Short communication

Testing reversed sexual dominance from an ontogenetic perspective: juvenile female House Finches *Carpodacus mexicanus* are dominant to juvenile males

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Dominance behaviour in songbirds tends to follow well-defined patterns throughout the year. During the breeding season, most agonistic interactions are between birds of the same sex, as individuals compete aggressively for mates, maintain pair bonds and defend nesting territories or sites (Andersson 1994, Ligon 1999). Outside the breeding season, aggressive encounters centre around more general contests over resources necessary for survival, such as food and cover (Gauthreaux 1978). During these interactions, there is often little or no co-operation between sexes, and intersexual aggression is much more common than in breeding contexts (Gowaty 1993). Males of most passerine species are larger than females, have higher androgen levels and compete more intensely for mates, so in nearly all species that have been studied males tend to be dominant over females (Piper 1997). Outside of the order Passeriformes, there are a few avian taxa in which females are typically dominant to males (e.g. raptors, shorebirds), but in these groups females are either larger than males (Amadon 1975, Jehl & Murray 1986) or there is a polyandrous mating system with females being the more ornamented and competitive sex (Oring 1986).

Among songbirds, a notable exception to this rule is found in certain cardueline finch species, where females typically are dominant to males (Newton 1972). Within the subfamily Carduelinae, reversed sexual dominance has been confirmed in all North American *Carpodacus* finches (Thompson 1960, Samson 1977, Shedd 1990), including one of the best studied of all, the House Finch *Carpodacus mexicanus* (Brown & Brown 1988, Belthoff & Gauthreaux 1991, Belthoff & Gowaty 1996). Despite the fact that *Carpodacus* females are dominant to males, females are smaller in body size, birds pair monogamously, and males display elaborate ornamental traits and have higher androgen levels (Hill 1993, Hahn 1996, Wootton 1996).

Thus, reversed sexual dominance in *Carpodacus* finches poses an interesting evolutionary puzzle. In contrast to what is observed in virtually all other passerine species, why would the smaller sex that has less exaggerated ornamentation aggressively outcompete the larger sex that has more elaborate ornamentation? One hypothesis is that males defer to females to enhance mating and breeding success (Smith 1980, Brown & Brown 1988, Shedd 1990). Because male *Carpodacus* finches do not defend territories during the year, selection may be weak for male aggression, and males may yield either to females with which they may eventually pair or to their social mate when resources are needed for breeding. We tested this hypothesis in the House Finch by observing intersexual aggression outside a reproductive context – among juvenile birds near the end of their pre-basic moult. Hatch-year (HY, also known as first-year) House Finches form large flocks and congregate at food sources in the late summer and autumn (Hill 1993). After completing their annual autumn moult, HY finches leave these flocks and disperse from their natal area; only about 6% of males and 3% of females annually return to their natal site to breed (Hill 1993, G.E. Hill unpubl. data). Because individuals in these juvenile flocks are unlikely to encounter one another as breeding adults, aggressive behaviour should have virtually no mating or reproductive consequences, and as a result we should see the true fighting ability of males in this setting.

METHODS

We quantified the dominance behaviour of juvenile House Finches by observing aggressive interactions at feeders in the wild as well as in two mixed-sex flocks of HY finches in captivity. All behavioural observations were conducted in Lee County, Alabama, USA (32°N 85°W), during early October 1998, a time when virtually all HY finches are completing or have just completed moult, and the earliest time in autumn when all HY finches can be sexed. HY birds were sexed by the differences in plumage colour that they develop; males deposit carotenoid pigments on the crown, breast and rump, whereas females are brightly coloured on the rump only (Hill 1993).

For wild birds and in both captive flocks, we observed aggressive behaviour during four 2-h periods that occurred within the first 3 h of morning daylight. An aggressive interaction was defined as any chase, attack or displacement at or near food sources (Thompson 1960). We took note of only those agonistic encounters that occurred between the sexes. For each interaction in which an individual was supplanted successfully, we determined a

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winner and loser and calculated the percentage of wins for males and females in each setting. Because we were unable to identify individual birds (see below), in all cases the percentages we report represent the proportion of aggressive interactions won by all members of a given sex. We used chi-square and sign tests to examine differences in dominance between the sexes.

Wild birds

Most of the local adult population was ringed as part of a long-term study of the breeding biology of House Finches (Hill *et al.* 1999, McGraw *et al.* 2001), but only about 10% of the birds seen at feeders in this study were ringed. We assume that virtually all of the unringed birds seen at feeders in this study were HY House Finches and not adult birds moving into the area. Consistent with this assumption, capture records indicate that 90% of birds that visit feeders during October are HY individuals (G.E. Hill unpubl. data). Also, autumn flocks of juveniles are large, and we routinely ringed 50 or more birds at a feeder during a morning of trapping. Thus, patterns we report here do not result from a few individuals, and although some birds may have been used more than once in our study, we believe that the number of encounters observed approximates to the number of birds included.

Captive flocks

We housed captive flocks of HY finches in large outdoor cages (McGraw & Hill 2000a, 2000b). *Ad libitum* supplies of sunflower seed, millet and water were available in dishes that we spaced evenly across the floor of the two cages. One flock of birds had equal numbers ($n = 7$) of males and females, whereas another flock consisted of 12 males and seven females. As the birds were not marked with unique colour-ring combinations, we do not have multiple observations of aggressive behaviour for individual birds. However, we followed birds well enough to note that finches rarely remained at food sources for long periods of time, which suggests that our observations do not consist simply of one or few individuals who aggressively displaced all others.

RESULTS

Cumulative data

During 24 observation hours, we tallied 611 aggressive interactions between the sexes, 58.4% ($n = 357$) of which were won by HY females and 41.6% ($n = 254$) of which were won by HY males ($\chi_1^2 = 17.4$, $P < 0.01$). Juvenile females won more interactions than juvenile males in 11 of the 12 observation periods (sign-test, $T = 11$, $P = 0.003$).

Wild birds

Wild HY females won significantly more aggressive intersexual interactions (60%) at feeders than did HY males (40%) (Table 1).

Captive flocks

In one cage of finches, HY females won significantly more aggressive encounters (63%) than did HY males (37%) (Table 1). In the other captive flock, the tendency for females to dominate males only approached statistical significance, as females won 55% and males 45% of all interactions (Table 1). However, this was the cage in which there were nearly twice as many males ($n = 12$) as females ($n = 7$). Although we cannot be sure of the precise sex ratio of juveniles in the wild, it is interesting that the male bias in this captive group resulted in males and females winning similar numbers of interactions per individual (M: 10 wins/bird; F: 20 wins/bird) as in the other cage (M: 10 wins/bird; F: 17 wins/bird), with females winning nearly twice as many interactions as males in both cases.

DISCUSSION

In this study, we investigated the mechanisms underlying reversed sexual dominance in the House Finch by quantifying the aggressive behaviour of juvenile males and females in the autumn. Intersexual aggression among juveniles has been considered in other taxa, including fish

Table 1. Outcomes of aggressive interactions between juvenile male and female House Finches during the autumn of 1998 in Auburn, Alabama, USA.

Source	Group	No. hours	No. interactions	Male wins	Female wins	χ_1^2	P
Wild		8	161	65	96	6.0	0.02
Captive	1	8	188	70	118	12.3	< 0.01
	2	8	262	119	143	2.2	0.15

We observed dominance behaviour of wild finches at pre-established sunflower seed feeding stations. Captive males and females competed for access to food that was placed in dishes on the floors of large outdoor flight cages. Captive group #1 consisted of seven males and seven females, whereas there were 12 males and seven females in captive group #2.

(Johnsson & Akerman 1998) and primates (Archie & Digby 1999), but it is poorly studied in birds. Some of the few studies of juvenile aggression in birds come from cardueline finch species that form large flocks prior to dispersal. In these carduelines, including species of Rosy Finch *Leucosticte* sp. and the White-winged Crossbill *Loxia leucoptera*, males are dominant over females in both adult and juvenile flocks (Johnson 1972, Shreeve 1977, Benkman 1997). Observations of aggressive behaviour among juvenile House Finches in this study afforded us the opportunity to investigate the ontogeny of dominance patterns in a species in which adult females are known to be dominant to adult males. In both wild and captive settings, we found that HY female House Finches are dominant to HY males.

Shedd (1990) and Brown and Brown (1988) argued that reversed sexual dominance in House Finches results from male deference behaviour because males are equally as aggressive at feeders toward Purple Finches *Carpodacus purpureus* and House Sparrows *Passer domesticus* as are females. However, our findings are inconsistent with the idea that male House Finches defer to females in competitive situations. In the autumn, there should be little selective advantage for males to allow females access to food resources. Juvenile males do not begin to associate with prospective mates until late into their first winter (Hill 1993), so the competitive behaviour of HY birds in the autumn is removed from a breeding context and should provide few if any reproductive advantages. In fact, moulting males should be highly motivated to compete for food during the critical period of feather replacement. Not only do male House Finches have to grow structurally sound feathers to be worn over the next year, but they also must deposit carotenoid pigments into their feathers during the pre-basic moult (Brush & Power 1976, Hill 1992). The brightness of carotenoid-based plumage ornamentation is affected by the nutritional condition of males during moult (Hill & Montgomerie 1994, Hill 2000), and contributes critically to the mate-choice decisions of female House Finches (Hill 1990, 1991, 1994, Hill *et al.* 1999). Thus, HY males have much to gain and little to lose by displacing HY females in competition over food during moult, and yet HY females still win the majority of aggressive encounters at this time.

Although we found no support for the mating advantages of deference behaviour in male House Finches, it is possible that males yield to females because they mistake them for drab males, who tend to be more aggressive than brightly coloured males throughout the year (Brown & Brown 1988, Belthoff & Gauthreaux 1991, McGraw & Hill 2000a, 2000b). However, it seems very unlikely that closely interacting birds would be unable to distinguish males from females visually, especially when sexual plumage patterns are so distinct in this species. Ultimately our findings suggest that, despite being smaller than males, female House Finches are indeed better at defending food resources than are males. Belthoff and Gauthreaux (1991)

found that female House Finches interacted more often with females of their species than did males with males, and similarly concluded that dominance patterns are proximately regulated by female aggression. But why should female House Finches be more aggressive than males? Females may show greater resource-holding potential during the breeding season for two reasons: (1) because they have greater energetic needs to complete reproduction (Samson 1977); (2) because they must defend their immediate nest site since males do not defend territories (Belthoff & Gauthreaux 1991). However, neither hypothesis necessarily predicts greater aggression by juvenile females in the autumn. As juveniles undergoing their first pre-basic (post-juvenile) moult, females do not have greater energetic needs than males, and they do not begin defending nest sites for about another 5 months (Hill 1993). We are left therefore with the explanation that aggressiveness of juvenile female House Finches is either simply an extension of aggressive behaviour that is needed in the winter and/or first breeding season to come, or that there is some undiscovered benefit to them in being dominant in the autumn.

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