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AGGRESSION AND DOMINANCE IN HOUSE FINCHES¹

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Key words: Aggression; reversed sexual dominance; House Finch; *Carpodacus mexicanus*; eastern population.

Among wintering birds, males generally dominate females and adults dominate immatures (Gauthreaux 1978). Reversed sexual dominance, when females dominate males during the nonbreeding season, is uncommon. Notable examples include species of raptors where females are larger than males (Amadon 1975) and shorebirds that have undergone sexual role reversals, e.g., Spotted Sandpipers (*Actitis macularia*; Maxson and Oring 1980). Among passerines, reversed sexual dominance is rare and occurs mainly among the *Carpodacus* finches (Thompson 1960a, Samson 1977).

Females dominate males during winter in native, western populations of House Finches (*Carpodacus mexicanus*; Thompson 1960a, Kalinoski 1975). Among recently introduced eastern populations, studies of unmarked birds at sunflower feeders suggest that females also dominate males (Brown and Brown 1988, Shedd 1990), but these studies offer little insight into factors other than sex (and associated plumage) that are known to influence dominance behavior in birds (e.g., body

size, mass, subcutaneous fat reserves or other morphological or physiological parameters). In this study, our objective was to examine phenotypic correlates of dominance among eastern House Finches. In contrast to previous studies of eastern populations, we used wild-caught, individually-marked House Finches that we maintained in captivity. This approach allowed us to measure morphological and physiological parameters and control for group size, sex ratio, and hunger. It also allowed a comparison of field and laboratory results.

MATERIALS AND METHODS

We captured House Finches throughout Pickens County, South Carolina during early January 1989 with mist nets. Birds were housed in individual cages (visually isolated from each other) with 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 color bands, and measured (to the nearest 0.5 mm) relaxed wing chord length, tarsus length, bill length (exposed culmen), medial rectrix length, abdominal fat class (Helms and Drury 1960), and body mass (to the nearest 0.1 g). We scored males for plumage brightness on the forehead, eyebrow, crown and nape, malar, throat, breast, abdomen, back, wrist (lesser secondary and marginal coverts), and rump. Body regions received a maximum of 3 points in each region

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TABLE 1. Comparison of mean (\pm SE) morphological and physiological characteristics between captive male and female House Finches.

Variable	Males (<i>n</i> = 18)	Females (<i>n</i> = 18)	<i>t</i> -statistic	<i>P</i>
Mass (g) ¹	19.7 \pm 0.33	20.0 \pm 0.30	0.706	>0.484
Wing length (mm)	78.2 \pm 0.46	76.3 \pm 0.38	3.187	<0.004
Tarsus length (mm)	20.1 \pm 0.19	19.9 \pm 0.19	0.517	>0.608
Bill length (mm)	10.2 \pm 0.09	10.3 \pm 0.08	0.902	>0.373
Tail length (mm)	59.1 \pm 0.45	57.7 \pm 0.50	2.093	<0.044
Net change in mass ² (g)	-0.4 \pm 0.15	-0.7 \pm 0.11	1.550	>0.130
Captivity mass change (g)	-1.8 \pm 0.30	-1.9 \pm 0.27	0.083	>0.934

¹ Mean of three pretrial masses.

² Mean of differences between three pretrial and post-trial masses.

as follows: 0—no pigmentation; 1—only small amounts of color, predominantly orange, gold or yellow; 2—red or pink color with only a few yellow or gold feathers; 3—red feathers only. Scores for the 10 regions were summed, and males receiving high and low scores were considered bright and dull, respectively. Because all captive finches possessed fully pneumatized skulls, we could not accurately age individuals.

We determined group size (six) based on observations of wild flocks and on space constraints in the arena. We randomly combined three male and three female House Finches until six groups were assembled (*n* = 36). We withheld food from individuals the evening before trials in an attempt to simulate naturally occurring conditions of reduced food during which finches would have to compete.

In January 1989 we conducted dominance trials in a hexagonal arena constructed of woven wire (130 cm in diameter and 31 cm high) complete with a perch, water jar, and food jar containing sunflower seeds. Although space in the arena was limited, density of birds was no greater than that observed on outdoor feeders during winter (pers. observ.). We modified the food jar so that only one finch could feed at a time. The arena floor was constructed of hardware cloth so that dropped seeds would pass through it. Thus, feeding was possible only at the feeder. Prior to trials, flocks occupied the arena for up to 30 min. Trials consisted of a 5-min pretrial period, a 1-hr observation period, and a 5-min post-trial period. From a blind located 5 m away, we counted the number of aggressive interactions for each group member for two randomly selected 5-min periods using 10 \times 40 binoculars. We observed each group on alternate days for a total of three trials (180 min) and returned birds to their individual cages between trials. We weighed birds before and after trials to determine changes in mass.

Wins were scored for supplanting attacks, high intensity head-forward displays, and beak fencing or actual combat at or away from the food jar (see Thompson 1960b for complete description of displays). Supplanting attacks occurred when one bird flew towards another, causing the bird approached to move away. We called the individual that moved away the loser. High intensity head-forward displays, usually accompanied by "chit" calls, were the most common form of aggression. Winners lunged at or motioned toward opponents and displaced them with head and

beak extended. Beak fencing and combat resulted when opponents failed to yield to attackers following either of the above displays. Combatants pecked vigorously at each other's beaks while rapidly calling *chit-chit-chit*. In each of the above interactions, we called the individual that moved away the loser. We constructed win/loss matrices by minimizing the number of reversals beneath the diagonal (Brown 1975) and assigned dominance ranks to birds within groups.

We compared morphological and physiological characters of males and females using Student's *t*-tests. Fat classes, which were not normally distributed, were compared using Mann-Whitney *U*-tests. For analyses of mass, we used an average of the three pretrial measurements. We estimated effects of captivity by subtracting mean pretrial mass from mass at time of capture. We used analysis of covariance (ANCOVA) to examine effects of sex, wing length, and mass on dominance rank with group as a blocking factor (Sokal and Rohlf 1981). We also conducted separate one-way analyses of variance (ANOVA) to determine effects of dominance rank on weight change and number of seeds obtained. To examine the potential effect of plastic leg band color on dominance status (see Burley 1981), we performed a Kruskal-Wallis single factor analysis of variance (Sokal and Rohlf 1981). All statistical tests were non-directional (two-tailed) and rejection levels were set at $\alpha = 0.05$. Means and their standard errors are given as $\bar{x} \pm$ SE throughout the text.

RESULTS

Males had significantly longer wings and tails than females, but mean bill length, tarsus length, body mass, change in mass during trials, and change in mass during captivity did not differ between the sexes (Table 1). Similarly, males and females did not differ significantly in mean fat index (2.3 ± 0.45 and 2.4 ± 0.09 , respectively; Mann-Whitney *U*-test; *U* = 121.5, *P* > 0.20).

Of the 2,629 interactions we observed, 875 (33.3%) were between females, and 379 (14.4%) were between males. Of 1,375 (52.3%) intersexual interactions, females won 1,163 (85%) and males 212 (15%). Relationships among group members were transitive, with few reversals. Female finches occupied the top three positions in five of six groups. In the remaining group a male dominated all three females; these females in turn dominated the remaining two males. Although not independent, females (*n* = 18) won 113 ± 30.0

interactions out of 174 ± 26.3 interactions per female (65%). In contrast, the average male won 33 ± 18.4 interactions out of 122 ± 77.4 interactions (27%). Most interactions were head-forward displays, beak fencing and combat, but 18 interactions (0.7% of bouts) escalated to biting, wing pulling, and feather pulling. In each instance, a female performed the behavior (17 times towards other females).

Sex had a significant effect on dominance rank ($F = 42.92$, $P < 0.001$), while neither wing chord length nor mass significantly affected rank ($F = 0.01$, $P > 0.90$ for each). Among females there was a significant effect of mass ($F = 10.79$, $P < 0.01$), with lighter females achieving higher rank than heavier females and males. Thus sex alone, rather than larger size correlated with sex, appeared important in determining dominance in House Finches. We also observed no relationship between dominance rank and change in mass during captivity ($F = 0.13$, $P > 0.72$) or change in mass during trials ($F = 1.03$, $P > 0.32$). There was no effect of plastic leg band color on dominance rank (Kruskal-Wallis test; $H = 2.667$, $P > 0.50$).

Among the 18 males, plumage scores averaged 19.8 ± 1.2 (range: 6–26). Males were brightest (i.e., the greatest mean plumage score) on the forehead (2.4 ± 0.1), nape (2.4 ± 0.2), and rump (2.3 ± 0.2), and least colorful on the abdomen (1.8 ± 0.2) and wrist (0.5 ± 0.2). Brighter males did not consistently achieve high dominance rank. In fact, the dullest male in four groups became most dominant among the males.

DISCUSSION

On the basis of scoring wins and losses during interactions, linear dominance hierarchies (Appleby 1983) were developed for each group of captive House Finches. As in studies of free-living, unmarked eastern populations, females achieved higher status than males. What attributes of females influence dominance in House Finches? Because size seems unimportant (i.e., smaller females dominated larger males), some other asymmetry favoring females may exist, such as sexual differences in fighting abilities or expected benefits from winning (Maynard Smith and Parker 1976). Whatever the asymmetry, it appears that dominance patterns in House Finches are mediated proximately through greater female aggressiveness. Our results indicated that females engaged in intrasexual bouts twice as often as males, and females exhibited higher levels of aggression (suggested by behaviors such as biting and wing pulling). Although Brown and Brown (1988) reported that male and female House Finches differed little in aggressiveness when interacting with House Sparrows (*Passer domesticus*), studies of intraspecific aggression in House Finches (e.g., Brown and Brown 1988, Shedd 1990, this study) showed that female–female interactions substantially outnumber male–male interactions. Thus, although both sexes are equally aggressive to members of other species, female House Finches are more aggressive than males intraspecifically.

Selection pressures favoring increased female aggression and its ultimate consequences remain unclear but may relate to their mating system (Smith 1980). In contrast to territorial species, male House Finches (and other *Carpodacus* males) do not defend territories,

and they may or may not defend the immediate area surrounding the nest site (Thompson 1960b, Samson 1976, Björklund 1990). Instead, females choose the nest site and often defend it without assistance from their mates (Thompson 1960b, Samson 1976, Björklund 1990). Björklund (1990) concluded that female reproductive success was largely determined by choice of nest site (which was unrelated to male behavior) among Common Rosefinches (*Carpodacus erythrinus*) in Sweden, and the probability of nesting success was independent of male physical characteristics or behavior. Thus, the reproductive success of a given *Carpodacus* female may be dependent on her ability to secure resources for nesting (e.g., high quality nest sites) and perhaps defend them against other individuals seeking resources. If so, selection for aggressive females is possible, and such aggression may be reflected during winter. Female dominance among *Carpodacus* finches may therefore be a product of selection for increased aggressiveness in females during the breeding season.

Are studies of captive House Finches representative of behavior in the field? To examine this relationship we compared our results of captive House Finches to those of both Brown and Brown (1988) and Shedd (1990), who examined free-living eastern House Finches. The present study corroborates results from field studies in several respects. First, all three studies concluded that females dominated males. Next, all indicated that females interacted with females approximately twice as often as males interacted with other males. In fact, reported percentages of such interactions were remarkably similar (30.7% vs. 16.1%, $n = 1,653$ interactions, Brown and Brown 1988; 34.1% vs. 15.7%, $n = 612$, Shedd 1990; 33.3% vs. 14.4%, $n = 2,629$, this study). Finally, both Brown and Brown (1988) and the present study found that dull males frequently dominated brighter males. We conclude, therefore, that studies of dominance among captive House Finches can accurately reflect behavior in the field and, because investigators can control many variables and individually tag and measure experimental subjects, the laboratory approach may be as valuable as field studies of behavioral dominance.

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A RETROSPECTIVE ANALYSIS OF RED-BAND EFFECTS ON RED-WINGED BLACKBIRDS¹

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Key words: Red-winged Blackbird; color bands; territoriality; reproduction; survival.

Color bands are probably the most common technique used by ornithologists to identify individual birds at a distance. Burley's (e.g., 1981, 1985, 1986) studies of captive Zebra Finches (*Poephila guttata*) showed that colored bands influenced several important aspects of reproduction and survival. Recent field studies have shown that bands matching the color of prominent secondary sexual traits had a negative impact on reproduction in Red-cockaded Woodpeckers (*Picoides borealis*) (Hagan and Reed 1988) and a positive effect on mate attraction in Rock Ptarmigan (*Lagopus mutus*) (Brodsky 1988), although the latter result may have

been confounded by other factors (Holder 1990). In a field experiment manipulating band color in Red-winged Blackbirds (*Agelaius phoeniceus*), Metz and Weatherhead (1991) found that red bands (matching the males' epaulets) provoked increased aggression from neighbors, which was associated with a higher rate of territory loss. Collectively these studies raise the concern that much of ornithological research could be compromised by the use of colored bands. Here we investigate this possibility using data from our own research on Red-winged Blackbirds.

Because Red-winged Blackbirds have bright red epaulets, the size of which appears to be associated with aspects of social dominance (Eckert and Weatherhead 1987a) and parental behavior (Eckert and Weatherhead 1987b), Metz and Weatherhead (1991) chose red bands as their experimental color. Black bands were used on controls because they matched the color of the rest of the birds' bodies. They found that the red-banded males that lost their territories had larger epaulets than those that retained their territories, indicating that the red bands somehow interacted with the natural epaulet. A further experiment using red, blue and black bands confirmed the importance of red bands (Metz

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