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Pairing success relative to male plumage redness and pigment symmetry in the house finch: temporal and geographic constancy

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Male house finches (*Carpodacus mexicanus*) have carotenoid-based ornamental plumage coloration. In previous research it was shown that for a single population of house finches in a single year, males that paired were on average redder in plumage coloration than males that did not pair, and males with redder plumage tended to nest earlier than males with less red plumage. Here we show that these patterns continued over 6 years and at two widely separated locations. We also tested whether the symmetry of carotenoid-based crown pigmentation differed between paired and unpaired males and found that paired males have, on average, more perfect symmetry of crown pigmentation than males not paired. These observations support the idea that expression of carotenoid-based plumage coloration by males is a persistent and widespread criterion in female mate choice in the house finch. *Key words:* carotenoids, *Carpodacus mexicanus,* fluctuating asymmetry, mate choice, sexual selection. *[Behav Ecol 10:48–53 (1999)]*

Over the past few decades, field studies of wild birds have greatly increased our understanding of the evolution and maintenance of ornamental traits (reviewed in Andersson, 1994; Møller, 1994). By necessity, such studies are generally conducted on a single population of birds, at a single location, over 1 or a few years. What is observed in the study population is taken as representative of the entire population of animals or even representative of an entire class of ornaments across a diverse array of species. However, every field biologist is aware of annual and geographic variation in the morphological and behavioral traits of animals, and one must wonder about the universality of some conclusions about the function of ornamental traits drawn from localized, short-term studies.

In only a few species of birds has the evolution of an ornamental trait been studied for more than 5 years and at widely separated locations. In the barn swallow (*Hirundo rustica*), female mate choice for males with long and/or symmetrical tails has been demonstrated over 15 years (Møller, 1993) and at study sites across Europe (Denmark: Møller, 1993; Spain: Møller et al., 1995; Italy: Saino and Møller, 1994) and North America (Smith and Montgomerie, 1991). The function of melanin-based plumage coloration in the pied flycatcher (*Ficedula hypoleuca*) and in the closely related collared flycatcher (*Ficedula albicollis*) has also been studied across Europe for more than a decade (e.g., Lundberg and Alatalo, 1992; Part and Quvarnstrom, 1997; Potti and Montalvo, 1991; Saetre and Slagsvold, 1996). In the case of these *Ficedula* flycatchers, however, it has been shown that there is substantial geographic variation in expression of both plumage blackness and the size of the white forehead patch (Lundberg and Alatalo, 1992; Saetre et al., 1997). In some studies females show a mating preference relative to these plumage traits, whereas in other studies they do not (e.g., Alatalo et al., 1986; Lundberg and Alatalo, 1992; Saetre and Slagsvold, 1996). These studies of *Ficedula* flycatchers underscore the importance of testing the function of ornamental traits over as many seasons and at as many geographic locations as possible.

One of the most widespread ornamental traits among birds is carotenoid-based red, orange, and yellow plumage coloration. Carotenoid-based coloration is particularly interesting to students of sexual selection because it is a condition-dependent trait (Gray, 1996; Hill, 1996). Carotenoid pigments cannot be synthesized *de novo* by birds or by any vertebrates; they must be ingested (Goodwin, 1984). Because carotenoid pigments must be derived from food, expression of carotenoid pigmentation is dependent on access to sufficient amounts of foods that provide the right type of carotenoid pigments (Brush and Power, 1976; Fox and McBeth, 1970; Fox et al., 1970; Hill, 1992, 1996). Moreover, after carotenoids are ingested, various parasites can inhibit uptake, transport, or deposition of carotenoid pigments and therefore can alter expression of plumage coloration independent of diet (Brawner, 1997; Hill and Brawner, 1998; Thompson et al., 1997). The physiological condition of a bird at the time of molt, independent of parasitic infection, has also been invoked as a factor in the efficiency with which ingested carotenoids might be used to pigment feathers (Bortolotti et al., 1996; Negro et al., 1998). Models of sexual selection predict that condition-dependent ornamental traits such as carotenoid-based plumage coloration should be of particular interest to females when they choose a mate (see Andersson, 1994; Møller, 1994).

Not only is carotenoid-based plumage coloration condition dependent, but apparently so is the bilateral symmetry of carotenoid pigmentation. Oranger male house finches (*Carpodacus mexicanus*) have less symmetrical carotenoid-based crown pigmentation than do redder males (Hill, 1998). The degree of this sort of fluctuating asymmetry has been proposed as a measure of developmental stability and hence as an indicator of individual quality (Møller, 1990; Thornhill, 1992). In the case of feathers that are replaced once per year, such as the crown feathers of house finches, pigment symmetry potentially reflects individual condition at the time of molt. In a feeding experiment with European starlings (*Sturnus vulgaris*), it was shown that nutritional stress during feather growth affects the symmetry of non-carotenoid pigmenta-

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tion (Swaddle and Witter, 1994). No equivalent experiments have been conducted on carotenoid-based coloration.

In both laboratory and field experiments, female house finches have been shown to prefer mates with redder and more intensely pigmented plumage (Hill, 1990, 1991, 1994). One result of female preference for redder males is that the mean redness of paired male house finches is greater than the mean redness of unpaired males (Hill, 1990). In addition, among male house finches that pair, redder males tend to initiate nesting earlier (i.e., their mates lay eggs earlier) than less red males (Hill et al., 1994). The effects of symmetry of carotenoid-based plumage pigmentation on female mate choice have not been tested in the house finch or in any bird species.

The above results come from studies made in a single population of house finches and over one or two seasons. We examined the effect of male plumage coloration on pairing success and date of nest initiation over six breeding seasons and for two breeding populations of house finches separated by 1200 km. We also looked at the relationship of pigment symmetry to pairing success and nest initiation date.

METHODS

This study was conducted on the main campus of the University of Michigan in southeastern Michigan, USA over four breeding seasons from 1988 to 1991 and on the campus of Auburn University in east-central Alabama, USA for the breeding seasons of 1996 and 1997. At both locations, we trapped house finches at feeding stations and marked them with a unique combination of one aluminum and three colored plastic bands. Red bands were not used on male finches at any location in any year.

The ornamental plumage coloration of males was recorded in two ways. During the 4 years of study in Michigan, the coloration of each of seven plumage regions (four areas on the underside, plus the crown, eyestripe, and rump) was recorded with a separate hue, intensity, and tone score based on comparison with color chips in the *Methuen Handbook of Colour* (Kornerup and Wanscher, 1983). We then summed the 21 scores that were generated to derive a single index value, which was used as an estimate of overall plumage brightness (see Hill, 1992, for details). For the Alabama portion of this study in 1996 and 1997, we scored male plumage coloration using a Colortron (Light Source, San Rafael, California), a Macintosh-compatible reflectance spectrophotometer (see Hill, 1998, for details). The Colortron measures the light reflection from a 3 mm × 3 mm area, and three Colortron measurements were taken at each of three body regions—crown, breast, and rump. For each body region, we used the Colortron software to calculate the mean hue, saturation (intensity), and brightness (tone, blackness) for the three measurements taken, and, for this study, we focused on plumage hue. Color scores attained through visual assessment and scores attained from the Colortron were highly correlated (Hill, 1998). It should be noted that for scores generated by comparison to the *Methuen Handbook of Colour,* higher scores correspond to redder plumage, whereas for scores generated by the Colortron, lower scores correspond to redder plumage.

In 1996 and 1997 we scored the right versus left symmetry of carotenoid-based pigmentation of crown feathers on a 1–5 scale: (5) perfect symmetry; (4) 1–5% of feathers different; (3) 5–50% of feathers different; (2) 50–95% of feathers different; (1) 95–100% of feathers different. Feathers were counted as asymmetrical when the equivalent feather on the opposite side of the crown was obviously a different hue (see Hill, 1998, for details). Symmetry scores were estimated for most but not all males banded in 1996 and 1997, so sample sizes for comparisons of symmetry are consistently smaller than sample sizes for comparisons of plumage coloration. For 142 males, crown symmetry score was estimated by two or more observers, and we calculated repeatability (r) using the interclass correlation coefficient (Lessells and Boag, 1987). Crown symmetry scores were repeatable between observers ($r = .48$, $F_{142, 241} = 3.49$, $p < .0001$).

In Michigan, we began banding each year in January and continued through the breeding season. About 90% of the breeding population was banded in each year of the Michigan study. In Alabama, banding was conducted throughout the year, and about 95% of the breeding population of house finches was banded each year. Male song and the first pair associations become evident in early January in Alabama and early February in Michigan. At these times, daily ad libitum sampling of the populations began.

House finches form strong pair associations (Hill, 1993a; Thompson, 1960), so once a pair is formed, the paired individuals are seldom seen alone (Hill, 1991, 1993a). Therefore, before females begin incubating, it is relatively easy to determine the pairing status of individuals as well as the identity of mates. In addition, females are conspicuous in their efforts to build nests (Hill, 1993a; Thompson, 1960), so it was possible to record virtually all nesting activity on the study sites. Throughout the breeding season at both sites, each time a male was observed it was described as ‘‘paired’’ if it was associating with a female and ‘‘unpaired’’ if it was not associating with a female. Observation of a male simply in proximity to a female was not sufficient to rank that male as paired. The female with which the male was associating had to show some indication that she was encouraging the male’s presence. Such encouragement was generally in the form of the female following the male, but also included the male and female together driving off intruding house finches and any courtship activities by the male to which the female was receptive (see Hill, 1993b, for additional details of field techniques). If a male was observed in such an association with a female at any time during the breeding season, it was counted as paired for that season.

We checked nests once every 3–4 days in Michigan and every other day in Alabama. Nest activity was monitored in Alabama only in 1997; in 1996 only the pair status of males was recorded. House finches lay one egg per day, early in the morning (Hill, 1993a), so when a nest had more than one egg when first checked, first-egg date was determined by backdating. There are two main ways that first nesting date could be incorrectly assigned to birds: if birds nested and failed before they were detected or if birds moved onto the study area after a first nesting attempt outside the study area. In both cases, the incorrect first-nest dates that would result would tend to obscure patterns of redness and nesting date. Therefore, we believe that our test of male coloration and nest initiation is conservative.

We used a one-tailed Mann-Whitney U test to make comparisons of pairing status to plumage redness and pigment symmetry. We had clear a priori predictions about the expected direction of differences between males that paired and males that did not pair based on sexual selection theory and previous findings from a single year of observation (Hill, 1990). A Bonferroni correction was made for simultaneously testing two hypotheses.

RESULTS

Compared to unpaired males, paired males had redder plumage in both Michigan and Alabama and in all 6 years of observation. The probability that by chance the mean redness of paired males would be greater than that of unpaired males

Table 1

The plumage coloration of males observed to be paired versus males not observed to be paired over 4 years in Michigan and 2 years in Alabama

Location	Year	Pair status[a]	*n*	Mean[b]	SD	*U*[c]	*p*
Plumage redness							
Michigan	1988	Paired	66	148.7	8.0	5586	.06
		Unpaired	149	146.3	10.2		
	1989	Paired	66	149.4	10.6	5040	.001*
		Unpaired	119	143.5	14.1		
	1990	Paired	72	149.7	8.3	4200	.0001*
		Unpaired	82	141.1	12.0		
	1991	Paired	67	148.4	9.1	7437	.0003*
		Unpaired	172	141.1	15.2		
Alabama	1996	Paired	20	3.10	4.22	1177	.002*
		Unpaired	83	5.45	4.37		
	1997	Paired	45	2.04	2.65	7016	.0002*
		Unpaired	233	4.99	6.27		
Pigment symmetry							
Alabama	1996	Paired	22	4.23	0.69	1054	.02*
		Unpaired	74	3.64	1.11		
	1997	Paired	44	3.82	0.92	7017	.0001*
		Unpaired	235	3.18	0.96		

[a] Paired birds are those seen associating with a female at any time during the breeding season. Unpaired birds are those males never observed associating with a female; hence, this group includes birds that did not pair and males that paired but were not observed associating with a female. These data underestimate the true differences between paired and unpaired males and constitute conservative tests of hypotheses.

[b] Color scores are based on book scores for 1988–1991 in Michigan (higher scores correspond to redder and brighter plumage) and spectrophotometric scores for 1996–1997 in Alabama (lower scores correspond to redder plumage). Symmetry was recorded on a 5-point scale from perfect symmetry (5) to complete asymmetry (1). See text for details of methods.

[c] One-tailed Mann-Whitney *U* test.

* $p < .05$ after Bonferroni correction.

in 6 of 6 years of observation is 0.016 (sign test). After Bonferroni correction for testing two hypotheses simultaneously (color and symmetry related to redness), the mean difference in plumage coloration between paired males and unpaired males was significant in 5 of 6 years (Table 1). In 2 years of observation in Alabama, paired males also had significantly less pigment asymmetry than unpaired males (Table 1).

Because pigment symmetry is highly correlated with plumage redness (1996: $r_s = -.36$, $n = 93$, $p = .0004$; 1997: $r_s = -.39$, $n = 263$, $p = .0001$), we also compared the effect of plumage redness and pigment symmetry independently. To derive the degree of asymmetry independent of redness, we retained the residual values from the regression of pigment symmetry (dependent variable) on plumage redness (independent variable). Similarly, to derive the degree of plumage redness independent of pigment symmetry, we retained the residual values from the regression of redness (dependent variable) on pigment symmetry (independent variable). Using these residual values as measures of symmetry independent of plumage hue, and plumage hue independent of symmetry, we

Table 2

Residual values for crown pigment symmetry score plotted against plumage redness and for plumage redness plotted against pigment symmetry score

Year	Trait	Pair status	*n*	Mean residual[a]	SD	*U*[b]	*p*
1996	Pigment symmetry	Paired	20	0.375	0.769	908	.048
		Unpaired	73	−0.103	1.020		
	Plumage redness	Paired	20	−0.974	4.304	923	.035
		Unpaired	73	0.267	3.428		
1997	Pigment symmetry	Paired	42	0.350	0.915	5629	.015*
		Unpaired	221	−0.067	0.886		
	Plumage redness	Paired	42	−1.422	3.021	5326	.065
		Unpaired	221	0.270	5.913		

[a] Lower plumage scores correspond to redder plumage; higher symmetry scores correspond to more perfect symmetry.

[b] One-tailed Mann-Whitney *U* test.

* $p < .05$ after Bonferroni correction.

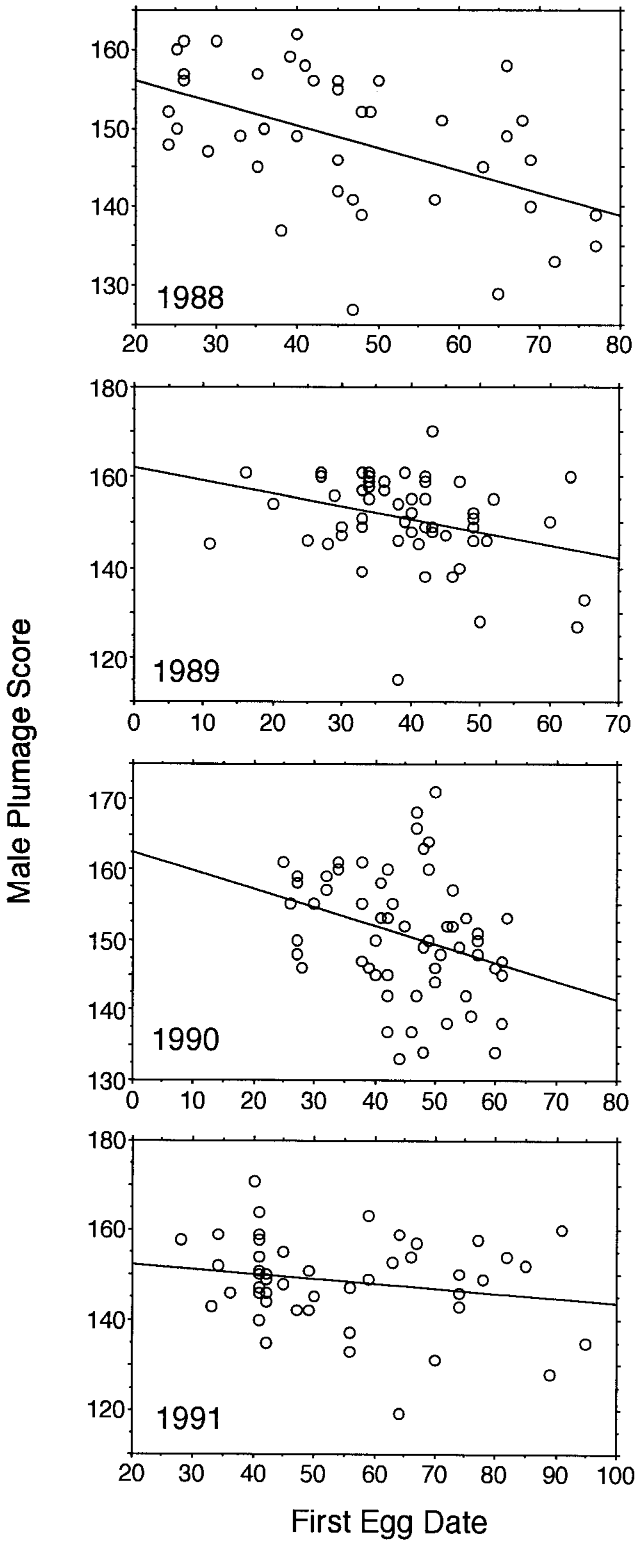

Figure 1
Relation between the plumage brightness of a male house finch and the date the first egg was laid in its nest. Four years of observations from Michigan are shown; March 1 = day 1.

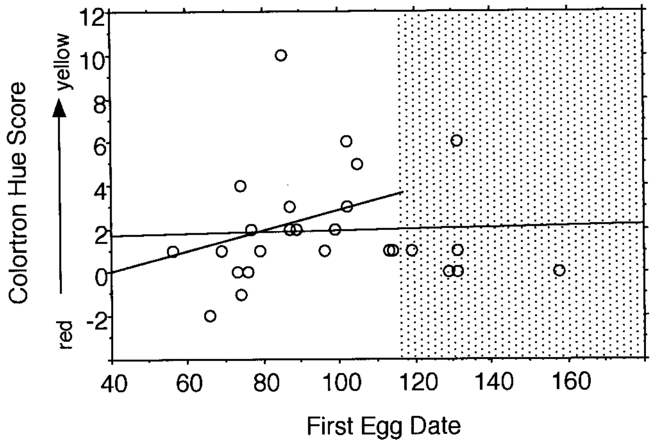

Figure 2
Relation between the plumage brightness of a male house finch and the date the first egg was laid in its nest in Alabama in 1997. The shaded portion of the figure shows nests initiated 61 or more days after the first nest in population. Analysis was run with points in the shaded region both included (the regression line that runs the length of the figure) and with points in the shaded excluded (the regression line that stops at the shaded region). See text for details. January 1 = day 1.

compared the residual values of paired males versus unpaired males paired. Paired males had lower residual plumage values (redder plumage) than unpaired males, but after Bonferroni correction, the difference was not significant in either year (Table 2). After Bonferroni correction, paired males had significantly greater residual symmetry values (more perfect symmetry) than unpaired males in 1 of 2 years (Table 2).

In 3 of 4 years in Michigan, there was a significant negative relationship between the plumage brightness of a male and the first date in which an egg appeared in a nest he was attending (1988: $r_s = -.48$, $n = 41$, $p = .003$; 1989: $r_s = -.28$, $n = 57$, $p = .03$; 1990: $r_s = -.33$, $n = 60$, $p = .01$; Figure 1). In the fourth year, the trend was for brighter males to nest earlier, but the result was not significant (1991: $r_s = -.16$, $n = 47$, $p = .27$; Figure 1). In the 1 year of data for Alabama, there was no significant relationship between male plumage coloration and nest initiation date when all males were included ($r_s = .11$, $n = 26$, $p = .57$; Figure 2). However, although first-nest initiation dates spanned a range of about 60 days in Michigan, some Alabama males were first recorded nesting up to 95 days after the first nest in the population was initiated. We believe that all males in the population had initiated their first nest within 60 days of the first nest initiation and that males first sighted nesting after about 60 days are renesting birds moving into the study area from outlying areas. Thus we repeated the analysis excluding nests that were initiated more than 60 days after the first nest in the population. With this correction, there was again a significant relationship between male plumage brightness and the first date on which an egg appeared in the nest of the attending male ($r_s = .46$, $n = 20$, $p = .04$; Figure 2). (Note that the correlation coefficient is now positive because male coloration was measured with a Colortron, for which redder hues are given lower scores.) When the 60-day cutoff was applied, males with more symmetrical plumage tended to nest earlier than males with less symmetrical plumage, but the relationship was not significant ($r_s = -.36$, $n = 22$, $p = .09$).

DISCUSSION

Across 6 years of study at two widely separated sites, male house finches that paired with a female had redder plumage coloration, on average, than unpaired males. This difference was significant in 5 of 6 years. Among males that paired, there was also a significant relationship between plumage redness and first egg date in 4 of 5 years, and a nonsignificant trend in the same direction in the year 5. These data suggest that over a wide geographic area and across at least a decade, female house finches remained consistent in their choice of brightly colored mates. These observations, combined with laboratory experiments on female mate choice in the house finch (Hill, 1990, 1994), make a convincing case that female choice based on plumage redness is a general phenomenon in house finches.

The observation that females remained constant in their choice of brightly colored mates across all years of study is particularly interesting when one considers that between 1996 and 1997 in Alabama, an epidemic of mycoplasmosis caused by *Mycoplasma gallicepticum* swept through the population (Nolan et al., 1998). Between 1996 and 1997 approximately 60% of the house finches in our study population in Alabama developed gross symptoms of the disease, and many of these birds died as a result (Nolan et al., 1998). The sex ratio was shifted from male biased to female biased, and the mean plumage redness of males increased (Nolan et al., 1998). With a shift in sex ratio from male biased to female biased, the intensity of sexual selection undoubtedly was lower in 1997 than in previous years (see Hill, 1994, for a discussion of the role of sex ratio in sexual selection in the house finch) and because the males remaining in the population were shifted away from the previous mean toward redder plumage (presumably because drab males died from the disease; Nolan et al., 1998), there was less variation in male plumage coloration on which females could base their mate choice. Nevertheless, males that paired were redder than unpaired males.

The tendency for redder males to initiate nesting earlier might be interpreted in at least two ways. Darwin (1871) and later Møller (1988) suggested that one way for variance in reproductive success to exist in monogamous birds is if there is variation in the quality of females such that more attractive males pair with higher quality females. Higher quality females would nest earlier in the season. Therefore, a relationship is predicted between the speed with which males pair and nest and the quality of their ornamentation (Darwin, 1871; Møller, 1988). It is possible, however, that bright males might actually instigate earlier nesting by providing more food to females during courtship. Either way, the observation that across years bright males tend to begin nesting earlier than drab males supports the idea that plumage redness is tied to reproductive success in male house finches because early nesting leads to increased reproductive success in the house finch (McGraw et al., unpublished data).

This is the first study to look at the effect of symmetry of carotenoid-based plumage pigmentation on male pairing success. Previous studies of female mate choice relative to ornament symmetry have focused primarily on elongated tails (Balmford et al., 1993). The only studies on pigment symmetry have focused on melanin-based coloration, and both found a significant female preference for more symmetrically pigmented males (Swaddle and Cuthill, 1994; Swaddle and Witter, 1994). In house finches it was previously observed that pigment symmetry is significantly correlated with plumage redness (Hill, 1998), so in this study it was important to tease apart the independent contribution of symmetry from the independent contribution of redness to the relationship between plumage characteristics and pairing success. We found that independent of plumage redness, there was, on average, greater pigment symmetry of crown plumage in paired males than in males not observed with a female. This suggests that females assess male pigment symmetry as well as plumage coloration when choosing mates. Indeed, from these observations alone, it would appear that females show a stronger preference for pigment symmetry than for redness because the effect of pigment symmetry on pairing success of males remained significant in one year when the effects of redness were removed, but the effect of redness on pairing success was no longer significant when the effects of symmetry were removed. However, female mate choice for symmetrically pigmented males in the house finch needs to be corroborated with an experiment in which pigment symmetry is uncoupled from all potential correlated effects.

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REFERENCES

Alatalo RV, Glynn C, Lundberg A, 1986. Female pied flycatchers chose territory quality and not male characteristics. Nature 323:152–153.

Andersson MB, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.

Balmford A, Jones IL, Thomas ALR, 1993. On avian asymmetry: evidence of natural selection for symmetrical tails and wings in birds. Proc R Soc Lond B 252:245–251.

Bortolotti G, Negro JJ, Tella JL, Marchant TA, Bird DM, 1996. Sexual dichromatism in birds independent of diet, parasites and androgens. Proc R Soc Lond B 263:1171–1176.

Brawner WR III, 1997. The effects of coccidial and mycoplasmal infection on plumage pigmentation in male house finches (*Carpodacus mexicanus*): a test of the Hamilton-Zuk hypothesis (MSc thesis). Auburn, Alabama: Auburn University.

Brush AH, Power DM, 1976. House finch pigmentation: carotenoid metabolism and the effect of diet. Auk 93:725–739.

Darwin C, 1871. The descent of man, and selection in relation to sex. London: Murray.

Fox DL, McBeth JW, 1970. Some dietary and blood carotenoid levels in flamingos. Comp Biochem Physiol 34:707–713.

Fox DL, McBeth JW, MacKinney G, 1970. Some dietary carotentoids and blood-carotenoid levels in flamingos. II γ-carotene and α-carotene consumed by the American flamingo. Comp Biochem Physiol 36:253–262.

Goodwin TW, 1984. The biochemistry of carotenoids, vol. 2. Animals, 2nd ed. New York: Chapman and Hall.

Gray DA, 1996. Carotenoids and sexual dichromatism in North American passerine birds. Am Nat 148:453–480.

Hill GE, 1990. Female house finches prefer colorful males: sexual selection for a condition-dependent trait. Anim Behav 40:563–572.

Hill GE, 1991. Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339.

Hill GE, 1992. Proximate basis of variation in carotenoid pigmentation in male house finches. Auk 109:1–12.

Hill GE, 1993a. House finch (*Carpodacus mexicanus*). In: The birds of North America, no. 46 (Poole A, Gill F, eds). Washington, DC: The American Ornithologists' Union.

Hill GE, 1993b. Male mate choice and the evolution of female plumage coloration in the house finch. Evolution 47:1515–1525.

Hill GE, 1994. Geographic variation in male ornamentation and female mate preference in the house finch: a comparative test of models of sexual selection. Behav Ecol 5:64–73.

Hill GE, 1996. Redness as a measure of the production cost of ornamental coloration. Ethol Ecol Evol 8:157–175.

Hill GE, 1998. Plumage redness and pigment symmetry in the house finch. J Avian Biol 29:86–92.

Hill GE, 1998. An easy, inexpensive means to quantify plumage colouration. J Field Ornithol. 69:353–363.

Hill GE, Brawner WR, III, 1998. Melanin-based plumage colouration in the house finch is unaffected by coccidial infection. Proc R Soc Lond B. 265:1105–1109.

Hill GE, Montgomerie R, Roeder C, Boag P, 1994. Sexual selection and cuckoldry in a monogamous songbird: implications for sexual selection theory. Behav Ecol Sociobiol 35:193–199.

Kornerup A, Wanscher JH, 1983. Methuen handbook of colours, 3rd ed. London: Methuen.

Lessells CM, Boag PT, 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Lundberg A, Alatalo RV, 1992. The pied flycatcher. London: T. & A. D. Poyser.

Møller AP, 1988. Female choice selects for male sexual tail ornaments. Nature 332:640–642.

Møller AP, 1990. Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. Anim Behav 40:1185–1187.

Møller AP, 1993. Sexual selection in the barn swallow *Hirundo rustica*. III. Female tail ornaments. Evolution 47:417–431.

Møller AP, 1994. Sexual selection and the barn swallow. Oxford: Oxford University Press.

Møller AP, De Lope F, Lopez-Caballero JM, 1995. Foraging costs of a tail ornament: experimental evidence from two populations of barn swallows *Hirundo rustica* with different degrees of sexual size. Behav Ecol Sociobiol 37:289–295.

Negro JJ, Bortolotti GR, Tella JL, Fernie KJ, Bird DM, 1998. Regulation of integumentary colour and plasma carotenoids in American kestrels consistent with sexual selection theory. Funct Ecol 12:307–312.

Nolan PM, Hill GE, Stoehr AM, 1998. Sex, size, and plumage redness predict house finch survival in an epidemic. Proc R Soc Lond B 265:961–965.

Part T, Quvarnstrom A, 1997. Badge size in collared flycatchers predicts outcome of male competition over territories. Anim Behav 54: 893–899.

Potti J, Montalvo S, 1991. Male colour variation in Spanish pied flycatcher *Ficedula hypoleuca*. Ibis 133:293–299.

Saetre GP, Moum T, Bures S, Kral M, Adamjan M, Moreno J, 1997. A sexually selected character displacement reinforces premating isolation. Nature 387:589–592.

Saetre GP, Slagsvold T, 1996. Female pied flycatchers prefer brightly coloured males. Anim Behav 48:1407–1416.

Saino N, Møller AP, 1994. Secondary sexual characters, parasites and testosterone in the barn swallow (*Hirundo rustica*). Anim Behav 48: 1325–1333.

Smith HG, Montgomerie R, 1991. Sexual selection and the tail ornaments of North American barn swallows. Behav Ecol Sociobiol 28:195–201.

Swaddle JP, Cuthill IC, 1994. Female zebra finches prefer males with symmetric chest plumage. Proc R Soc Lond B 258:267–271.

Swaddle JP, Witter MS, 1994. Food, feathers and fluctuating asymmetries. Proc R Soc Lond B 255:147–152.

Thompson CW, Hillgarth N, Leu M, McClure HE, 1997. High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. Am Nat 149:270–294.

Thompson WL, 1960. Agonistic behavior in the house finch. Part II: Factors in aggressiveness and sociality. Condor 62:378–402.

Thornhill R, 1992. Fluctuating asymmetry and the mating system of the Japanese scorpionfly *Panorpa japonica*. Anim Behav 44:867–879.