Plumage Color as a Composite Trait: Developmental and Functional Integration of Sexual Ornamentation

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ABSTRACT: Most studies of condition-dependent sexual ornaments have treated such ornaments as single traits. However, sexual ornaments are often composites of several components, each produced by partially independent developmental pathways. Depending on environmental and individual condition, components of these ornaments may reflect different behavioral or physiological properties of an individual. One of the best-known, condition-dependent ornaments is carotenoid-based plumage coloration, which has at least four distinct components: pigment elaboration, patch area, pigment symmetry, and patch area symmetry. Here we examined fitness consequences of variation in individual components of carotenoid ornamentation in male house finches (*Carpodacus mexicanus*). Over 5 yr and several selection episodes, we studied variation in the plumage components in a large sample ($n = 498$) of males from a Montana population. The ornament components were partially independent of each other and had distinct fitness consequences. Selection for higher fecundity favored an increase in redness of coloration and a decrease in pigment asymmetry and patch area asymmetry but did not act on patch area itself. In contrast, viability selection favored larger and more symmetrical ornamental patches but did not act on pigment elaboration. Developmental and functional interrelationships among individual components of ornamentation strongly differed between house finch populations. Distinct patterns of selection on individual components of condition-dependent ornaments, combined with partially independent development of components, should favor the evolution of composite sexual traits whose components reliably reflect condition across a wide array of environments.

Keywords: Carpodacus mexicanus, composite trait, morphological integration, sexual ornaments, plumage color, phenotypic selection.

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Expression of secondary sexual traits is often closely linked to the overall physical condition and health of an individual (Kodric-Brown and Brown 1984; Andersson 1986; Berglund et al. 1996). Because overall condition is closely associated with the fitness of an organism, condition-dependent traits are typically under strong directional selection (Price et al. 1988, 1993). When individual condition is heritable and genetically correlated with expression of a condition-dependent trait, directional selection can lead to elaboration of the trait (Schluter and Price 1993; Iwasa and Pomiankowski 1994). However, the production of an indicator trait can be affected by many organismal processes with varying degrees of condition dependence (Pomiankowski and Møller 1995; Rowe and Houle 1996; Merilä and Sheldon 1999), leading to different intensity of selection on different aspects of an indicator trait (Burley 1981; Zuk et al. 1990). Thus, knowledge of developmental and functional interrelationships (i.e., integration) among the components of a condition-dependent trait is essential for an understanding of the evolutionary change in such a trait (Kodric-Brown and Brown 1984; Endler 1992, 1993, 1995; Moore 1997; Kodric-Brown 1998).

Significant progress has been made in uncovering the composite nature of structural morphological traits and identifying which components of such traits are the target of specific forms of selection. Typically, these traits are highly intercorrelated, and variation in a trait is often related to the overall size of an organism rather than to specific attributes of a trait (Lande and Arnold 1983). Partitioning of the variation of structural traits into overall size and trait-specific "shape" variation has allowed researchers to evaluate trait-specific selection pressures (Wright 1923; Crespi and Bookstein 1989). However, progress toward uncovering the composite nature of or-

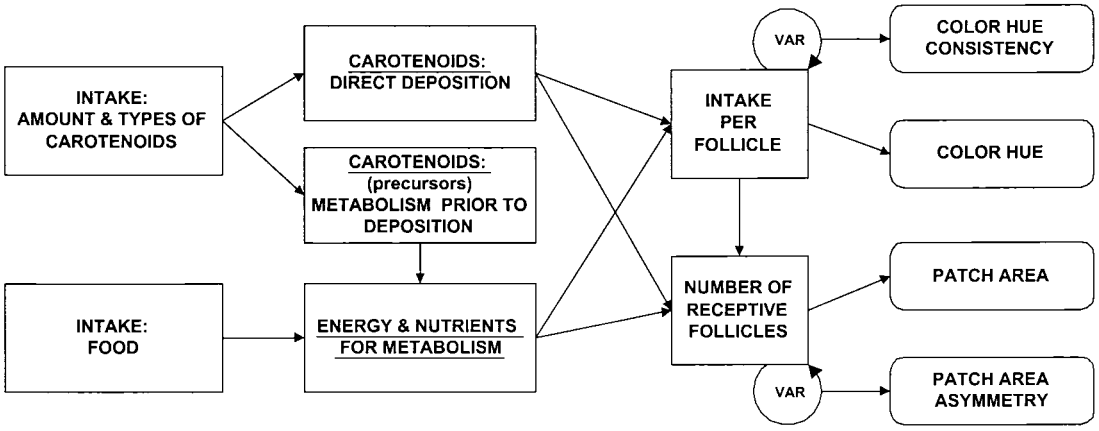

Figure 1: A schematic illustration of the pathways for the development of components of carotenoid-based plumage coloration. Food and carotenoid intake are separated for the ease of presentation. Pigmentation involves two primary processes—carotenoid acquisition and carotenoid utilization (see Hill 1999, 2000). Carotenoid pigments that are used to color feathers are either ingested directly or metabolized from suitable carotenoid precursors. Direct use of dietary pigments moves carotenoids along the top of the figure and avoids most dependency of body condition. Use of carotenoids metabolized from dietary precursors leads to greater dependency on the energy and health state of the individual. The elaboration of pigmentation (hue and intensity of coloration) is thus variably dependent on dietary pigments and body condition. Expression of patch area is also dependent on dietary pigments and body condition, but the contribution of these factors to patch size can be quite different than the contribution of these factors to pigment elaboration. Circular arrows indicate the variance (among follicles between right and left side) in intake per follicle and the number of receptive follicles, which determines pigment consistency and patch area symmetry across the midline of the organism.

namental traits in general and, in particular, plumage color ornaments has lagged behind the advances that have occurred in studies of other morphological traits. Despite a long interest in the evolution of brightly colored plumage, researchers have only recently begun treating carotenoid-, melanin-, and structurally based coloration as distinct plumage ornaments (Gray 1996; Hill 1996; Owens and Hartley 1998; Badyaev and Hill 2000*a*). Still, within each of these broad classes of color display, studies often assume a noncomposite nature of plumage ornaments (reviewed in Badyaev and Hill 1999).

Carotenoid-based ornaments provide a particularly good example of the standard approach that has been adopted in studies of ornamental traits. No animals are known to synthesize carotenoids (reviewed in Fox 1976; Goodwin 1973, 1984; Britton 1995), so production of carotenoid-based coloration is ultimately linked to ability to acquire carotenoids from food (Brush and Power 1976; Brush 1978, 1990; Slagsvold and Lifjeld 1985). As a result, expression of carotenoid-based plumage ornamentation is commonly assumed to be a good indicator of the physical condition and health of the bearer (Endler 1983; Kodric-Brown 1985, 1989; Hill 1990; Frischknecht 1993; Hill and Montgomerie 1994; reviewed in Hill 1999). However, while commonly treated as a simple trait with a single direction of elaboration (Björklund 1990; Hill 1990, 1991, 1994; Seutin 1994; Sundberg 1995; Badyaev 1997*a*, 1997*b*), carotenoid-based "plumage coloration" is actually a complex trait with several distinct and partially developmentally independent components.

We recognize four distinct components of carotenoid-based plumage coloration. First, pigment elaboration is a function of the type and quantity of carotenoid pigments deposited in growing feathers (Troy and Brush 1983; Hill 1992; Inouye et al., in press). Carotenoid-based pigment elaboration has generally been quantified using tristimulus color notation, and under this system, the pigment (redness/yellowness) and intensity of coloration have been the focus of most studies (Hill 1999). Second, patch area is the area of plumage (i.e., number of feathers) with carotenoid pigmentation. Third, pigment symmetry is the bilateral consistency of feather pigmentation, generally recorded as deviation from perfect symmetry (Hill 1998*b*). Fourth, patch area symmetry is the bilateral symmetry in the area of carotenoid pigmentation. These four components of carotenoid-based coloration can be partially developmentally independent (fig. 1). For example, expression of patch area could be a function of the number of follicle cells that are receptive to the uptake of carotenoid pigments during feather growth (Brush 1990). In contrast, expression of pigment elaboration is a function of the type and quantity of pigments available to receptive follicles during feather growth. Symmetry of both patch area and pigmentation is a function of how well processes of follicle receptivity and feather pigmentation, respectively, are car-

ried out and may be related to additional processes during development (fig. 1).

The best evidence for independent expression of components of carotenoid-based plumage coloration comes from studies of house finches (*Carpodacus mexicanus*). House finches have carotenoid plumage coloration on the crown, breast, and rump (Brush and Power 1976; Inouye et al., in press). Males vary in pigment elaboration from pale yellow to bright red; they vary in ventral patch area from about 30% to 90% of ventral surface pigmented with carotenoids; and they strongly vary in the symmetry of both pigmentation and patch area (Hill 1993, 1998*b*). In a series of controlled feeding experiments, Hill (1992, 1993) showed that when access to carotenoid pigments was standardized, all males grew feathers with nearly identical coloration and with equally symmetrical pigmentation, regardless of their coloration or pigment symmetry at the start of the feeding experiment. However, the patch area of males in the feeding experiments was less affected by standardization of carotenoid access—on low-carotenoid diets patches got smaller and on high-carotenoid diets patches got bigger, but substantial variation in patch area remained. These observations indicate partly independent developmental pathways of the components of plumage coloration. Partial independence between the size of an area pigmented with carotenoids and the deposition of carotenoid pigments within an area has also been documented in studies of nonavian vertebrates (Kodric-Brown 1989; Endler and Houde 1995; Grether et al. 1999).

Here we examine the developmental and functional interrelationships among components of carotenoid-based plumage ornamentation in male house finches in a large population in northwestern Montana. First, we establish that there is low integration among different components of carotenoid ornamentation, which indicates that "plumage coloration" is indeed a composite trait. Second, in a long-term field study of fecundity and viability selection episodes, we examine fitness correlates of variation in individual components of carotenoid ornamentation. Finally, we discuss our findings in the context of studies in other populations of the house finch. Strong differences in selection on components of ornamentation among house finch populations underscore the importance of treating carotenoid-based plumage ornamentation as a composite trait.

Methods

Assessing Components of Fitness

We studied a resident population of the house finches inhabiting an isolated area of suitable habitat near Missoula, Montana (for details of the study site and field protocol, see Badyaev and Hill 2000*b*; Badyaev and Martin 2000*a*). The study site was a cluster of buildings and ornamental shrubs set in an open grassland. Finches used 2-m-high ornamental shrubs for nesting and several large coniferous trees at the edge of the complex for roosting. Each year, from 1995 to 2000, all resident male finches were captured during January–March, measured, and marked with a unique combination of one aluminum and three colored plastic rings. At any time during the breeding season, the resident population consisted of about 20 breeding pairs, their nestlings, and about 60–70 adult finches that were either between nesting attempts or unpaired. All resident finches remained in the vicinity of the study area throughout the breeding season (see Badyaev and Martin 2000*b* for details).

House finches form strong pair associations (G. E. Hill et al. 1999; Badyaev et al. 2000), and the pairing status of individuals is easily determined from the beginning of the breeding season. A male was considered not paired when it was a resident at the study site from the beginning of the breeding season but was never seen in close association with a female. The open landscape of the study site made it easy to monitor pairing status of all birds. In addition, over 5 yr of this study, all but three pairs initiated a nest. High levels of extrapair paternity could bias estimates of pairing success (Webster et al. 1995). However, while copulations between social mates were observed regularly, we never observed copulations with extrapair birds. In previous studies, we assumed that extrapair fertilizations were too rare to bias estimates of fecundity in our population (Badyaev and Martin 2000*b*). Here, we quantified the frequency of extrapair fertilizations to test this assumption.

Strong fidelity of adult house finches to the location of previous breeding (G. E. Hill et al. 1999; Badyaev et al. 2000) and the isolation of our study site allowed us to assign survival status to the resident birds (Badyaev and Martin 2000*b*). A male was considered to have "survived postbreeding season"—recorded as 1—when it was a resident at the site during a summer and was then present at the site at the onset of the subsequent breeding season (February–March). A resident male that was not present in the study site the following year was assigned "did not survive postbreeding season" status—recorded as 0. We used a survival period that excluded the breeding season (i.e., postbreeding season) to evaluate both fecundity and survival selection on the same group of birds. Despite capturing more than 3,500 house finches in fall and early winter flocks around the study site and in Missoula, we never encountered an individual previously assigned "did not survive" status. No resident individuals appeared at the study site after missing a breeding season. Moreover, most of the overwinter mortalities of resident birds occurred within the study site. Dead birds were recovered

by one of us (A.V.B.) or by local personnel near roosting trees following heavy snowstorms or unusually cold overnight temperatures during fall and winter. In 1995–2000, 11 males died as a result of collisions with glass, vehicles, and fences; these individuals were not included in the viability analyses. See Badyaev and Martin (2000*b*) and Badyaev et al. (2001) for further justification of measuring viability selection in the study site.

Nesting censuses were conducted daily, and all nests were found as they were being constructed. For all breeding pairs, we determined the first egg date, number of eggs per clutch, and number of broods per season. As a measure of within-season fecundity, we used a total number of offspring fledged during a breeding season (number of nestlings in a nest multiplied by number of broods). Note that this measure is different from the one used for other studies of this population (i.e., a combination of the first egg date and number of eggs in the first clutch; Badyaev et al. 2000), although the two measures are highly correlated $r = 0.86$, $P < .0001$). There was no nest predation at the study site. For univariate analyses, we assigned a breeding bird to a high-fecundity status if its fecundity was higher than the average in the population that year and to a low-fecundity status if its fecundity was lower than the average. We used a continuous measure of fecundity for other analyses.

Within each year, the estimates of male fitness (pairing success, fecundity, and survival) were converted to relative fitness by dividing absolute fitness measures by mean absolute fitness for males in a given year (Lande and Arnold 1983). Because extrapair paternity was exceedingly low and not associated with the traits that were the focus of this study (see below), we did not include extrapair paternity in our estimates of male fitness. We calculated male net fitness as within-season fecundity × postbreeding survival (Arnold and Wade 1984). Both episodes were recorded in the same year for each individual. Estimates of fitness for each episode were made for all individuals present during the episode. Net male fitness was estimated for a subset of individuals whose survival and fecundity was recorded for the entire year. To avoid pseudoreplication, for all selection analyses we used data for only one—the first—year of residence at the study site per bird. Thus our selection estimates are not confounded by age-related changes in pairing success or fecundity.

Paternity Analysis

To assess whether extrapair paternity is likely to bias our estimates of male pairing success and fecundity, we conducted DNA fingerprinting of 111 birds (19 families, 77 nestlings). The subset of birds (males: 2-yr-old, 7; older, 12) used for this analysis was selected to account for the entire range of variation in male ornamentation in the study population. Pigment hue in selected males varied from 0 to 9, patch area varied from 178 to 1,205 mm^2, pigment asymmetry from 1 to 9. Blood samples of 15 μL were taken from a puncture of the brachial vein and stored in Queen's lysis buffer (Seutin et al. 1991) at 4°C. We used standard techniques of multilocus DNA fingerprinting (Lifjeld et al. 1993). In brief, Hae III was used to digest the DNA, which was then subjected to electrophoresis (8 mg of DNA per lane) and Southern blotted onto Hybond N^+ transfer membranes. All membranes were probed with *per* (Shin et al. 1985) and then autoradiographed. Several membranes were reprobed with 33.15 (Jeffreys et al. 1985) when there appeared to be nestlings close to our criteria for exclusion. On average, 15 (range = 10–27) bands were scored using *per*.

We used presence of novel fragments and band sharing to determine parentage (Westneat 1990). If a nestling is the true descendant of two parents, then it will inherit all of its bands from those parents, barring any mutation. Mutation rates for minisatellite DNA are in the order of 1–5 per 1,000 meiotic events (Burke and Bruford 1987; Westneat 1990), which implies that a few novel fragments may occur in a small proportion of genetic offspring. The probability that a given number of novel fragments arose from mutation can be calculated from the Poisson distribution using the mean number of novel fragments found in offspring (see Burke and Bruford 1987). In our case, the probability that a nestling would have one mutant band was 0.067, and 0.002 for two mutant bands. Therefore, we excluded young with two or more novel bands as offspring of one or both putative parents. For the excluded young, we used the proportion of bands shared between a nestling and each of its parents (Wetton et al. 1987) to determine which of the two parents (if not both) was unrelated to the nestling. Band sharing between true parents and descendants should average 50% based on Mendelian inheritance, while band sharing between putative parents and young produced by extrapair fertilization or egg dumping should be similar to the background level of band sharing in the population. Thus, we used the distribution of band-sharing values between mothers and their unexcluded young to estimate a cutoff (lower 99% one-tailed confidence interval [CI]) for band sharing between parents and their direct descendants. This cutoff value did not overlap with the distribution of background band sharing in the population (see "Results").

Ornamentation Measurement

Upon capture in January–March, carotenoid-based breast plumage patch of each male ($n = 498$) was photographed using a 35-mm camera mounted in a standard position.

Individuals were kept in a standardized position—on dorsal side with anterior point of beak held in place by a wire loop. All photography was done with a constant distance and light settings against a neutral gray (Kodak) background with scale markings. To prevent shifting of individual feathers at the boundaries of the ornaments, all feathers were combed by moving a bird through a circular bristle-comb before the photography. All resulting images were transferred to digital image files. To assess the effect of bird position in the photostand on repeatability of measured traits (repositioning error), each male was repositioned (i.e., taken from a photo setup, put back again, and rephotographed) three times. Each resulting image of the breast patch was further remeasured two times (measurement error) under ×6 magnification in SigmaScan software (SPSS 1999).

For the ventral plumage region of each male we recorded pigment hue, pigment asymmetry between left and right side, patch area, and patch area asymmetry between left and right side. Pigment hue was recorded on a 0–10 scale (0, no pigmentation; ca. 2–4, yellow; ca. 5–8, orange and orange-red; and 9–10, red) following the protocol for visual assessment of hue outlined in Hill (1990). Pigment hue was the average of the hue assessment in three different areas (ca. 3 × 2 feathers) within a breast patch. Visual assessment of carotenoid-based ornamentation of male house finches was both precise (i.e., highly correlated with measures obtained by a reflectance spectrophotometer; Hill 1998*a*) and biologically accurate (i.e., correctly representing spectrum visible to birds; Hill 1998*a*; Badyaev and Hill 2000*a*). For other measures, breast patch was divided into a left and right side along the plane of bilateral symmetry by drawing a line passing through anteriormost point (middle) of the lower mandible, and anteriormost point at posterior end of lower mandible. Fixed position of a bird head in the photo stand enabled an accurate delineation of left and right side of a breast patch. Following Hill (1998*b*) and G. E. Hill et al. (1999), pigment asymmetry was recorded on a 1–10 scale as a percentage of feathers different in hue group (unpigmented, yellow, orange, and red) between left and right side at tenths of percentiles: 0–10, 11–20, 21–30, 31–40, 41–50, 51–60, 61–70, 71–80, 81–90, 91–100. High magnification of original digital images allowed us to assess pigment asymmetry for each feather of the breast ornamentation. Because of the methods used, the pigment asymmetry cannot be attributed to fluctuating or other asymmetries. Here, we used pigment asymmetry values as a measure of consistency in pigment deposition. Patch area was measured with SigmaScan software by tracing, under ×6 magnification, the edges of carotenoid-colored feathers of breast patch separately for left and right side. Patch area asymmetry was an absolute difference between the measured area of the left and right sides. ANOVA indicated absence of directional asymmetry in path area (table 1), while visual examination of data distribution and significant tests for normality with mean zero ($W = 0.81$, $P < .001$) allowed elimination of antisymmetry. Thus, our measure of patch area asymmetry is fluctuating asymmetry (Palmer and Strobeck 1986).

Data Analysis

All color measures (by A.V.B.) and area measures (by J.C.G.) were conducted without prior tabulation of fitness data. In addition, left and right side areas were measured without actually seeing the numbers as SigmaScan software fills out the data sheet automatically while the observer works with an image. Repeated measures of three sets of images (498 images each) were separated by measuring of all 498 individuals within each set. As a result, each bird

Table 1: Nested ANOVA to assess measurement error—a combination of repositioning and repeated measurement of individual birds—for patch area, pigment hue, and pigment hue asymmetry in male house finches

Trait and source of variation	df	Mean square (mm^4)
Breast patch area:		
Individual	497	1,898.32***
Side	1	.074
Individual × side	496	452.91***
Repositioning	166	81.35*
Measurement	992	15.05
Repeatability[a]		.76 ± .007***
Repeatability[b]		.39 ± .019**
Pigment hue:		
Individual	495	42.74***
Repositioning	162	.02
Measurement[c]	2,490	.03
Repeatability		.99 ± .001***
Pigment asymmetry:		
Individual	495	27.93***
Repositioning	162	1.14
Measurement	2,490	.23
Repeatability		.77 ± .013***

[a] For patch area.

[b] For patch area nondirectional asymmetry; F value ($F = 4.20$) is a ratio of MS for individual × side, and MS for combination of individual × side × repeat (repositioning and measurement errors combined) and individual × repeat.

[c] Total df for a measurement error—repositioning and remeasurement.

* $P < .1$.

** $P < .05$.

*** $P < .001$.

was measured six times, with 2-wk intervals between the measures for patch area, and with 1-wk intervals between the measures for color. Variances associated with repositioning ($n = 3$ repeats) and remeasuring ($n = 2$ repeats) of breast ornamentation components were calculated with a mixed-model nested ANOVA and are shown in table 1. For analysis of repeatability, we used a combined measurement error ($n = 6$ repeats).

For area and pigment measures, the repeatability (R) was $R = \sigma_W^2/(\sigma_W^2 + \sigma_E^2)$, where σ_W^2 is the variance among n individuals and σ_E^2 is the variance among k measures within n individuals. Standard error of R was $\mathrm{SE}(R) = \{2(1 - R)^2[1 + (k - 1)R]^2/[k(k - 1)(n - 1)]\}^{1/2}$. The F value was a ratio of MS_W and MS_E (Becker 1984). For area asymmetry, the repeatability and associated F value was calculated as a ratio of MS for individual × side, and MS for a combination of individual × side × repeat and individual × repeat (after Swaddle et al. 1994). Data were pooled across years because year was not a significant covariate in any of the analyses. Pigment hue and pigment asymmetry scores were arcsine transformed, area and area asymmetry were natural log transformed. For selection analyses, each trait was standardized to a mean of 0 and standard deviation of 1.

Results

Variation in Components of Carotenoid Ornamentation

Measurements of all components of carotenoid-based ornamentation were highly repeatable (table 1). Repeated measures allowed precise estimation of fluctuating asymmetry in patch area. The variance associated with asymmetry was significantly greater than the variance produced by measurement error (table 1).

For 498 males in the Montana population, pigment hue averaged 7.11 ± 3.55 (SD) and ranged from 1 to 10. Twenty percent of males had pigment hue within range of yellow (1–4.5), 42% had color within the orange range (4.6–7), and 38% of males were within the range of red colors (7.1–10). Pigment asymmetry averaged 4.2 ± 2.89 (range 1–10). Most males (64%) had less than 30% asymmetrically pigmented feathers; 25% of males had 31%– 60% asymmetrically pigmented breast feathers; only 11% had more than 61% asymmetrically pigmented feathers. Patch area averaged 937.04 ± 359.51 mm^2 (range 82.64–1,702.78 mm^2). Fluctuating asymmetry of patch area averaged 54.1 ± 42.06 mm^2 (range 0–397.35 mm^2), or 5.76% of the patch area (range 0%–25.02%).

Bivariate regressions of ornamentation components revealed partial independence between pigment elaboration and patch area measures. Elaboration of pigment hue was not associated with changes in pigment asymmetry; for example, red males were as likely to be asymmetrical in color as yellow males (fig. 2*A*). Males with redder breast plumage had larger breast patches (fig. 2*B*), but pigment hue was not associated with patch area asymmetry (fig. 2*C*) and pigment asymmetry was unrelated to patch area (fig. 2*D*). Males with larger breast patches had more symmetrical patches (fig. 2*E*), and there was a weak but significant negative association between pigment asymmetry and patch area asymmetry (fig. 2*F*).

Male Fitness and Components of Carotenoid Ornamentation

Extrapair Paternity. Among 77 young sampled, only five (6.5%) young in three (15.8%, 3/19) families were the result of extrapair fertilization. There was no evidence of intraspecific brood parasitism (egg dumping). Sixty-three young had no novel fragments and 10 had at least one (range = 1–7). The 63 young with no novel fragments had high levels of band sharing with both the putative father (0.570 ± 0.113; range = 0.402–0.846) and mother (0.624 ± 0.135; range = 0.403–0.933), indicating that they were direct descendants. The lower 99% CI (one tailed) for band sharing between these offspring and their mothers was 0.317. We used this value as a general cutoff for excluding paternity because this distribution did not overlap with the distribution of band sharing among putatively unrelated adults (mated males and females: 0.139 ± 0.092, range = 0–0.258, $n = 18$ pairs). Five of the 10 young with novel fragments each had one novel fragment but relatively high levels of band sharing with both the putative father (range = 0.410–0.625) and mother (range = 0.462–0.727), suggesting that they were related and that the novel fragments arose by mutation. The five remaining young had three or more novel fragments. All five of these young had low levels of band sharing with the putative father (0.244 ± 0.099; range = 0.118–0.345) and high levels with the mother (0.608 ± 0.068; range = 0.500–0.667), suggesting that they were the result of extrapair fertilizations. For one family, we did not recover DNA from the putative mother and, thus, we used the band-sharing cutoff of 0.317 to determine paternity. In this family, we concluded that all four of the young were produced by the putative father, as all father-young band-sharing values were well above our cutoff of 0.317 (0.615 ± 0.011, range = 0.606–0.629). Because only three males lost some paternity and there was no association between loss of paternity and ornamentation components in this study (e.g., males had pigment hue scores of 2.3, 7.1, and 9.5), we concluded that extrapair fertilization was unlikely to bias the male fitness estimates reported here (see also Hill et al. 1994).

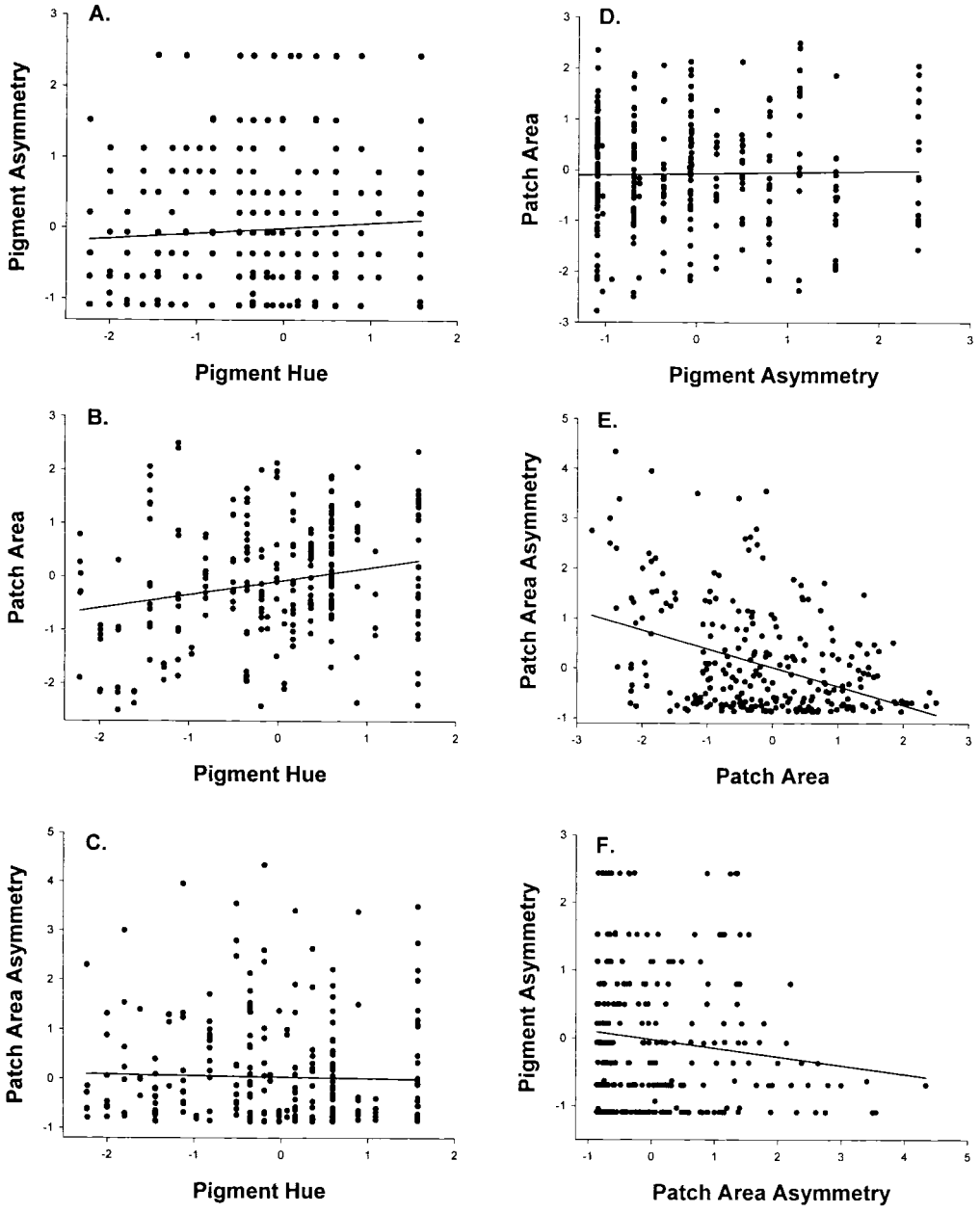

Figure 2: Partial regression plots illustrating the relationships among components of carotenoid-based breast ornamentation in the house finch. Regression coefficients are as follows: *A*, $b = 0.07 \pm 0.04$ (SE), $t = 1.8$, $P = .07$; *B*, $b = 0.26 \pm 0.06$, $t = 4.33$, $P = .0001$; *C*, $b = -0.007 \pm 0.06$, $t = -0.14$, $P = .89$; *D*, $b = 0.002 \pm 0.05$, $t = 0.04$, $P = .96$; *E*, $b = -0.42 \pm 0.05$, $t = -7.89$, $P < .0001$; *F*, $b = -0.12 \pm 0.06$, $t = -2.02$, $P = .04$. Only regression coefficients of *B* and *E* are significant after correction for multiple comparisons.

Univariate Analysis. Paired and unpaired males did not differ in pigment hue, pigment asymmetry, or patch area (fig. 3*A*, all F's < 3.54). However, paired males had more symmetrical breast patch compared to unpaired males ($F = 50.91$, $P < .0001$). To account for significant negative correlation between patch area and area asymmetry (fig. 2*E*), variation due to patch area was statistically removed from asymmetry values used here. Males that produce a greater number of offspring per season had redder breast plumage ($F = 25.59$, $P < .0001$), as well as larger ($F = 8.78$, $P = .002$) and more symmetrical ($F = 7.31$, $P = .006$) breast patch area (fig. 3*B*). Males that survived post-

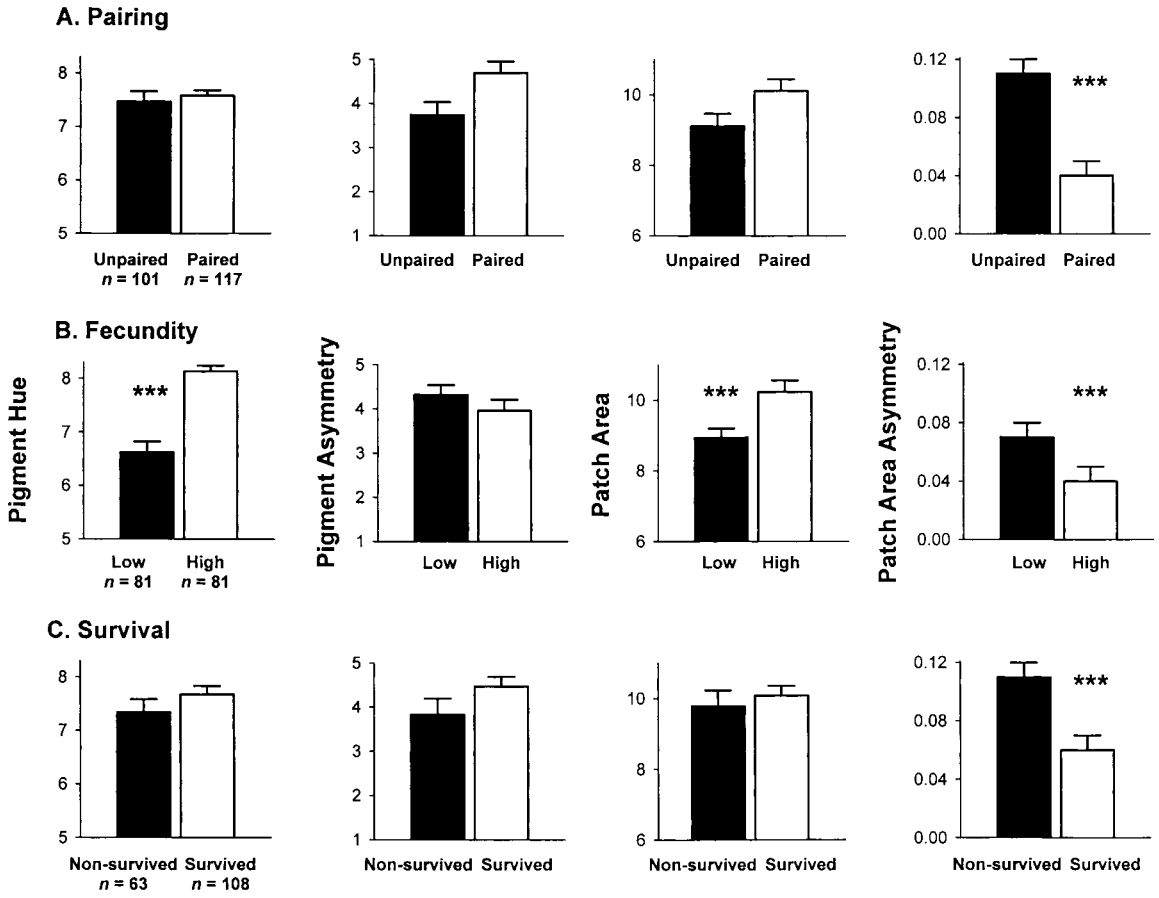

Figure 3: Differences in components of carotenoid-based breast ornamentation between (*A*) paired and unpaired males, (*B*) males with above average (high) and below average (low) fecundity (total number of offspring per season), and (*C*) males that survived and did not survive postbreeding season. Three asterisks indicate significant difference between groups after correction for multiple comparisons for each trait ($n = 3$, $\alpha < 0.013$). Patch area is in cm^2; patch area asymmetry is adjusted by a patch area. See "Methods" for more details.

breeding season and those that died did not differ in any component of carotenoid ornamentation except patch area asymmetry (survived males had more symmetrical patches, $F = 21.09$, $P < .0001$; fig. 3*C*). Overall, the only consistent difference in carotenoid ornamentation between selection groups was a difference in patch area asymmetry (fig. 3).

Multivariate Selection Analysis. To identify targets of selection while accounting for correlations among components of ornamentation (fig. 2), we used the path analysis to estimate multivariate selection gradients for all traits and both fecundity and survival episodes of selection. Path analysis (fig. 4) revealed significant positive partial correlations between breast patch area and pigment hue, and significant negative correlation between patch area and patch area asymmetry, as well as between pigment asymmetry and patch asymmetry. When we accounted for interactions between ornamentation components, greater within-season fecundity was most strongly associated with lower patch area asymmetry (standardized multivariate selection gradient = −0.56), lower pigment asymmetry (−0.24), and redder pigmentation (0.26; fig. 4). Greater survival was most closely associated with lower patch area asymmetry (−0.48) and larger patch area (0.28). Overall, male net fitness (a combination of relative fitness of fecundity and survival) in a Montana population was most strongly correlated with patch area components—patch area (standardized multivariate selection gradient = 0.18) and patch area asymmetry (−0.64), followed by pigment hue (0.16; fig. 5).

Thus, these analyses confirmed partial independence of

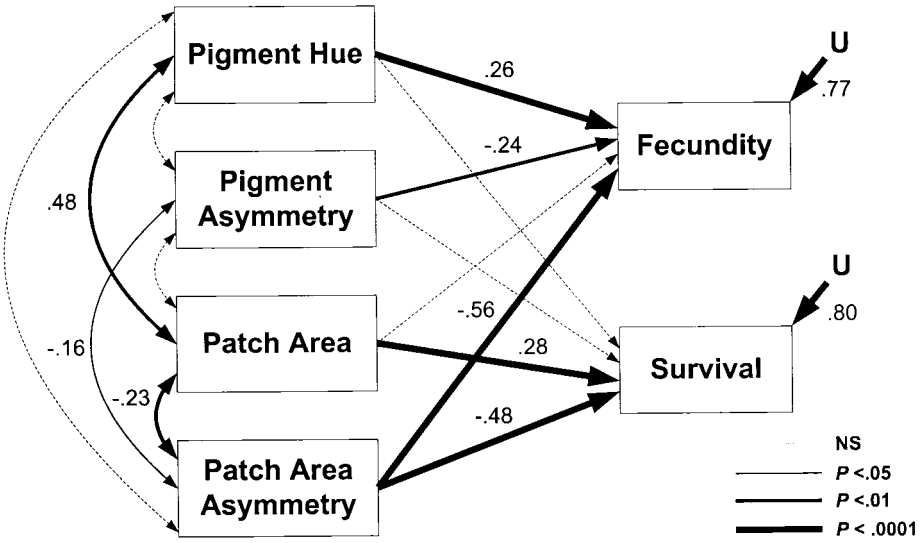

Figure 4: Path diagram illustrating joint effects of within-season fecundity (number of offspring produced) and survival of postbreeding period on components of carotenoid breast ornamentation in male house finches ($n = 161$). Numbers at the single-headed arrows are standardized directional selection coefficients on individual traits. Numbers at the double-headed arrows are partial covariations between ornamentation components. The single-headed arrows with *U* indicate effects of unmeasured factors. The model explains about 41% of total variance in fecundity and 37% of total variance in survival of male house finches.

ornamentation components not only in patterns of variation and covariation (fig. 2) but also in fitness correlates (figs. 4, 5).

Discussion

Mating preference for individuals of high condition often leads to directional selection for elaboration of condition-dependent (i.e., indicator) traits (Iwasa and Pomiankowski 1994) and to selection for greater integration of such display traits with aspects of individual fitness (Schluter and Price 1993). As a result, expression of secondary sexual traits is commonly observed to be closely linked to the physical condition and health of an individual. However, many of the ornamental traits that have been a focus of research are actually composites of multiple components. Comparing gross categorization of a complex ornament to a generalized measure of overall condition can lead to oversimplifications because the processes that generate different components of ornamentation may have different dependencies on environmental and individual variation. Thus, under different conditions, the specific components of an ornament may reflect different information about an individual (Zuk et al. 1990; Sullivan 1994; Johnstone 1996), which results in population variation both in the relative contribution of components to overall ornamentation and in the selection patterns on individual components (Price et al. 1991; Møller and Pomiankowski 1993*a*; Schluter and Price 1993; J. A. Hill et al. 1999).

Our study of the developmental and functional interrelationships (hereafter, developmental and functional integration) among components of carotenoid-based ornamentation in the house finch produced three important results. First, integration among components of carotenoid ornamentation was relatively low. This finding corroborated previous observations (Hill 1992, 1993) that different components of carotenoid plumage coloration may be proximately produced by partially independent mechanisms. Second, variation in different components of ornamentation had distinct fitness consequences because pairing, fecundity, and viability selections operated on different components of ornamentation. Third, developmental and functional integration of ornamentation components differed among populations of the house finch. Thus, variable patterns of selection across populations may favor flexible correlations among ornament components (Cheverud 1996), ultimately producing a composite and dynamic secondary sexual trait.

These results enable us to discuss the relative contribution of developmental and functional integration to the evolution of carotenoid ornaments. In the Montana population of house finches, we found that the variation in

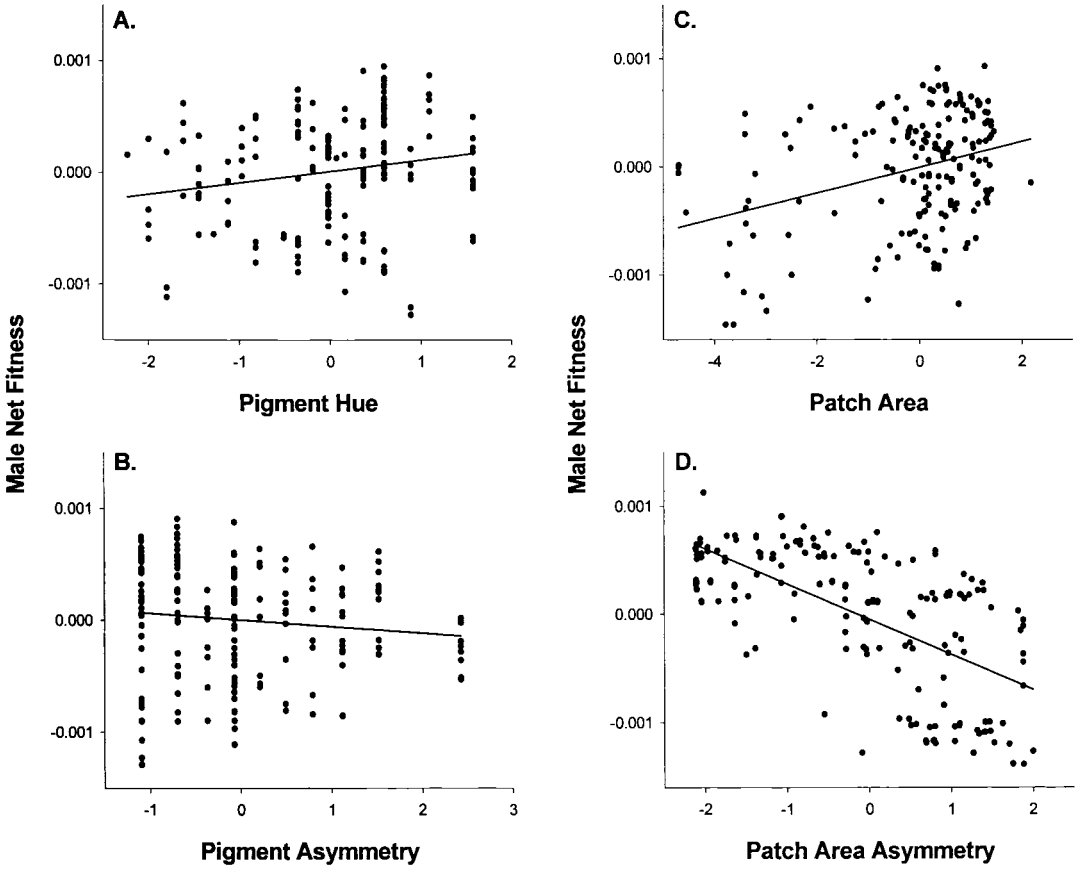

Figure 5: Partial multiple regression plots illustrating the relationships between components of carotenoid-based breast ornamentation and net fitness (survival of postbreeding season and breeding season fecundity) in male house finches. Standardized regression coefficients are as follows: *A*, $b_{ST} = 0.16$, $t = 2.42$, $P = .02$; *B*, $b_{ST} = -0.09$, $t = -1.52$, $P = .13$; *C*, $b_{ST} = 0.18$, $t = 2.71$, $P = .01$; and *D*, $b_{ST} = -0.64$, $t = -10.13$, $P < .0001$.

patch area and variation in pigment hue were affected by processes that were often independent. For example, variation in access to carotenoid pigments can influence the physiological mechanisms linking uptake of carotenoid pigments per follicle (pigment elaboration) as well as the number of follicles that uptake carotenoids (patch area; Hill 1993), resulting in the frequently observed positive correlation between carotenoid pigment elaboration and patch area (Hill 1992; this study). It is unclear, however, whether ingesting more carotenoid pigments actually stimulates more follicles to take up carotenoid pigments or whether it simply pushes circulating carotenoid concentrations above a threshold that allows all activated follicles to express carotenoid pigmentation. Regardless, the result is correlated expression of these traits driven by integration of their development. Differences in fitness correlates of ornament components, however, strongly suggest partial functional independence of these traits, that is, low functional integration. In this study we found that the pigment elaboration and patch area asymmetry were the target of fecundity selection, while attributes of patch area were the target of viability selection. Moreover, in mate choice experiments, females responded differently to pigment elaboration and patch area (Hill 1994). These studies indicate functional independence of the components of plumage coloration. The net result is that the forces acting to change expression of plumage coloration in male house finches are complex, and an understanding of plumage coloration requires an understanding of both the proximate control and the selective pressures acting on each component of the trait.

The strong negative relationship that we observed between patch area and fluctuating asymmetry of patch area suggests that there are high costs associated with the production of a plumage patch that is both large and symmetrical (Møller and Pomiankowski 1993*b*). However, de-

spite a significant correlation between patch area and patch area asymmetry—which suggests partially shared production pathways—the fitness consequences of these traits were largely distinct. While there was no significant covariation between patch area and fecundity, patch area asymmetry accounted for more than half of the variation in male fecundity. Similarly, variation in patch area asymmetry contributed twice as much to variation in survival probability than did patch area. Distinct selection pressures on trait size and trait fluctuating asymmetry have also been found in other studies (Møller 1990; Møller et al. 1996; Morris 1998).

The relationship between pigment elaboration and pigment symmetry may be an example of the opposite pattern—weak developmental integration but strong selection for functional integration. In both Alabama and Montana populations of house finches, fecundity selection favored correlated expression of these traits; higher fecundity was positively related to both pigment elaboration and pigment symmetry. However, the relationship between pigment hue and pigment symmetry was distinct among populations—no relationship was found in this study, but there was a strong negative relationship ($r = -0.39$) in the Alabama population of the house finches (Hill 1998*b*; G. E. Hill et al. 1999). Feeding experiments suggest that, for carotenoid-based plumage coloration, development of pigment elaboration and expression of pigment symmetry are largely independent. In captive feeding experiments, male house finches that were provided with abundant but carotenoid-deficient food grew dull yellow feathers that nonetheless had perfect pigment symmetry (Hill 1992, 1998*b*). Conversely, males provided with abundant red pigments but with restricted food access grew red plumage patches with substantial pigment asymmetry (Hill 2000). Thus, pigment symmetry seems to be more closely related to organism-wide condition than to the costs of carotenoid utilization per se (fig. 1). These different proximate controls could explain why we observed a strong relationship between pigment symmetry and pigment elaboration in Alabama but no relationship in Montana. In Alabama, strong selection on pigment elaboration and a correlation between individual condition and individual acquisition/utilization of carotenoids (Brawner et al. 2000) generate the positive correlation between pigment elaboration and pigment symmetry; in Montana, weak selection on pigment elaboration and a weaker relationship between condition and acquisition/utilization of carotenoids (possibly linked to lesser parasite infestation of the Montana population; A. V. Badyaev, unpublished observations) result in no relationship between pigment elaboration and pigment symmetry. Thus, the variation in relationship between pigment elaboration and pigment symmetry may be due to selection for correlated expression in the absence of high developmental integration.

An important implication of the observation that plumage coloration in the house finch is really a composite of multiple component traits, each with a different proximate control and function, is that the cost of production and the patterns of selection on individual components are likely to differ across environments (Endler 1995; Endler and Houde 1995). For example, expression of a particular plumage hue is likely to have different production costs depending on the type and quantity of carotenoid pigments in a particular environment. Some dietary carotenoid pigments can be deposited unchanged (Goodwin 1984; Stradi et al. 1997), which is a metabolically cheap route to ornament display (Hill 1996), while other dietary carotenoids serve as precursors to feather pigments (Stradi et al. 1997; Inouye et al., in press) and must be metabolically converted, which is a costly route to ornament display (Hill 1996). The total quantity and the types of carotenoids available in the diets in various environments will affect pigment elaboration (Slagsvold and Lifjeld 1985; Hill 1993; Linville and Breitwisch 1997) and to a lesser extent patch area (Hill 1993) but may have little effect on pigment symmetry or patch area symmetry. Alternatively, environmental stressors such as food access (Hill 2000) or parasites (Thompson et al. 1996; Nolan et al. 1998; Brawner et al. 2000) may affect patch and/or pigment symmetry more than pigment elaboration.

What we observed in our studies of carotenoid-based plumage ornamentation is not likely to be unique to carotenoid traits. Distinct patterns of selection on individual components of condition-dependent ornaments, combined with partially independent development of components, should favor the evolution of composite sexual traits whose components reliably reflect conditions across a wide array of environments. Most studies of condition-dependent traits have focused on one component of the trait (e.g., hue or length) and one type of selection (e.g., pairing success). Perhaps not surprisingly, the results of these studies have been mixed in their support of the hypothesis that condition-dependent traits are maintained through selection. For instance, previous work on eastern populations of house finches—which focused primarily on one component of a trait and one aspect of selection—indicated that a key signaling function of plumage coloration in this species was pigment elaboration relative to pairing success (Hill 1990; G. E. Hill et al. 1999). If pigment elaboration and pairing success had been the exclusive focus of the current study, however, we would have erroneously concluded that there is no selection on plumage coloration in the Montana population of house finches. With a broader perspective, we observed that there is significant selection on plumage coloration but that in

the Montana population pigment elaboration is not selected by pairing success (Badyaev and Martin 2000*b*). Such a broadening of perspective in studies of condition-dependent traits to include an examination of the interaction between developmental and functional integration of signal components should provide important insight into the evolution of sexual signals (Endler 1993, 1995; Price and Pavelka 1996; Moore 1997).

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