invest in both of these traits. Why then are dull males socially dominant in this population? And why is testosterone elevation not associated with dominance behavior in free-living males?

The ability of less ornamented males to dominate more ornamented males may reflect their higher motivation to access resources or mates (Maynard Smith and Harper, 1988). Many studies have shown that individual motivation can play an important role in determining the outcome of dominance interactions (Cristol, 1992; Lemel and Wallin, 1993), especially if there is a large difference between individuals in the benefits of accessing a particular resource (Enquist and Leimar, 1987). For example, in house crickets (*Acheta domesticus*), body size usually determines the outcome of dominance interactions, however, when motivation is maximized by food deprivation, this overrides the effects of male body size on dominance interactions (Nosil, 2002). Furthermore, in natural populations of birds, the effects of motivation have been shown to be an important determinant of dominance outcome even in species in which the largest or most ornamented males usually win contests (Lemel and Wallin, 1993). Dull males are

presumably in poorer condition than are redder male house finches and therefore may value access to food resources more than do redder males. Thus, the motivation of dull males to access food resources may explain the observed patterns of dominance in house finches. However, future studies will be necessary to test this idea.

Contrary to the relationship between dominance and testosterone elevation in free-living males, in captive males dominance behavior was clearly influenced by elevation of testosterone levels. These results are in contrast to the results of Belthoff et al. (1994). However, in their study they were specifically interested in the effects of testosterone on dominance status during the nonbreeding season, and the testosterone levels that they report in nonbreeding males were 10 times lower than the average level of testosterone we found in males that were pairing. Furthermore, several recent studies have found that testosterone's effects on the phenotype can differ, depending on the season and the life-history stage of birds (Wingfield and Soma, 2002).

The effects of testosterone elevation on dominance may depend on the context of the interaction between two individuals (Wingfield et al., 1990). In captive flocks, males were provided with an abundance of food for all individuals in the flock, and thus, motivation owing to the nutritional state of an individual should have played a small role in dominance interactions. The positive influence of testosterone on aggressive behavior is likely to be the proximate cause of the increased dominance rank of T-males. The link between testosterone and aggression is well established (Wingfield et al., 1987), and increased aggressiveness often translates into a higher dominance rank. Observations that T-males were the most active and initiated the most interactions during the dominance trials (Duckworth RA, personal observation) support this interpretation. However, it is clear that higher levels of aggression cannot explain all of the variance in dominance rank between males. For example, one high-ranking G-male retained the number one dominance rank in a flock despite his decreased testosterone levels. This male showed low levels of activity and initiated few interactions; however, he resisted all attempted displacements by other males (Duckworth RA, personal observation), suggesting that his dominance status was more affected by his previous high ranking than by decreased testosterone. These observations confirm the growing consensus that the structure of dominance hierarchies results from many different factors and perhaps, most importantly, depends on the current context of the interaction (Chase et al., 2002).

The positive correlation between plumage color and testosterone elevation in free-living males may reflect selection by females for males to invest in multiple condition-dependent traits. In house finches, testosterone has been shown to increase male song rate (Stoehr and Hill, 2000) and, as shown in the present study, also to increase male competitive ability. These behaviors could serve as a secondary signal of condition to females, reinforcing the information that they obtain from male plumage coloration (Møller and Pomiankowski, 1993). These traits change on different time scales—plumage color is renewed annually during fall molt (Hill, 2002), whereas testosterone elevation can fluctuate within hours or even minutes during the breeding season (Wingfield et al., 1990)—and thus may provide females with both long- and short-term information on male condition. Although all current studies on dominance and plumage color in house finches show that dull males tend to be dominant to redder males, all of these studies have been conducted over access to food resources. No study has yet described the relationship between male dominance and plumage color in contests over females, a context that is likely

more relevant to the notion that testosterone-dependent behaviors are sexually selected in this species. Further study is also needed to determine whether female house finches base mate choice decisions on testosterone-dependent traits, as has been shown in other species (Hill et al., 1999).

Our results indicate that male house finches of high quality are able to invest in multiple costly sexual traits, and do not support the hypothesis that there are alternative mating tactics in this population. This is contrary to results found in a population of house finches in western Montana, USA, where dull males invest more in parental care than do redder males, indicating a trade-off between investment in mate attraction versus parental behavior (Badyaev and Hill, 2002). This variation between populations in male reproductive behaviors may be a common occurrence as indicated by a growing number of studies that show population variation in reproductive strategies (e.g., *Carpodacus mexicanus*: Badyaev and Hill, 2002; Hill, 1991; *Passer domesticus*: Griffith et al., 1999; Møller, 1988; *Tachycineta bicolor*: Dunn and Robertson, 1992). These studies suggest that reproductive strategies are labile and can closely track changes in environmental conditions. Understanding the ecological, social, and historical factors that produce such distinct patterns in reproductive traits and behaviors between populations remains an important challenge for future studies of sexual selection.

We thank Alex Badyaev, Jim Belthoff, and one anonymous reviewer for comments that improved this manuscript; Anne Dervan, Kevin McGraw, Paul Nolan, and Andrew Stoehr for help with the capture and banding of birds; and Jeannine Ott for assistance with the radioimmunoassays. This research was supported by a National Science Foundation grant (numbers IBN 9722171 and DEB 0077804) to G.E.H. and grants from the Society for Integrative and Comparative Biology and the Auburn University Graduate School to R.A.D. Birds were collected under state of Alabama permit no. 12 and Federal permit 784373. The procedures described in this article were approved by the Auburn University Institutional Animal Care and Use Committee (no. 0106-R2170).

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