Individual variation in growth trajectories: phenotypic and genetic correlations in ontogeny of the house finch (*Carpodacus mexicanus*)

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Abstract

We studied patterns of growth in a recently established natural population of the house finch (*Carpodacus mexicanus*) to examine whether phenotypic and genetic covariation among age-specific trait values is likely to constrain morphological change favoured by selection acting on adults. We found variable patterns of allometric relationships during ontogeny, and documented relatively weak covariations among ages or among traits in individual growth trajectories. Frequent compensatory growth largely cancelled out the initial differences among nestlings, potentially enabling house finches to raise offspring under diverse and unpredictable environmental conditions. Moderate levels of additive genetic variance in morphological traits throughout ontogeny, and relatively low and fluctuating phenotypic and genetic covariation among ages imply strong potential for evolutionary change in morphological traits under selection. This conclusion is consistent with the profound population-level divergence in morphological patterns that accompanied very successful colonization of most of North America by the house finch over the last 50 years.

Introduction

For evolution to occur, a population must have phenotypic and heritable variation. Individual differences in developmental processes produce the within-population morphological variation on which selection can act (Gould, 1977; Alberch *et al*., 1979; Alberch, 1982), while the potential of a population to respond to selection is limited by the extent to which ontogenetic variation is heritable (e.g. Atchley & Rutledge, 1980; Atchley, 1987; Cowley & Atchley, 1992). Thus, knowledge of phenotypic and genetic aspects of ontogenetic variation is essential for understanding the potential for evolutionary change in a population (Price & Grant, 1985; Kirkpatrick & Lofsvold, 1992; Grant & Grant, 1995; Björklund, 1996a; Larsson *et al*., 1998).

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Developmental systems are often under strong stabilizing selection to maintain homeostasis (e.g. Cheverud *et al*., 1983). Patterns of developmental and functional integration produced by this stabilizing selection strongly influence direction in which a population evolves, and often opposes selection pressures acting on adults (Cheverud, 1984; Lande, 1985). However, patterns of developmental variation and covariation often change during ontogeny (e.g. Zelditch & Carmichael, 1989; Cowley & Atchley, 1992). The observation that growth is often optimized with the local environmental conditions (reviewed in Gebhardt-Henrich & Richner, 1998) and the results of successful artificial selection on growth chronology and rate (e.g. Kinney, 1969; Atchley *et al*., 1997) suggest that growth trajectories themselves can evolve.

Empirical evidence from many species points to conservatism of developmental systems that often manifests itself in similarities between patterns of trait covariation within a particular ontogenetic stage (i.e. static allometry), and trait covariation across all ontogenetic stages (i.e. ontogenetic allometry) (e.g.

Cheverud, 1982; Creighton & Strauss, 1986; Wayne, 1986; Voss *et al*., 1990; Björklund, 1994; Fiorello & German, 1997). Such conservatism in ontogenies is often produced by close covariation among ages (e.g. Hazel *et al*., 1943; Eisen, 1976; Cheverud *et al*., 1983; Leamy & Cheverud, 1984). High genetic and phenotypic correlations and autocorrelations throughout ontogeny could strongly reduce independent variation of traits at different ages, limit the number of dimensions in growth trajectories, and thus present a powerful constraint on the evolution of ontogeny (McCarthy & Bakker, 1979; Kirkpatrick & Lofsvold, 1992; Klingenberg, 1996; Björklund, 1997).

Here we examine the patterns of phenotypic and genetic variation in growth of the house finch (*Carpodacus mexicanus*). We specifically examine whether available ontogenetic variation is likely to limit, or bias, the morphological changes favoured by strong current selection on adult finches in Montana (Badyaev & Martin, 2000). We address three questions. First, do growth trajectories vary among individuals within a population? Second, how constrained is the phenotypic and genetic variation across ages, and how likely is it to limit morphological change in adults? Third, is there heritable genetic variation in the ontogeny of morphological traits, and do heritability estimates vary during ontogeny? Finally, we discuss the potential ecological and evolutionary consequences of ontogenetic patterns found in the house finches.

Methods

Data collection

We studied a large, resident population of house finches that occupy an isolated area of suitable nesting habitat in western Montana (USA). The data were collected during March–July 1995–1999. The study site is located in an open field, and contained several hundred 2-m-high ornamental bushes used by finches for nesting, and several large coniferous trees used by finches for roosting. All resident finches were trapped during January–March and August–October, measured, and marked with a unique combination of one aluminium and three coloured plastic rings. All pairing and nesting affiliations of breeding adults were reliably determined (see Badyaev & Martin, 2000, for detailed description of field techniques). The hatching was continuously monitored and nestlings were individually marked within a few hours of hatching. Longitudinal growth data were collected on day 2 after hatching (hereafter age 2), 4, 6, 8, 10, 12, 14 and 16 (fledging day). After fledging, individually marked juveniles were repeatedly recaptured, and their age was categorized as follows: 25–40 days after hatching – age 33, 45–55 days – age 50, 60–70 days – age 65, 71–75 days – age 73, 80–85 days – age 83, and 87–144 days – age 117. In April 1995 and 1996 some 2–6-day-old nestlings were not measured, and thus sample sizes vary. Sample sizes were as follows: 88 nestlings from 29 nests were measured every 2 days for the entire nesting period (age 2 to age 16) and at age 33. Age-specific sample sizes: age 2, 89 nestlings (29 families); age 4 and age 6, 91 (29); age 8, 121 (41); age 10, 132 (50); age 12, 158 (61); age 14, 122 (51); age 16, 124 (52); age 33, 101 (47); age 50, 34 (16) males and 28 (16) females; age 65, 20 (17) males and 25 (19) females; age 73, 24 males and 22 females; age 83, 27 males and 29 females; age 117, 29 males and 23 females; and known-age sample of at least 2-year-old (adult) birds randomly selected for this study, 38 males and 36 females.

We measured (with digital calipers to an accuracy of 0.05 mm): bill length from angle of the skull to the tip of the upper mandible; bill width at the anterior end of the nostrils; bill depth in a vertical plane at the anterior end of the nostrils over both mandibles; tarsus length (left and right); wing (left and right, flattened), and body mass (with Pesola balance, to an accuracy of 0.05 g). 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. Repeatabilities for all traits are presented in Badyaev & Martin (2000). Briefly, in nestlings, error variance did not exceed 12% of the total variance and was the largest for bill width and depth (6–12%) and smallest for body mass, wing and tarsus (3–4%). All linear data were ln-transformed, body mass was cube-root transformed, and all data were zero-mean standardized before the analyses.

Data analysis

Static and ontogenetic allometries

We calculated bivariate allometry coefficients and compared them with the isometric vector coefficients. Bivariate allometry coefficient of a trait with size at a particular age is the standardized loading of that trait on the first principal component. The isometric vector has the standardized loadings $(1/p)^{1/2}$ where p is a number of traits. With six traits in this study $(1/p)^{1/2}$ was 0.408, so that the ratio of each trait's loading with 0.408 is the bivariate allometry coefficient of that trait with overall body size. Calculated for each age separately, these allometric relationships represent static allometric coefficients (Table 1). Because of significant deviations of age-specific vectors from isometry (e.g. Table 3), we also estimated bivariate coefficients of traits in relation to each other (Shea, 1985). Similarity of age-specific and isometric vectors was illustrated with vector correlations and corresponding angles. To estimate the significance of the angle between two vectors, we calculated the range of angles for the 10 000 pairs of random six-element vectors with randomly substituted elements (Cheverud, 1982; Klingenberg & Zimmerman, 1992).

To estimate variability in phenotypic ontogenetic vectors over the entire growth sequence, we performed

MANOVA of individuals and ages. Ontogenetic allometry coefficients (see below) can be estimated from the principal component analysis as the PC1 of the among-age matrix of the sum of squares and cross-products (SSCP matrix) (after Klingenberg, 1996). In this case, PC1 of the matrix is a vector of ontogenetic allometry. Standard errors for the PC1 were estimated from 2640 random resamplings with replacement of individual nestling values. In most studies, ontogenetic allometry coefficients are estimated as PC1 of the conventional principal component analysis on data pooled across all individuals and all ages (e.g. Cock, 1966; Gould, 1977; Shea, 1985). However, the use of the SSCP matrix allowed us to take full advantage of our longitudinal data set.

Individual variation in growth trajectories

First, for each trait we calculated phenotypic and genetic correlations among all age-specific trait values (see below) to construct phenotypic and genetic variation matrices for the growth sequence through ages 2 and 33. Second, to examine patterns of variation and covariation across growth sequence, we calculated longitudinal Common Principal Component (CPC) coefficients, eigenvalues and individual scores. CPC analysis was used because phenotypic and genetic patterns of covariation among morphological traits are partially similar across ontogenetic stages (e.g. Cock, 1966; Gould, 1977). The longitudinal CPC model assumes that the different ages share the same principal components, thus it is especially appropriate for studies such as ours (Klingenberg & Zimmermann, 1992; Klingenberg *et al*., 1996; Klingenberg, 1996). In addition, the longitudinal CPC model assumes that different components are uncorrelated not only within but also across ages (e.g. Klingenberg *et al*., 1996). Unlike the original measurements, in which separate analyses of covariation among ages for each age ignore the correlations among traits, each CPC can be analysed without any loss of information on correlation among traits (reviewed in Klingenberg *et al*., 1996; see also Flury, 1988; Klingenberg & Zimmermann, 1992). Third, to examine individual variability in ontogenetic trajectories, we calculated conventional principal component (PCA) coefficients from a covariance matrix of CP1 scores for each age (after Klingenberg, 1996). High covariation among ages would produce a highly integrated ontogeny where variation in one age would affect all subsequent groups. This ontogenetic pattern would produce consistently increasing or decreasing principal component (PC) loadings for each age (Björklund, 1993; Klingenberg, 1996; see also Kirkpatrick & Lofsvold, 1992). Highly variable and distinct PC1 loadings among ages, and especially loadings of the opposite signs indicate negative covariation among some ages. Such ontogenetic patterns are considered 'relatively unconstrained' and could be produced by compensatory growth of traits at different ages (Cheverud *et al*., 1983; Riska *et al*., 1984; Klingenberg, 1996; Björklund, 1997). We tested the uniqueness of individual eigenvalues with the SAS/IML program provided in Klingenberg (1995); we evaluated the CPC model for each age period with Flury's (1988) decomposition of chi-squared tests conducted with algorithms provided in Phillips (1997).

Genetic analysis

Genetic correlations among age-specific values for each of the six traits were calculated from the full-sib design (Falconer & Mackay, 1996, p. 312). Genetic relatedness among nestlings within each nest and between social parents and offspring (see below) was confirmed with the DNA fingerprinting analysis (A. V. Badyaev & P. O. Dunn, unpublished data). Although sex of all nestlings was determined by PCR amplification of the avian CHD gene (A. V. Badyaev & L. A Whittingham, unpublished data), sexes of offspring were pooled for these analyses because our sample size (88 nestlings from 29 families) was not sufficient to detect differences between sex-specific genetic correlations. Our sample was also too small to calculate standard errors for genetic correlation estimates.

The midparent–midoffspring regression for a trait can be used to estimate the genetic covariation between parents and offspring for a trait (Falconer & Mackay, 1996). We estimated the regression coefficients for ages 2–50, and standard errors for each age were generated by resampling with replacement of values for each family. Measurements of a character at different times, such as parental wing length and still-growing wing of offspring at day 5, are not identical traits, and thus cannot be used to estimate heritabilities (except at age 50 when most growth is completed). However, in this study we were interested in ontogenetic changes in parent–offspring genetic covariances that can be estimated by the midparent–midoffspring regressions. Moderate assortative mating for the measured traits in our population (r) can inflate midparent variance, and thus the variance for each trait was adjusted by $(1 + r)$ (Falconer & Mackay, 1996, p. 179). Male and female phenotypic variances for the measured traits were equal (Badyaev & Martin, 2000; Badyaev & Hill, in review), and therefore are unlikely to bias our estimates of genetic covariances.

Results

Nestling growth and static allometry

Variation in static allometric relationships illustrates the differences among traits in an onset and intensity of growth (Tables 1 and 2, Fig. 1). The most pronounced contrast in growth was between bill traits (bill length, depth, width) and body traits (wing, tarsus, body mass). Overall, relative increase in body traits was most prominent early in ontogeny (i.e. before fledging, Fig. 1, Table 1), while relative increase in bill traits was most pronounced late in ontogeny (after fledging, Fig. 1, Table 2). At age 2 most traits had a negative allometric

Table 1 Multivariate allometry and integration of morphological traits during early ontogeny of the house finch. Shown are the first eigenvectors, and the proportion of total variance (%) accounted for by the first eigenvalue from the variance–covariance matrix of ln-transformed values.

Trait	Age 2	Age 4	Age 6	Age 8	Age 10	Age 12	Age 14	Age 16
Bill length	0.397	0.534	0.324	0.473	0.121	0.241	0.615	0.531
Bill depth	0.442	0.533	0.403	0.101	0.135	0.165	0.497	0.352
Bill width	0.397	0.127	0.399	0.173	0.295	0.231	0.431	0.416
Wing	0.395	0.589	0.494	0.734	0.654	0.601	0.424	0.521
Tarsus	0.450	0.329	0.426	0.350	0.370	0.531	0.350	0.451
Body mass	0.364	0.012	0.444	0.602	0.605	0.495	0.325	0.391
% var	83.18	58.35	81.32	58.71	43.87	52.71	49.71	44.65

relationship (i.e. relationship less than one) to tarsus length and bill depth (e.g. wing/tarsus = 0.395/0.450 = 0.878; bill length/bill depth = 0.397/0.442 = 0.898). Growth pattern from age 4 to age 12 was dominated by negative allometries of traits in relation to wing and body mass. These patterns changed drastically near (ages 14 and 16) and after fledging when most traits had negative allometries in relation to bill traits, especially bill length and width (Tables 1 and 2). In addition to these general patterns, at age 4, bill length, bill depth, and wing were larger relative to other traits. At age 12, relative increase in tarsi and wing were the most prominent in relation to other traits.

The first eigenvector showed considerable departures from isometry throughout ontogeny; the angle between the first eigenvector and the isometric vector ranged from 4.4° at age 2 to 29.8° at age 10 (Table 3). Angles between vectors for all ages were smaller than angles of any of the randomly generated pairs of vectors. The most significant deviations from isometry (e.g. 35.8° at age 73) occurred after fledging; these deviations were most likely associated with accelerated growth of sexually dimorphic traits in males.

Ontogenetic allometry and individual variation in growth trajectories

Analyses of ontogenetic allometry revealed variable phenotypic patterns of development (Fig. 2). The first eigenvalue of the SSCP among-age phenotypic matrix accounted for 59.4% of the total variance, and the first two eigenvalues accounted for 71.1% of the total variance. Static and ontogenetic allometries were distinct (Fig. 2), possibly reflecting the contrast between early and late maturing traits (i.e. body vs. bill traits, Tables 1 and 2, Fig. 1).

Phenotypic and genetic correlations (calculated from the full-sib analyses, see Methods) across age groups (not shown) were generally low and often near zero or slightly negative. Age-specific covariance matrices, both phenotypic and genetic, were mostly distinct, even between consecutive ages (e.g. phenotypic matrices for ages 6 and 8, ages 8 and 10, and ages 16 and 33 shared no common principal components (CPCs), $\chi^2 = 62.7$, d.f. = 5, $P < 0.001$; $\chi^2 = 22.5$, d.f. = 5, $P < 0.001$; and $\chi^2 = 20.4$, d.f. = 5, $P = 0.001$, respectively). The most similar were ages 10 and 12, where matrices shared three of four CPCs: $\chi^2 = 18.7$, d.f. = 12, $P = 0.05$; and ages 12 and 14, where matrices shared two CPCs: $\chi^2 = 23.1$, d.f. = 9, $P = 0.006$.

Relatively low phenotypic and genetic covariation across ages, and high individual variation in covariance patterns were evident in the patterns of age-specific variability, where the largest eigenvalue of the PCA on CPC1 scores accounted for only 45.4% of the total variation in phenotypic matrix (44.8% in genetic correlation matrix), and the first three eigenvalues accounted for 92.0% and 87.8% of the total variation, respectively

Table 2 Multivariate allometry and integration of morphological traits during late ontogeny of the house finch. Shown are the first eigenvectors and the proportion of total variance (%) accounted for by the first eigenvalue from the variance–covariance matrix of ln-transformed values.

Trait	Age 33	Age 50*	Age 65	Age 73	Age 83	Age 117	Adults
Bill length	0.618	0.621	0.386	0.631	0.521	0.571	0.448
Bill depth	0.475	0.363	0.341	0.478	0.592	0.341	0.367
Bill width	0.481	0.442	0.682	0.641	0.454	0.350	0.458
Wing	0.201	0.301	0.321	0.087	0.109	0.112	0.316
Tarsus	0.110	0.130	0.159	0.091	0.053	0.021	0.252
Body mass	0.417	0.355	0.121	0.127	0.239	0.370	0.540
% var	53.17	49.12	35.65	33.50	41.20	37.40	40.10

*Effects of sex are removed in ANCOVA for ages 50 and older.

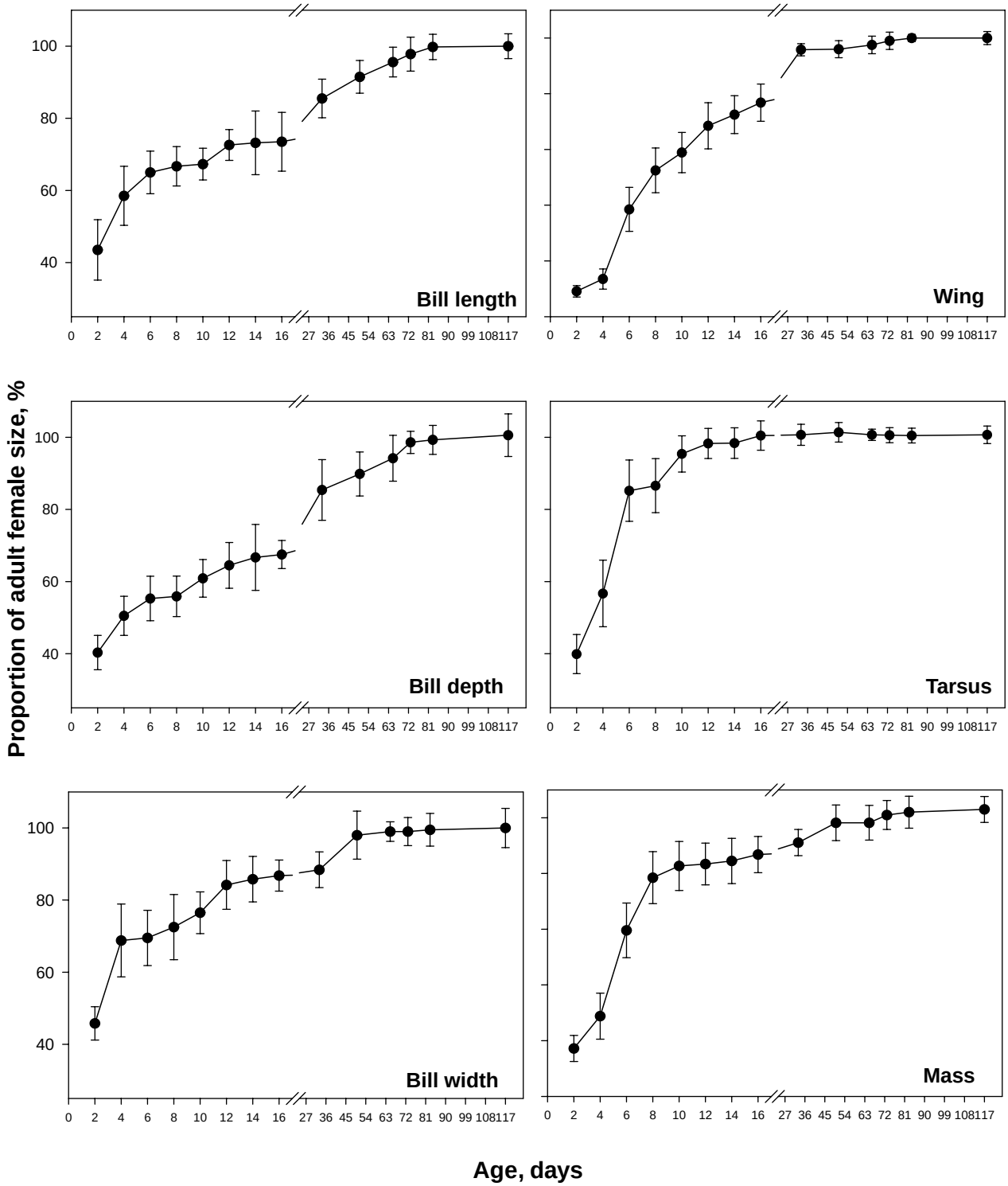

Fig. 1 Growth curves (mean ± SE) illustrating the relationship between age (days) and the proportion of adult size (size of adult female) for bill traits and body traits in the house finch.

Table 3 Ontogenetic vector correlations (r_v) and corresponding angles (α) in the house finch. Shown are correlations and angles between age-specific vector and an isometric vector.

Age	r_v	α
Age 2	0.997	4.4°
Age 4	0.850	31.8°
Age 6	0.992	7.3°
Age 8	0.875	28.9°
Age 10	0.868	29.8°
Age 12	0.912	24.2°
Age 14	0.977	12.3°
Age 16	0.989	8.5°
Age 33	0.911	24.4°
Age 50	0.928	21.9°
Age 65	0.878	28.6°
Age 73	0.811	35.8°
Age 83	0.847	32.1°
Age 117	0.852	31.6°
Adults	0.972	13.6°

(Fig. 3A,B). None of the PCs accounted for most of the variation during *all* ages (Fig. 3). Instead, PC1 of the phenotypic matrix primarily explained variability during early ages in contrast to ages 4, 14 and 33, PC2 accounted for variability in ages 4, and 8–33 in contrast to ages 2 and 6, and PC3 mostly explained variation during the first 4 days of the nestling period (Fig. 3). In genetic correlation matrix, PC1 contrasted variation at ages 2, 8 and 14 with ages 4, 6, 12, 16 and 33. No single component accounted for variability in all ages simultaneously (Fig. 3). While a large portion of variation in growth was still associated with one growth trajectory (PC1, Fig. 3II), suggesting some constraints during growth, there were at least three distinct directions (eigenfunctions) for which considerable phenotypic variation is present.

The negative covariance observed between consecutive stages points to occurrence of compensatory growth, especially between ages 2 and 4, and 16 and 33. Such compensatory growth is likely to balance the differences that were present among nestlings in the earlier ages (Fig. 4), and closely corresponds to the periods of maximum growth gains (Fig. 1). A decrease in both total phenotypic variance of standardized untransformed traits with age (Fig. 4) and in sample variances for principal components (expressed as eigenvalues, Tables 1 and 2) strongly suggests that compensatory growth is widespread in ontogeny of the house finch.

Ontogenetic variation in genetic covariance between adult and juvenile traits

Patterns of genetic covariation between midparent and midoffspring were similar among traits (Fig. 5). The genetic covariances generally increased with age, and most reached significance by age 12 (Fig. 5). All covariations were significantly different from zero after age 14, and by age 50, when most growth is completed (Fig. 1), midparent vs. midoffspring regression can be used to estimate heritabilities for each trait. Estimates of heritabilities at age 50 were high and varied from 0.35 to 0.49 for bill traits, and from 0.22 to 0.41 for body traits.

Discussion

Evolutionary change in morphology requires heritable ontogenetic variation. Thus, understanding phenotypic and genetic parameters of growth trajectories and their variation among individuals in a population is important for predicting evolutionary change. Several problems need to be investigated. First, examination of an association between morphological patterns of adults and

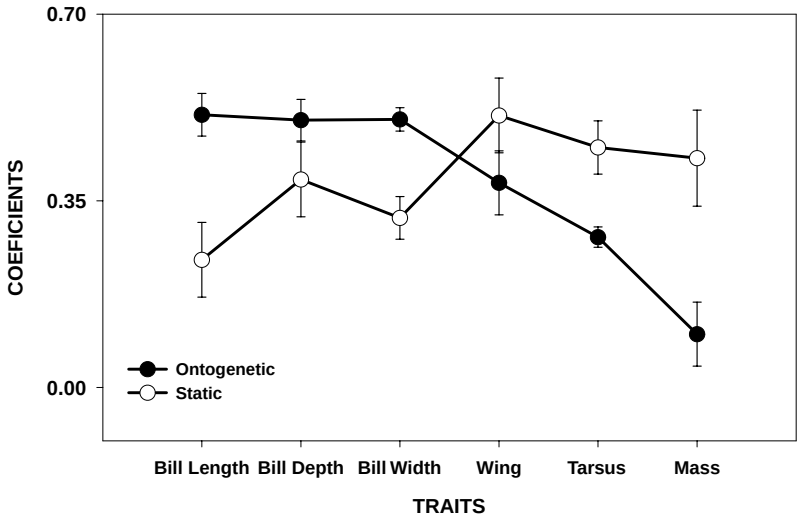

Fig. 2 Static and ontogenetic allometry of the house finch growth. Static allometry is presented as the first common component (CPC1) of covariance matrices for each age; ontogenetic allometry is presented as the first principal component (PC1) of the among-age matrix of sums of squares and cross-products. Error bars are the bootstrapped SE of the estimates obtained by resampling of the entire ontogenetic sequence of an individual.

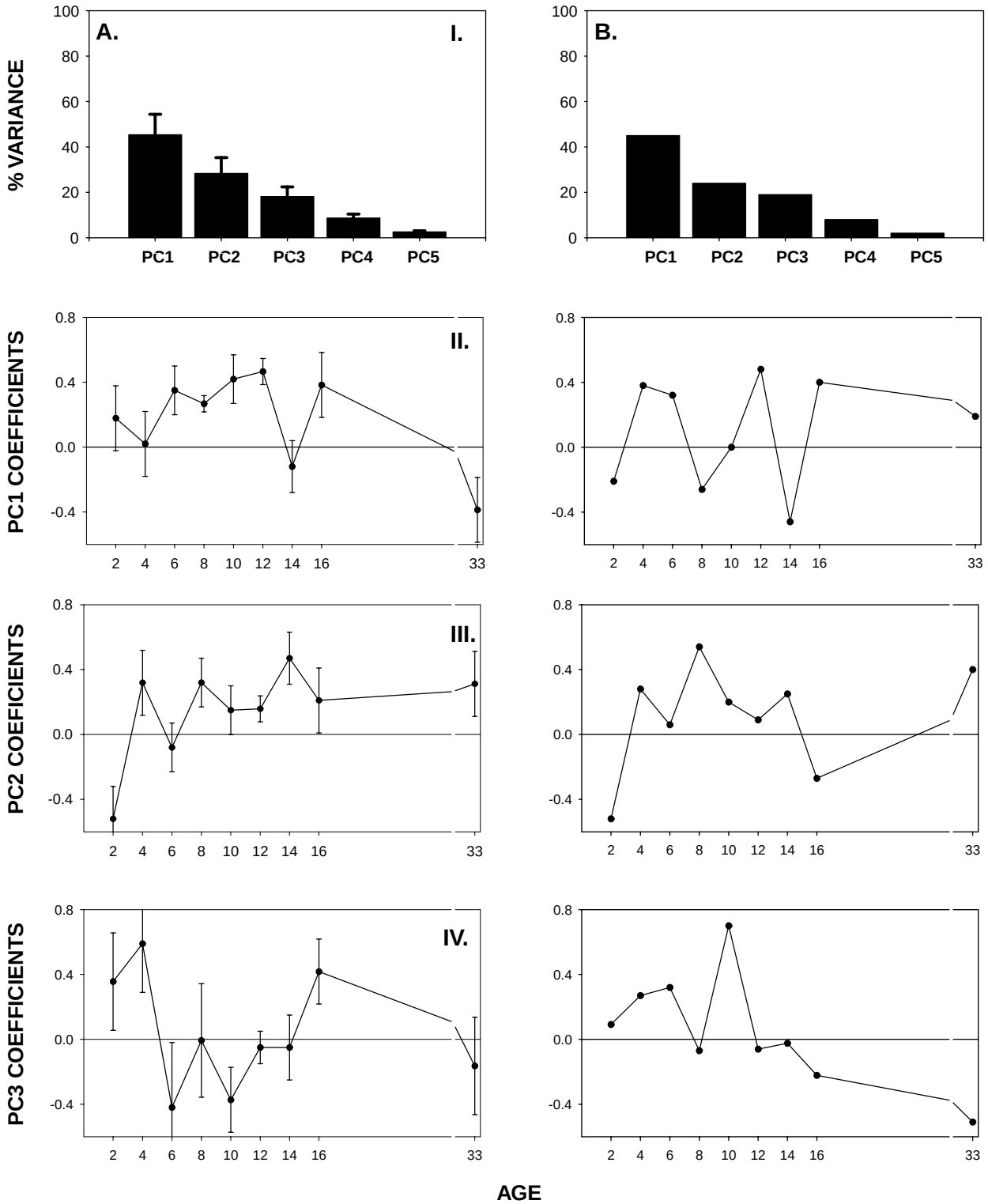

Fig. 3 Patterns of individual phenotypic (A) and genetic (B) variation and covariation in growth trajectories across ages of the house finches. (I) Percentage of total variance explained by principal-component (PC) eigenvalues from covariance matrix of individual scores of the first common component (CPC) in all ages. Coefficients of the (II) PC1, (III) PC2 and (IV) PC3 for each age group. Error bars are the bootstrapped standard errors, and are only estimated for the phenotypic correlations.

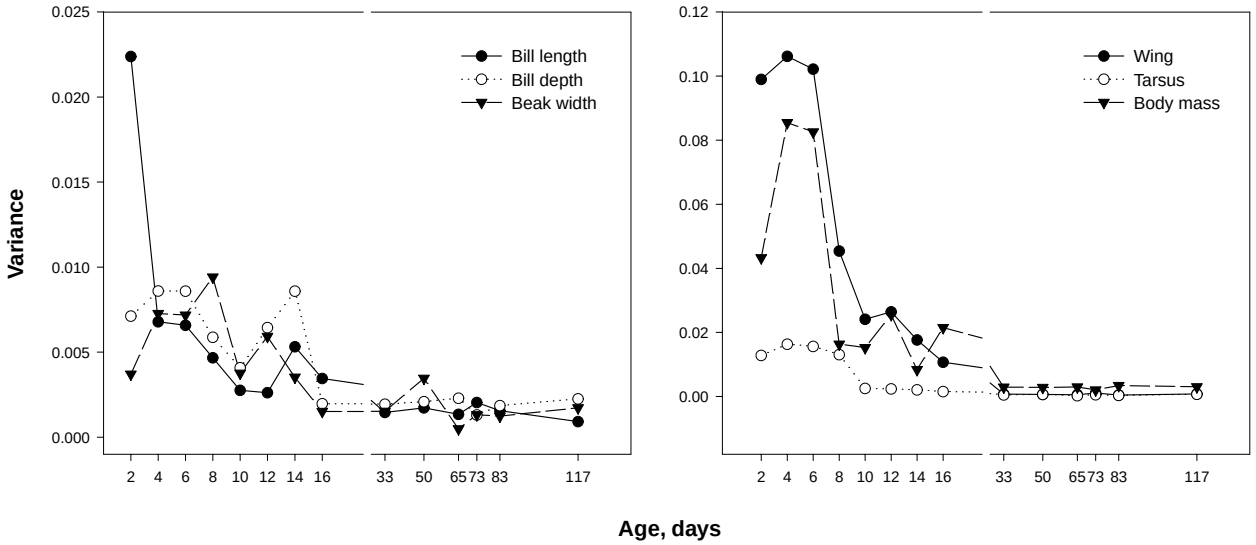

Fig. 4 Total phenotypic variance of untransformed trait values in relation to age in the house finch.

morphological patterns prevailing during growth can reveal how closely adult static allometries correlate with ontogenetic allometries. Similarities between these allometries would imply that adult morphological patterns could be reliably predicted from morphological patterns during developments (e.g. Voss *et al.*, 1990; Klingenberg & Zimmermann, 1992; Björklund, 1996b). Second, analyses of phenotypic and genetic covariation among traits at different ages can indicate potential for evolutionary change in ontogenies (Cheverud, 1984; Lande, 1985; Cowley & Atchley, 1992). Specifically, close covariation among ages implies that selection on a trait at one age would result in changes in this trait in consecutive ages (e.g. Riska *et al.*, 1984; Kirkpatrick & Lofsvold, 1992). In addition, if close covariation among ages is accompanied by close integration among traits at each age, the overall short-term change in morphology will be limited to a few directions only, irrespective of directions favoured by current selection (Cheverud *et al.*, 1983; Cheverud, 1984; Wagner, 1988; Kirkpatrick & Lofsvold, 1992). Third, the amount of additive genetic variance at each age, and differences among ages in the amount of genetic variance could strongly affect the evolutionary change (e.g. Atchley, 1987; van Noordwijk & Marks, 1998).

Static allometric relationships varied during development mostly due to differences in the onset of growth and growth rates between bill and body traits (Tables 1 and 2). Growth in body size traits (i.e. tarsus, wing and body mass) started earlier and continued at higher rates compared with later maturing bill traits (bill length, width and depth) (Tables 1 and 2, Figs 1 and 2). Heterochrony in body and bill traits apparently is common in Cardueline and Emberizidae finches (Grant, 1981; Boag, 1984; Björklund, 1994), and may be related to the resources preferentially allocated to the traits with immediate functional importance at a certain age (e.g. O'Connor, 1977; reviewed in Starck, 1998). For example, fast growth in body mass may be a priority for thermoregulatory reasons (Cane, 1993), while rapid growth of tarsi may be adaptive for intrabrood competition (Monk, 1998), or for early leaving of the nest in areas with high nest predation (e.g. Ricklefs, 1968; Björklund, 1994).

The contrast between early and late maturing traits was illustrated in differences between ontogenetic and static allometries of nestlings (Fig. 2; see also Boag, 1984; Björklund, 1994). Close concordance between static and ontogenetic allometries would imply that most of the morphological variation among individuals results from variable growth along relatively constant allometric trajectories (e.g. Cock, 1966; Leamy & Bradley, 1982). Because it is clearly not the case in our study population (Tables 1–3), static allometry of adult finches does not immediately follow from ontogenetic allometric variation.

Principal component analysis of CPC scores for each age provides an estimate of individual variation in phenotypic and genetic patterns in ontogenies (Klingenberg *et al.*, 1996). If most of the total variation is limited to the first principal component (i.e. approximation of size at each age), this would imply a constraint on changes in directions other than an increase or decrease in overall size (Klingenberg, 1996; see also Kirkpatrick & Lofsvold, 1992; Björklund, 1993, 1996a, 1997; Schluter, 1996). We found that in both genetic and phenotypic matrices, the first eigenfunction illustrated variation in only some ages, and accounted for only a moderate amount of the total ontogenetic variation (Fig. 3). Large amounts of variation accounted for by the first three eigenvalues implies significant potential for evolutionary change in these three directions. This pattern also points to significant constraints in ontogeny of the house finch –

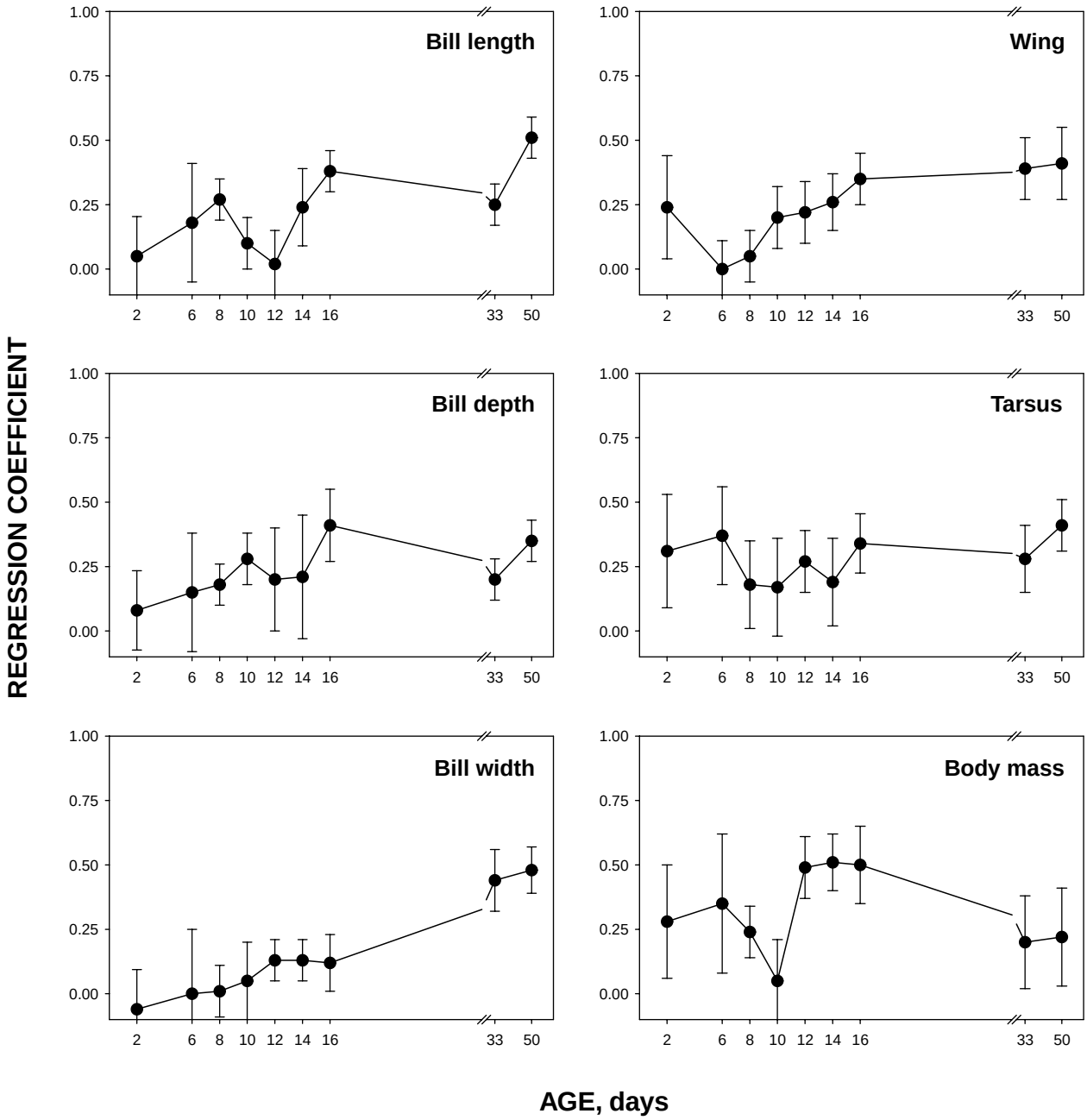

Fig. 5 Ontogenetic variation in genetic covariance between midparent and midoffspring traits for each age in the house finch. Values at age 50 estimate heritability of a trait.

no variation was present in about half of all possible eigenvalues (Fig. 3). Thus, our results suggest that as long as selection favours morphological change in directions described by these three eigenvalues, phenotypic and genetic constraints during ontogeny are unlikely to strongly limit evolutionary change.

Several recent studies documented that close covariation among age-specific trait values, and low individual variation for growth trajectories lead to the general lack of genetic and phenotypic variation for ontogenetic change other than change in overall size (e.g. Kirkpatrick & Lofsvold, 1992, and references therein; Klingenberg, 1996). For example, Björklund (1993) used the infinite-dimensions method (Kirkpatrick & Lofsvold, 1992) to analyse the phenotypic variation in ontogeny of three Cardueline finches, including a close relative of the

house finch – common rosefinch (*C. erythrinus*). He found significant phenotypic ontogenetic variation in only one growth trajectory – the 'size' trajectory that accounted for the largest amount of variation in all ages simultaneously (see also Björklund, 1997). Klingenberg's (1996) re-analysis of available data-sets on growth indicated that phenotypic constraints on growth may not be as stringent when analyses account for autocorrelation among ages. Our analyses, using common principal component scores, suggest that while there are strong constraints in the ontogeny of the house finch (i.e. variation was limited to three directions), the amount of ontogenetic phenotypic and genetic variation is not as strongly constrained as in other finches, and production of a morphological change within limits outlined by the three dimensions (eigenvectors) may be possible. These results may provide an explanation for the patterns of strong multivariate morphological divergence among house finch populations (Badyaev & Hill, in review). The house finch populations in Mexico, Alabama, California, Michigan, Hawaii, New York and Montana were significantly different not only in overall size but also in morphological covariance patterns, i.e. in 'shape' (Badyaev & Hill, in review). Lack of concordance between within- and among-population morphological variation suggested that persistent constrains on morphological change are unlikely in this species (see also Merilä & Björklund, 1999, for a similar result in populations of the Greenfinch, *Carduelis chloris*).

While the first eigenvalue accounted for only a moderate amount of the total variation, the first two eigenvalues summarized a considerable amount of the variation (Fig. 3), suggesting the alternation of positive and negative covariations between consecutive ages (see principal component plots, Fig. 3II–IV). Absence of strong autocorrelation among ages, and negative covariations between ages suggests widespread occurrence of compensatory growth in ontogeny of the house finch in our population. Patterns of compensatory growth are evident in the ontogenetic variance patterns (Fig. 4); total phenotypic variance of untransformed traits is high during early ages and then reduced (compensated for) as individual growth trajectories converge to a 'target' morphology (*sensu* Tanner, 1963) at the end of growth (Fig. 4).

Compensatory growth is adaptive if it enables individuals to achieve the same adult size under diverse environmental conditions (Riska *et al*., 1984; Cooch *et al*., 1991; Smith & Wettermark, 1995; Larsson *et al*., 1998). For example, accelerated compensatory growth is often associated with intensive feeding after periods of malnutrition (reviewed in Gebhardt-Henrich & Richner, 1998). The house finches in the recently established population in Montana often hatch nestlings under extreme environmental conditions. First nests are initiated in late February to March when repeated snow storms and prolonged subzero temperatures severely limit food provisioning by parents (A.V.B., unpublished data). Under such unpredictable and harsh conditions, flexible intrabrood growth rates should be highly beneficial. Under these conditions, selection can act on correlations among traits and among ages, strongly favouring individuals which are able to compensate for environmental fluctuations with flexible (among traits and among ages) growth rates. Later in the nestling period, during more favourable conditions, initial differences in size are often compensated by periods of accelerated growth (Fig. 4). In early nesting pairs, females often start incubating with the first of the five eggs, which leads to pronounced (up to 4 days) hatching asynchrony in our study population (A.V.B., personal observation). In turn, hatching asynchrony leads to strong initial differences in size within a brood. Incubation from the first egg and pronounced differences in hatchling sizes are common in other cardueline finches, especially those that breed at high elevations (Badyaev, 1997a,b). While compensatory growth is widespread in several high-elevation finches, among-age ontogenetic covariations are often high (Badyaev, 1993, 1994), similar to that described by Björklund (1993). However, the house finch populations are exposed to a greater range and variation in environmental conditions that any extant species of cardueline finches (e.g. Badyaev & Ghalambor, 1998). Thus, low covariation among ages and strong compensatory growth during periods of maximum growth gains could be especially beneficial for this species.

Genetic covariations among adult and juvenile traits were significant for most traits, starting at age 12 and older. Genetic covariations at age 50 approached the estimates of heritability for adult traits (Badyaev & Martin, 2000). For all traits, except body mass, genetic associations between adults and juveniles were generally high at late ages (Fig. 5). Body mass had relatively low heritability, but also low repeatability in adults (Badyaev & Martin, 2000). Because the amount of evolutionary change is determined by the amount of additive genetic variance at each age where selection acts, moderate genetic covariations indicate that evolutionary response to selection is likely to be fast in the house finch. Strong response to selection is further favoured by relatively low covariation among ages and traits, thus providing both opportunities for morphological change in several directions and opportunities for selection to act on individual traits. Furthermore, traits examined in this study are the targets of current selection on adult finches in the Montana population (Badyaev & Martin, 2000).

This study suggests that the considerable amount of variation in individual ontogenetic trajectories, comparatively low genetic and phenotypic covariations among age-specific trait values, and significant genetic variance throughout most of the ontogeny may have accounted for close congruence between current net selection and current morphology in adult house finches in our study

population (Badyaev & Martin, 2000). Evolutionary response to selection could also manifest itself in a strong adaptive divergence in morphological patterns among recently established house finch populations (Badyaev & Hill, in review). In addition, widespread occurrence of compensatory growth in the house finch ontogeny may have allowed development under a wide variety of environmental conditions, and ultimately contributed to the unusually high colonization abilities of this species.

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References

Alberch, P., Gould, S.J., Oster, G. & Wake, D. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* **5**: 296–317.

Alberch, P. 1982. Developmental constraints in evolutionary processes. In: *Evolution and Development* (J. T. Bonner, ed.), pp. 313–332. Springer-Verlag, Berlin.

Atchley, W.R. 1987. Developmental quantitative genetics and the evolution of ontogenies. *Evolution* **41**: 316–330.

Atchley, W.R. & Rutledge, J.J. 1980. Genetic components of size and shape. I. Dynamics of components of phenotypic variability and covariability during ontogeny in the laboratory rat. *Evolution* **34**: 1161–1173.

Atchley, W.R., Xu, S. & Cowley, D.E. 1997. Altering developmental trajectories in mice by restricted index selection. *Genetics* **146**: 629–640.

Badyaev, A.V. 1993. Breeding biology of the gold-fronted serin (*Serinus pusillus*) in a subalpine zone of Pamir Mountains. *Biol. Sciences (Biol. Nauk)* **348**: 89–99.

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

Badyaev, A.V. 1997a. Avian life history variation along altitudinal gradients: an example with Cardueline finches. *Oecologia* **111**: 357–364.

Badyaev, A.V. 1997b. Covariation between sexually selected and life history traits: an example with Cardueline finches. *Oikos* **80**: 128–138.

Badyaev, A.V. & Ghalambor, C.K. 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. & Martin, T.E. 2000. Sexual dimorphism in relation to current selection in the house finch. *Evolution* **55**: in press.

Björklund, M. 1993. Phenotypic variation of growth trajectories in finches. *Evolution* **47**: 1506–1514.

Björklund, M. 1994. Allometric relations in three species of finches (Aves: Fringillidae). *J. Zool.* **233**: 657–668.

Björklund, M. 1996a. Similarity of growth among great tits (*Parus major*) and blue tits (*P. caeruleus*). *Biol. J. Linn. Soc.* **58**: 343–355.

Björklund, M. 1996b. The importance of evolutionary constraints in an ecological time scale. *Evol. Ecol.* **10**: 423–431.

Björklund, M. 1997. Variation in growth in the blue tit (*Parus caeruleus*). *J. Evol. Biol.* **10**: 139–155.

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.

Cane, W.P. 1993. The ontogeny of postcranial integration in the common tern, *Sterna hirundo*. *Evolution* **47**: 1138–1151.

Cheverud, J.M. 1982. Relationships among ontogenetic, static, and evolutionary allometry. *Am. J. Phys. Anthropol.* **59**: 139–149.

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

Cheverud, J.M., Rutledge, J.J. & Atchley, W.R. 1983. Quantitative genetics of development: genetic correlations among age-specific trait values and the evolution of ontogeny. *Evolution* **37**: 895–905.

Cock, A.G. 1966. Genetical aspects of metrical growth and form in animals. *Q. Rev. Biol.* **41**: 131–190.

Cooch, E.G., Lank, D.B., Dzubin, A., Rockwell, R.F. & Cooke, F. 1991. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology* **72**: 503–512.

Cowley, D.E. & Atchley, W.R. 1992. Quantitative genetic models for development, epigenetic selection, and phenotypic evolution. *Evolution* **46**: 477–494.

Creighton, G.K. & Strauss, R.E. 1986. Comparative patterns of growth and development in cricetine rodents and the evolution of ontogeny. *Evolution* **40**: 94–106.

Eisen, E.J. 1976. Results of growth curve analysis in mice and rats. *J. Anim. Sci.* **42**: 1008–1023.

Falconer, D.S. & Mackay, T.F.C. 1996. *Introduction to Quantitative Genetics*. Longman, London.

Fiorello, C.V. & German, R.Z. 1997. Heterochrony within species: craniofacial growth in giant, standard, and dwarf rabbits. *Evolution* **51**: 250–261.

Flury, B. 1988. *Common Principal Components and Related Multivariate Models*. Wiley, New York.

Gebhardt-Henrich, S. & Richner, H. 1998. Causes of growth variation and its consequences for fitness. *Avian Growth and Development* (J. M. Starck & R. E. Ricklefs, eds), pp. 324–339. Oxford University Press, Oxford.

Gould, S.J. 1977. *Ontogeny and Phylogeny*. Harvard University Press, Cambridge, Mass.

Grant, P.R. 1981. Patterns of growth in Darwin's finches. *Proc. Roy. Soc. Lond. B* **212**: 403–432.

Grant, P.R. & Grant, B.R. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* **49**: 241–251.

Hazel, L.N., Baker, M.L. & Reinmiller, C.F. 1943. Genetic and environmental correlations between the growth rates of pigs at different ages. *J. Anim. Sci.* **2**: 118–128.

Kinney, T.B. Jr. 1969. *A Summary of Reported Estimates of Heritabilities and of Genetic and Phenotypic Correlations for Traits of Chickens*. Agric. Handbook 363. USDA, Washington, DC.

Kirkpatrick, M. & Lofsvold, D. 1992. Measuring selection and constraints in the evolution of growth. *Evolution* **46**: 954–971.

Klingenberg, C.P. 1995. *Common Principal Components for Dependent Random Vectors*. http://life.bio.sunysb.edu/morph/dcpc.exe.

Klingenberg, C.P. 1996. Individual variation of ontogenies: a longitudinal study of growth and timing. *Evolution* **50**: 2412–2428.

Klingenberg, C.P. & Zimmermann, M. 1992. Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. *Am. Nat.* **140**: 601–620.

Klingenberg, C.P., Neuenschwander, B.E. & Flury, B.D. 1996. Ontogeny and individual variation: analysis of patterned covariance matrices with common principal components. *Syst. Biol.* **45**: 135–150.

Lande, R. 1985. The dynamics of peak shifts and the patterns of morphological evolution. *Paleobiology* **12**: 343–354.

Larsson, K., der Jeugd, H.P., van der Veen, I.T. & Forslund, P. 1998. Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. *Evolution* **52**: 1169–1184.

Leamy, L. & Bradley, D. 1982. Static and growth allometry of morphometric traits in randombred house mice. *Evolution* **36**: 1200–1212.

Leamy, L. & Cheverud, J.M. 1984. Quantitative genetics and the evolution of ontogeny. II Genetic and environmental correlations among age-specific characters in randombred house mice. *Growth* **48**: 339–353.

McCarthy, J.C. & Bakker, H. 1979. The effects of selection for different combinations of weights at two ages on the growth curve of mice. *Theoret. Appl. Genet.* **55**: 57–65.

Merilä, J. & Björklund, M. 1999. Population divergence and morphological integration in the Greenfinch (*Carduelis chloris*) – evolution against the trajectory of least resistance? *J. Evol. Biol.* **12**: 103–112.

Monk, D.S. 1998. Parental allocation by birds: Analysis of parent and sibling interactions with a new statistical model. *Proc. VII Congr. Internat. Soc. Behav. Ecol.* Pacific Grove, CA.

van Noordwijk, A.J. & Marks, H.L. 1998. Genetic aspects of growth. In: *Avian Growth and Development* (J. M. Starck & R. E. Ricklefs, eds), pp. 305–323. Oxford University Press, Oxford.

O'Connor, R.J. 1977. Differential growth and body composition in altricial passerines. *Ibis* **119**: 147–166.

Phillips, P. 1997. *CPC – Common Principal Analysis Program*: http://wbar.uta.edu/software/cpc.html.

Price, T.D. & Grant, P.R. 1985. The evolution of ontogeny in Darwin's finches: a quantitative genetic approach. *Am. Nat.* **125**: 169–188.

Ricklefs, R.E. 1968. Patterns of growth in birds. *Ibis* **110**: 419–451.

Riska, B., Atchley, W.R. & Rutledge, J.J. 1984. A genetic analysis of targeted growth in mice. *Genetics* **107**: 79–101.

Shea, B.T. 1985. Bivariate and multivariate growth allometry: statistical and biological consideration. *J. Zool.* **206**: 367–390.

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

Smith, H.G. & Wettermark, K.-J. 1995. Heritability of nestling growth in cross-fostered European starlings *Sturnus vulgaris*. *Genetics* **141**: 657–665.

Starck, J.M. 1998. Structural variants and invariants in avian embryonic and postnatal development. *Avian Growth and Development* (J. M. Starck & R. E. Ricklefs, eds), pp. 59–88. Oxford University Press, Oxford.

Tanner, J.M. 1963. Regulation of growth in size in mammals. *Nature* **199**: 845–850.

Voss, R.S., Marcus, L.S. & Escalante, P. 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.

Wayne, R.K. 1986. Cranial morphology of domestic and wild canids: The influence of development on morphological change. *Evolution* **40**: 243–261.

Zelditch, M.L. & Carmichael, A.C. 1989. Ontogenetic variation in patterns of developmental and functional integration in skulls of *Sigmodon fulviventer*. *Evolution* **43**: 814–824.

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