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SEXUAL DIMORPHISM IN RELATION TO CURRENT SELECTION IN THE HOUSE FINCH

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Abstract.—Sexual dimorphism is thought to have evolved in response to selection pressures that differ between males and females. Our aim in this study was to determine the role of current net selection in shaping and maintaining contemporary sexual dimorphism in a recently established population of the house finch (*Carpodacus mexicanus*) in Montana. We found strong differences between sexes in direction of selection on sexually dimorphic traits, significant heritabilities of these traits, and a close congruence between current selection and observed sexual dimorphism in Montana house finches. Strong directional selection on sexually dimorphic traits and similar intensities of selection in each sex suggested that sexual dimorphism arises from adaptive responses in males and females, with both sexes being far from their local fitness optimum. This pattern is expected when a recently established population experiences continuous immigration from ecologically distinct areas of a species range or as a result of widely fluctuating selection pressures, as found in our study. Strong and sexually dimorphic selection pressures on heritable morphological traits, in combination with low phenotypic and genetic covariation among these traits during growth, may have accounted for close congruence between current selection and observed sexual dimorphism in the house finch. This conclusion is consistent with the profound adaptive population divergence in sexual dimorphism that accompanied very successful colonization of most of the North America by the house finch over the last 50 years.

Key words.—Fecundity, house finch, local adaptation, overwinter survival, pairing success, peripheral population, sexual dimorphism.

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The relative importance of selection in evolution and maintenance of sexual dimorphism is a much debated issue. On one hand, sexual dimorphism is regarded as an outcome of sex-specific patterns of current sexual and natural selection (e.g., Darwin 1871; Ralls 1976; Lande 1980; Slatkin 1984; Arak 1988; Shine 1989). Indeed, concordance between current environmental conditions and degree of dimorphism is well documented (e.g., Earhart and Johnson 1970; Johnston and Fleischer 1981; Payne 1984; Moore 1990; Webster 1992; Promislow et al. 1994; Martin and Badyaev 1996; Mitani et al. 1996; Badyaev 1997a,b; Poulin 1997; Wikelski and Trillmich 1997). The importance of current selection in explaining observed patterns of sexual dimorphism is further supported by the considerable heritable genetic variation in many sexually dimorphic traits (e.g., Cowley et al. 1986; Cowley and Atchley 1988; Reeve and Fairbairn 1996) and by the examples of rapid phenotypic changes in dimorphism under artificial selection (e.g., Wilkinson 1993). On the other hand, studies of sexual dimorphism suggest that allometric and developmental patterns (Alberch 1982; Leutenegger and Cheverud 1982; Wagner 1988), differences in such patterns among phylogenetic lineages (i.e., phylogenetic constrains; Cheverud et al. 1985; Kappeler 1996), and the patterns of genetic correlations of a species (e.g., Cheverud 1984; Lande 1985; Lofsvold 1988; Rogers and Mukherjee 1992) strongly bias or limit changes in sexual dimorphism in response to changing selection pressures.

The relative importance of various selective forces in shaping current variation in sexual dimorphism is not well understood (reviewed in Badyaev and Hill 1999). For example, sexual dimorphism is generally interpreted to be a result of sexual selection. However, close concordance between contemporary sexual selection and current degree of sexual dimorphism is not necessarily expected. First, sexual dimorphism in a species may be ancestral to ecological divergence or speciation (e.g., Björklund 1991a; Schluter and Price 1993; Price 1998) and thus variation in sexual dimorphism in response to changes in selection may be reduced by patterns set over evolutionary time. Second, sexual selection favoring dimorphism may be opposed by natural selection on the same traits (e.g., Howard 1981; Price 1984a,b; Weatherhead et al. 1987; Fairbairn and Preziosi 1996; Wikelski and Trillmich 1997), selection on closely correlated traits in the opposite sex (Lande 1980; Reeve and Fairbairn 1996), or selection during different life stages (reviewed in Schluter et al. 1991). Alternatively, no relationship is expected when sexually dimorphic traits lack appropriate genetic variability or are highly genetically correlated (e.g., by linkage, epistasis, or pleiotropy) or when phenotypic plasticity (such as behavioral modification of displays) reduces selection pressures on sexually dimorphic traits (Badyaev and Hill 1999). Moreover, the concordance between current selection and current dimorphism does not necessarily imply the adaptiveness of sexual dimorphism, because sexual dimorphism may arise independently of adaptations within each sex if there is sex-biased variance in traits (e.g., Johnston and Fleischer 1981; Cheverud et al. 1985). Finally, once a population is adapted to a particular environment, selection may be detectable only on unusual phenotypes and a large amount of phenotypic variation in sexual dimorphism may be selectively neutral (e.g., Lande 1976). Thus, study of an association between observed sexual dimorphism and current net selection on

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morphology in natural populations is especially needed to examine the relative importance of evolutionary forces and constraints in the evolution of sexual dimorphism (e.g., Björklund and Linden 1993, Preziosi and Fairbairn 1996).

Examination of morphological variation and selection in recently established populations allows greater inference about evolutionary forces and constraints that affect sexual dimorphism (e.g., Endler 1986; Rising 1987; Wikelski and Trillmich 1997). This is because strong selection, immigration, and dispersal, which are typical of peripheral or recently established populations (Holt and Gomulkiewicz 1997; Kirkpatrick and Barton 1997), greatly influence genetic and phenotypic correlations among traits (e.g., Shaw et al. 1995), thus modifying forces and constraints acting on dimorphism. A recently established (15–18 yr ago) population of house finches (*Carpodacus mexicanus*) in northwestern Montana provided a unique opportunity to examine the relationship between dimorphism and current selection. First, given the peripheral location and recent establishment of the Montana population, as well as continuous immigration of juveniles from ecologically distinct locations (Badyaev and Hill 2000a), we expect to find strong directional selection on morphology in our population (e.g., García and Kirkpatrick 1997). Second, the explosive colonization of much of North America by the house finch over the last 50 years, produced populations that strongly differ in phenotypic sexual dimorphism (Badyaev and Hill 2000a). However, it is unclear whether such divergence is due to selection differences among populations (e.g., Vazquez-Phillips 1992; see Badyaev et al. 2000).

Our aim was to determine the role of current selection in shaping and maintaining contemporary sexual dimorphism in the house finches in Montana. We studied large, individually marked, resident population over four years and several selection episodes to examine the fitness consequences of variation in sexual dimorphism. Whereas considerable attention has been paid to sexual dichromatism in this species (reviewed in Hill et al. 1998), variation in size dimorphism was not studied. Thus, we primarily focused on variation in sexual size dimorphism. We first described current sexual dimorphism in the house finch in size and shape factors based on a path analysis model. Second, we used the same path analysis model to calculate selection differentials for pairing (paired vs. nonpaired birds), survival (survived vs. did not survive), and fecundity (above- vs. below-average fecundity). Finally, we examined concordance between the direction and magnitude of current selection and observed sexual dimorphism. We used the same multivariate model to describe both sexual dimorphism and current selection to estimate concordance between current morphology and selection. For example, if current selection favored increased sexual dimorphism, the difference in selection differentials between males (larger sex) and females (smaller sex) should be positive; whereas, if current selection favored decreases in dimorphism, the difference in selection differentials between the larger and smaller sex should be negative (Crespi and Bookstein 1989; Björklund and Linden 1993). In addition, if current selection favored greater dimorphism, then for each trait we should find a positive correlation between the magnitude of difference in selection differentials between sexes and magnitude of sexual dimorphism. A negative or no correlation is expected when current selection favors monomorphism (Björklund and Linden 1993) or selection is not acting on sexually dimorphic traits.

MATERIALS AND METHODS

Data Collection

This study was carried out on a resident house finch population in an isolated area, 3 km west of Missoula, Montana. The study site was located in an open field that contained several hundred 2-m-high ornamental bushes used by finches for nesting and several large coniferous trees used by finches for roosting. In 1995–1998, all resident finches were trapped during January–March and August–October, measured, and marked with a unique combination of one aluminum and three colored plastic rings. All individuals captured in the fall were aged as hatching-year birds and after-hatching-year birds (hereafter adults) according to Hill (1993a), and only adult birds will be used in the subsequent analysis. Finches foraged within the area and on shortgrass prairie and agricultural fields surrounding the site. 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. A bird was considered a resident if it roosted on the area for 14 consecutive days. All resident finches were present in the vicinity of the area throughout the breeding season, and despite extensive searches, we documented no breeding by resident marked finches outside of our study site. The closest suitable breeding habitat and the closest nest of an unmarked house finch pair was about 4 km from our study site.

House finches form a strong pair association (Hill 1993a), and pairing status of individuals is easily determined from the beginning of the breeding season (e.g., Hill et al. 1998; Badyaev et al. 2000). A bird was considered not paired when it was a resident at the study site from the beginning of the breeding season, but was never seen with a mate. The open landscape of the study site made it easy to observe pairing status of birds. Several birds that appeared at the study site late in the season and became residents were not included in the pairing selection analyses in their year of arrival to the site. High levels of extrapair paternity could bias estimates of pairing success (Webster et al. 1995). However, we did not find significant levels of extrapair fertilizations in our study population ($< 12\%$; A. V. Badyaev and P. O. Dunn, unpubl. ms.). Similarly, whereas copulations between social mates were frequently observed, we never observed copulations with extrapair birds. Thus, we conclude that extrapair fertilizations are too rare to bias estimates of pairing selection in our population.

House finches show strong nest site fidelity and typically return to renest at the same location year after year (Hill 1991, 1993a; Hill et al.1998; A. V. Badyaev, pers. obs.). Strong fidelity of adult house finches to the location of previous breeding and isolation of our study site allowed us to assign overwinter survival status to the resident birds. A bird was considered to have ''survived'' when it was a breeding adult in the previous summer and was seen the following year after March. A breeding adult that did not appear in the study site the following year was assigned ‘‘did not survive’’ status. Despite capturing more that 2100 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 (AVB) near roosting trees following snow storms or unusually cold overnight temperatures. Six birds that died as a result of collisions with glass, vehicles, and fences were not included in the survival analyses.

Field observations were conducted daily from 04:30 to 08:00 and 14:00 to 16:00 during March and April and 04:30 to 13:00 and 16:00 to 20:00 during May through August. All but six nests were found at the stage of early nest building, and first-egg date was reliably determined for all breeding pairs. Nest initiation date is the most important predictor of overall reproductive success in the house finch (e.g., Hill et al. 1994, 1998; Badyaev et al. 2000). Pairs that nest earliest produce more broods and have larger clutch sizes than pairs that nest later (Hill 1993a; this study). In addition, offspring from earlier nests were in better conditions and experienced lower mortality compared to offspring from later nests (A. V. Badyaev and L. A. Whittingham, unpubl. data). Thus, we used a linear combination of the first-egg date (eigenvector $= -0.79$) and the first clutch size (eigenvector $= 0.79$) as a measure of fecundity. This measure was most consistently and highly correlated with the number of broods per season, eggs laid per season, and renesting intervals than any other variable we have considered (see also Hill et al. 1994). We assigned a breeding bird a ‘‘high fecundity’’ status if its fecundity was higher than the average in the population that year. ‘‘Low fecundity’’ status was assigned if the fecundity measure was lower than the average. We used categorical classification of fecundity to facilitate comparison between pressures of selection episodes and the levels of sexual dimorphism in finches. To avoid pseudoreplication, for all selection analyses we used data for only one year of residence (i.e., three selection episodes) at the study site per bird or the first year of survival.

We measured the following (with digital calipers to an accuracy of 0.02 mm): bill length from angle of the skull to the tip of upper mandible; bill width at the anterior end of nostrils; bill depth in a vertical plane at the anterior end of nostrils over both mandibles; tarsus length (left and right); wing length (left and right, flattened); and body mass (with Pesola balance, to an accuracy of 0.05 g); and plumage coloration (males only, see below). All morphological measures were repeated twice (i.e., four times for the bilateral traits), and the average of repeated measures was used for further analyses. Measurements of adults were taken during either pre- or postbreeding season short capture sessions, thus minimizing the effects of seasonal variation. All linear data were natural-log transformed, body mass was cube-root transformed, and all data were zero-mean standardized before the analyses.

To estimate measurement error for each trait, we calculated repeatabilities for all traits from variance components of ANOVA. Resident birds were recaptured several times during year, and all available repeated measures for all individuals and traits within each capture season (7–14 days) were included. Within-capture session measurement error accounted for about 7–10% of variation in most morphological traits, and for 23% of variation in body mass.

In males, carotenoid-based coloration of crown, lores, breast, and rump was evaluated for brightness, extent, and hue (for details of measurements, see Badyaev and Hill 2000b). All characters were evaluated on 0–10 scale and hue was estimated on the yellow-to-red scale (0–10). The first principal component of brightness, extent, and hue measures was calculated for each body part separately. Plumage score was then the sum of these eigenvectors for all body parts (Badyaev and Hill 2000b).

Description of Dimorphism, Selection, and Genetic Variation

When morphological traits are highly correlated (as they are in the house finch), it is biologically appropriate to describe their variation in size and shape factors (Wright 1923; Crespi and Bookstein 1989). Thus, we used path analysis to examine both sexual dimorphism and selection on morphology (Crespi and Bookstein 1989; Björklund and Linden 1993). Size and shape factors were calculated separately for bill (bill length, depth, and width) and body (tarsus length, wing length, body mass) measurements. We first assessed homogeneity of covariance matrices between males and females for bill and body characters. Tests for homogeneity of covariances showed no significant differences between male and female matrices for each group of traits (e.g., $\chi^2 = 23.31$, df $= 28$, $P = 0.72$). Thus, pooled matrices were used in subsequent analyses. We then extracted first eigenvectors of the pooled covariance matrices. These vectors were general size (bill size and body size) in subsequent analyses. Sexual dimorphism in shape factors for bill and body was the difference in least-squared means of each trait calculated from ANCOVA of sex and each trait with general size (bill size or body size) and year as covariates (Rohlf and Bookstein 1987; Björklund and Linden 1993).

Similarly, selection differentials used in this study, i.e., directional selection (a) were the differences in adjusted means between groups (i.e., paired and not paired) from ANCOVA with selection group, year, and each trait (Crespi and Bookstein 1989). Calculations were made separately for each sex. As before, general size and year were used as covariates for estimating selection differentials on shape factors. Stabilizing selection (C) was estimated by comparing variances in each trait between groups. Selection on plumage coloration was calculated separately from other morphological traits. Means were compared with two-tailed t-tests and variances with an F-test. For ease of the interpretation, we also present raw morphological data for selection during 1995–1998. To facilitate comparisons with other studies, we also report conventional selection differentials. These selection differentials were calculated for each trait as a difference in standardized values between before and after selection divided by a square root of the before-selection value variance (e.g., Endler 1986).

The midparent-midoffspring regression for a trait can be

TABLE 1. Descriptive statistics (mean [SD]) of morphological traits measured in the known-sex adult house finches (194 males, 185 females) in a Montana population in 1995–1998.

Trait	Males	Females	P[1]
Bill length	10.33 (0.56)	10.21 (0.48)	0.051
Bill depth	7.91 (0.38)	7.85 (0.40)	0.210
Bill width	7.12 (0.33)	7.18 (0.44)	0.192
Wing length	79.48 (1.79)	77.39 (2.07)	**< 0.0001**
Tail length	63.52 (3.54)	61.48 (2.97)	**< 0.0001**
Tarsus length	20.67 (0.82)	20.53 (0.72)	0.098
Body mass	21.72 (1.54)	21.86 (1.54)	0.253
Plumage score	20.06 (6.08)		

[1] One-tailed test for difference in means between sexes; P-values in bold indicate significance after adjustment for multiple comparisons (Bonferroni $\alpha = 0.007$).

TABLE 2. Current sexual dimorphism in house finches, described by the differences between sexes in the size and shape factors of the path analysis model.[1] All differences are multiplied by 100.

Trait	Difference	P
Bill size	10.26	0.312
Body size	95.39	**< 0.0001**
Bill shape factors		
Bill length	0.67	0.172
Bill depth	0.33	0.248
Bill width	−0.89	0.065
Body shape factors		
Wing length	1.19	**< 0.0001**
Tail length	0.18	0.389
Tarsus length	−0.86	**0.011**
Mass	−2.67	**0.002**

[1] Dimorphism in size is the difference between sexes in the first eigenvector values of the pooled covariance matrices for bill and body traits; dimorphism in shape factors is the difference in adjusted means of each trait calculated from ANCOVA of sex and each trait with general size (bill size or body size) and year as covariates. Bold values indicate significance after the tablewide Bonferroni adjustments.

used to estimate the genetic covariation between parents and offspring for a trait (Falconer and Mackay 1996). When offspring are fully grown this covariation can be used to estimate heritability of a trait. We estimated the regression coefficients for 62 fully- grown (75–83 days old) offspring from 32 nests (details of genetic analyses described in Badyaev and Martin 2000). Standard errors of heritability estimates were generated by replicating family estimates. Genetic relatedness between social parents and offspring was confirmed with the DNA macrosatellite analysis (A. V. Badyaev and P. O. Dunn, unpubl. ms.). Moderate assortative mating (r) for the measured traits in our population can inflate midparent variance; thus, the variance was adjusted by $(1 + r)$ (Falconer and Mackay 1996; p. 179). Male and female phenotypic variances for the measured traits were equal (Table 1), and therefore are unlikely to bias our heritability estimates.

RESULTS

Sexual Dimorphism in the House Finch

In adult birds ($n = 379$), the first principal component of the pooled covariance matrix accounted for 47% of the total variance in bill characters and 45% of the total variance in body characters. The first eigenvectors of both matrices were highly concordant with the isometric vector (vector correlations = 0.979 and 0.988, $\alpha = 11.7°$ and $8.9°$). Thus, first eigenvectors represented general size vectors in both groups of traits.

In addition to sexual dichromatism in plumage coloration, male house finches were larger than females in bill, wing, and tail length (Table 1). When we used path analysis model to partition sexual dimorphism into variation in size and shape factors, we found that males had larger body sizes and disproportionally longer wings than females (Table 2). Females were disproportionally heavier for their size and had narrower bills and longer tarsi than males (Table 2).

Current Selection in the House Finch

Pairing selection

A total of 154 adult males and 122 adult females were used in the analysis of pairing selection. Paired males tended to have longer bills and longer wings (Table 3), but did not differ from unpaired males in plumage score ($P = 0.41$; Table 3). Paired females had significantly shallower and narrower bills and shorter wings than unpaired females (Table 3). Path analysis models of pairing selection during 1995–1998 (Table 4) indicated that pairing selection favored males that had disproportionally longer wings and larger bill and body sizes. Also, bill length variance differed between paired and unpaired males, thus indicating disruptive selection (Table 4). In females, pairing selection acted on the same traits as in males, but in the opposite direction; pairing selection favored a decrease in bill and body sizes and disproportionally shorter wings (Table 4). Also, paired and unpaired females significantly differed in variance in bill shape characters (Table 4).

Fecundity selection

A total of 102 adult males and 99 adult females were used in fecundity analyses. In both sexes, univariate analyses indicated differences between low- versus high-fecundity individuals. High-fecundity males had longer wings, shorter tarsi, shallower and narrower bills, and higher plumage score than low-fecundity males (Table 3). High-fecundity females had longer and shallower bills and shorter wings than low-fecundity females (Table 3). Multivariate analyses of fecundity selection over 1995–1998 revealed strong selection in both sexes. In males, selection for higher fecundity favored smaller bill size, larger body size, disproportionally longer and shallower bills, disproportionally longer wings, and shorter tarsi (Table 4). In females, fecundity selection favored a decrease in both bill and body sizes and a decrease in bill depth and in relative wing length, but an increase in body mass and tarsus length (Table 4).

Survival selection

A total of 107 adult males and 72 adult females were used in the survival selection analysis. Males that survived had narrower and deeper bills and more variable bill width compared to males that died during the winter (Table 3). Males that survived and males that did not survive were similar in plumage score ($P = 0.27$; Table 3). Females that survived

TABLE 3. Morphology (mean [SD]) of house finches with respect to pairing success, breeding season fecundity, and overwinter survival. Mean trait values shown in bold indicate significant difference between groups (e.g., paired vs. unpaired) after within-selection group adjustments for multiple comparisons. Bold values in parentheses indicate significant differences in variances between groups.

		Pairing		Fecundity		Survival	
	Trait	Paired	Unpaired	High	Low	Survived	Did not survive
Males	*n*	76	78	51	51	70	37
	Bill length	10.76 (0.36)	10.24 (0.48)	10.39 (0.62)	10.36 (0.47)	10.22 (0.62)	10.36 (0.76)
	Bill depth	8.06 (0.37)	7.96 (0.34)	**7.90 (0.39)**	8.18 (0.21)	**8.19** (0.42)	7.94 (0.40)
	Bill width	7.15 (0.23)	7.12 (**0.41**)	**7.06 (0.49)**	7.19 (0.24)	**7.05 (0.31)**	7.30 (0.07)
	Wing length	**79.97** (1.54)	78.24 (1.88)	**80.47** (1.35)	79.38 (1.67)	79.59 (1.70)	79.85 (1.88)
	Tail length	63.68 (2.49)	62.95 (**4.12**)	62.94 (3.40)	63.18 (5.19)	63.21 (**3.35**)	62.25 (5.07)
	Tarsus length	20.62 (0.90)	20.75 (0.79)	**20.35** (1.02)	20.96 (0.82)	20.43 (1.00)	20.60 (0.78)
	Body mass	21.58 (1.37)	22.04 (1.60)	21.78 (1.45)	21.31 (1.51)	20.80 (1.53)	21.80 (1.42)
	Plumage	21.47 (4.58)	21.16 (5.74)	**22.95** (3.37)	20.15 (5.05)	21.71 (5.44)	20.55 (5.42)
Females	*n*	74	48	51	48	35	37
	Bill length	10.12 (**0.36**)	10.28 (**0.60**)	10.13 (0.42)	10.29 (0.28)	10.28 (0.48)	10.28 (0.37)
	Bill depth	**8.01 (0.32)**	8.24 (**0.11**)	**7.95** (0.28)	8.10 (0.34)	8.12 (0.66)	8.10 (**0.32**)
	Bill width	**7.10 (0.34)**	7.56 (0.85)	7.07 (0.27)	7.07 (0.48)	7.24 (0.29)	7.09 (0.45)
	Wing length	**76.84** (1.64)	78.54 (1.81)	**76.03** (1.73)	78.72 (1.59)	**78.58** (1.40)	76.95 (1.21)
	Tail length	60.70 (3.64)	62.00 (2.80)	60.21 (2.57)	60.86 (4.04)	61.34 (3.35)	60.18 (4.06)
	Tarsus length	20.47 (0.85)	20.67 (0.83)	20.50 (0.95)	20.45 (0.84)	**21.20** (0.79)	20.30 (0.50)
	Body mass	22.31 (1.39)	22.26 (1.61)	22.19 (**0.75**)	22.30 (1.95)	21.86 (1.18)	22.26 (1.76)

had longer tarsi and wings and less variable bill depth compared to females that died (Table 3). A path analysis of survival selection over 1995–1998 indicated that, in males, selection favored smaller body size, disproportionally deeper but narrower bills, disproportionally shorter wings, and less variable bill length (Table 4). In females, survival selection favored larger body and bill sizes, deeper bills, and longer wings and tarsi (Table 4).

Comparisons of Selection Episodes

Selection often operated on the same traits in males and females, but in opposite directions (Tables 4–6). The intensity of selection (absolute values of selection differentials) was similar between sexes (Table 4). However, directional survival selection on relative bill depth and width, and wing length was stronger in males than in females (corresponding differences: $\Delta = 0.009$, $t = 14.0$, $P = 0.005$; $\Delta = 0.01$, $t = 34.0$, $P = 0.009$; and $\Delta = 0.002$, $t = 4.0$, $P = 0.05$), whereas survival selection on bill size was stronger in females than in males ($\Delta = -0.17$, $t = -8.83$, $P = 0.01$). Similarly, directional fecundity selection on relative bill depth and tarsus length was stronger in males than in females (corresponding differences $\Delta = 0.007$, $t = 4.14$, $P = 0.02$; $\Delta = 0.009$, $t = 4.04$, $P = 0.02$), but the pattern was the opposite for bill width ($\Delta = -0.016$, $t = -5.49$, $P = 0.01$).

Current Selection in Relation to Sexual Dimorphism in the House Finch

Pairing selection strongly favored sexual dimorphism in every year (Spearman *r*-values = 0.23–0.85, Tables 5, 6),

TABLE 4. Directional (*a*) and stabilizing (*C*) selection on pairing success, breeding season fecundity, and overwinter survival in the house finches.

	Pairing				Fecundity				Survival			
	Males		Females		Males		Females		Males		Females	
Trait	*a*[1]	*C*[2]	*a*	*C*	*a*	*C*	*a*	*C*	*a*	*C*	*a*	*C*
Bill size[3]	**61.0**	50.7	**−119.4**	−79.1	**−63.0**	108.2	**−37.7**	−72.6	4.4	75.8	23.4	**−171.1**
Body size	55.0	97.2	**−85.1**	72.6	**43.1**	−141.8	**−17.0**	−29.4	**−10.0**	−204.8	**42.3**	−83.2
Shape factors[4]												
Bill length	0.3	**−0.2**	1.6	**−0.2**	**2.0**	−0.0	−0.7	0.1	−0.2	**0.3**	−1.6	0.1
Bill depth	0.2	0.0	1.1	**−0.1**	**−1.2**	0.0	**−0.5**	0.0	**1.5**	0.0	**0.5**	**0.1**
Bill width	−0.4	0.0	−2.4	**−0.3**	−0.1	0.1	1.1	−0.1	**−1.7**	0.0	0.6	0.1
Wing length	**1.2**	0.0	**−1.0**	0.0	**1.4**	0.0	**−0.6**	0.0	**−0.7**	0.0	**0.3**	0.0
Tail length	−1.2	0.1	0.7	0.0	−1.1	−0.1	−0.5	**−0.2**	0.9	−0.1	0.0	0.0
Tarsus length	−0.3	0.0	0.4	0.0	**−1.2**	−0.0	0.4	0.0	−0.2	0.0	**0.9**	0.0
Mass	−1.4	0.1	1.2	0.0	1.1	−0.2	0.4	−0.4	−0.2	−0.1	−2.5	−0.1

[1] Directional selection differentials are the differences in adjusted means between groups (e.g., paired and unpaired) from ANCOVA with selection group, year, and each trait; general size and year are used as covariates for estimating selection differentials on shape factors.

[2] Stabilizing selection differentials are the differences of variances in each trait between selection groups.

[3] Values are first eigenvectors of the pooled covariance matrices for bill and body traits.

[4] Shape factors for bill and body are least-squared means of each trait calculated from ANCOVA of sex and each trait with general size and year as covariates. All values are multiplied by 100. Bold values indicate significance after within-selection-group Bonferroni adjustments.

TABLE 5. Summary of the current selection for sexual dimorphism in a Montana population of the house finch.[1] Δa_P, sex differences in selection for pairing success; Δa_F, selection for breeding season fecundity; and Δa_S, selection for overwinter survival. All differentials are multiplied by 100.

	Δa_P				Δa_F				Δa_S		
Trait	1995	1996	1997	All	1995	1996	1997	All	1996	1997	All
Bill size	180.7	55.2	284.7	125.5	−7.6	−144.0	12.6	−25.3	−13.2	−19.0	−19.0
Body size	126.0	86.5	71.2	90.6	140.6	−67.0	35.7	60.1	155.6	−128.7	32.3
Bill shape factors											
Bill length	−8.1	2.6	−10.1	−1.3	2.9	8.1	−3.4	2.7	1.4	1.4	1.4
Bill depth	−3.0	−0.9	−3.5	−0.9	−0.8	−2.0	1.5	−0.8	0.8	1.0	1.0
Bill width	7.5	−0.9	9.6	2.0	−2.1	−3.9	1.1	−1.2	−1.8	−2.3	−2.3
Body shape factors											
Wing length	3.7	1.3	1.4	2.2	0.7	2.7	0.1	2.0	−2.0	0.2	−0.8
Tail length	−8.6	2.8	−2.8	−1.9	1.1	−3.3	3.8	−0.6	2.2	1.3	0.9
Tarsus length	−0.3	−1.3	−0.6	−0.7	−1.3	−1.2	−2.0	−1.6	−0.6	−2.5	−1.1
Mass	3.0	−8.1	1.6	−2.6	−1.2	−1.0	−1.9	0.7	1.3	4.4	2.3

[1] Difference between male and female selection differentials for a trait.

and overall current pairing selection was highly concordant with observed dimorphism (Spearman $r = 0.70$, $P < 0.01$; Fig. 1A). When pooled over the years of study, fecundity selection pressures favored increased sexual dimorphism (Spearman $r = -0.28$–0.53; overall fecundity selection: Spearman $r = 0.42$, $P = 0.04$; Tables 5, 6, Fig. 1B). On the contrary, survival selection strongly opposed sexual dimorphism (Spearman $r = -0.57$–(-0.05), overall survival selection: Spearman $r = -0.51$, $P = 0.003$; Tables 5, 6, Fig. 1C). The current net selection (combined standardized differentials of pairing, survival, and fecundity selections over 1995–1998) was highly concordant with observed sexual dimorphism in Montana house finches (Spearman $r = 0.82$, $P = 0.001$; Tables 5, 6, Fig. 1D).

Estimates of heritability were moderately high and significant for all traits (Fig. 2). Heritability estimates varied from 0.35 to 0.51 for bill traits and from 0.22 to 0.41 for body traits (Fig. 2).

DISCUSSION

We found strong current selection on sexually dimorphic traits in the Montana population of house finches. Whereas individual selection components often exerted opposite pressures on sexually dimorphic traits (Fig. 1A–C), the overall selection pressures were highly concordant with observed magnitude of sexual dimorphism (Fig. 1D). Because sexually dimorphic traits of the house finch have significant heritabilities (Fig. 2), the finding of strong current selection on these traits points to significant potential for evolutionary change.

The potential for the evolution of sexual dimorphism is partially determined by sex differences in strength and intensity of selection (e.g., Lande 1980; Arak 1988). Many studies have implicated such intersexual differences in selection as a causal basis for the evolution of sexual dimorphism (e.g., Ralls 1976; Price 1984a; Weatherhead et al. 1987; Arak 1988; Moore 1990; Martin and Badyaev 1996; Wikelski and Trillmich 1997). Similarly, we found that variation in sexually dimorphic traits in both sexes of the house finch had strong fitness consequences (Tables 3, 4). Current selection operated with similar intensity on both sexes, but selection often acted in opposite direction on the same traits of males versus females, thus favoring sexual dimorphism (Tables 5, 6, Fig. 1). Our results suggest that sexual dimorphism in this species is maintained by adaptive responses in each sex (Table 4) and arises from directional differences in the selection pressures on both sexes.

The finding of strong directional selection on house finch morphology in our population suggested that both sexes are far from their optimal morphology for the local ecological conditions. Alternatively, strong directional selection could result from fluctuating environmental pressures (e.g., differences between years, seasons, and selection episodes such as in Table 5; Benkman and Miller 1996; Reznick et al. 1997). For example, pairing and fecundity selection favored smaller size in females, but larger size in males (Tables 3–6). Se-

TABLE 6. Standardized selection differentials (mean, in standard deviations) for three episodes of selection in Montana house finches in 1995–1998. Values in bold indicate significant difference from zero.

	Pairing		Fecundity		Survival	
Trait	Males	Females	Males	Females	Males	Females
Bill length	+0.05	−0.18	+0.07	−0.24	−0.09	−0.02
Bill depth	**+0.35**	**−0.38**	−0.20	−0.14	**+0.51**	+0.43
Bill width	+0.12	**−0.28**	−0.10	**−0.41**	−0.02	+0.20
Wing length	**+0.75**	**−0.69**	**+0.34**	**−0.33**	−0.08	**+0.50**
Tail length	+0.05	−0.25	−0.07	−0.18	+0.03	+0.07
Tarsus length	−0.09	−0.11	−0.05	+0.04	−0.00	**+0.29**
Body mass	−0.02	+0.14	+0.14	**−0.28**	−0.08	−0.10

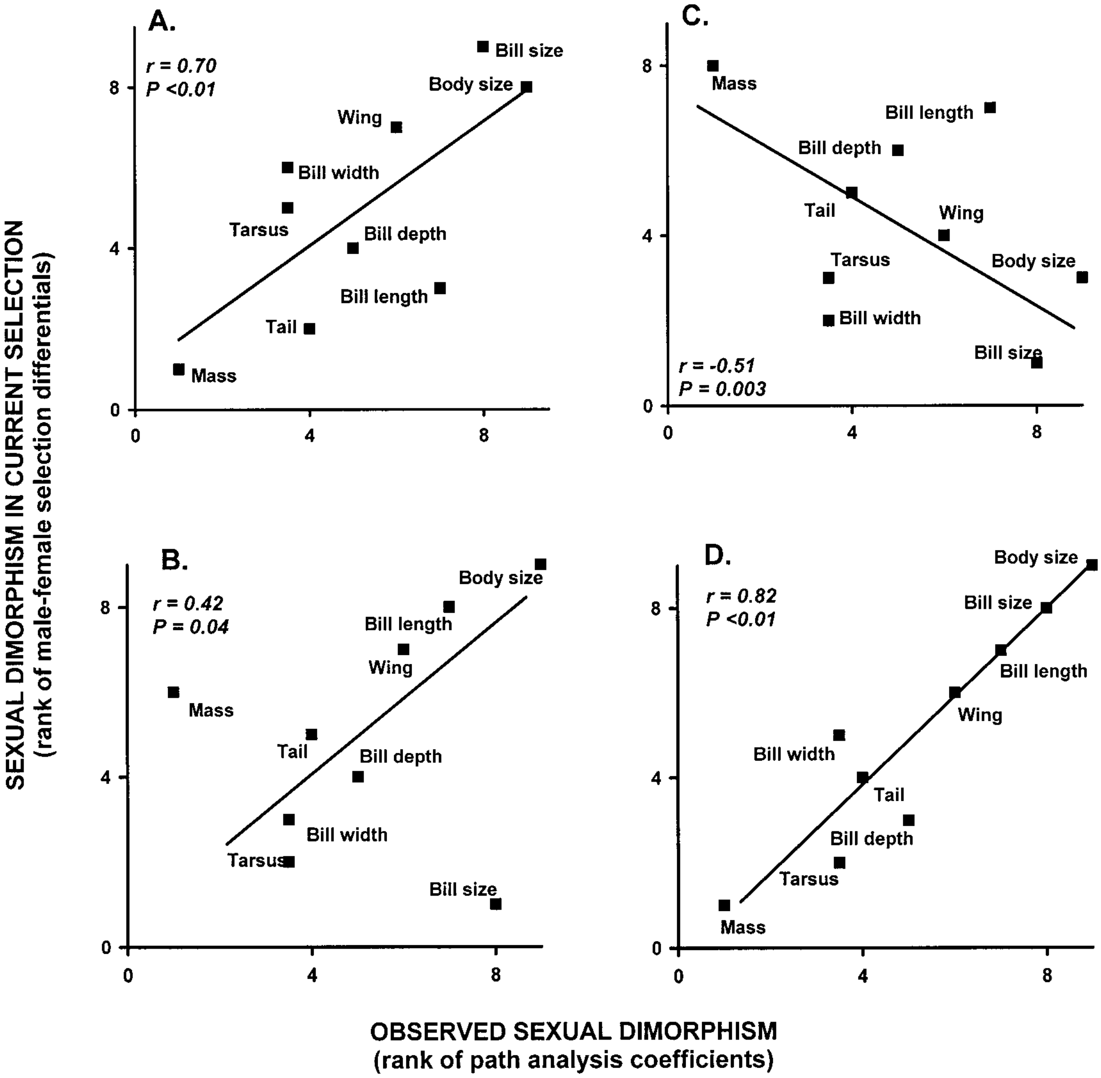

FIG. 1. Plots illustrating the relationship between observed sexual dimorphism (rank of standardized path analysis coefficients) and selection (1995–1998) for (A) pairing success, (B) high breeding season fecundity, (C) overwinter survival, and (D) net selection in a Montana population of the house finches.

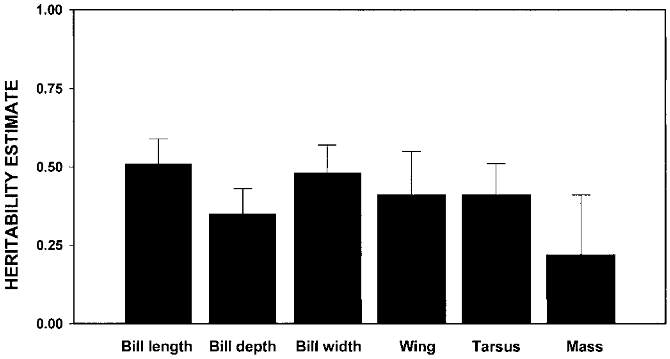

FIG. 2. Heritability values estimated with the midparent versus midoffspring regression for fully grown (75–83 days) offspring in a Montana population of the house finch. Shown are mean ± SE (replicates of family estimates, $n = 32$).

lection for smaller size in females is frequently documented (e.g., Perrins 1979; Murphy 1986). Such selection could arise from a physiological advantage to small body size because smaller females may reach the energetic requirements for self-maintenance faster and therefore breed earlier and convert a greater proportion of consumed resources into reproduction (e.g., Downhower 1976). In turn, early breeding is commonly associated with greater fecundity (e.g., Perrins 1979). Similarly, in our population smaller females initiated nests earlier and laid larger clutches compared to larger females (Tables 3, 4, 6). In contrast, pairing and fecundity selection favored larger structural size in males (Tables 3, 4, 6). Larger size in male house finches may be favored because larger males provided more food to their mates and nestlings than smaller males (A. V. Badyaev, unpubl. data); in the house finch, sufficient provisioning of incubating females by males is essential to reproductive success (e.g., Hill 1991, 1993a).

In both sexes, changes in morphological traits that increased fecundity and pairing success also reduced overwinter survival (Tables 4, 6). For example, survival selection favored larger body size in females, whereas selection for pairing success and high fecundity favored smaller female body size. Similarly, selection for pairing success and high fecundity favored larger body size in males, while overwinter survival favored smaller male body size (Table 4). Similar trade-offs were observed in other systems. For example, in a population of Darwin's finches (*Geospiza fortis*), females with smaller bills had higher fecundity, but lower survival than individuals with larger bills (Price 1984b). In marine iguanas (*Amblyrhynchus cristatus*), larger males had higher mating success, but lower survival than smaller males (Wikelski and Trillmich 1997). Such opposing selection pressures may also operate across life stages (reviewed in Schluter et al. 1991). For example, immature female song sparrows (*Melospiza melodia*) with long bills survived their first winter better than short-billed individuals, but the latter had higher reproductive success (Schluter and Smith 1986). In the Darwin's finch, small birds of both sexes survived poorly as adults, but better as juveniles (Price 1984b; Price and Grant 1984).

Strong concordance between current selection on sexually dimorphic traits and observed level of sexual dimorphism in the house finch (Table 4, Fig. 1D) is surprising in the light of studies of morphological variation in other Cardueline finches. Björklund (1991b; 1994; Björklund and Merilä 1993) found low level of variation in morphological traits in carduelines and suggested that the among-species variance could be most easily explained by long-term stabilizing selection (Björklund 1991b; see also van den Elzen et al. 1987). Moreover, in three species of cardueline finches, including the close relative of the house finch, the scarlet rosefinch (*C. erythrinus*), nestling growth trajectories showed high positive among-age and among-trait covariation, thus significantly limiting potential for morphological change under selection (Björklund 1993, 1994). Consequently, most morphological differentiation among finch species was related to structural size (van den Elzen and Nemeschkal 1991; Björklund and Merilä 1993) and plumage patterns (Badyaev 1997a; Badyaev and Hill 2000b).

The close concordance between current selection and morphology of the house finches in the face of the conservatism of morphological variation in other cardueline finches could be due to several reasons. First, in recently established marginal populations, such as in our study population (Badyaev and Hill 2000a), continuous gene flow from the central areas of the house finch geographical range may prevent the local population from reaching their ecological optima and thus facilitate strong directional selection on heritable traits (García and Kirkpatrick 1997; Holt and Gomulkiewicz 1997). Unusually high dispersal rates of house finches and colonization of diverse ecological conditions (Vazquez-Phillips 1992; Veit and Lewis 1996; Badyaev et al. 2000) may further contribute to high potential for evolutionary change in this species. Consequently, recently established house finch populations strongly differed in the patterns of sexual dimorphism (Badyaev and Hill 2000a). Second, the analysis of phenotypic and genetic variation in the house finch growth revealed that, in contrast to other carduelines (e.g., Badyaev 1994; Björklund 1993), house finch ontogeny is the least constrained (Badyaev and Martin 2000). Low and variable among-age and among-trait phenotypic and genetic covariations and moderate levels of additive genetic variance throughout the ontogeny (Badyaev and Martin 2000) imply significant potential for the evolutionary change, especially under the strong short-term selection that is likely to accompany colonization. Low levels of integration during development may enable house finches to respond to strong current selection and may ultimately contribute to the highest colonization ability and the widest gradient of ecological conditions occupied by this species compared to other carduelines (e.g., appendix 1 in Badyaev 1997a; Badyaev and Ghalambor 1998).

The response of both males and females to selection is composed of the direct response of each sex to selection on itself and the indirect response to selection on the other sex (Lande 1980; Cheverud et al. 1985). However, if sexes differ in the amount of genetic variance for the trait, sexual dimorphism can evolve even under similar selection pressures and high genetic correlation between sexes (Cheverud et al. 1985). We found no evidence for sex-biased phenotypic or genetic variation in morphological traits in this study (Table 1, Badyaev and Martin 2000). Moreover, genetic correlation between sexes were high and for most traits not significantly different from one (A. V. Badyaev and L. A. Whittingham, unpubl. ms.), a result similar to that of other avian studies (Price 1984a; Price 1996; Merilä et al. 1998). Thus, it is likely that the evolutionary change in sexual dimorphism is strongly constrained by high levels of genetic correlation between sexes (e.g., Price 1996; Merilä et al. 1998). Although greater sexual dimorphism favored by current selection in adults may be constrained by genetic correlations between sexes, selection acting on developmental time or other aspects of growth trajectories may strongly influence sexual dimorphism even in the presence of high between-sex genetic correlations (e.g., Reeve and Fairbairn 1996). In the house finch, growth curves for males and females were not parallel during late ontogeny and growth of sexes was terminated at different time (i.e., 37–50 days for females and 110–117 days for males; Badyaev and Martin 2000). Thus, sex differences in growth parameters may influence the potential for evolutionary change in sexual dimorphism in the house finch (see also Cooch et al. 1996).

Traits with a greater amount of sex-limited additive genetic variance, a lower degree of integration, and greater relevance to fitness under current conditions should be favored by selection for sexual dimorphism (Møller and Pomiankowski 1993; Schluter and Price 1993; Badyaev and Hill 1999). Among-trait variation in sex-limited additive genetic variance and the information the traits provide in different environments may account for one of the most surprising results of this study—the lack of strong selection for elaborate carotenoid-based coloration in males (Table 3). Long-term study of two populations in the eastern United States showed consistent and strong selection for brighter carotenoid-based coloration in male house finches (e.g., Hill 1991, 1993a). In a series of work, Hill (reviewed in Hill et al. 1998) documented strong pairing, fecundity, and survival selection for brighter carotenoid-based coloration in the house finch.

Strong selection in eastern populations of house finches persisted even as the available variation in carotenoid plumage declined (Hill et al. 1998; G. E. Hill, pers. comm.). In contrast, we observed much more extensive variability in carotenoid coloration of males in our study population (Table 1), but we detected only weak fecundity selection on this trait. Morphological traits such as body size and bill traits may provide more accurate information on individual quality and parental abilities than do plumage characteristics in conditions of newly established population. Alternatively, extensive variation in carotenoid-based plumage in our population may be maintained by male-male interactions (but see Belthoff et al. 1994; Belthoff and Gowaty 1996), gene flow from other populations, and pleiotropic relations with other traits. Weak directional fecundity selection for brighter plumage (Table 3) in combination with high availability of carotenoid-rich foods in suburban areas (e.g., Linville and Breitwisch 1997) may be sufficient to maintain variation in this trait in our population.

To summarize, we found strong fitness consequences of variation in sexual dimorphism in the house finch. Directional selection on sexually dimorphic morphological traits and similar intensities of selection on each sex suggests that sexual dimorphism in the house finch may arise from adaptive responses in both sexes. Continuous gene flow from the central areas of the house finch geographical range may prevent the local population from reaching their local fitness optima, thereby facilitating strong directional selection on morphological traits. In addition, widely fluctuating selection pressures found in this study can maintain moderate levels of additive genetic variance in sexually dimorphic morphological traits. Strong current selection in combination with low levels of ontogenetic integration in heritable sexually dimorphic traits may account for the close correspondence between current selection and observed sexual dimorphism in Montana population of the house finch.

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LITERATURE CITED

Alberch, P. 1982. Developmental constraints in evolutionary processes. Pp. 313–332 *in* J. T. Bonner, ed. Evolution and development. Springer, Berlin.

Arak, A. 1988. Sexual dimorphism in body size: a model and a test. Evolution 42:820–825.

Badyaev, A. V. 1994. Breeding biology of white-winged grosbeak (*Mycerobas carnipes*) in the Pamir Mountains. Bull. MOIP (Biol. Div.) 99:20–28.

———. 1997a. Altitudinal variation in sexual dimorphism: a new pattern and alternate hypotheses. Behav. Ecol. 9:675–690.

———. 1997b. Covariation between sexually selected and life history traits: an example with Cardueline finches. Oikos 80: 128–138.

Badyaev, A. V., and C. K. Ghalambor. 1998. Does a trade-off exist between sexual ornamentation and ecological plasticity? Sexual dichromatism and occupied elevational range in finches. Oikos 82:319–325.

Badyaev, A. V., and G. E. Hill. 1999. Variation in avian sexual dichromatism in relation to phylogeny and ecology: a review. Pp. 1687–1705 *in* N. Adams and R. Slotow, eds. Proceedings of the 22nd International Ornithological Congress. University of Natal, Durban, South Africa.

———. 2000a. The evolution of sexual size dimorphism in the house finch: I. Population divergence in morphological covariance structure. Evolution 54: *In press*.

———. 2000b. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. Biol. J. Linn. Soc. 69:153–172.

Badyaev, A. V., and T. E. Martin. 2000. Individual variation in growth trajectories: phenotypic and genetic correlations in ontogeny of the house finch (*Carpodacus mexicanus*). J. Evol. Biol. 13:290–302.

Badyaev, A. V., G. E. Hill, A. M. Stoehr, P. M. Nolan, and K. J. McGraw. 2000. The evolution of sexual size dimorphism in the house finch. II. Population divergence in relation to local selection. Evolution 54: *In press*.

Belthoff, J. R., and P. A. Gowaty. 1996. Male plumage coloration affects dominance and aggression in female house finches. Bird Behav. 11:1–7.

Belthoff, J. R., A. M. Dufty, Jr., and S. A. Gauthreaux, Jr. 1994. Plumage variation, plasma steroids, and social dominance in male house finches. Condor 96:614–625.

Benkman, C. W., and R. E. Miller. 1996. Morphological evolution in response to fluctuating selection. Evolution 50:2499–2504.

Björklund, M. 1991a. Evolution, phylogeny, sexual dimorphism and mating system in the grackles (*Quiscalus* spp.: Icterinae). Evolution 45:608–621.

———. 1991b. Patterns of morphological variation among cardueline finches (Fringillidae: Carduelinae). Biol. J. Linn. Soc. 43: 239–248.

———. 1993. Phenotypic variation of growth trajectories in finches. Evolution 47:1506–1514.

———. 1994. Processes generating macroevolutionary patterns of morphological variation in birds: a simulation study. J. Evol. Biol. 7:727–742.

Björklund, M., and M. Linden. 1993. Sexual size dimorphism in the great tit (*Parus major*) in relation to history and current selection. J. Evol. Biol. 6:397–415.

Björklund, M., and J. Merilä. 1993. Morphological differentiation in *Carduelis* finches: adaptive vs. constraint models. J. Evol. Biol. 6:359–373.

Cheverud, J. M. 1984. Quantitative genetics and developmental constraints in evolution by selection. J. Theor. Biol. 110: 115–171.

Cheverud, J. M., M. M. Dow, and W. Leutenegger. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. Evolution 39:1335–1351.

Cooch, E. G., D. B. Lank, and F. Cooke. 1996. Intraseasonal variation in the development of sexual size dimorphism in a precocial bird: evidence from the lesser snow goose. J. Anim. Ecol. 65:439–450.

Cowley, D. E., and W. R. Atchley. 1988. Quantitative genetics of *Drosophila melanogaster*. II. Heritabilities and genetic correlations between sexes for head and thorax traits. Genetics 119: 421–433.

Cowley, D. E., W. R. Atchley, and J. J. Rutledge. 1986. Quantitative genetics of *Drosophila melanogaster*. I. Sexual dimorphism in genetic parameters for wing traits. Genetics 114:549–566.

Crespi, B. J., and F. L. Bookstein. 1989. A path-analytical model for the measurements of selection on morphology. Evolution 43: 18–28.

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

Downhower, J. F. 1976. Darwin's finches and the evolution of sexual dimorphism in body size. Nature 263:558–563.

Earhart, C. M., and N. K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72:251–264.

Endler, J. A. 1986. Natural selection in the wild. Princeton Univ. Press, Princeton, NJ.

Fairbairn, D. J., and R. F. Preziosi. 1996. Sexual selection and the evolution of sexual size dimorphism in the water strider, *Aquarius remigis.* Evolution 50:1549–1559.

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. Longman, London.

García, G., and M. Kirkpatrick. 1997. Genetic models of adaptation and gene flow in peripheral populations. Evolution 51:21–28.

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

———. 1993a. House finch. Vol. 46 *in* A. Poole, P. Stettenheim, and F. Gill. eds. The birds of North America. The Academy of Natural Sciences, Philadelphia, PA.

———. 1993b. Geographic variation in the carotenoid plumage pigmentation of male house finch (*Carpodacus mexicanus*). Biol. J. Linn. Soc. 49:63–86.

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

Hill, G. E., P. M. Nolan, and A. Stroehr. 1998. Pairing success relative to male plumage brightness and pigment symmetry in the house finch: temporal and geographic constancy. Behav. Ecol. 10:48–53.

Holt, R. D., and R. Gomulkiewicz. 1997. How does immigration influence local adaptation? A reexamination of a familiar paradigm. Am. Nat. 149:563–572.

Howard, R. D. 1981. Sexual dimorphism in bullfrogs. Ecology 62: 303–310.

Johnston, R. F., and R. C. Fleischer. 1981. Overwinter mortality and sexual size dimorphism in the house sparrow. Auk 98: 504–511.

Kappeler, P. M. 1996. Intrasexual selection and phylogenetic constraints in the evolution of sexual canine dimorphism in strepsirhine primates. J. Evol. Biol. 9:43–65.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. Am. Nat. 150:1–23.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.

———. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292–305.

———. 1985. The dynamics of peak shifts and the patterns of morphological evolution. Paleobiology 12:343–354.

Leutenegger, W., and J. Cheverud. 1982. Correlates of sexual dimorphism in primates: ecological and size variables. Int. J. Primat. 3:387–402.

Linville, S. U., and R. Breitwisch. 1997. Carotenoid availability and plumage coloration in a wild population of northern cardinals. Auk 114:796–800.

Lofsvold, D. 1988. Quantitative genetics of morphological differentiation in *Peromyscus.* II. Analysis of selection and drift. Evolution 42:54–67.

Martin, T. E., and A. V. Badyaev. 1996. Sexual dichromatism relative to nest height and nest predation: contributions of females versus males. Evolution 50:2454–2460.

Merilä, J., B. C. Sheldon, and H. Ellengren. 1998. Quantitative genetics of sexual size dimorphism in the collared flycatcher, *Ficedula albicollis.* Evolution 52:870–876.

Mitani, J. C., J. Gros-Louis, and A. F. Richards. 1996. Sexual dimorphism, the operational sex ratio, and the intensity of mate competition in polygynous primates. Am. Nat. 147:966–980.

Møller, A. P., and A. Pomiankowski. 1993. Why have birds got multiple ornaments? Behav. Ecol. Sociobiol. 32:167–176.

Moore, A. J. 1990. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual and intersexual selection. Evolution 44:315–331.

Murphy, M. T. 1986. Body size, and condition, timing of breeding, and aspects of egg production in eastern kingbirds. Auk 103: 465–475.

Payne, R. B. 1984. Sexual selection, lek and arena behavior, and sexual dimorphism in birds. Ornithol. Monogr. 33:1–52.

Perrins, C. M. 1979. British tits. Collins, London.

Poulin, R. 1997. Covariation of sexual size dimorphism and adult sex ratio in parasitic nematodes. Biol. J. Linn. Soc. 62:567–580.

Preziosi, R. F., and D. J. Fairbairn. 1996. Sexual size dimorphism and selection in the wild in the waterstrider *Aquarius remigis*: body size, components of body size, and male mating success. J. Evol. Biol. 9:317–336.

Price, D. K. 1996. Sexual selection, selection load, and quantitative genetics of zebra finch bill colour. Proc. R. Soc. Lond. B 263: 217–221.

Price, T. D. 1984a. The evolution of sexual dimorphism in Darwin's finches. Am. Nat. 123:500–518.

———. 1984b. Sexual selection in body size, territory, and plumage variables in a population of Darwin's finches. Evolution 38: 327–341.

———. 1998. Sexual selection and natural selection in bird speciation. Philos. Trans. R. Soc. Lond. B 353:251–260.

Price, T. D., and P. R. Grant. 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. Evolution 38:483–494.

Promislow, D. E. L., R. D. Montgomerie, and T. E. Martin. 1994. Sexual selection and survival in North American waterfowl. Evolution 48:2045–2050.

Ralls, K. 1976. Mammals in which females are larger than males. Quart. Rev. Biol. 51:245–276.

Reeve, J. P., and D. J. Fairbairn. 1996. Sexual size dimorphism as a correlated response to selection on body size: an empirical test of the quantitative genetic model. Evolution 50:1927–1938.

Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934–1937.

Rising, J. D. 1987. Geographical variation of sexual dimorphism in size of savannah sparrows (*Passerculus sandwichensis*): a test of hypotheses. Evolution 41:514–524.

Rogers, A. R., and A. Mukherjee. 1992. Quantitative genetics of sexual dimorphism in human body size. Evolution 46:226–234.

Rohlf, F. J., and F. L. Bookstein. 1987. A comment on shearing as a method of size correction. Syst. Zool. 36:356–367.

Schluter, D., and T. Price. 1993. Honesty, perception, and population divergence in sexually selected traits. Proc. R. Soc. Lond. B 253:117–122.

Schluter, D., and J. N. M. Smith. 1986. Natural selection on beak and body size in the song sparrow. Evolution 40:221–231.

Schluter, D., T. D. Price, and L. Rowe. 1991. Conflicting selection pressures and life history trade-offs. Proc. R. Soc. Lond. B 246: 11–17.

Shaw, F. H., R. G. Shaw, G. S. Wilkinson, and M. Turelli. 1995. Changes in genetic variances and covariances: **G** whiz! Evolution 49:1260–1267.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. 64:419–461.

Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution 38:622–630.

van den Elzen, R., and H.-L. Nemeschkal. 1991. Radiation in African canaries (Carduelidae): a comparison of different classifactory approaches. Acta Congr. Int. Ornithol. 20:459–467.

van den Elzen, R., H.-L. Nemeschkal, and H. Classen. 1987. Morphological variation of skeletal characters in the bird family Carduelinae. I. General size and shape patterns in African canaries shown by principal component analyses. Bonn. Zool. Beitr. 38:221–239.

Vazquez-Phillips, M. A. 1992. Population differentiation of the house finch (*Carpodacus mexicanus*) in North America and the Hawaiian Islands. M.Sc. thesis. The University of Toronto, Toronto, Canada.

Veit, R. R., and M. A. Lewis. 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. Am. Nat. 148:255–274.

Wagner, G. P. 1988. The influence of variation and of developmental constraints on the rate of multivariate phenotypic evolution. J. Theor. Biol. 1:45–66.

Weatherhead, P. J., H. Greenwood, and R. G. Clark. 1987. Natural and sexual selection on body size in red-winged blackbirds. Evolution 41:1401–1403.

Webster, M. S. 1992. Sexual dimorphism, mating system, and body size in New World blackbirds (Icterinae). Evolution 46: 1621–1641.

Webster, M. S., S. Pruett-Jones, D. F. Westneat, and S. J. Arnold. 1995. Measuring the effects of pairing success, extra-pair copulations, and mate quality on the opportunity for sexual selection. Evolution 49:1147–1157.

Wikelski, M., and F. Trillmich. 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. Evolution 51:922–936.

Wilkinson, G. S. 1993. Artificial selection alters allometry in the stalk-eyed fly *Cyrtodiopsis dalmanni.* Genet. Res. Cambridge 62: 213–222.

Wright, S. 1923. The theory of path coefficients. Genetics 8: 239–255.

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