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PLUMAGE VARIATION, PLASMA STEROIDS AND SOCIAL DOMINANCE IN MALE HOUSE FINCHES[1]

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Abstract. In male House Finches (*Carpodacus mexicanus*), the extent and color of plumage varies depending on access to carotenoid pigments. "Colorful" males exhibit extensive red pigmentation, while less colorful (i.e., "drab") males exhibit carotenoid pigmentation over a smaller percentage of their plumage, pigmentation of a color besides red (e.g., yellow, gold, orange, or pink), or both. One explanation for maintenance of plumage variation is that it reliably reflects social status, allowing males to correctly assess their status in relation to others and avoid or minimize costly fights. Social relationships may also be related to endogenous factors, such as circulating levels of the hormones testosterone and corticosterone. High levels of testosterone may promote or facilitate increased aggression, and stress associated with receiving aggression from individuals of higher status may increase adrenal activity and secretion of corticosterone.

We examined the relationship between plumage variability, steroid hormones, and social status in captive male House Finches during the non-breeding period in: (1) groups of males in which individuals varied by age, size, and plumage, and (2) pairs (dyads) of males matched for several measurable parameters except plumage. Testosterone and social status were not related in males competing in either groups or dyads, and levels of testosterone were routinely low. Corticosterone and status were not related in groups but, in dyads where subordinate individuals had little chance of escaping aggression from more dominant birds, subordinates exhibited significantly greater levels of corticosterone. Although drab males tended to achieve higher status than colorful males in both experiments, which is consistent with previous studies on free-living individuals, we could not reject the null hypothesis that plumage and status were unrelated. We conclude that dominance relationships among male House Finches during the non-breeding season may not be related to testosterone, but they are reflected by levels of corticosterone in some circumstances. Additionally, colorful plumage appears to be a poor predictor of high social status among male House Finches during the non-breeding season.

Key words: Social dominance; hormones; testosterone; corticosterone; plumage coloration; House Finch; Carpodacus mexicanus; *South Carolina.*

INTRODUCTION

Use of plumage cues to signal dominance status may explain the occurrence of plumage variability in some winter flocks of birds (Rohwer 1975, Rohwer and Rohwer 1978, Rohwer and Ewald 1981). Such signals may benefit both flock members and immigrants by allowing them to correctly assess their relative status without resorting to costly fights, especially when flocks are large and unstable (Rohwer 1975). Plumage signals of social status operate in several previously examined species of flocking birds (e.g., Fugle et al. 1984, Jarvi and Bakken 1984, Rohwer 1985, Watt 1986, Holberton et al. 1989) where, in general, individuals with the greatest coloration achieve high status.

Although external plumage characteristics influence aggressiveness and status (e.g., Ficken et al. 1978, Parsons and Baptista 1980), they may do so only in the presence of elevated plasma androgen levels (e.g., Rohwer and Rohwer 1978). In past studies, androgen levels correlated most closely with aggression in situations of social instability, typically for the few days to a week when dominance relationships were being established. During this time, winners (i.e., individuals with high social status) exhibited significantly higher levels of testosterone than losers (Ramenofsky 1984, Wingfield 1985, Wingfield and Ramenofsky 1985, Hegner and Wingfield

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1987). After this time and during socially stable periods, androgen levels are often indistinguishable for winners and losers (Wingfield et al. 1987, Wingfield et al. 1990). Stress-related hormones, such as corticosterone, may also reflect dominance relationships. Individuals with low status may experience stress in relation to losing encounters or prolonged subordinate status, at which time adrenal activity increases and high levels of corticosterone are observed (Ely and Henry 1978). Thus, in addition to plumage cues, endogenous factors such as circulating testosterone and corticosterone levels may be important indicators of dominance relationships.

House Finches (*Carpodacus mexicanus*) are seed-eating, gregarious birds that form semi-colonial breeding assemblages throughout many urban and suburban regions of the United States (Thompson 1960a, 1960b). Beginning in October and continuing through early November, many individuals in the eastern subpopulation migrate south to winter (Belthoff and Gauthreaux 1991a), at which time they join flocks that spend the winter feeding from weedy fields and feeders baited with seed. Social dominance is important in these flocks in determining access to critical resources (Brown and Brown 1988, Shedd 1990).

Male and female House Finches are sexually dichromatic, and both undergo a single annual molt during late summer. Females are brown and white with contrasting dark streaks on the breast. Pigmentation in males grades from yellow to bright red (Michener and Michener 1931, 1940; Gill and Lanyon 1965; Yunick 1987) and is influenced by access to carotenoid-rich food prior to the molt (Brush and Power 1976, Hill 1992). The sources of carotenoids used by wild male House Finches to pigment their plumage and factors that mediate access to such resources remain unknown (Hill 1992, 1994). First-year males tend to be less colorful than adults, but there is considerable variation in both age classes (Yunick 1987).

Our study examined aggressive behavior in captive, male House Finches in relation to plumage variation and two plasma steroid hormones, testosterone and corticosterone. Using newly established groups of males, and males paired in dyadic competitions, we assessed: (1) the relationship between plumage variability and dominance status, and (2) the hormonal correlates of dominance. We hypothesized that colorful males would achieve higher status than drab males, individuals of high status would exhibit greater levels of testosterone, and subordinates would exhibit increased levels of corticosterone.

METHODS AND MATERIALS

GENERAL METHODS

We captured House Finches with mist nets as they approached artificial feeders baited with sunflower seeds throughout Pickens County, South Carolina, between late October and early December in 1989, 1990, and 1991. During this time of the year, most individuals have completed their late-summer molt, and it is possible to accurately age individuals based on skull characteristics (see below). We housed birds indoors in individual cages (30 cm wide × 30 cm high × 60 cm long) visually isolated from each other and provided unlimited access to sunflower seeds, millet, and water until dominance trials began. Light on/off cycles simulated the natural photoperiod.

We banded finches with uniquely numbered aluminum leg bands and, because morphological parameters can be important in influencing dominance relationships (e.g., Chase 1974, Gauthreaux 1978), we measured their relaxed wing chord length, tarsus length, medial rectrix length (all to the nearest 0.5 mm), and body mass (to the nearest 0.5 g using a pesola scale). We classified individuals with incompletely pneumatized skulls as hatching year (i.e., HY) and individuals with fully pneumatized skulls as adults. We quantified plumage on the forehead, eyebrow, crown, and rump. Individuals received a maximum of 3 points in each region as follows: 0—no red or orange in body region; 1—orange, gold, or yellow feathers only; 2—predominantly red or pink, with a few yellow or gold feathers; 3—red feathers only. We placed a grid (see Hill 1992) that divided the underside of birds into four regions (area 1 = throat; area 2 = upper breast; area 3 = lower breast; area 4 = abdomen) over the anterior portion of each male. Except for area 3 where we found it easier to score the number of squares lacking pigmentation, we counted the number of squares containing pigmentation in each region. In all birds, pigmentation completely filled areas 1 and 2, corresponding to the throat and upper breast, so we excluded these areas from further analyses. We included areas corresponding to the lower breast and abdomen, which varied much more. We also measured the length and width of rump patches following Yunick (1987). We entered scores for the eight variables into a Principal Components Analysis (Johnson and Wichern 1988) that collapsed observations into the variables describing much of the variation. We used scores along Principal Component I (PC I) as an index of plumage coloration and considered individuals receiving high PC scores to be colorful males. None of the males was used in more than one experiment, and we released all birds at original capture locations following the study. Throughout the paper, we set rejection levels at $\alpha = 0.05$ and present means and their standard errors ($\bar{x} \pm$ SE).

GROUPS OF MALES

During late November 1989, we conducted dominance trials with groups of males in a hexagonal arena constructed of wire hardware cloth (230 cm in diameter and 40 cm high) complete with a water jar, food jar containing sunflower seeds, and a 45-cm perch over which individuals competed for access. The probability that birds in a group would compete was increased by covering much of the feeding area on the food jar with cardboard, so that only one finch could feed at a time. Additionally, the floor of the arena was hardware cloth through which dropped seeds passed; this rendered the seeds unavailable and made feeding possible only at the feeder.

A total of 43 males comprised four groups (n = 12, 12, 10, and 9 birds). Groups were relatively large to limit potential for individual recognition (Shields 1977) and to develop a situation where plumage cues of dominance may be important. Although group densities were high, they were not much greater than those observed in free-living flocks occupying areas near feeders ($\bar{x}$ = 10.4 ± 0.7; maximum = 18; n = 21). Individuals competing in groups were in captivity 9.5 ± 1.7 days before trials began. Groups were assembled randomly with respect to each individual's age, size, and length in captivity, but we attempted to maximize the range of plumage color within each group. Each bird wore plastic colored legbands so that they could be identified; there was no relationship between color bands and dominance status during an earlier experiment (Belthoff and Gauthreaux 1991b). To simulate naturally occurring conditions of reduced food during which wild finches may have to compete, we withheld food from individuals on the evening before trials began (beginning 1 hr before lights out).

Dominance trials began near sunrise and included a 2-hr observation period during which interactions were recorded. We observed each group of finches on alternate days for three trials (6 hr per group) and returned birds to their individual cages between trials. From a blind located 5 m away, we recorded the frequency of overt aggressive interactions for each member of a group using 10 × 40 binoculars and scored wins for supplanting attacks, high intensity head-forward displays, beak fencing, and actual combat occurring at or away from the food jar (see Thompson 1960a for a complete description of these displays). For each interaction, we classified the individual that moved away as the loser. We constructed win/loss matrices by minimizing the number of reversals beneath the diagonal (Brown 1975) and assigned dominance ranks to individuals (1 = most dominant). Within a group, individuals received the same rank if neither won a greater proportion of interactions, or if they did not interact. Generally, pairs of birds that did not interact were birds that were dominated by many other finches and, subsequently, both ranked low in the hierarchy.

We used Spearman's correlation analysis (Sokal and Rohlf 1981) to examine relationships between dominance status, morphology, plumage coloration, and hormone levels. Because we posed directional hypotheses, we used 1-tailed tests. To examine effects of age, we divided groups into thirds to represent birds with high, moderate, and low dominance ranks. Four birds were assigned moderate dominance status in group 3, which contained 10 birds. Sample sizes were too small to perform statistical analyses within groups (i.e., expected values for cells were too low) and data across groups could not be pooled. Thus, we present percentages for age classes attaining each level of dominance. We compared mean plumage scores between age classes using Mann-Whitney tests and examined effects of age on testosterone and corticosterone levels with ANOVA.

MALE DYADS

During December 1989 (n = 8), between December 1990 and February 1991 (n = 16), and during early January 1992 ($n = 6$), we conducted 30 dyadic competitions between 60 male House Finches. Individuals competing in dyads were in captivity 30.7 ± 4.3 days before experiments began. We matched males for age (adult or HY birds), tarsus length (to within 1 mm), wing chord length (to within 1.5 mm), mass (to within 1.5 g), and length of captivity to the extent possible (average difference in captivity between combatants = 14.4 days), so that birds differed noticeably only in pigmentation. We called members of a dyad with greater plumage scores "colorful" males and birds with lower scores "drab" males. However, "drab" males generally had considerable pigmentation. We introduced experimental pairs simultaneously into a neutral cage on the evening before trials were to begin, where they spent the last hour of light each day without food. The experimental cage measured approximately 60 cm long × 30 cm wide × 30 cm high and had separate water jars and perches at each end. We separated males by placing an opaque divider between them. Each morning (between 07:00 and 09:00 hr) for four consecutive days we removed the divider, placed a food jar filled with sunflower seeds centrally in the cage, and isolated the cage in a container (Skinner box) complete with a 1-way mirror and light. Finches were allowed to interact for 15 min while we recorded the number of interactions at and away from the food jar. To avoid site dominance from becoming a factor, we returned finches to their individual cages between trials. We considered one member of a dyad dominant over the other if it won 75% or more of its interactions (Piper and Wiley 1989). Use of predominantly HY birds in the dyads allowed us to accurately control for age (i.e., birds aged as adults could be any age >1 year old). Of the 30 dyads, 26 pitted HY birds against one another, and four paired adults against each other. Using a Chi-square goodness of fit test (Sokal and Rohlf 1981) we tested the null hypothesis that dominance status was independent of plumage coloration. Using paired sample *t*-tests (Sokal and Rohlf 1981), we compared circulating levels of testosterone and corticosterone between (1) dominant and subordinate males, and (2) colorful and drab males. We examined effects of month on hormone titers using 1-way ANOVA or, in the case of one analysis of testosterone levels, with a Mann-Whitney test (Sokal and Rohlf 1981).

BLOOD COLLECTION AND ANALYSIS OF HORMONES

Immediately after final observation periods for a group or pair of birds, we collected 100–300 μl of whole blood from each combatant into heparinized capillary tubes after puncture of the brachial vein. Blood was transferred to 1.5 ml centrifuge tubes and centrifuged at 2,500 rpm for 15 min within 1 hr of collection, after which plasma was stored at −80°C. Testosterone and corticosterone were measured in two radioimmunoassays after partial purification on diatomaceous earth/glycol columns (Wingfield and Farner 1975, Wingfield et al. 1982), using modifications described by Ball and Wingfield (1987). Water blanks for each assay averaged <2 pg and 4.9 pg testosterone, and 4.5 pg and 2 pg corticosterone. Two samples containing 250 pg testosterone and 500 pg corticosterone were taken through each assay procedure. Values calculated for testosterone were 249 pg and 208 pg for one assay and 257 pg and 230 pg for the other. Values for corticosterone were 463 pg and 494 pg, and 437 pg and 513 pg, respectively. We were unable to obtain enough plasma for hormone analyses from one male in the dyad experiment (a bright male who was subordinate) and one male in the group experiment (the most dominant individual [rank = 1] in Group 2). Many (51/102 or 50%: 24 of 59 in the dyad experiment; 27 of 43 in the group experiment) testosterone samples were at or below the level of detection of the assay. Corticosterone was present in detectable levels in all birds. Although handling time can influence both hormones, effects on corticosterone are much more rapid (Wingfield et al. 1982, Le Maho et al. 1992). Therefore, we recorded sampling time for each member of a group as the number of minutes since entering the cage to sample the first individual and regressed plasma corticosterone levels on this sampling time. In none of the experiments were handling time and corticosterone titer significantly related.

RESULTS

GROUP TRIALS

Plumage. PC I (eigenvalue = 392.1) explained more than 88% of variation in plumage among the 43 finches, with abdomen (area 4), lower breast (area 3), and rump patch length generating the greatest loadings along this axis (eigenvectors

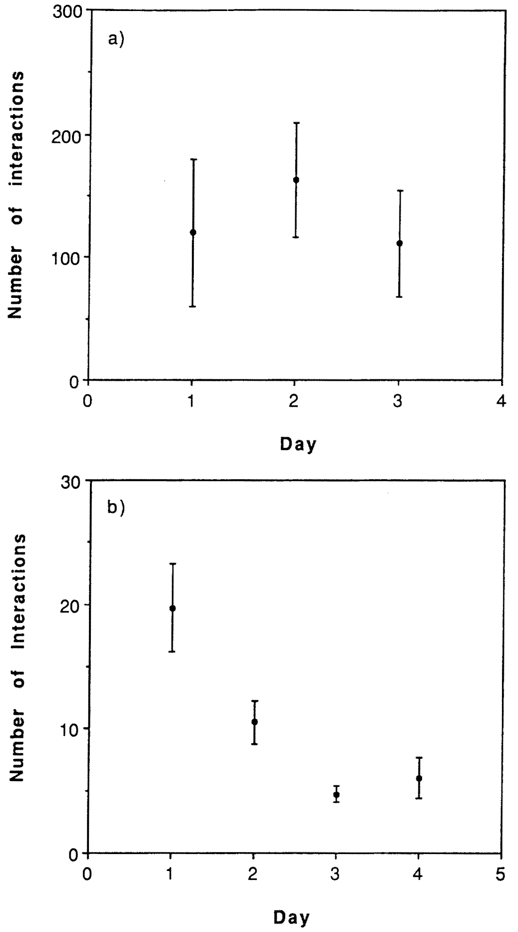

FIGURE 1. (a) Mean (±SE) number of interactions scored by day in four groups of wintering male House Finches. (b) Mean (±SE) number of interactions scored by day in 30 dyads.

= 0.9786, −0.1496, and 0.1248, respectively). Plumage score (PC I) averaged −8.1 ± 2.98, −8.0 ± 3.28, 12.0 ± 8.02, and 8.0 ± 7.91 in groups 1–4, respectively. Although the range was comparable for adult and HY males (adults: −21.1–42.6; HY: −21.3–39.0), adult males had significantly greater plumage scores (Mann-Whitney test, $U = 285$, $P < 0.05$).

Dominance patterns. Dominance ranks among group members were assigned based on 208 ± 35, 236 ± 22, 37 ± 12, and 85 ± 28 interactions per trial (i.e., per day) for Groups 1–4, respectively, with the mean number of interactions ($n = 4$ groups) peaking on Day 2 (Fig. 1a). Because we assigned dominant birds (i.e., alpha birds) the rank of 1, and the birds they dominated received higher scores, a negative correlation between plumage score (PC I) and dominance rank is expected if colorful plumage were related to high status. In no group was dominance rank significantly correlated with plumage score and, despite lack of significance, all correlation coefficients were positive rather than negative (Fig. 2). This indicates that many drab individuals dominated more colorful ones. There also were no significant relationships between dominance rank and wing length or mass, but tarsus length may have been important in Groups 1 and 3 where the relationship approached statistical significance (Table 1). Because HY birds achieved high status more often than adults (Table 2), greater age did not promote higher dominance status in these birds.

Hormones. In no group was there a significant relationship between dominance rank and levels of testosterone or corticosterone (Table 1). There was also no significant relationship between number of wins by individuals and testosterone ($P > 0.22$ for all groups). Testosterone did not differ between adult and HY individuals ($F_{1,25} = 2.20$, $P = 0.151$), nor was there an effect of age on corticosterone ($F_{1,37} = 0.21$, $P > 0.645$).

MALE DYADS

Plumage. Among 60 finches matched in dyadic competitions, PC I accounted for 86.6% of variation among measures of plumage (eigenvalue = 303.2). As in finches used for group trials, abdomen, lower breast, and rump patch length generated the greatest loadings along the first PC (eigenvectors = 0.9686, −0.1474, and 0.1641, respectively). Patterns of plumage variation were similar among finches competing in the two types of experiments.

Dominance patterns. We based our assignment of dominance on 41 ± 4.4 interactions per pair, and no relationship was based on fewer than five interactions (range: 5–98). Average number of interactions between paired males was greatest on Day 1, declined until Day 3, and then increased on Day 4 (Fig. 1b). Of 30 dyads, 29 met the criterion for establishing dominance (wins were evenly distributed in one dyad), and individuals classified as dominant won 96 ± 1.4% of interactions. Drab males dominated more colorful males in 18 (62.1%) dyads, while colorful males achieved dominance in 11 (37.9%). We

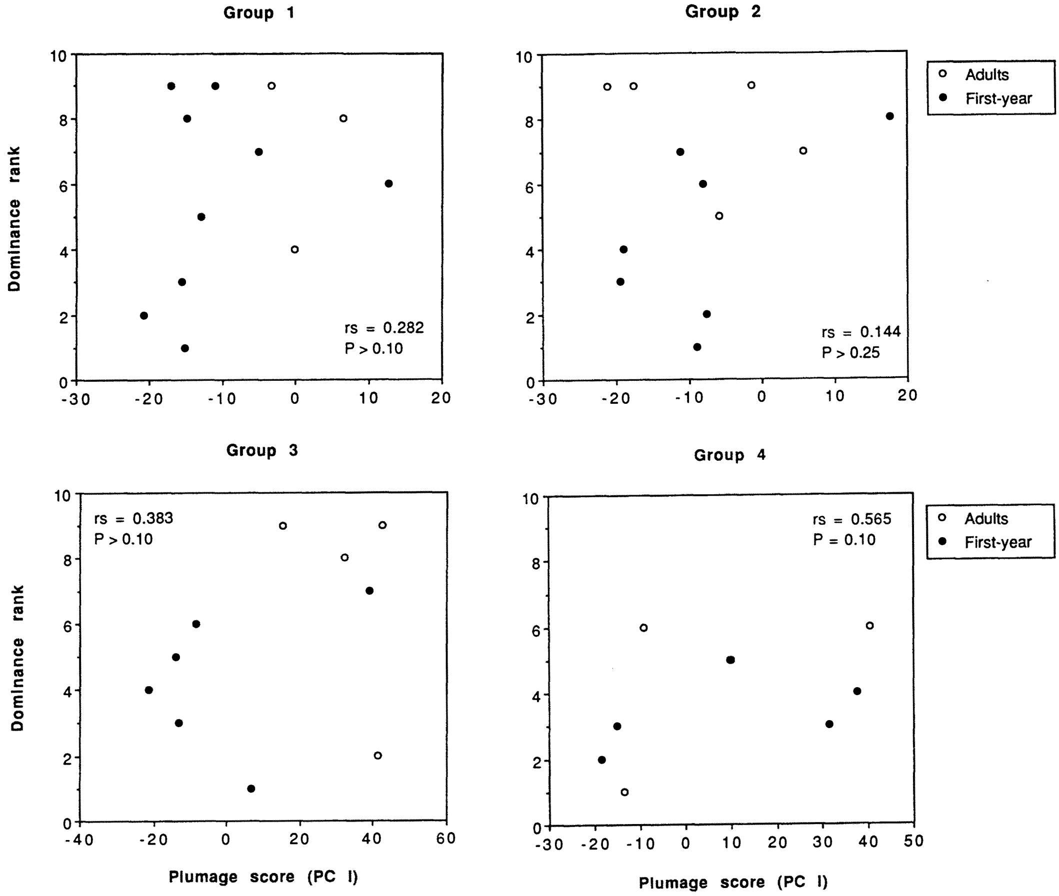

FIGURE 2. Relationship between plumage coloration and dominance status in four groups of wintering male House Finches. Larger PC scores represent more colorful males. Dominance rank equal to 1 represents individuals with the highest status (i.e., the alpha bird), while increasing scores for dominance rank represent birds with lower status (rs = Spearman correlation coefficient).

could not reject the null hypothesis that dominance status was independent of plumage (X^2 = 1.689, df = 1, $0.10 < P < 0.25$), and there was no effect of month (Dec., Jan., or Feb.) on the frequency with which each plumage type became dominant (Contingency analysis; $g = 0.137$, $P = 0.934$). Among four dyads in which adult males were paired, drab males became dominant in three.

Did one plumage type become dominant when there were small differences in plumage scores between combatants, and the other type achieve dominance when this difference was large? If so, mean difference scores (defined as PC I score for colorful individual minus PC I score for drab individual within a dyad) should have differed between dyads dominated by colorful birds and those dominated by drab birds. There was no significant difference in such scores (30.1 ± 5.07 for colorful males win; 24.3 ± 3.98 for drab males win; Mann-Whitney test; $U = 110$, $P > 0.20$). There was also no significant difference in number of interactions between dyads dominated by colorful (45 ± 8.54) and drab birds (39.4 ± 5.13; Mann-Whitney test; $U = 111.5$, $P > 0.20$). Finally, we detected no significant relationship between plumage score difference and number of interactions in a dyad (Spearman correlation analysis: $r_s = -0.20$, $P = 0.297$).

Hormones. Circulating levels of testosterone for male House Finches competing in dyads averaged 133.2 ± 7.1 pg/ml (n = 24). Testos-

TABLE 1. Relationship between dominance status and morphological and physiological parameters in four groups of captive male House Finches. Sample sizes for groups 1–4 = 12, 12, 10, 9, respectively, unless indicated.

Variable	Group 1 ($\bar{x}$ ± SE) r_s P	Group 2 ($\bar{x}$ ± SE) r_s P	Group 3 ($\bar{x}$ ± SE) r_s P	Group 4 ($\bar{x}$ ± SE) r_s P
Wing (mm)	79.3 ± 0.6	77.4 ± 0.4	78.8 ± 0.3	77.8 ± 0.6
	0.084	−0.282	0.093	0.353
	>0.25	>0.10	>0.25	>0.10
Tarsus (mm)	20.4 ± 0.1	20.4 ± 0.2	20.3 ± 0.1	20.1 ± 0.2
	−0.562	0.246	−0.536	0.067
	=0.055	>0.25	=0.09	>0.25
Mass (g)	20.6 ± 0.4	20.5 ± 0.4	20.6 ± 0.3	19.4 ± 0.3
	0.112	0.171	0.261	0.314
	>0.25	>0.25	>0.25	>0.25
Testosterone (pg/ml)	234.3 ± 22.8[a]	269.4 ± 69.8[a]	296.3 ± 33.0[a]	237.2 ± 39.0[a]
	0.262	−0.080	0.295	—
	>0.45	>0.82	>0.48	—
	$n = 9$	$n = 7$	$n = 7$	$n = 4$
Corticosterone (ng/ml)	40.8 ± 5.4	31.8 ± 3.1	35.8 ± 3.7	28.8 ± 2.8
	−0.099	−0.142	0.237	−0.523
	>0.25	>0.25	>0.25	>0.10

[a] Samples with detectable levels.

terone levels did not differ significantly between dominant and subordinate males or between colorful and drab males (Table 3). Circulating levels of testosterone were significantly greater in February than in December (Table 3). This increase may reflect initial changes related to the onset of the breeding season, where a relationship between testosterone and dominance behavior could develop as birds become sufficiently photostimulated. However, our data on wintering birds do not address this breeding season phenomenon.

TABLE 2. Percentage of individuals in each age class attaining high, moderate, and low dominance status within and across four groups of captive male House Finches. HY = hatching year birds; AD = adults.

Group/ age class	N	Relative dominance status High	Moderate	Low
Group 1				
HY	9	33.3	33.3	33.4
AD	3	33.3	33.3	33.4
Group 2				
HY	7	57.1	28.6	14.3
AD	5	0.0	40.0	60.0
Group 3				
HY	6	33.3	66.7	0.0
AD	4	25.0	0.0	75.0
Group 4				
HY	6	33.3	50.0	16.7
AD	3	33.3	0.0	66.7
Across groups				
HY	28	39.3	42.8	17.9
AD	15	20.0	20.0	60.0

Circulating corticosterone averaged 17.2 ± 1.2 ng/ml ($n = 59$) and, in contrast to testosterone, there was a significant difference between dominant and subordinate finches. As predicted, dominant finches exhibited significantly lower corticosterone levels than subordinate finches (Table 3). Corticosterone in colorful and drab males did not differ significantly. Finally, for unknown reasons birds competing in January exhibited significantly lower corticosterone levels than birds in December or February (Table 3).

DISCUSSION

RELATIONSHIP BETWEEN PLASMA STEROIDS AND SOCIAL DOMINANCE

Glucocorticoids are important for mobilizing energy reserves used in combating stress (Siegel 1980), and birds fit the general vertebrate pattern in showing a sustained increase in secretion of corticosterone in response to stressor stimuli (Wingfield 1987). We observed a significant relationship between corticosterone and dominance status among male House Finches in one experimental situation. Within dyads, birds scored as subordinate exhibited significantly

TABLE 3. Dominance, plumage, and seasonal (monthly) effects on testosterone (pg/ml) and corticosterone (ng/ml) in captive, male House Finches competing in dyads. Values are $\bar{x} \pm$ SE.

	Dominance effects				
	Dominant	Subordinate	df	t-value[b]	Prob.
Testosterone	146.6 ± 19.8^{a}	140.6 ± 11.4^{a}	4	0.50	= 0.322
Corticosterone	14.7 ± 1.3	20.1 ± 1.9	27	3.20	<0.004
		Plumage effects			
	Colorful	Drab	df	t-value[b]	Prob.
Testosterone	147.6 ± 20.5^{a}	139.6 ± 10.0^{a}	4	0.680	= 0.260
Corticosterone	17.2 ± 1.7	17.3 ± 1.7	28	0.15	= 0.879
		Seasonal effects			
	December	January	February		
Testosterone	118.1 ± 7.4^{a}	85.0^{a}	162.1 ± 8.4^{a}		$^{d}U = 112.5$
	$n = 14^{e}$	$n = 1^{e}$	$n = 9^{e}$		$P = 0.002$
Corticosterone	19.6 ± 1.7	9.3 ± 1.6	18.9 ± 2.1		$^{c}F_{2,56} = 6.57$
	$n = 25^{e}$	$n = 12^{e}$	$n = 22^{e}$		$P = 0.003$

[a] Samples with detectable levels only.
[b] T-values from paired t-tests.
[c] Based on 1-way analysis of variance.
[d] Mann-Whitney test between samples from December and February.
[e] Number of birds.

greater circulating corticosterone than individuals scored as dominant. This is consistent with previous information suggesting that subordinate individuals experience stress and increase adrenal activity in relation to low social status or the loss of aggressive interactions (e.g., Fretwell 1969, Murton et al. 1971, Harding 1983).

Our results with respect to corticosterone and social status, however, varied across experiments. Avian species differ in their adrenal responses to stress (i.e., variation in the secretion of corticosterone; see Etches 1976, Dawson and Howe 1983) and, within a species, this stress response can vary seasonally (Wingfield et al. 1982, Wingfield 1987) or with climatic changes (Rohwer and Wingfield 1981, Rogers et al. 1993). Our results suggest that relationships between corticosterone secretion and dominance status may also differ with the social situation in which an individual competes. The degree of social stability within a group appears to affect glucocorticoid responses in some species (e.g., Ely and Henry 1978, Sapolsky 1983). During unstable periods, such as during hierarchy formation in newly established groups, corticosterone levels are comparable among high and low ranking individuals. However, when relationships are well established, high ranking individuals exhibit lower corticosterone levels than subordinates (Ely and Henry 1978, Sapolsky 1983). Patterns of corticosterone secretion in our study may indicate that dominance relationships were well established in dyads but not in groups of males where many more individuals competed. House Finches may also be accustomed to competing in groups (i.e., they are adapted to group living), and this competitive situation elicited less obvious stress responses in subordinates. Finally, the different results may reflect testing conditions. Subordinate birds competing in dyads had little opportunity to avoid aggression from dominant birds, whereas subordinates in groups could remain "peripheral" and very often avoid interacting with more dominant individuals. Whatever the cause, our study indicates that dominance relationships among male House Finches are reflected by corticosterone levels in at least some circumstances.

Despite evidence that exogenously-administered testosterone increases aggressive behavior in male birds (e.g., Rohwer and Rohwer 1978, Baptista et al. 1987), correlative studies frequently find no relationship between testosterone and dominance status (e.g., Wingfield and Ramenofsky 1985, Schwabl et al. 1988, Ramenofsky et al. 1992). One explanation is that testosterone may be important only during early encounters when flocks are forming (Ramenofsky 1984), or when existing relationships are "challenged" (Hegner and Wingfield 1987). Thus, as Schlinger (1987) suggested, autumn may be especially important for investigating the social organization of flocks of birds. Many House Finches in the eastern United States migrate beginning in October and early November (Belthoff and Gauthreaux 1991a). It follows that winter flocks begin forming in mid- to late-November, the time period during which we conducted group experiments and many of the dyads. Therefore, if testosterone was related to social dominance in groups of male House Finches, our design should have detected this relationship. Circulating levels of testosterone in captive male House Finches were low but comparable to those found in other species that form flocks during the non-breeding period (see Rohwer and Wingfield 1981, Hegner and Wingfield 1987, Schlinger 1987). Despite comparable levels, and an observed increase in testosterone among males as the breeding season approached, we found no significant relationship between dominance status and testosterone in either experiment. However, the power of our statistical tests was routinely low. Power averaged 0.31 (range: 0.12–0.57) for correlation analyses in group experiments and 0.14 for the paired *t*-test in the dyad experiment. Given the observed variation in levels of testosterone, much larger sample sizes (between 15 and 250 for the group experiments; greater than 500 pairs for the dyad experiment) would be necessary to achieve power (e.g., 0.80) sufficient to protect against Type II errors (Cohen 1988). Additionally, because birds were sampled only once, the possibility that correlations between testosterone and social status appeared some time earlier (such as on day 1 or 2 when the mean number of interactions peaked in dyads and groups, respectively) or later cannot be eliminated. However, in comparison to previous studies, birds in the present study spent relatively little time together (a total of 6 hr for groups, and 1 hr for dyads); therefore, if peaks in testosterone occurred before we sampled, they would have had to be extremely brief in duration, or they occurred when birds were returned to their original cages between trials. Also, our results concur with recent studies concluding that aggression outside of the breeding season (in contexts of either winter territorial behavior or in establishing dominance hierarchies) occurs independently of testosterone (Holberton et al. 1989, Logan and Wingfield 1990, Schwabl and Kriner 1991, Ramenofsky et al. 1992, Wingfield and Monk 1992, Wingfield and Hahn 1994). Thus, dominance relationships among male House Finches outside the breeding season may not be related to testosterone, and different neuroendocrine systems may be operating (Holberton et al. 1989, Schlinger et al. 1992, Wingfield and Monk 1992).

RELATIONSHIP BETWEEN PLUMAGE AND DOMINANCE

We could not reject the null hypothesis that dominance status was independent of plumage coloration among captive male House Finches during the non-breeding season. Therefore, colorful male plumage, at least as we measured it, did not indicate high social status. Our results may be informative with respect to drab plumage, however. That is, there was a consistent tendency across experiments for drab males, independent of age, to dominate more colorful ones. In relation to more colorful males, less colorful males also achieve high rank when competing in captive, mixed-sex groups of House Finches (Belthoff and Gauthreaux 1991b), and these results from laboratory experiments are consistent with those from field studies. For example, among House Finches competing at a feeder in Connecticut, 61% of male-male interactions included a male displacing another male with more red than itself. In only 12% of bouts did a male displace another male with less red than itself (Brown and Brown 1988).

Unlike many passerines, female House Finches achieve higher status than males (i.e., they dominate males; Thompson 1960a, 1960b; Brown and Brown 1988; Belthoff and Gauthreaux 1991b). Therefore, drab males may gain a competitive advantage over colorful males by mimicking females in appearance and deceiving colorful males into yielding to them (Brown and Brown 1988). However, if "female mimicry" were to explain dominance of drab males over more colorful ones, drab males may be most likely to win when differences in plumage scores between combatants are large. Because the opponent's plumage is much less colorful than its own, this may be the most likely situation in which a male could be fooled into thinking its opponent is a female. Plumage difference scores in the present study did not vary between dyads dominated by colorful and drab birds, and the mean difference was greater for dyads in which more colorful males achieved higher status (the opposite of what may be expected with female mimicry). In addition, "drab" House Finches in the present study exhibited considerable pigmentation, which presumably easily identified them as males and not females. Thus, although it may influence dominance relationships, female mimicry by itself does not appear to explain the tendency for drab male House Finches to dominate more colorful ones.

IMPLICATIONS FOR MATE CHOICE IN HOUSE FINCHES

Our results may also be informative with respect to mate choice in House Finches. Male plumage coloration is an important criterion in female mate choice, with females preferring colorful males as mates (Hill 1990, 1991, 1994). Male plumage coloration appears to be correlated with at least one trait related to fitness, i.e., the capacity for parental care (Hill 1991), and Hill suggests that male plumage coloration in House Finches is precisely the sort of condition-dependent trait that is predicted by the honest advertisement model of sexual selection (Zahavi 1975, Kodric-Brown and Brown 1984). Could females also be choosing colorful males because these males have higher social status than drab males? The available data (Brown and Brown 1988, Belthoff and Gauthreaux 1991b, this study) suggest that colorful males frequently lose in interactions with drab males, and colorful males often occupy low positions in hierarchies. Thus, it appears that female House Finches do not choose mates on the basis of a male's social status. However, as Hegner and Wingfield (1987) cautioned, it may not be appropriate to generalize hierarchies observed in one context (e.g., competing at feeders or in captivity) to all others (e.g., competing for carotenoid-rich food prior to molting). In any event, although colorful plumage may be a good predictor of pairing status in male House Finches during the breeding season, results of the present study suggest that it is not a reliable indicator of high status during non-breeding periods.

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