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Plumage redness predicts breeding onset and reproductive success in the House Finch: a validation of Darwin's theory

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Darwin (1871) and later Fisher (1958) suggested that sexual selection can drive the evolution of ornamental traits in monogamous species when female preferences for these traits allow well-ornamented males to begin breeding earlier in a season and, as a result, gain reproductive advantages over poorly ornamented males. However, few studies have been conducted to test this fundamental concept upon which much of the sexual selection theory for monogamous species has been based. In this study, we examined the relationship between breeding onset, reproductive success, and male ornamentation in the House Finch *Carpodacus mexicanus*, a species in which males display bright carotenoid-based plumage pigmentation. In previous work, it has been shown that bright male House Finches are preferred as social mates by females and, as a result, begin nesting earlier in the season than do drab orange and yellow males. Here we show that, by initiating breeding earlier in the season, brightly colored males fledge more offspring in a season than do drab males. Thus, differential timing of breeding generates considerable variance in reproductive success among male House Finches and contributes to sexual selection for male plumage ornamentation in this species.

Sexual selection is the result of variance in reproductive success among members of one sex. When reproductive success is related to the expression of an ornamental trait, sexual selection can drive the evolution of such traits. A number of mechanisms have been proposed for generating variance in reproductive success in relation to ornamental traits (see review in Andersson 1994). In polygynous species, differential male mating success can occur through the monopolization of many females by a few well-ornamented males (Trivers 1972). Species that are socially monogamous present a special problem for sexual selection theory. Darwin (1871) and later Fisher (1958) suggested that, in monogamous species, differences in the seasonal onset of breeding is the primary source of variance in reproductive success. By this idea, individuals of birds that begin breeding early in a season are able to produce more offspring or offspring of higher quality than pairs that begin nesting later in the season. Thus, if females prefer well-ornamented males as mates, well-ornamented males will pair with early-breeding females and experience a fitness advantage over later-breeding, poorly ornamented males.

Directional selection on breeding onset has been considered at length theoretically (O'Donald 1972, Price et al. 1988, Kirkpatrick et al. 1990), and a number of studies have found that the timing of breeding influences the number of offspring produced in a year (e.g. O'Donald 1980, Wolfenbarger 1999a). Yet, to date there is little empirical evidence in support of the notion that female preferences for male ornamentation drive the evolution of male ornamentation through differential timing of breeding. Only Møller (1988, 1990a) in his studies of the Barn Swallow *Hirundo rustica* has shown that males with extravagant ornaments are preferred by females and thus begin nesting earlier and fledge more offspring in a season than males displaying less elaborate forms of the ornament.

Here we consider the relationship between nesting asynchrony, male ornamentation, and annual reproductive success in the House Finch *Carpodacus mexicanus*. The House Finch is a sexually dichromatic monogamous North American passerine. Females are drab brown while males exhibit carotenoid-based ornamentation that varies in color from red to orange to yellow (Hill 1993a). In this species, male coloration is an honest indicator of carotenoid access during molt (Hill 1992, 1993b), nutritional condition (Hill and Montgomerie 1994), parental ability (Hill 1991), parasite load (Thompson et al. 1997, Brawner et al. in press), and survivorship (Hill 1991, Nolan et al. 1998). Females prefer to mate with the brightest males (Hill 1990) and, as a result, redder males pair more often (Hill 1991) and earlier (Hill et al. 1994, 1999) than do drab orange and yellow males.

Because the 6-month breeding season of the House Finch allows pairs of birds to fledge between 2 and 5 broods in a year, and because the range of dates during which pairs initiate breeding covers a period of nearly 60 days (Hill et al. 1999), there is great opportunity for the timing of breeding to strongly influence the number of offspring that House Finch pairs may fledge in a year. As a result, we conducted a two-year study of the relationship between male plumage coloration and annual reproductive success in the House Finch to determine if, as proposed by Darwin (1871), early nesting is a mechanism by which brightly colored males gain a reproductive advantage over drably colored males. Because there seems to be an age component to ornament expression in this species (Hill 1992), we also considered the possibility that male age might have a more significant effect on reproductive success than male plumage coloration.

Methods

This study was conducted on the campus of Auburn University, Alabama, USA in 1997 and 1998. Finches were trapped at feeders and at nests, and each was banded with a unique combination of one aluminum U.S. Fish and Wildlife Service band and three colored plastic leg bands. Birds had been captured and banded at this site since 1993, so many of the resident breeding birds had been marked before our study. Thus, we assumed that all unbanded birds were first-year birds, and we subsequently assigned minimum ages for previously banded birds by counting forward from the year in which they were banded. Male plumage coloration was quantified using a Colortron reflectance spectrophotometer (Light Source, San Rafael, CA) (Hill 1998). We measured plumage hue in each of the three body regions showing carotenoid-based plumage pigmentation in males (crown, breast, and rump), and used the arithmetic average of nine hue values as our index of plumage coloration (mean hue). By arbitrary convention, the Colortron hue scores increase as hues vary from red to orange to yellow. Thus, the reddest, most highly ornamented males have the lowest Colortron hue scores.

To provide accessible nesting sites, open nest cups constructed from the bottom of 1.89 l (0.5 gallon) plastic milk containers were placed inside small wooden boxes. We attached these boxes beneath overhangs on buildings and other structures at sites that mimicked traditional nesting locations in the urban habitat. In both years, we monitored boxes in the afternoon of every other day from February to August for the presence of nest material, eggs, and nestlings. We also observed the behavior of pairs to help locate nests outside of the boxes.

We assigned first nest initiation dates for House Finch pairs by scaling them relative to the day on which the first egg was laid in the entire population. Thus, in each year the first breeding pair in the population began nesting on Day 1; timing of breeding for all other pairs was determined by counting the number of days since this first pair began nesting. Because House Finches lay one egg per day in the early morning (Hill 1993), we back-dated first egg dates when a nest was found with more than one egg. We followed the progress of nests to determine the number of young fledged from each. Because most pairs bred together for the duration of the breeding season (Hill 1993, pers. obs.), we located all of the nests for stable pairs in each season and determined the total number of offspring fledged during the year by each pair.

To obtain the most accurate and conservative estimates of reproductive success among birds in the population, we included data only for those pairs whose first nest was started less than 60 days after the very first nest was initiated in the population each year (after Hill et al. 1999), as we believe that birds whose first nest appeared after this date were birds that had moved into the area to re-nest. Furthermore, we included data from only those pairs for which we found at least two nests, as this behavior suggests that these birds have a tendency to re-nest in the same area. Birds showed distinct preferences for nesting in our boxes and experienced low rates of nest failure (see Results), so we have little reason to believe that birds left our study site during a season to breed elsewhere. When we had two years of plumage color or reproductive success data for birds that remained paired across years, we randomly selected data from one of those years for use in our analyses.

We found differences in first nest initiation dates between the two years and eliminated these seasonal differences by standardizing the data for all variables in both years to a mean of 0 and standard deviation of 1. Original means and standard deviations are given in Table 1. We subsequently pooled data across years for statistical analysis. The data were not normally distributed (Shapiro-Wilks W-test, $p > 0.05$), so we used Spearman's rank correlations to test for associations

Table 1. Comparison of means of first clutch initiation dates, male plumage color scores, and reproductive success during the two years of this study for the birds for which we obtained complete annual reproductive success data. Means ± standard deviations are given for each variable and sample sizes are listed in parentheses. First nest initiation dates were significantly different between years (Mann-Whitney $U = 78$, $p = 0.02$). For all other comparisons, $p > 0.1$.

	1997	1998
Initiation date of first clutch[a]	31.4 ± 26.3 (16)	46.7 ± 16.2 (19)
Male plumage color (mean hue)	2.3 ± 3.3 (13)	0.9 ± 1.5 (16)
Total number of offspring fledged	8.7 ± 3.1 (16)	7.2 ± 5.2 (19)

[a] First nest initiation dates were calculated as the number of days after the first nest of the year in the population (27 February in 1998 and 12 February in 1999).

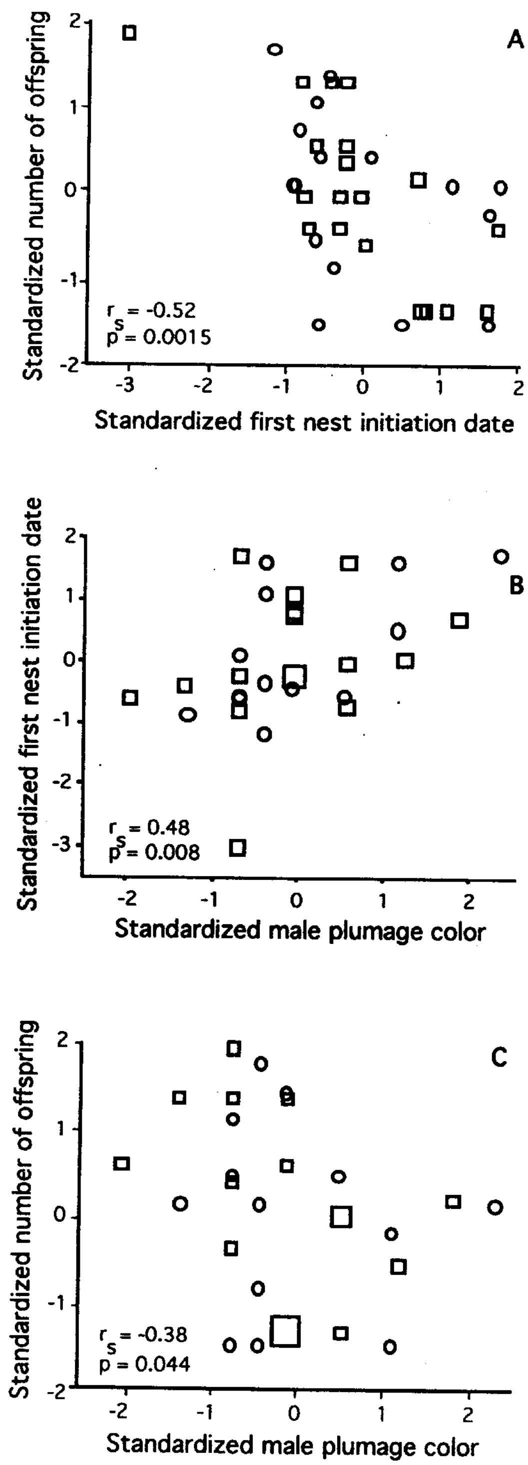

Fig. 1. Relationship between (A) standardized first nest initiation date and standardized number of offspring (n = 35), (B) standardized male plumage coloration and standardized first nest initiation date (n = 29), and (C) standardized male plumage coloration and standardized number of offspring fledged (n = 29). Recall that redder males were assigned lower hue values than were duller birds. ○ = 1997, □ = 1998. Point size is proportional to the number of overlapping observations.

between male plumage brightness, annual reproductive success, and timing of breeding. All tests are two-tailed and the assumed level of significance for all tests is $p < 0.05$.

Results

We found a total of 164 nests during the study and few nests (18%) were found outside of our boxes in the two years. Nest failures at both the egg and nestling stages were uncommon (71% of all nests found fledged at least one offspring), and patterns of nest success were consistent across the two years (1997 = 73%; 1998 = 70%). We obtained complete reproductive success data for a total of 35 unique pairs – 16 in 1997 and 19 in 1998 – and 99 (60%) of the total nests found were from these birds (44 in 1997, 55 in 1998). We were able to capture and quantify plumage coloration for only 29 of the 35 males from these pairs during the two years

Breeding onset was significantly related to annual reproductive success, such that earlier nesting birds fledged more offspring than those that began breeding later in the season (Fig. 1A). Timing of breeding was also significantly associated with male plumage coloration (Fig. 1B), with redder birds breeding earlier than orange and yellow males. In the end, we found that bright males fledged more offspring in a season than did dull males (Fig. 1C). Male age was unrelated to both the number of offspring fledged in a season ($r_s = 0.02$, n = 35, p = 0.90) and male plumage color ($r_s = -0.16$, n = 29, p = 0.39) among the breeding birds in our study.

Discussion

The Darwin-Fisher theory of sexual selection for monogamous birds provides an eloquent explanation for the maintenance of elaborate ornamentation in males of these species. Darwin (1871) and Fisher (1958) recognized that variation in female reproductive effort may directly affect the reproductive success of males to which they are mated, and specifically the time at which females begin breeding in a season can strongly influence both the quantity and quality of offspring produced that year. Female preferences for exaggerated male ornaments consequently provide considerable reproductive benefits to well-ornamented males and drive sexual selection for male ornamentation in these species.

A number of studies have in fact detected a relationship between male ornamentation, breeding onset, and reproductive success. O'Donald (1980) found that the earliest pairing Arctic Skuas *Stercorarius parasiticus* tended to be males that exhibited brown, melanin-based pigmentation (dark morph) as opposed to males that were pale and non-melanic in coloration (light morph), and that earlier skua pairs reared more chicks to fledging than did birds that paired later. Wolfenbarger (1999a) found the same relationship between breeding date, male ornamentation, and reproductive success in Northern Cardinals *Cardinalis cardinalis*. However, in these studies, the role of female choice in the sexual selection system remains unclear. O'Donald (1980) could not rule out the possibility that male competition, and not female choice, maintained the ornamental trait in that system, and Wolfenbarger (1999b) failed to provide experimental evidence for female choice of male plumage coloration in her study species.

To our knowledge, the only study that has carefully corroborated Darwin's theory, where female choice maintains a male ornamental trait through differential timing of breeding, is that by Møller (1988, 1990a) on the Barn Swallow. Using both observational and experimental techniques in the field, Møller (1988, 1990a) demonstrated that longer-tailed males paired sooner than males having shorter tails and that this resulted in increased annual reproductive output for long-tailed males. He also found female choice to be an inherent component of the Barn Swallow mating system. Females visited males individually on their territories, males performed tail-fanning displays to visiting females, and females subsequently accepted or rejected males both as intra-pair and extra-pair mates using tail length as their primary criterion (Møller 1988, 1990a).

Here we provide the second study in which sexually preferred ornamentation, breeding onset, and reproductive success are linked. Experimental work with the House Finch has shown that brighter males are preferred as social mates by females (Hill 1990) and, as a result, begin nesting earlier in a season than do drab orange and yellow males (Hill et al. 1994, 1999). However, it has never been demonstrated that these conditions allow bright male House Finches to fledge more offspring in a given season than do drab males. In this study, we showed that early nesting allowed pairs to achieve higher annual reproductive success than later nesting pairs, and that redder males, by nesting earlier, fledged more offspring in a year than did orange and yellow males. We considered the possibility that the relationship between male plumage color and reproduction has been driven by variables correlated with ornamentation, such as age, but male age was unrelated to both the number of offspring fledged in a season and male plumage color. Thus, differential timing of breeding generates considerable variance in reproductive success among male House Finches and contributes to sexual selection for male plumage ornamentation in this species.

Studies of sexual selection and ornamentation often focus on single mechanisms by which variance in reproductive success may be generated with respect to an ornamental trait, when in fact multiple, interactive mechanisms may work to maintain the sexually selected condition. Thus, differential timing of breeding is not the only means by which variance in reproductive success among male House Finches may be generated with respect to plumage redness. Hill (1991) demonstrated that a male-biased adult sex ratio in House Finches differentially excludes certain drab males from the breeding population. Thus, a male-biased sex ratio and differential timing of breeding work jointly to maintain ornamental plumage coloration in this species.

In addition to a male-biased sex ratio and differences in breeding onset, differential access to extra-pair fertilizations (Westneat et al. 1990) may also increase reproductive output for a subset of ornamental males. However, we believe that sexual selection pressures exerted through choice of extra-pair mates may be weak in this species. Hill et al. (1994) failed to detect a relationship between male plumage coloration and incidence of cuckoldry in a one-year study of extra-pair paternity in Michigan House Finches. The annual EPF rate was low in their study (8%); presumably the intensity of reciprocal mate guarding and the rarity of extra-pair interactions constrained EPF rates (GEH, pers. obs.). Pair behavior of Michigan and Alabama House Finches is very similar (GEH, pers. obs.) and, although additional genetic paternity analyses are needed to determine the full opportunity for sexual selection through extra-pair mate choice in this species, we feel that our focus on social reproductive success in this study is likely to be a fair representation of the true, genetic reproductive success realized by individuals.

Increasing offspring quality is another means by which reproductive advantages may be conferred to brightly pigmented male House Finches. Male genetic quality may increase offspring fitness (Fisher 1958, Andersson 1986) and, because redder males are in better nutritional condition (Hill and Montgomerie 1994), have fewer parasites during molt (Thompson et al. 1997, Brawner et al. in press) and have increased survival (Hill 1991, Nolan et al. 1998), it is possible that parasite resistance (Hamilton and Zuk 1982, Møller 1990b) and/or foraging ability are heritable traits that are passed on to offspring. Increased parental investment (Hoelzer 1989) may also increase offspring quality. In fact, bright red males feed their mates more during incubation than do drab orange and yellow males (Hill 1991), and by feeding their mates more during courtship and incubation, redder males may better help their mates prepare for energy-demanding reproductive efforts (Lack 1940, Carlson 1989). These male feeding behaviors early in the nesting cycle may also foreshadow future performance during nestling and/or fledgling provisioning (Wiggins and Morris 1986). Lastly, offspring quality seems to decline with season in this species, both because late-hatching birds are at a disadvantage in accumulating sufficient resources before molt, thus leaving them with a low likelihood of survival (Murphy 1986, Hochachka

1990), and also because hematophagous mites *Pellonyssus reedi* (Acari: Macronyssidae) appear in House Finch nests in Alabama in the second half of the breeding season and have a considerable impact on the condition of offspring (Stoehr et al. in press). While it is unclear how long House Finches have been subjected to this selection pressure, one would presume it to be beneficial to fledge as many offspring as possible before the seasonal appearance of these mites. Early nesting by the reddest males would certainly allow them to do so. From all of this, it is clear that future work will be needed to explore the full spectrum of direct and indirect benefits female House Finches receive from mating with the reddest males.

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