Plumage color as a dynamic trait: carotenoid pigmentation of male house finches (*Carpodacus mexicanus*) fades during the breeding season

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Abstract: Evolutionary biologists studying sexually selected bird plumage generally consider this trait to be static throughout a breeding season and assign trait values to individuals on the basis of single measurements. We investigated the propensity for carotenoid-based color of feather patches in male house finches (*Carpodacus mexicanus* (Muller, 1776)) to change during the breeding period. We recaptured and rescored 63 males and found that the hue of feathers faded significantly over the season. The degree of hue change was a direct function of the amount of time between plumage scores; feathers faded more as the interval between measurements increased. The magnitude of hue change was not, however, related to an individual's age or initial plumage redness, which suggests that certain birds are not more or less prone to fading. Collectively, these findings imply that researchers should more carefully track plumage color expression during the course of a year, as seasonal color shifts may have important consequences for late-season male–male competitive interactions and flexible female mating tactics (e.g., social mate switching, choice of extra-pair partners). Potential mechanisms for this seasonal plumage color shift are discussed.

Résumé : Les biologistes spécialistes de l'évolution qui étudient le plumage des oiseaux, un caractère soumis à la sélection sexuelle, estiment généralement qu'il s'agit d'une caractéristique statique au cours de la saison de reproduction et se contentent d'une seule mesure pour assigner une valeur au plumage de chaque individu. Nous avons examiné la tendance des taches de couleur à base de caroténoïdes sur les plumes des roselins familiers (*Carpodacus mexicanus* (Muller, 1776)) mâles à changer au cours de la saison de reproduction. Nous avons capturé une seconde fois et réévalué 63 mâles: leurs plumes changent significativement de teinte au cours de la saison de reproduction. L'importance du changement de teinte est fonction directe du temps entre les deux évaluations du plumage: les plumes pâlissent d'autant plus que l'intervalle entre les évaluations est long. Cependant, l'importance du changement de teinte n'est pas reliée à l'âge de l'individu ni à l'intensité initiale de la couleur rouge du plumage, ce qui indique qu'il n'y a pas d'oiseaux dont le plumage est plus ou moins enclin à pâlir. Dans leur ensemble, ces résultats indiquent que les scientifiques devraient suivre plus attentivement l'expression de la couleur du plumage au cours de l'année, car les changements saisonniers peuvent avoir d'importantes conséquences pour les interactions de compétition entre mâles en fin de saison et les tactiques flexibles d'accouplement des femelles (e.g., changement de partenaire social, choix d'un partenaire hors du couple). Les mécanismes possibles qui expliquent ce changement saisonnier de couleur du plumage font l'objet d'une discussion.

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Introduction

Many sexually selected characters, such as courtship dances or vocalization bouts, are generally thought of as dynamic traits that are subject to change over space and time, whereas others, such as feather ornaments (e.g., crests, tails) or hardened horns and antlers, are considered more static traits. The plasticity of sexual traits largely shapes the sexual signaling systems of animals, as conspecific receivers must continually reassess display intensity and other aspects of signal quality to gain reliable, global information about their potential sexual partners or combatants (Bradbury and Vehrencamp 1998). The temporal stability of ornament expression also bears critically on the means by which biologists quantify these signals. A single snapshot of trait expression may not adequately represent the true quality of signalers.

Plumage coloration in birds is typically recognized as a fixed form of sexual signal (with a few exceptions, such as the cosmetic coloration of waterfowl, shorebirds, and vultures; Negro et al. 1999; Piersma et al. 1999). Bird feathers are most commonly colored either by the incorporation of

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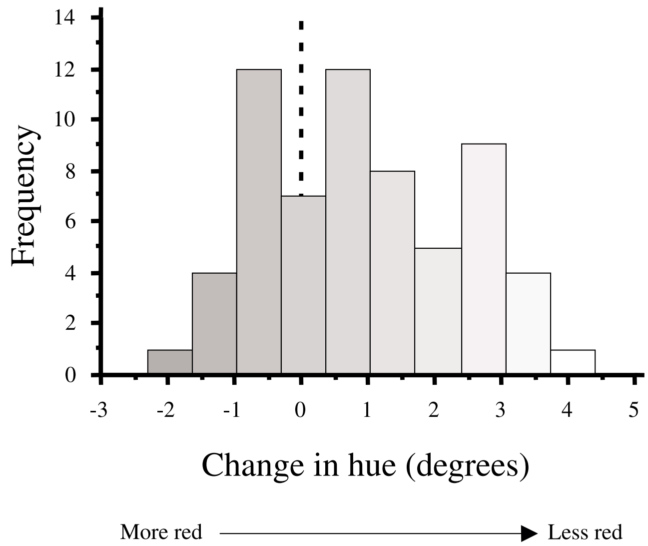
pigments (e.g., carotenoids, melanins) into the matrix of keratin or by the structural arrangement of feather tissues (known as structural coloration) (Fox and Vevers 1960). Because birds grow feathers during periodic molts and retain the dead tissues for extended periods of time (e.g., through the breeding season or for an entire year), most studies of avian color ornaments quantify coloration only once during the year and make the implicit assumption that plumage displays remain constant. However, feathers are subject to abrasion, damage, soiling, and degradation by many abiotic and biotic factors (e.g., Bonser 1995; Burtt and Ichida 1999). Thus, we have reason to suspect that feather colors may not be entirely static.

Here, we investigate the temporal constancy of carotenoid-based plumage coloration in male house finches (*Carpodacus mexicanus* (Muller, 1776)), which serves as a classic sexually selected trait in animals. Male finches that deposit more carotenoids into feathers to acquire redder plumage are more likely to acquire mates, begin breeding earlier, and fledge more offspring in a year (reviewed in Hill 2002). Rather than examine population-wide changes in color over time, which may be subject to temporal sampling biases, we used within-individual comparisons (by recapturing and rescoring the same birds) to analyze the extent to which carotenoid colors change during the 6-month breeding season of house finches.

Fig. 1. Frequency distribution of the seasonal changes in plumage hue in male house finches (*Carpodacus mexicanus*). Because the Colortron™ reflectance spectrophotometer arbitrarily assigns lower hue scores to redder birds, positive values on the *x* axis represent decreases in hue (i.e., hue becoming less red over time).



Methods

As part of a larger study of the breeding biology of house finches in east-central Alabama (Hill et al. 1999; Hill 2002), we recaptured and rescored plumage coloration for 63 males during the breeding season(s) (late January to mid-July) of 1997–1999. Birds were captured using basket traps at feeding stations on the campus of Auburn University, Auburn, Alabama. We marked each bird with a unique combination of colored leg bands for later identification.

We scored plumage color using a Colortron™ reflectance spectrophotometer (Light Source Inc., San Rafael, California; Hill 1998), which is a 32-band hand-held instrument that objectively quantifies colors visible to the human eye (house finches see poorly, and their ornamental feathers reflect weakly, in the UV portion of the spectrum; McGraw and Hill 2000) using a tristimulus scoring system (HSB, or hue/saturation/brightness). We took two measurements from each of the three primary patches of plumage color in house finches (crown, breast, rump) and averaged the six scores to obtain mean HSB values for each bird (see Hill 2002 for additional details). We subtracted initial from final scores to compute seasonal plumage color change, which we used in statistical analyses. Because hue captures most of the meaningful variation in plumage color in house finches (Hill 2002), we focus particular attention on this variable. Note that because hue is measured around a 360° color wheel with red set arbitrarily at 0°, hue values increase as one proceeds from red through orange to yellow.

We used paired *t* tests to examine within-season temporal changes in plumage hue, saturation, and brightness. Individual birds appear only once in the analyses; when they were studied in multiple years, we randomly selected data from one year for analysis. To test for a more specific effect of time on color change, we used Fisher's *r*-to-*z* correlational tests to compare the relationship between color change and the number of days between measurements, predicting that plumage color would change more as the time between sampling dates increased.

We were also interested in whether plumage color change might be a function of a male's age or plumage appearance (bright or drab). We used nonparametric Spearman's rank correlation tests to examine the link between color change and a male's initial plumage color (which were not normally distributed). We determined the age of males in two ways (sensu McGraw et al. 2001*a*): (1) by capturing and marking hatch-year birds (easily identified by their first-year plumage; Hill 2002) and following them in successive years and (2) by capturing unbanded adults early in the breeding season and assuming that they were in their second calendar year. Because the second assumption is weak and because there were too few males in each of the older age classes, we applied two statistical models (both using unpaired *t* tests) to compare age and color change: (1) known second-year birds (banded in their hatch year) versus birds followed as adults for more than 2 years (>2 years of age) and (2) all birds known or presumed to be in their second year versus birds >2 years of age.

Results

Changes in plumage hue

The initial hue scores of the 63 males that we studied ranged from –3 to 33, thus spanning the full spectrum of red to yellow plumage colors displayed in this population (also see Hill 2002). Males showed a significant decrease in plumage redness (increase in hue) over the season (mean ± SE of first score = 3.75 ± 0.88; second score = 4.78 ± 0.88; paired *t* test, $t_{62} = -5.38$, $P < 0.0001$) (Fig. 1). Of the 63 males, 41

Table 1. Differences in seasonal plumage color change as a function of age in male house finches (*Carpodacus mexicanus*).

	Model 1				Model 2			
Color measure	2 years old (n = 15)	>2 years old (n = 11)	t	P	2 years old (n = 52)	>2 years old (n = 11)	t	P
Hue change (degrees)	1.20±0.36	0.72±0.40	0.9	0.38	1.09±0.22	0.72±0.40	0.73	0.47
Saturation change (%)	1.47±0.97	1.96±1.06	–0.37	0.74	2.00±0.51	1.96±1.06	0.04	0.97
Brightness change (%)	–0.33±0.83	–1.87±0.80	1.3	0.21	–0.18±0.43	–1.87±0.80	1.69	0.10

Note: Values are means ± SE. Model 1 is more conservative, using only known second-year birds, whereas model 2 incorporates both known and presumed second-year birds (see Methods for more details).

showed an increase in hue, 5 did not change, and 17 were scored as redder. The small number of birds that did not undergo a change in hue in this breakdown is a result of the precision with which we assigned hue scores (to the nearest 0.1, a result of averaging six integer scores for each bird). When we consider the margin of measurement error in these analyses, which is 0.67 hue units (determined by averaging the absolute values of the differences between the two hue scores for each plumage patch on each bird), 32 of the 63 males showed an increase in hue beyond the measurement error, 26 did not change, and only 5 showed a decrease in hue. The average increase was 2.28 ± 0.16 hue units for the faded birds; the five redder birds underwent a decrease of 1.40 ± 0.24 hue units.

Among the birds that faded, the magnitude of hue change was predicted significantly by the number of days between scoring periods (Fig. 2); birds faded more when there was a longer time interval between measurements. The initial hue of individuals did not predict the extent to which they changed color (Fig. 3); this was true regardless of whether we included all birds in the sample or only males that faded. Also, older and younger birds did not differ in the degree of plumage hue change within a season (Table 1).

Changes in plumage saturation and brightness

Carotenoid-containing plumage patches became significantly more saturated as the breeding season progressed (first score = 53.08 ± 0.53%; second score = 55.14 ± 0.61%; t_{62} = –4.5, P < 0.0001) but did not change in brightness (t_{62} = –1.4, P = 0.18). Fourty-four males underwent an increase in saturation, 4 did not change, and 15 became less saturated. Again, if we modify these categories with a consideration of measurement error (1%), 35 showed an increase in saturation, 19 underwent no change, and 9 became less saturated. Among the birds that became more saturated, there again was a significant positive association between color change and the interval between measurements (r = 0.31, P = 0.025). There were no links between seasonal saturation change and initial plumage saturation (all birds, r = –0.24, P = 0.06; birds that became more saturated only, r = –0.17, P = 0.34), although there was a tendency for birds that began the season with less saturated plumage to become more saturated. Saturation and brightness did not change predictably during the year as a function of a male's age (Table 1).

Discussion

Seasonal color change in sexually selected bird plumage is a common and predictable phenomenon when it is the result of a complete feather molt. For example, American goldfinches (*Carduelis tristis* (L., 1758)), a close relative of house finches, shed their drab winter plumage and grow brilliant lemon yellow body feathers just prior to the breeding season (Middleton 1993). Until recently, however, there were few quantitative studies that examined systematic changes in the color of intact bird plumages.

Fig. 2. Scatterplot of the relationship between plumage hue change and the number of days between plumage hue measurements. Higher "shift" scores denote birds that faded more. Birds faded significantly more as the interval between measurements increased.

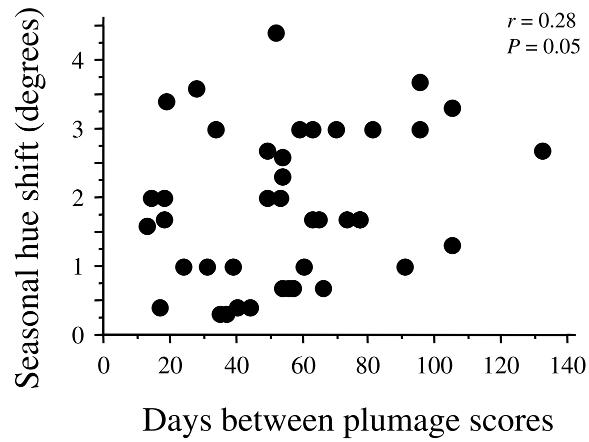
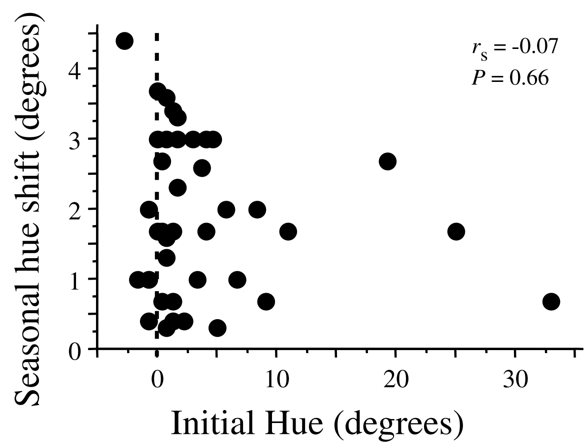


Fig. 3. Scatterplot of the relationship between plumage hue shift and the initial plumage redness of males.



Here, we document a seasonal change in the expression of carotenoid-based plumage coloration in male house finches. Colorful plumage patches, which are grown in late fall and retained for one calendar year, shifted along two axes of elaboration over the course of the breeding season, becoming less red and more saturated. Örnborg et al. (2002) characterized a similar color change in structurally colored ornamental feathers of male blue tits (*Parus caeruleus* L., 1758) from Europe. Our longitudinal study allowed us to track precise temporal effects on feather color; in fact, we found that the hue of house finches faded more over longer time intervals. Senar (2004) reported similar seasonal fading of carotenoid-based plumage coloration in great tits (*Parus major* L., 1758). Certain plumages (bright versus drab, those of old males versus young) in house finches were not more likely to fade, suggesting that fading may be a general phenomenon for this sexual signal and not a predictable aspect of individual quality. Still, follow-up tests are needed to determine whether these small changes in color are used by males or females to gauge relative mate quality throughout the breeding period.

We propose three mechanisms, which are not mutually exclusive, that may explain the observed color changes. (1) Feather degradation: bird feathers commonly abrade over time because of damage and the action of feather-eating bacteria. This can result in feather brightening, as is the case with Lawrence's goldfinch (*Carduelis lawrencei* Cassin, 1850, Willoughby et al. 2002), where the abrasion of dark feather portions coincides with the onset of breeding and leaves behind only the colorful yellow-pigmented portions, but physical changes to feather structure may also impair the reflectivity of colored surfaces. Melanin pigments are often used to improve feather integrity and reduce abrasion (Bonser 1995), but biochemical analyses of carotenoid-pigmented portions of house finch feathers show that they contain few melanins (McGraw et al. 2004) and may be subject to wear. (2) Plumage soiling: feathers often accumulate dirt and lipids over the course of a year, either accidentally or as a result of adaptive strategies employed by birds to become more sexually attractive (e.g., cosmetic preen waxes in shorebirds; Piersma et al. 1999) or camouflaged (e.g., soiling in ptarmigans; Montgomerie et al. 2001). Dirt and oils can alter spectral characteristics of feathers, specifically by absorbing short wavelengths of light (Örnborg et al. 2002). This phenomenon may account for the observed increase in plumage saturation (spectral purity) during our study. (3) Pigment degradation: with their extended conjugated electron systems, carotenoid pigments are easily oxidized and subject to photobleaching (Mortensen and Skibsted 1999). Thus, it is possible that plumage carotenoids themselves are chemically damaged or modified to less colorful forms by long-term exposure to sunlight. UV irradiation is touted as a significant cause of feather deterioration in birds (Burtt 1986), but it is not known to what extent carotenoids are rendered less susceptible to photodamage within the feather–keratin matrix. Bacterial keratin-degrading enzymes may also damage carotenoid structure or coloration.

The likelihood of plumage fading over the course of the breeding season may serve as an important selective pressure for the evolution of feather morphology, as well as seasonal mating behaviors in house finches. Given the fitness benefits of displaying brightly colored plumage, birds might be expected to evolve strategies to minimize color change; one such strategy in house finches and other cardueline finches (Newton 1972) may be the initial "covering" of their carotenoid-pigmented feathers with buff-colored tips that progressively wear away up until the start of the breeding season. Late-season social interactions may also be affected by this color shift. Among birds that use bright plumage to acquire mates early in the season, individuals may lose social partners or competitions with rivals if they display faded plumage. Females using plumage pigmentation to make late-season extra-pair mating decisions may avoid males with faded colors.

Based on the results of this study, we encourage behavioral ecologists studying plumage color to more carefully quantify color expression in their study species, to better represent individual phenotypes over time. Ideally, field biologists would capture all animals at around the same time to avoid the effects of color change. In practice, however, many researchers score plumage colors over a range of dates and draw conclusions about an individual's reproductive potential for the entire year (e.g., Wolfenbarger 1999; Dale 2000; McGraw et al. 2001*b*) without accounting for seasonal color shifts. Studies of plumage coloration and sexual selection that use museum specimens (e.g., Endler and Théry 1996; Zahn and Rothstein 1999; McNaught and Owens 2002) should also consider long-term shifts in color that might confound results.

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References

Bonser, R.H.C. 1995. Melanin and the abrasion resistance of feathers. Condor, **97**: 590–591.

Bradbury, J.W., and Vehrencamp, S.L. 1998. Principles of animal communication. Sinauer Associates, Sunderland, Mass.

Burtt, E.H., Jr. 1986. An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. Ornithol. Monogr. **38**: 1–126.

Burtt, E.H., Jr., and Ichida, J.M. 1999. Occurrence of feather-degrading bacilli in the plumage of birds. Auk, **116**: 364–372.

Dale, J. 2000. Ornamental plumage does not signal male quality in red-billed queleas. Proc. R. Soc. Lond. B Biol. Sci. **267**: 2143–2149.

Endler, J.A., and Théry, M. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. Am. Nat. **148**: 421–452.

Fox, H.M., and Vevers, G. 1960. The nature of animal colors. Macmillan, New York.

Hill, G.E. 1998. An easy, inexpensive method to quantify plumage coloration. J. Field Ornithol. **69**: 353–363.

Hill, G.E. 2002. A red bird in a brown bag: the function and evolution of ornamental plumage coloration in the house finch. Oxford University Press, Oxford.

Hill, G.E., Nolan, P.M., and Stoehr, A.M. 1999. Pairing success relative to male plumage redness and pigment symmetry in the house finch: temporal and geographic constancy. Behav. Ecol. **10**: 48–53.

McGraw, K.J., and Hill, G.E. 2000. Carotenoid-based ornamentation and status signaling in the house finch. Behav. Ecol. **11**: 520–527.

McGraw, K.J., Nolan, P.M., Stoehr, A.M., and Hill, G.E. 2001*a*. Intrasexual differences in age-specific parental effort in the house finch (*Carpodacus mexicanus*). Etologia, **9**: 35–41.

McGraw, K.J., Stoehr, A.M., Nolan, P.M., and Hill, G.E. 2001*b*. Plumage redness predicts breeding onset and reproductive success in the house finch: a validation of Darwin's theory. J. Avian Biol. **32**: 90–95.

McGraw, K.J., Wakamatsu, K., Clark, A.B., and Yasukawa, K. 2004. Red-winged blackbirds use carotenoid and melanin pigments to color their epaulets. J. Avian Biol. In press.

McNaught, M., and Owens, I.P.F. 2002. Species-specific plumage in birds: species-recognition or light environment? J. Evol. Biol. **15**: 505–514.

Middleton, A.L.A. 1993. American goldfinch (*Carduelis tristis*). *In* Birds of North America. No. 80. *Edited by* A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia, Pa. pp. 1–24.

Montgomerie, R., Lyon, B., and Holder, K. 2001. Dirty ptarmigan: behavioral modification of conspicuous male plumage. Behav. Ecol. **12**: 429–438.

Mortensen, A., and Skibsted, L.H. 1999. Carotenoid photobleaching. Methods Enzymol. **299**: 408–421.

Negro, J.J., Margalida, A., Hiraldo, F., and Heredia, R. 1999. The function of the cosmetic coloration of bearded vultures: when art imitates life. Anim. Behav. **58**: F14–F17.

Newton, I. 1972. Finches. Taplinger Publishing Co., New York.

Örnborg, J., Andersson, S., Griffith, S.C., and Sheldon, B.C. 2002. Seasonal changes in an ultraviolet structural colour signal in blue tits, *Parus caeruleus*. Biol. J. Linn. Soc. **76**: 237–245.

Piersma, T., Dekker, M., and Damste, J.S.S. 1999. An avian equivalent of make-up? Ecol. Lett. **2**: 201–203.

Senar, J.C. 2004. Mucho más que plumas. Monografies del Museu de Ciéncias Naturales 2, Barcelona.

Willoughby, E.J., Murphy, M., and Gorton, H.L. 2002. Molt, plumage abrasion, and color change in Lawrence's goldfinch. Wilson Bull. No. 114. pp. 380–392.

Wolfenbarger, L.L. 1999. Red coloration of male northern cardinals correlates with mate quality and territory quality. Behav. Ecol. **10**: 80–90.

Zahn, S.N., and Rothstein, S.I. 1999. Recent increase in male house finch plumage variation and its possible relationship to avian pox disease. Auk, **116**: 35–44.