Evolution, 54(5), 2000, pp. 1784–1794

THE EVOLUTION OF SEXUAL DIMORPHISM IN THE HOUSE FINCH. I. POPULATION DIVERGENCE IN MORPHOLOGICAL COVARIANCE STRUCTURE

ALEXANDER V. BADYAEV[1,2,3] AND GEOFFREY E. HILL[3]
[1]*Division of Biological Sciences, The University of Montana, Missoula, Montana 59812-1002*
[2]*E-mail: abadyaev@selway.umt.edu*
[3]*Department of Biological Sciences, Auburn University, Auburn, Alabama 36849*

Abstract.—Patterns of genetic variation and covariation strongly affect the rate and direction of evolutionary change by limiting the amount and form of genetic variation available to natural selection. We studied evolution of morphological variance-covariance structure among seven populations of house finches (*Carpodacus mexicanus*) with a known phylogenetic history. We examined the relationship between within- and among-population covariance structure and, in particular, tested the concordance between hierarchical changes in morphological variance-covariance structure and phylogenetic history of this species. We found that among-population morphological divergence in either males or females did not follow the within-population covariance patterns. Hierarchical patterns of similarity in morphological covariance matrices were not congruent with a priori defined historical pattern of population divergence. Both of these results point to the lack of proportionality in morphological covariance structure of finch populations, suggesting that random drift alone is unlikely to account for observed divergence. Furthermore, drift alone cannot explain the sex differences in within- and among-population covariance patterns or sex-specific patterns of evolution of covariance structure. Our results suggest that extensive among-population variation in sexual dimorphism in morphological covariance structure was produced by population differences in local selection pressures acting on each sex.

Key words.—*Carpodacus mexicanus*, genetic correlation, phenotypic covariance, sexual size dimorphism.

Received November 1, 1999. Accepted April 2, 2000.

Patterns of genetic variation and covariation strongly affect the rate and direction of evolutionary change (Lande 1976, 1980; Lande and Arnold 1983). Although genetic variance-covariance structure (hereafter covariance structure) that results from developmental or functional interrelationships among traits may be adaptive when it is formed (Berg 1960; Cheverud 1984; Wagner 1988), it can bias evolutionary change in response to new environments (e.g., Maynard Smith et al. 1985; Arnold 1992).

Two issues related to covariance structure of populations are of a particular interest to studies of evolution: the relative temporal constancy of genetic covariances and the relationship between phenotypic and genetic covariance structures (Lande 1980, 1985; Turelli 1988). Genetic covariance structure may remain constant during the initial periods of taxa divergence, but eventually it is expected to evolve under selection or drift (e.g., Lande 1980, 1985; Zeng 1988; Schluter 1996). Indeed, theoretical and empirical studies have suggested that genetic correlations can strongly bias short-term evolution, but their importance should diminish over time (Cheverud 1984; Lofsvold 1986, 1988; Turelli 1988; Zeng 1988; Shaw et al. 1995; Schluter 1996) especially when the correlations themselves are the subject of selection (e.g., Berg 1960; Wilkinson et al. 1990), and constancy of genetic covariance patterns vary among groups of traits (e.g., Cheverud 1996; Wagner et al. 1997). Empirical and theoretical studies also emphasized the distinction between phenotypic and genetic divergence in covariance structures (Cheverud 1988; Roff 1995, 1997; Armbruster and Schwaegerle 1996; Deng et al. 1999), with divergence in phenotypic matrices being most closely related to multivariate patterns of phenotypic selection (Lande and Arnold 1983; Arnold and Phillips 1999).

Macroevolutionary predictions of quantitative genetics models depend on the assumption of relative constancy of genetic covariance structure (Lande 1976, 1985; Price and Grant 1985; Lofsvold 1988; Zeng 1988; Cheverud 1996; Roff et al. 1999). Thus, examination of covariance structure at different taxonomic levels is crucial both for an understanding of the mechanisms behind taxon divergence and for making predictions regarding the evolutionary change in populations (e.g., Grant and Grant 1995). However, whereas the temporal persistence of covariance structure has been a topic of considerable debate (reviewed in Roff 1997, p. 110; Steppan 1997 and references therein), only a few studies have explicitly examined the evolution of covariance structure; i.e., tested the congruence between hierarchical changes in covariance structure and the phylogenetic relationships among taxa (e.g., Goodin and Johnson 1992; Steppan 1997; Arnold and Phillips 1999; Roff and Mousseau 1999; Roff et al. 1999).

The history and distribution of the house finch (*Carpodacus mexicanus*) populations provided us with a unique opportunity to examine evolution of morphological covariance patterns in relation to a known history of population divergence. House finches have undergone a dramatic expansion of range over the last 150 years, resulting in populations whose historical relationships are well documented in the literature and that now occupy ecologically distinct regions across North America and Hawaii (Table 1, Fig. 1). The morphologies of male and female house finches vary strongly among populations (Fig. 2), resulting in extensive geographical variation in sexual size dimorphism (Table 2; Hill 1993; A. V. Badyaev and G. E. Hill, unpubl. ms.). Given such extensive divergence in the morphological traits of populations that have been separated for only a short period of time, it is interesting to ask whether changes in morphology (Fig. 2, A. V. Badyaev and G. E. Hill, unpubl. ms.) were accompanied by changes in morphological covariance structure.

Our goal in this paper was to analyze morphological variance-covariance matrices for seven house finch populations.

TABLE 1. Location and age of house finch (*Carpodacus mexicanus*) populations sampled between 1989 and 1993 and sample sizes for each sex.

Population	Location	Taxonomic subspecies	Age of population at the time of sampling	Males	Females
Mexico	Guerrero, Mexico	*C. m. griscomi*	historic range ($>10^4$ years)	74	70
California	San Jose, central coastal California	*C. m. frontalis*	historic range ($\sim10^3$ years)	102	86
Montana	Missoula, northwestern Montana	*C. m. frontalis*	30 years	91	91
Hawaii	Mona Loa, Hawaii Island, Hawaii	*C. m. frontalis*	125 years	76	53
New York	southern Long Island, New York	*C. m. frontalis*	50 years	60	59
Michigan	Ann Arbor, southeastern Michigan	*C. m. frontalis*	5 years	88	88
Alabama	Auburn, east-central Alabama	*C. m. frontalis*	10 years	90	90

If genetic covariance matrix remains constant over time since divergence and genetic drift is the primary cause of divergence, we expect (1) congruency or proportionality among population matrices (Lande 1980; Lofsvold 1988; Armbruster 1991; Björklund 1994; Roff and Mousseau 1999; Badyaev and Foresman 2000), i.e., the morphological diversification among house finch populations should occur in the directions predicted by within-population correlation or covariance structures (Schluter 1996); and (2) concordance in patterns of divergence in covariance matrices between males and females. Alternatively, if population divergence resulted from locally distinct selection pressures, no congruence would be expected both between within- and among-population covariance structures *and* between divergence of male and female covariance structures (Lande 1985; Riska 1985; Zeng 1988; Arnold and Phillips 1999; Camara and Pigliucci 1999). We also addressed whether temporal change in morphological covariance structure among populations follow phylogenetic trajectories (i.e., whether closely related populations are more similar in covariance structure than distantly related populations). Both random drift and especially long-term directional selection are expected to produce congruence between hierarchical patterns of population divergence and patterns of phylogenetic relationships (Lande 1980; Arnold 1992; Goodin and Johnson 1992; Schluter 1996; Steppan 1997; Roff and Mousseau 1999) and congruence between evolution of covariance structures of males and females (Arnold and Phillips 1999). Alternatively, if population divergence in genetic covariance structure results from responses to locally distinct and fluctuating selection pressures or if populations differ in sex-biased selection pressures or in the strength of between-sex genetic correlations, no concordance between morphological covariance structure and phylogenetic relatedness is expected for both sexes (Riska 1985; Kohn and Atchley 1988; Lofsvold 1988; Steppan 1997; Lynch and Walsh 1998, p. 75). In addition, to examine whether phenotypic matrix accurately represents genetic matrix, we evaluated the association between phenotypic and genetic correlations for all morphological traits.

METHODS

Data Collection

History of the house finch introduction.—The house finch is a small, granivorous passerine that is native to western North America. Before European colonization of North America, house finches occupied an area from southern Oregon and southern Wyoming south to Oaxaca, Mexico (Hill 1993). Across this broad range, there is substantial geographic variation in the size, shape, and plumage coloration of house finches, which lead Moore (1939) to recognize 21 subspecies. In the seventh edition of the *A.O.U. Checklist of North American Birds* (American Ornithologists' Union 1998) the number of recognized subspecies was reduced to 15, lumping into single subspecies many of the populations recognized by Moore (1939), including some populations that will be discussed in this paper. All ornithologists, however, have recognized house finches from south of the Mexican Plateau, Moore's ''Sur Group,'' as being distinct at least the subspecific level from house finches found north of the Mexican Plateau (Hill 1996; American Ornithologists' Union 1998). These birds likely form a phylogenetic species distinct from the northern house finch (Moore 1939; Hill 1996), but this question has not been formally addressed by systematists. We sampled one population of house finches from a subspecies of the ''Sur Group,'' *C. m. griscomi,* and six populations from a northern subspecies, *C. m. frontalis.*

Since colonization of North America by Europeans, house finches of the subspecies *C. m. frontalis* have undergone a remarkable expansion of range. Between 1850 and 1870 a small number of house finches from coastal California was introduced to Oahu Island (Grinnell 1911). By 1901 house finches were abundant on all the major islands in the Hawaiian chain (Grinnell 1911; Caum 1933). Approximately a century after the introduction of finches to the Hawaiian Islands, 40–100 house finches collected in southern coastal California were released in the vicinity of New York City (Elliot and Arbib 1953). By the early 1950s the New York population of house finches had became stable and was estimated at a few hundred birds (Mundinger and Hope 1982). From the 1960s through the 1990s this introduced population spread across virtually all of the eastern United States and southeastern Canada (Hill 1993). House finches first bred in southeastern Michigan in 1981 (Payne 1983) and were common breeders in Ann Arbor, Michigan, by 1986 (G. E. Hill, pers. obs.). In Alabama, this species first bred in 1981 (Dusi and Dusi 1982) and was common in Auburn, Alabama, by 1984 (J. L. Dusi, pers. comm.). The house finch expanded its range not just through introductions into entirely new regions, but also by expanding at the edges of its historic range. In the 1940s and 1950s house finches expanded their range along the eastern edge of the Rocky Mountains from southern Wyoming into southern and then into northwestern Montana (Hill 1993; Fig. 1). The first record of the house

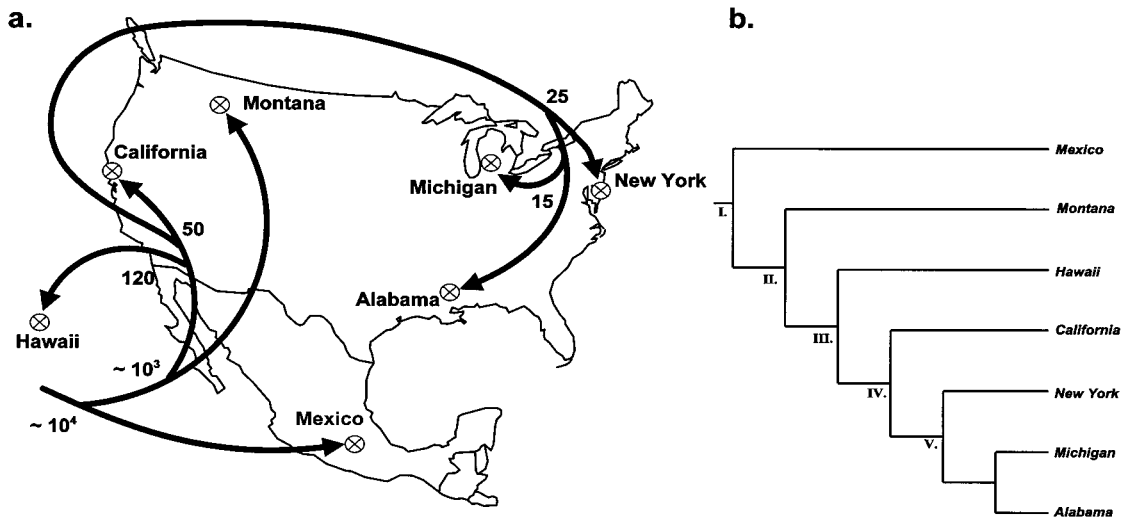

FIG. 1. Phylogenetic relationships among house finch (*Carpodacus mexicanus*) populations. (a) History of introductions and range expansions for the seven study populations. Numbers at nodes give the years since divergence of lineages. See Methods for exact locations and historical background. (b) Simplified depiction of phylogenetic relationships with levels of comparison indicated: level I: *C. m. griscomi* subspecies (Mexican population) versus *C. m. frontalis* subspecies (all other populations); level II: interior *frontalis* (Montana populations) versus *frontalis* of recent coastal California origin (California, Hawaii, New York, Michigan, Alabama); level III: Hawaii population versus Californian and eastern North American populations; level IV: recently diverged populations (California, New York, Michigan, and Alabama); level V: divergence of populations of New York origin (Michigan and Alabama).

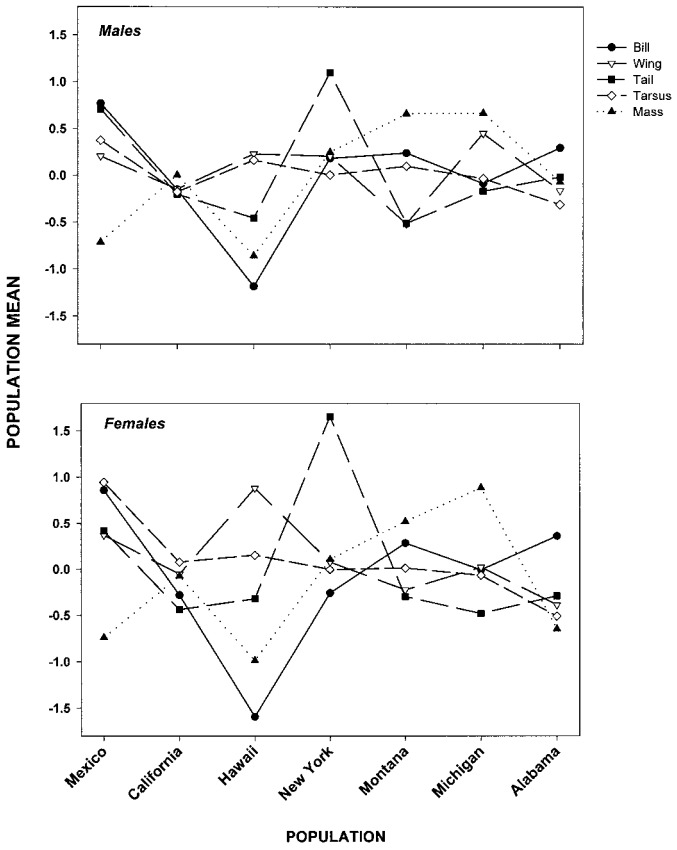

FIG. 2. Variation in morphological traits and sexual dimorphism among populations of the house finch. Shown are standardized (mean = 0, SD = 1) within-population means of each trait.

finch in Missoula, northwestern Montana, was in the summer of 1955 (P. L. Wright, pers. comm), and by mid-1970s house finches were a common breeding bird.

Measurements.—Between 1988 and 1993, we measured 1118 live house finches from seven populations (Table 1). The phylogenetic relationships of these populations (Fig. 1, Table 1) are known through direct observation of introductions (see above) and range expansions or can be inferred with confidence from the degree of geographic isolation of populations (Hill 1996). We measured (with dial Mitutoyo calipers to an accuracy of 0.02 mm): bill length from anterior end of nostril to the tip of upper mandible; tarsus length (left and right); and wing (right, flattened), tail, and body mass (with a balance, to an accuracy of 0.05 g). To estimate measurement error, all morphological measures were repeated twice (i.e., four times for the bilateral traits) in the Montana sample. In all populations the average of repeated measures was used for further analyses. In each population, measurements of fully-grown adult finches were taken during short capture sessions (1–3 months) in the prebreeding season, thus minimizing the effects of seasonal variation. Within all populations, birds were captured in a single location. Repeatabilities for all traits were high; briefly, within-capture session measurement error estimated from a one-way ANOVA accounted for about 7–10% of variation in most morphological traits and for 18% of variation in body mass (Badyaev and Martin 2000a). When means of morphological traits are proportional to their variances, populations can exhibit distinct covariance structure simply because of differences in means (Fig. 2). However, because in our data coefficient of variation was independent of the mean for all traits, log-transformation of original variables had achieved the decoupling of mean and variance (e.g., Lynch and Walsh 1998, p.

TABLE 2. Descriptive statistics, mean (SD) of untransformed morphological traits measured in male and female house finches from seven North American populations. *P*-values are for two-tailed *t*-tests of differences between sexes.

Trait	Males	Females	*t*	*P*
Mexico				
Bill length	9.08 (0.32)	8.99 (0.25)	1.19	0.237
Wing length	80.74 (1.99)	78.32 (2.04)	5.04	<0.001
Tail length	62.80 (2.15)	61.15 (2.07)	3.25	0.002
Tarsus length	17.43 (0.55)	17.73 (0.56)	−1.64	0.109
Body mass	19.51 (1.26)	19.39 (1.22)	0.39	0.696
California				
Bill length	8.64 (0.40)	8.50 (0.38)	1.99	0.048
Wing length	80.00 (1.59)	77.61 (1.64)	8.78	<0.001
Tail length	59.50 (2.01)	57.60 (2.02)	5.56	<0.001
Tarsus length	17.10 (0.53)	17.09 (0.55)	0.09	0.930
Body mass	20.64 (1.00)	20.44 (1.06)	1.19	0.236
Montana				
Bill length	8.84 (0.47)	8.73 (0.45)	2.40	0.017
Wing length	79.30 (1.81)	77.32 (2.06)	10.35	<0.001
Tail length	59.11 (3.15)	57.98 (2.88)	3.56	<0.001
Tarsus length	17.23 (0.67)	17.09 (0.63)	2.20	0.028
Body mass	21.71 (1.38)	21.57 (1.40)	1.03	0.303
Hawaii				
Bill length	8.20 (0.37)	7.99 (0.40)	1.97	0.053
Wing length	80.98 (2.15)	79.37 (1.50)	3.38	0.002
Tail length	58.58 (2.63)	58.11 (1.70)	1.09	0.217
Tarsus length	17.27 (0.69)	17.14 (0.93)	0.67	0.500
Body mass	19.40 (1.36)	19.17 (1.32)	0.62	0.536
New York				
Bill length	8.82 (0.29)	8.54 (0.28)	4.16	<0.001
Wing length	80.55 (1.52)	77.87 (1.01)	8.83	<0.001
Tail length	67.10 (8.49)	67.94 (5.55)	0.67	0.502
Tarsus length	17.23 (0.58)	17.03 (0.45)	1.61	0.113
Body mass	21.25 (1.37)	20.67 (0.87)	2.00	0.051
Michigan				
Bill length	8.71 (0.34)	8.68 (0.34)	0.93	0.353
Wing length	80.06 (1.96)	77.87 (1.89)	18.49	<0.001
Tail length	59.56 (2.16)	57.70 (2.30)	12.99	<0.001
Tarsus length	17.17 (0.60)	17.19 (0.61)	0.74	0.459
Body mass	21.45 (1.24)	22.12 (1.46)	7.82	<0.001
Alabama				
Bill length	8.92 (0.58)	8.68 (0.37)	3.81	<0.001
Wing length	79.72 (1.91)	77.13 (2.02)	16.23	<0.001
Tail length	59.32 (2.49)	57.49 (2.68)	8.91	<0.001
Tarsus length	17.45 (1.19)	16.80 (0.65)	9.03	<0.001
Body mass	20.49 (1.41)	20.22 (1.36)	2.61	0.009

301). Body mass was cube-root transformed. For some analyses data were standardized to zero-mean and one standard deviation.

Data Analysis

Genetic analysis.—Families were divided according to sex of offspring and, for each sex, we calculated genetic correlations between traits from covariances of midparent values and fully-grown midoffspring values (males or females; Lynch and Walsh 1998, p. 634). For each pair of traits, an average of two theoretically identical values was obtained: $r_1(G) = \text{cov}(X'Y)/\sqrt{[\text{cov}(X'X)\text{cov}(Y'Y)]}$ and $r_2(G) = \text{cov}(XY')/\sqrt{[\text{cov}(X'X)\text{cov}(Y'Y)]}$, where X′ and Y′ are midparent values and X and Y are midoffspring values for X and Y traits. Genetic relatedness among nestlings within each nest and between social parents and offspring was confirmed with the DNA macrosatellite analysis (A. V. Badyaev and P. O. Dunn, unpubl. ms.). Sex of all offspring used in this analysis (52 families) was determined by polymerase chain reaction (PCR) amplification of the avian CHD gene (Badyaev et al. 2000b). We compared phenotypic and genetic correlations using simple correlations for individual values (e.g., Cheverud et al. 1989; Preziosi and Roff 1998). Heritabilities were estimated from the midparent-midoffspring regression for each trait and were corrected for assortative mating and sex-biased phenotypic variance (Lynch and Walsh 1998, p. 547). The analysis of heritability in Montana house finches is presented in Badyaev and Martin (2000a,b).

Hierarchical analysis of covariance structure.—We calculated sex-specific within-population correlation and covariance matrices by pooling standardized data from all populations. We also calculated among-population correlation and covariance matrices with means for each population. From these matrices we extracted the first two eigenvectors (characteristic roots of additional eigenvectors were not distinct from each other). We used correlation matrices to compare within- versus among-population patterns of variation. Correlation matrices were more suitable for this analysis for two reasons. First, unit-free and mean-independent correlations are more appropriate for within- versus among-population comparisons (e.g., Zeng 1988). Second, considering the traits used in this study, correlation matrices were more easily decomposed into size- and shape-related variation than were covariance matrices (e.g., Preziosi and Roff 1998). Correlation matrices were constructed for two levels of analysis: including only recently diverged populations of ''California origin'' (i.e., Hawaii, New York, Michigan, and Alabama; see Data Collection) and including all seven populations. Similarity of within- and among-population eigenvectors was evaluated with vector correlations and corresponding angles. To estimate the significance of an angle between two vectors, we calculated the range of angles for the 1000 pairs of random five-element vectors with randomly substituted elements (e.g., Klingenberg and Zimmerman 1992). Parallelism of corresponding within- and among-population eigenvectors would indicate that among-population patterns of morphological divergence can be reliably predicted from the within-population morphological structure (that is equality or proportionality). All possible pairwise vector comparisons were conducted at different hierarchical levels (see below) corresponding to the historical patterns of taxa divergence (Fig. 1; after Steppan 1997). The resulting mean vector correlation was calculated for each phylogenetic level (Fig. 1). See Steppan (1997) for statistical justification of multiple comparisons and discussion of degrees of freedom in this analysis.

We used the common principal component analysis (CPCA; Flury 1988) of variance-covariance population matrices to test a hypothesis that divergence among house finch populations followed a hierarchically structured pattern (Arnold 1992) that reflected the phylogeny of the populations (Fig. 1). The model underlying CPCA assumes that covariance matrices of all populations share the same eigenvectors, common principal components (CPCs), but the eigenvalues associated with these CPCs are not necessarily equal among

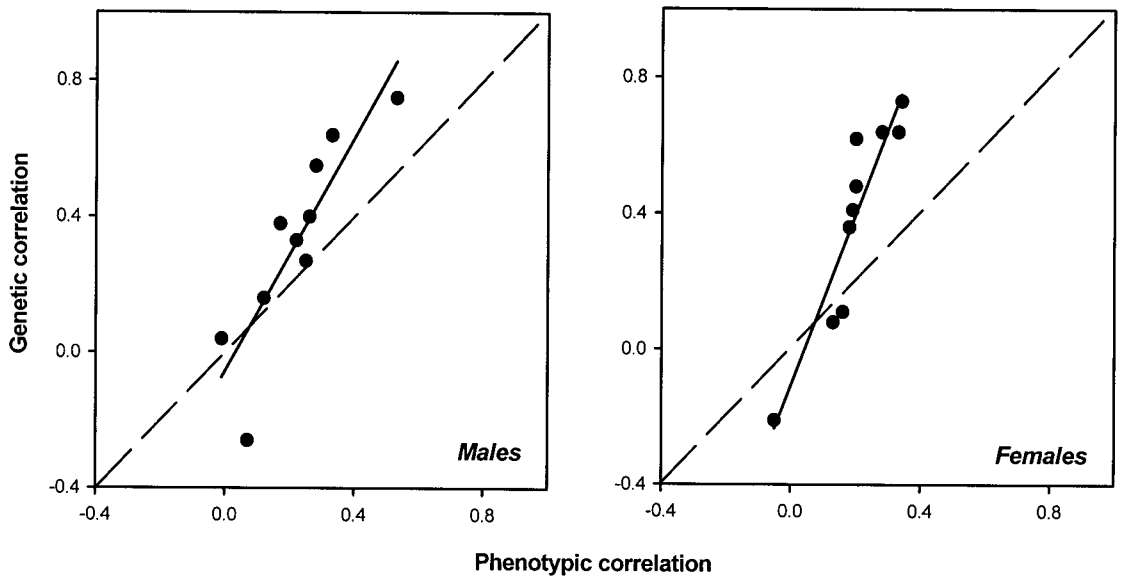

FIG. 3. Phenotypic versus genetic correlations for male ($r = 0.88$, $P = 0.0009$) and female ($r = 0.93$, $P = 0.0001$) Montana house finches. Dotted line is 1:1 relationship; solid line is fitted regression.

populations (Flury 1988; Klingenberg and Zimmermann 1992; Phillips and Arnold 1999). The component elements for each population, which are estimated as the eigenvectors of the population covariance matrix, are considered to differ only by a sampling error (Flury 1988). In contrast the eigenvalues associated with CPCs are estimated separately. Thus, our CPC model tests, in hierarchical fashion, whether morphological covariance patterns are similar across all populations. Multiple matrix comparison in CPCA proceeds by evaluating a goodness-of-fit for all hierarchical levels, from unrelated matrices to partially shared principal structure to equal covariance structure of all matrices (Phillips 1997; Phillips and Arnold 1999). Because differences between χ^2-statistics are distributed as χ^2, the models can be statistically tested for the best fit. To further evaluate the most optimal fit independently of the number of parameters included into the comparison, we choose the model with the smallest value of the Akaike information criterion (AIC) and the smallest value of the ratio χ^2/df (Flury 1988; Phillips and Arnold 1999). We evaluated the CPC models with Flury's (1988) decomposition of χ^2-tests conducted with algorithms provided in Phillips (1997).

All seven populations were used in comparisons, and analyses were conducted from the most inclusive (i.e., level I, Fig. 1) to least inclusive (i.e., Michigan vs. Alabama) comparisons. In the more inclusive analysis, covariance matrices were used as a set rather than pooled (after Steppan 1997), thus taking the full advantage of the CPCA. The highest level of hierarchy in the step-up model-building approach (Flury 1988; Phillips and Arnold 1999) for which the null hypothesis can be accepted was mapped on the historical patterns of taxa divergence (Fig. 1b). The congruence between the hierarchy of covariance matrix association and historical pattern of population divergence would indicate relative constancy of covariance patterns and suggest that the pattern of population divergence could be reliably predicted from the within-taxa covariance structure and the time since divergence (Arnold 1992; Schluter 1996; Steppan 1997; Arnold and Phillips 1999).

RESULTS

Genetic and Phenotypic Correlations

In males, genetic correlations between traits varied from 0.26 to 0.75, and phenotypic correlations varied from −0.01 to 0.53 (Fig. 3). In females, genetic correlations varied from −0.21 to 0.73, whereas phenotypic correlations varied from −0.05 to 0.34. In both sexes, genetic correlations were greater than corresponding phenotypic correlations (average phenotypic vs. genetic correlation; males: 0.22 vs. 0.33, females: 0.20 vs. 0.39; Fig. 3). All traits examined in this study were significantly heritable in both sexes. Heritability estimates for morphological traits in the Montana population of the house finches (given in Badyaev and Martin 2000a,b) ranged from 0.23 for body mass to 0.53 for bill length, with an average heritability of 0.42.

Within- Versus Among-Population Correlations

In males, first eigenvectors of within-population correlation matrices were approximations of isometric size (Table 3). Second eigenvectors of within-population variation mostly reflected variation in tail length (Table 3). Most of the variation among recently diverged populations were in bill length, whereas all populations mostly differed in structural size (Table 3). Second eigenvectors of among-population variation mostly featured variation in wing in recently diverged populations and in bill and tail in all populations (Table 3). In females, first within-population eigenvectors featured variation in wing and tarsus length, whereas second eigenvectors emphasized the contrast between bill length and other traits (Table 3). Most of the variation among populations was due

TABLE 3. First and second eigenvectors of within- and among-population correlation matrices and associated eigenvalues (λ) calculated for house finches from recently diverged and all populations. See Methods for more details.

	Recently diverged populations				All populations			
	Eigenvector I		Eigenvector II		Eigenvector I		Eigenvector II	
Trait	Within	Among	Within	Among	Within	Among	Within	Among
Males								
Bill	0.466	0.660	−0.334	0.071	0.429	0.068	0.287	0.751
Wing	0.481	−0.270	0.435	0.696	0.526	0.518	−0.374	−0.162
Tail	0.371	0.361	0.662	0.321	0.452	0.485	−0.573	0.509
Tarsus	0.413	−0.507	−0.141	0.377	0.460	0.524	0.248	−0.065
Mass	0.491	0.420	−0.490	0.514	0.351	−0.467	0.623	0.383
λ	2.00	2.68	1.04	1.57	1.88	1.86	1.18	1.55
% variance	40.1	53.7	20.9	31.3	37.5	37.3	23.5	30.9
Females								
Bill	0.042	−0.581	0.731	0.082	0.258	−0.392	0.597	0.619
Wing	0.612	0.584	−0.306	−0.007	0.572	0.659	−0.377	−0.072
Tail	0.245	−0.011	−0.361	0.668	0.253	0.112	−0.586	0.530
Tarsus	0.578	0.505	0.017	0.420	0.591	0.402	0.063	0.575
Mass	0.478	−0.251	0.491	0.608	0.440	−0.488	0.392	0.000
λ	1.45	2.90	1.24	1.26	1.47	2.11	1.21	1.37
% variance	28.9	58.1	25.0	25.4	29.6	42.2	24.1	27.3

to contrast between bill length and wing and tarsus lengths (e.g., bill: −0.581 vs. wing: 0.581 for the first eigenvectors of recently diverged populations, and −0.392 vs. 0.659 for all populations; Table 3).

In both sexes, strong differences in patterns of within- and among-population variation were evident in low correlations between corresponding vectors (Table 4). In both recently diverged populations and all populations, vectors of within- and among-population variation were not collinear (vector correlations varied from 0.13 to 0.60; Table 4). Random simulation of vector angles produced confidence intervals of ~30°, rendering most estimates in Table 4 not significantly different from each other and from 90° (i.e., complete unrelatedness).

Overall, despite recent divergence of examined populations, among-population divergence was not predictable from the within-population correlation patterns. Both male and female morphologies showed high and multidirectional divergence among populations, and the patterns of within-population variation were different between sexes.

Magnitude and Directionality of Taxa Divergence in Covariance Structure

For both sexes, vector correlations were similar at all hierarchical levels and varied between 0.84 and 0.91 (Table 5). Recently diverged populations were as similar in covariance patterns as were the populations of higher hierarchy of historical divergence (e.g., in males, average r_v = 0.91 vs. 0.84 for the level I and level V correspondingly; Table 5). Overall, the high correlations found here indicate a relatively small magnitude of divergence among house finch populations.

CPC analyses allowed a more detailed test of hierarchical association among populations (Fig. 4). Of special interest here is whether divergence among historically nested populations shows consistent directionality. We found that morphological and historical hierarchies were mostly distinct (Fig. 4, Table 5). For example, male morphology from Mexico, Montana, and New York populations did not share any common principal structure (Table 5, Fig. 4). Moreover, for both sexes, the New York population was no more similar to other recently diverged populations (e.g., Michigan and Alabama) than it was to the population in Mexico, Hawaii, California, or Montana (Fig. 4, Table 5). Females from different populations were more similar in their covariance structure than were males (Fig. 4). For example, most populations shared at least two CPCs, and covariance structure of Mexico, Montana, and Hawaii females was especially similar (Fig. 4). However, as in males, morphological hierarchy was distinct from the historical one. Indeed, females from most recently diverged populations were the most different (Table 5, Fig. 4). For example, most recently diverged pop-

TABLE 4. Correlations between the within- and among-population eigenvectors r_v (and corresponding angles). Data from Table 2.

Comparisons	Eigenvectors I	Eigenvectors II
Males		
Within vs. among populations (recently diverged populations)	0.32 (71.3°)	0.21 (78.0°)
Within vs. among populations (all populations)	0.60 (53.1°)	0.21 (78.1°)
Females		
Within vs. among populations (recently diverged populations)	0.52 (58.7°)	0.14 (81.9°)
Within vs. among populations (all populations)	0.33 (70.7°)	0.13 (83.5°)

TABLE 5. Mean first eigenvector correlations, r_v (and corresponding angles) among all pairwise comparisons within specified phylogenetic levels and the common principal component analysis (CPCA) of shared hierarchical structure in covariance matrices of specified phylogenetic levels.

	Mean r_v (range), α	Best fit CPCA model	χ^2/df[1]	AIC[2]
Males				
Level I	0.91 (0.68–0.99), 25.1°	unrelated structure	1.90	148.0
Level II	0.89 (0.68–0.99), 26.5°	unrelated structure	1.91	118.5
Level III	0.89 (0.68–0.99), 27.5°	CPC (2) model	1.49	80.3
Level IV	0.88 (0.75–0.99), 28.3°	CPC (1) model	0.91	54.8
Level V	0.84 (0.75–0.97), 33.6°	CPC (2) model + unrelated[3]	0.33	25.1
Females				
Level I	0.86 (0.60–0.99), 31.1°	CPC (3) model	0.65	119.5
Level II	0.90 (0.69–0.99), 25.9°	CPC (3) model	0.58	101.8
Level III	0.89 (0.74–0.99), 26.5°	CPC (3) model	0.81	69.8
Level IV	0.87 (0.74–0.98), 29.4°	CPC (2) model	0.16	41.3
Level V	0.85 (0.84–0.98), 31.3°	CPC (1) model + unrelated[3]	0.58	19.5

[1] Estimates the amount of lack-of-fit for given degrees of freedom in the model.
[2] Akaike Information Criterion.
[3] In both sexes, New York versus other populations at level V are unrelated, but Michigan and Alabama populations share two common principal components in males and one common principal components in females.

ulations of Michigan and Alabama shared just one CPC (Fig. 4).

Overall, patterns of morphological divergence among populations were distinct from the hierarchical patterns described by documented history of introductions; we found no evidence for long-term directionality in divergence among house finch populations. In addition, CPCA revealed highly distinct patterns of evolution of covariance structure between males and females.

DISCUSSION

Patterns of genetic variance and covariance play a central role in evolutionary change (Lande 1976, 1980, 1985). On one hand, genetic covariance structure can bias the direction and rate of population divergence in response to diversifying selection pressures (e.g., Lande and Arnold 1983; Schluter 1996). On the other hand, genetic correlations may themselves reflect patterns of developmental and functional integration produced by long-term stabilizing selection (Cheverud 1984; Lande 1985; Wagner 1988); genetic covariances may evolve by selection or random drift, thus their importance for long-term evolutionary change may be limited (Turelli 1988; Armbruster 1991; Arnold 1992; Björklund 1994). However, despite a considerable amount of theoretical and empirical work, the evolution of genetic covariance structure is poorly understood and empirical evidence for constancy

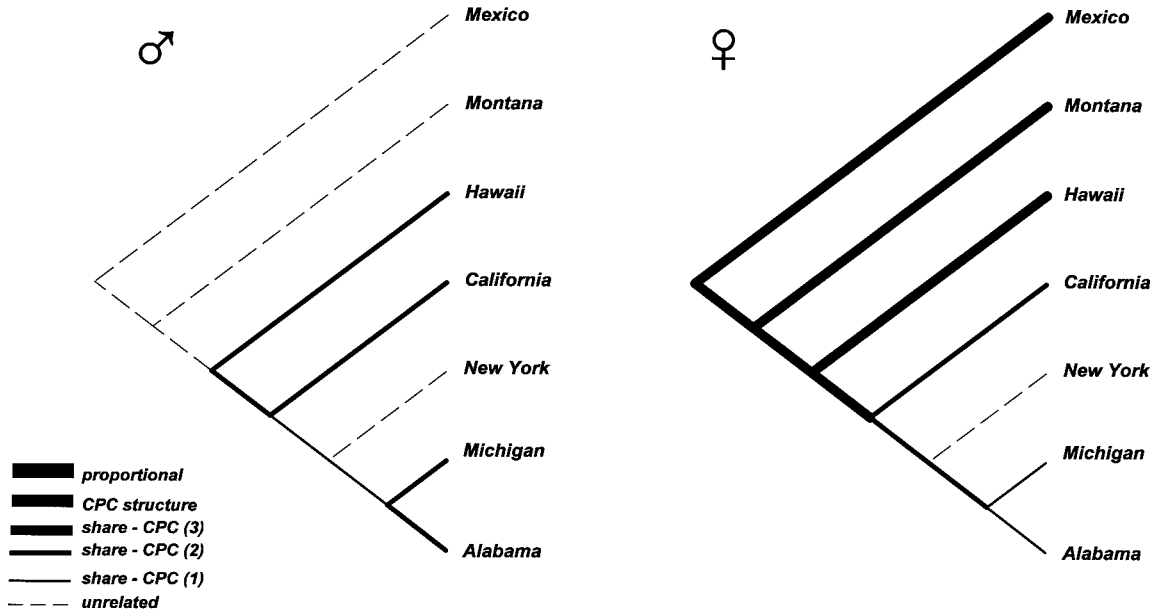

FIG. 4. Common principal components analysis of shared structure in covariance matrices of the house finch populations. Line thickness indicates the hierarchy of the shared common principal structure. Males and females differ in patterns of covariance structure, but in both sexes the hierarchy of shared morphological structure is different from the historical relationships among populations.

of genetic covariance and its effect on adaptive evolution is inconclusive. Of a special theoretical and empirical interest is the question of temporal persistence of genetic covariance structure. In particular, understanding temporal constancy of genetic covariance patterns can enable us to explore mechanisms behind population divergence (Lande 1985; Price and Grant 1985; Grant and Grant 1995; Cheverud 1996; Arnold and Phillips 1999; Camara and Pigliucci 1999; Roff et al. 1999; Badyaev and Foresman 2000).

Our study of morphological differentiation among house finch populations has produced three principal results. First, in both sexes, we found small but significant among-population differences in morphological correlation and covariance structure (Tables 3 and 5), in addition to population divergence in means and variances (Fig. 2, Table 2; A. V. Badyaev and G. E. Hill, unpubl. ms.). Second, among-population divergence was not proportional to the within-population correlation patterns (Table 4), and the morphological and a priori described historical hierarchy of taxa divergence were not congruent (Figs. 1, 4; Table 5). Third, population divergence in covariance structure, and more importantly, the hierarchy of this divergence was highly distinct between sexes (Tables 3, 5; Fig. 4). In at least one population of house finches, phenotypic correlations between morphological traits reliably estimated corresponding genetic correlations (Fig. 3). Thus, within- and among-population phenotypic divergence described in this study could reflect divergence in genetic covariance structure (see below). It is unlikely that random drift alone could accomplish multidirectional and, most importantly, sexually dimorphic divergence in covariance structure among house finch populations. Instead, this divergence is most likely due to population differences in locally distinct selection pressures acting on each sex.

High vector correlations among populations on all levels of comparison (Table 5) suggest that population differences in covariance structure are small. A low magnitude of morphological divergence among house finch populations is expected given the recent history of these populations and likely gene flow among some of the populations (Vazquez-Phillips 1992). What is more surprising is the significant multidirectionality of the population divergence, in which patterns of among-population divergence, even over the relatively short period of time, cannot be predicted by within-population morphological structure (Table 4). The proportionality among population covariance matrices is expected if genetic drift or consistent correlational selection are the primary mechanisms behind population divergence (Lande 1980; Lande and Arnold 1983; Lofsvold 1988; Armbruster 1991; Steppan 1997). However, the lack of proportionality in matrix evolution can also indicate unequal gene flow between populations, even with divergence under drift (Roff 1997). Nevertheless, drift is unlikely to account for sexually dimorphic patterns of population divergence found in this study (see below). Thus, our results are most parsimoniously explained by divergence under locally distinct and sexually dimorphic natural selection.

In the recent study of population divergence in the greenfinch (*Carduelis chloris*), Merilä and Björklund (1999) found distinct patterns of among- and within-population correlation and covariance patterns, and suggested that population divergence in this species was due to local selection pressures. In addition, divergence in covariance structure among greenfinch populations, despite generally conservative morphological patterns across cardueline finches (Björklund 1993, 1994; Björklund and Merilä 1993), was associated with low integration between bill traits and body traits (Merilä and Björklund 1999; see also Schluter and Smith 1986; van den Elzen et al. 1987; Merilä 1997; Badyaev and Martin 2000a). Decoupling of bill and body trait evolution in finches may be enabled by differential phenotypic and genetic patterns of growth between these groups of traits (Boag 1984; Björklund 1993; Badyaev and Martin 2000b). Contrary to other studies (Johnston 1973; Voss et al. 1990; Björklund 1993, 1994, 1996; Björklund and Merilä 1993; Badyaev 1997), we found that most of the recent morphological divergence in the house finch involved small and relatively independent changes in individual traits (Table 3) and not changes in general size (e.g., eigenvectors I and II in Table 4). However, this result may be expected for traits with initially low integration (e.g., feather traits and body mass).

Detailed analysis of covariance structure by CPCA revealed no congruence between hierarchical patterns of morphological divergence and phylogenetic relationships among house finch populations (Fig. 4). While some recently diverged populations (e.g., males of Michigan and Alabama populations) shared more covariance structure than did populations at a higher phylogenetic level, this pattern was not consistent. For example, female covariance patterns in recently diverged populations were less similar than covariance pattens of females in populations that diverged long ago, and in both sexes, morphological covariance structure of the recently established New York population was highly distinct from all other recent populations (Table 5, Fig. 4). Similar discordance between patterns of similarity in covariance matrices and geographic or phylogenetic relationships among taxa was found in several other studies (Riska 1985; Lofsvold 1986; Kohn and Atchley 1988; Cheverud 1989; Wagner 1990; Steppan 1997). Such divergence in covariance patterns among populations is most consistent with diverse responses to local fluctuating selection pressures (Riska 1985; Arnold 1992), especially in peripheral populations that are subject to frequent variation in population density (Felsenstein 1976; see also Power 1979).

Similarity between phenotypic and genetic correlation patterns in Montana house finches (Fig. 3) suggests that phenotypic correlations can reliably estimate genetic correlations in morphological traits (Cheverud 1988; Roff 1995; Preziosi and Roff 1998; Roff et al. 1999). However, we also found that in both sexes genetic correlations were consistently higher than the corresponding phenotypic correlations (Fig. 3; e.g., Koots et al. 1994). While this may reflect the estimation biases associated with small sample size (52 families; Cheverud 1988), the use of phenotypic correlations for predicting response to selection or drift in our study populations may overestimate the potential for independent evolution in each morphological trait, although producing qualitatively similar patterns compared to when genetic correlations are used.

Whether the strong phenotypic divergence found in this study reflects divergence in genetic covariance patterns depends on magnitude and constancy of environmental covariances across populations (Armbruster and Schwaegerle

1996; Roff et al. 1999). Large and variable environmental covariance can result in divergent phenotypic patterns despite constant genetic covariances. Alternatively, genetic covariance structure may evolve to reflect the contrasting selection pressures among populations (e.g., Cheverud 1996). Patterns of environmental covariance are rarely compared, and available empirical data is inconclusive, varying from unrelated environmental covariance structure (e.g., Kohn and Atchley 1988) to equal or proportional environmental covariance among populations (Arnold and Phillips 1999).

Field studies of house finches uncovered highly divergent patterns of natural selection among populations (Badyaev and Martin 2000a; Badyaev et al. 2000a). For example, wing length was the most frequent target of net selection in Montana, whereas tail length was the most frequent target of selection in Michigan. The high heritability of morphological traits in this study points to strong potential for morphological change in response to these contrasting selection pressures and may account for close concordance between patterns of current selection and phenotypic appearance of males and females in several house finch populations (Badyaev and Martin 2000a; Badyaev et al. 2000a). Fast and extensive divergence in morphologies across populations may be enabled by moderate levels of additive genetic variance in morphological traits throughout ontogeny and relatively low and variable phenotypic and genetic covariation among age-specific trait values in the house finch (Badyaev and Martin 2000b). Indeed, in Montana finches, morphological traits that were the target of most intense natural selection were the least ''constrained'' during ontogeny (i.e., had the lowest among-age and among-trait genetic correlations; Badyaev and Martin 2000b).

Field studies suggested that variation in sexual size dimorphism in the house finch is produced by changes in both male and female morphologies in response to highly dimorphic selection pressures in recently established populations (Badyaev et al. 2000a). Results of this study support this conclusion, but also point to more frequent morphological changes in males than in females (Fig. 4) that produce population variation in magnitude and direction of sexual dimorphism (e.g., Fig. 2). Higher historical lability of male morphology (Fig. 4) may reflect historically stronger selection on males compared to females, exacerbated by highly male-biased sex ratio of many populations of the house finch (e.g., Hill 1993). In addition, viability selection on juvenile house finches is significantly stronger on males compared to females (Badyaev et al. 2000b).

Sexually dimorphic evolution of morphological covariance structure found in this study (Tables 3–5, Fig. 4) is in apparent conflict with the observation of high (not significantly different from unity) between-sex genetic correlations in this species (A. V. Badyaev and L. A. Whittingham, unpubl. ms.). High genetic correlations between corresponding traits of sexes will strongly constrain the potential for variation in sexual dimorphism in adults (e.g., Price 1996; Merilä et al. 1998). However, selection acting on developmental time or other aspects of growth trajectories can strongly influence sexual dimorphism even in the presence of high between-sex genetic correlations of adults (e.g., Reeve and Fairbairn 1996). Indeed, in the house finch growth curves for males and females were not parallel, and growth of sexes was terminated at different times (e.g., for tail length, 43 days of age for females and 67 days of age for males), producing different levels of sexual dimorphism in adults (Badyaev et al. 2000b) Thus, extensive population divergence in sexual dimorphism could be enabled by changes in sexual dimorphism in growth parameters across populations of this species. The contribution of sexual dimorphism in growth to population divergence in adult sexual dimorphism can be assessed by comparing morphologies of fledglings from each populations (instead of adults used in this study) (J.A. Stamps, pers. comm., Badyaev et al. 2000b).

In summary, among-population divergence in morphological covariance structure in male and female house finches did not follow from the within-population covariance patterns. Hierarchical patterns of similarity of morphological structure were not congruent with a priori defined historical relationships among populations. Within- and among-population covariance patterns and patterns of evolution of covariance structure were highly sexually dimorphic. Taken together, these results suggest that extensive population variation in sexual dimorphism in the house finch was produced by locally distinct selection pressures acting on each sex.

Acknowledgments

We thank D. Emlen, C. Ghalambor, J. McKay, R. Ricklefs, P. Martin, D. Schluter, and M. Wootten for discussion and advice. We are grateful to two anonymous reviewers and T. A. Mousseau for a number of very helpful suggestions, most of which are incorporated here. We are grateful to the Cox family, J. and N. Van't Hof, the Mewaldt family, the Serano family, Pohakuloa State Endangered Species Facility, and B. McCue and the personnel of the Vigilante MiniStorage for logistical support and hospitality during collecting trips. GEH was supported by grants from the American Museum of Natural History, a grant from the Hawaii Audubon Society, and by National Science Foundation grant IBN-9722171. During writeup, AVB was supported by a postdoctoral fellowship from the College of Science and Mathematics at Auburn University. Banding and collecting were conducted under USFWS banding permit 21661 and collecting permit PRT-719116, and under Michigan (0065), Hawaii (88-30), New York (LPC89-428), California (0052), Alabama (06), Montana (21635), and La Secretaria de Relaciones Exteriores Mexico (302416) permits.

Literature Cited

American Ornithologists' Union. 1998. Check-list of North American birds. 7th ed. Lord Baltimore Press, Baltimore, MD.

Armbruster, W. S. 1991. Multilevel analysis of morphometric data from natural plant populations: insights into ontogenetic, genetic, and selective correlations in *Dalechampia scandens.* Evolution 45:1229–1244.

Armbruster, W. S., and K. E. Schwaegerle. 1996. Causes of covariation of phenotypic traits among populations. J. Evol. Biol. 9:261–276.

Arnold, S. J. 1992. Constraints on phenotypic evolution. Am. Nat. 140:S85–S107.

Arnold, S. J., and P. C. Phillips. 1999. Hierarchical comparison of genetic variance-covariance matrices. II. Coastal-inland diver-

gence in the garter snake, *Thamnophis elegans.* Evolution 53: 1516–1527.
Badyaev, A. V. 1997. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. Behav. Ecol. 8: 675–690.
Badyaev, A. V., and K. R. Foresman. 2000. Extreme environmental change and evolution: stress-induced morphological variation is strongly concordant with patterns of evolutionary change. Proc. R. Soc. Lond. B 267:371–379.
Badyaev, A. V., and T. E. Martin. 2000a. Sexual dimorphism in relation to current selection in the house finch. Evolution 54: 987–997.
———. 2000b. 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. 2000a. The evolution of sexual dimorphism in the house finch. II. Population divergence in relation to local selection. Evolution: *In press.*
Badyaev, A. V., L. A. Whittingham, and G. E. Hill. 2000b. The evolution of sexual dimorphism in the house finch. III. Developmental basis. Evolution: *In press.*
Berg, R. L. 1960. The ecological significance of correlational pleiades. Evolution 14:171–180.
Björklund, M. 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.
———. 1996. The importance of evolutionary constraints in an ecological time scale. Evol. Ecol. 10:423–431.
Björklund, M., and J. Merilä. 1993. Morphological differentiation in *Carduelis* finches: adaptive vs. constraint models. J. Evol. Biol. 6:359–373.
Boag, P. T. 1984. Growth and allometry of external morphology in Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos. J. Zool. 204:413–441.
Camara, M. D., and M. Pigliucci. 1999. Mutational contributions to genetic variance-covariance matrices: an experimental approach using induced mutations in *Arabidopsis thaliana.* Evolution 53:1692–1703.
Caum, E. L. 1933. The exotic birds of Hawaii. Occ. Pap. Bernice P. Bishop Mus. 10:1–56.
Cheverud, J. M. 1984. Quantitative genetics and developmental constraints in evolution by selection. J. Theor. Biol. 110: 115–171.
———. 1988. A comparison of genetic and phenotypic correlations. Evolution 42:958–968.
———. 1989. A comparative analysis of morphological variation pattern in the papionins. Evolution 43:1737–1747.
———. 1996. Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddle-back (*S. fuscicollis*) tamarins. J. Evol Biol. 9:5–42.
Cheverud, J. M., G. P. Wagner, and M. M. Dow. 1989. Methods for the comparative analysis of variation patterns. Syst. Zool. 38:201–213.
Deng, H.-W., V. Haynatzka, K. Spitze, and G. Haynatzki. 1999. The determination of genetic covariances and prediction of evolutionary trajectories based on a genetic correlation matrix. Evolution 53:1592–1599.
Dusi, J. L., and R. D. Dusi. 1982. House finch breeding in Auburn, Alabama. Alabama Birdlife 29:6.
Elliot, J. J., and R. S. Arbib. 1953. Origin and status of the house finch in the eastern United States. Auk 70:31–37.
Felsenstein, J. 1976. The theoretical population genetics of variable selection and migration. Annu. Rev. Genetics 10:253–280.
Flury, B. 1988. Common principal components and related multivariate models. Wiley, New York.
Goodin, J. T., and M. S. Johnson. 1992. Patterns of morphological covariation in *Partula.* Syst. Biol. 41:292–304.
Grant, P. R., and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. Evolution 49:241–251.
Grinnell, J. 1911. The linnet of the Hawaiian Islands: a problem in speciation. Univ. Calif. Pub. Zool. 7:179–195.
Johnston, R. F. 1973. Evolution in the house sparrow. IV. Replicate studies in genetic covariation. Syst. Zool. 22:219–226.
Hill, G. E. 1993. House finch. No. 46 *in* A. Poole, P. Stettenheim, and F. Gill, eds. The birds of North America. The Academy of Natural Sciences, Philadelphia, PA.
———. 1994. Geographic variation in male ornamentation and female mate preference in the house finch: a comparative test of models of sexual selection. Behav. Ecol. 5:64–73.
———. 1996. Subadult plumage in the house finch and tests of models for the evolution of delayed plumage maturation. Auk 113:858–874.
Klingenberg, C. P., and M. Zimmermann. 1992. Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. Am. Nat. 140:601–620.
Kohn, L. A. P., and W. R. Atchley. 1988. How similar are genetic correlation structures? Data from mice and rats. Evolution 42: 467–481.
Koots, K. R., J. P. Gibson, and J. W. Wilson. 1994. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Absts. 62: 825–853.
Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.
———. 1980. The genetic correlation between characters maintained by pleiotropic mutations. Genetics 94:203–215.
———. 1985. The dynamics of peak shifts and the patterns of morphological evolution. Paleobiology 12:343–354.
Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.
Lofsvold, D. 1986. Quantitative genetics of morphological differentiation in *Peromyscus.* I. Test of the homogeneity of genetic covariance structure among species and subspecies. Evolution 40:559–573.
———. 1988. Quantitative genetics of morphological differentiation in *Peromyscus.* II. Analysis of selection and drift. Evolution 42:54–67.
Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland, MA.
Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert. 1985. Developmental constraints and evolution. Q. Rev. Biol. 60:265–287.
Merilä, J. 1997. Quantitative trait and allozyme divergence in the greenfinch (*Carduelis chloris*; Fringillidae). Biol. J. Linn. Soc. 61:243–266.
Merilä, J., and M. Björklund. 1999. Population divergence and morphological integration in the Greenfinch (*Carduelis chloris*): evolution against the trajectory of least resistance? J. Evol. Biol. 12:103–112.
Merilä, J., B. C. Sheldon, and H. Ellegren. 1998. Quantitative genetics of sexual size dimorphism in the collared flycatcher, *Ficedula albicollis.* Evolution 52:870–876.
Moore, R. T. 1939. A review of the house finches of the subgenus *Burrica.* Condor 41:177–205.
Mundinger, P. C., and S. Hope. 1982. Expansion of the winter range of the house finch, 1947–1979. Am. Birds 36:347–353.
Payne, R. B. 1983. A distributional checklist of the birds of Michigan. Misc. Pub. Univ. Mich. Mus. Zool., no. 164.
Phillips, P. 1997. CPC: common principal analysis program. Available via http://wbar.uta.edu/software/cpc.html.
Phillips, P. C., and S. J. Arnold. 1999. Hierarchical comparison of genetic variance-covariance matrices. I. Using the Flury hierarchy. Evolution 53:1506–1515.
Power, D. M. 1979. Evolution in peripheral isolated populations: *Carpodacus* finches on the California islands. Evolution 33: 834–847.
Preziosi, R. F., and D. A. Roff. 1998. Evidence of genetic isolation between sexually monomorphic and sexually dimorphic traits in the waterstrider *Aquaruis remigis.* Heredity 81:92–99.
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., and P. R. Grant. 1985. The evolution of ontogeny in Darwin's finches: a quantitative genetic approach. Am. Nat. 125: 169–188.

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.

Riska, B. 1985. Group size and geographical variation of morphometric correlation. Evolution 39:792–803.

Roff, D. A. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. Heredity 74:481–490.

———. 1997. Evolutionary quantitative genetics. Chapman and Hall, New York.

Roff, D. A., and T. A. Mousseau. 1999. Does natural selection alter genetic architecture? An evaluation of quantitative genetic variation among populations of *Allonemobius socius* and *A. fasciatus.* J. Evol. Biol. 12:361–369.

Roff, D. A., T. A. Mousseau, and D. J. Howard. 1999. Variation in genetic architecture of calling song among populations of *Allonemobius socius, A. fasciatus,* and a hybrid population: drift or selection? Evolution 53:216–224.

Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance. Evolution 50:1766–1774.

Schluter, D., and J. N. M. Smith. 1986. Genetic and phenotypic correlations in a natural population of song sparrows. Biol. J. Linn. Soc. 29:23–36.

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.

Steppan, S. J. 1997. Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analyses. Evolution 51:571–586.

Turelli, M. 1988. Phenotypic evolution, constant covariances, and the maintenance of additive variance. Evolution 42:1342–1348.

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 Univiversity of Toronto, Toronto, Ontario, Canada.

Voss, R. S., L. S. Marcus, and P. Escalante. 1990. Morphological evolution in muroid rodents. I. Conservative patterns of craniometric covariance and their ontogenetic basis in the neotropical genus *Zygodontomys.* Evolution 44:1568–1587.

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.

———. 1990. A comparative study of morphological integration in *Apis mellifera* (Insecta, Hymenoptera). A. Zool. Syst. Evolut.-forsch. 28:48–61.

Wagner, G. P., G. Booth, and H. Bacheri-Chaichian. 1997. A population genetic theory of canalization. Evolution 51:329–347.

Wilkinson, G. S., K. Fowler, and L. Patridge. 1990. Resistance of genetic correlation structure to directional selection in *Drosophila melanogaster.* Evolution 44:1990–2003.

Zeng, Z. B. 1988. Long-term correlated response, interpopulation covariation and interspecific allometry. Evolution 42:363–374.

Corresponding Editor: T. Mousseau