

Population divergence and morphometric integration in the greenfinch (*Carduelis chloris*) – evolution against the trajectory of least resistance?

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Abstract

Theory predicts that genetic and phenotypic correlations among traits may direct the process of short-term evolution by limiting the directions of variation available to natural selection to act on. We studied correlations between 14 skeletal traits in 10 geographically distinct and relatively young greenfinch (*Carduelis chloris*) populations to unravel whether the divergence among populations has occurred into directions predicted by the within-population correlations (cf. drift/correlated responses models), or whether it is better explained by 'adaptive' models, which predict no necessary association between within- and among-population correlations (allometries). We found that the within-population character correlations (or covariances) did not predict character divergence between populations. This was because the first eigenvector of the among-population correlation/covariance matrix, summarizing the major dimension of divergence, was a bipolar body:beak dimension, and distinct from the (\approx isometric) first eigenvector of within-population matrix. Hence, as the divergence among greenfinch populations cannot be satisfactorily accommodated by drift/correlated response models, an adaptive basis for divergence is suggested. The second major axis of within-population variation was a classical 'group size' factor revealing that beak size was more or less free to vary independently of body size. Consequently, even if the divergence among populations cannot be simply accommodated to expectations of drift and correlated response models, it is striking that the most pronounced size-independent (nonallometric) changes had occurred along the second largest dimension of variance. This could mean that selection pressures which shape integration within populations are the same as those that cause divergence among populations. A relaxed beak:body integration could also occur as a result of species level selection favouring taxa in which independent evolution of beak and body is made possible.

Introduction

A common pattern among closely related animal taxa, such as a genus, is that species vary very little in shape, but almost exclusively in terms of overall size (e.g. Björklund, 1991, 1996). This implies that the evolutionary process creating this pattern involves an element of

internal constraints such as pleiotropy (Falconer, 1989) or epigenetic effects (cf. Cowley & Atchley, 1992). However, both quantitative genetic theory and the vast diversity of organismal forms suggest that these constraints can be broken down in the long term and are themselves subject to evolution (Lande, 1976; Zeng, 1988; Arnold, 1991). In this view, the high degree of similarity among closely related taxa might also be explained by a shared adaptive zone. For example, a recent analysis of morphometric variability in the avian genus *Carduelis* revealed that species vary very little in beak shape, while more divergence was observed in respect of body size and

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shape (Björklund & Merilä, 1993). Since beak is a functionally important trait that has been shown to be under strong selection in a number of species (Boag & Grant, 1981; Grant, 1985; Schluter & Smith, 1986a; Gibbs & Grant, 1987; Smith, 1991; Björklund, 1992), and even undergo evolutionary changes in ecological time-scale (Grant & Grant, 1995), it seems unlikely that such a cross taxonomic homogeneity in beak shape simply reflects an inability of selection to brake developmental constraints, but, more likely, shared adaptation to similar feeding modes. Furthermore, Darwin's finches (Geospizinae) and Hawaiian Honeycreepers (Drepanididae) provide some of the best known examples of adaptive radiations, both of which are characterized by enormous diversity of beak forms (e.g. Raikow, 1977; Grant, 1986). Likewise, beak size has been identified as the most variable trait in Carduelinae finches (Björklund, 1991). These broad patterns suggest that avian beak is an example of a trait which readily tracks changes in adaptive surfaces.

In a recent analysis of morphometric differentiation of greenfinch (*Carduelis chloris*) populations across the European continent, highly discordant patterns of population divergence in different quantitative traits were found (Merilä, 1997). Southern European birds (*C. c. aurantiiventris*) were small bodied but had much larger bills (also in absolute scale) than large-bodied birds in the north (*C. c. chloris*; Fig. 1). Because both beak and body size are ecologically and functionally important traits,

and have repeatedly be shown to be under natural selection in other species of finches, there is good reason to suspect an adaptive basis for this differentiation.

The aim of this study was to evaluate the hypothesis that the pattern of character divergence among different greenfinch populations (Fig. 1) is caused by natural selection. This was done by comparing the observed character divergence among populations with that to be expected under two different kinds of evolutionary models: 'adaptive' and 'neutral' (Lande, 1980; Riska, 1989). In short, we investigated whether the divergence among different populations has occurred in directions predicted by character correlations within populations, the null hypothesis being that the divergence has occurred in directions parallel to within-population correlations, i.e. in directions of maximum variance ('least resistance'; Schluter, 1994). This corresponds to the expectation under drift (Lande, 1979; Lofsvold, 1988), correlated response (Lande, 1979) or 'constraint' models (Björklund & Merilä, 1993; Schluter, 1994), which emphasize the role of ancestral developmental pathways and genetic correlations in directing the process of divergence. For example, if the populations have diverged because of natural selection acting on overall body size, the changes in other characters being correlated responses, then there should be a precise relationship between among-population correlations and correlations of characters within populations (Reeve,

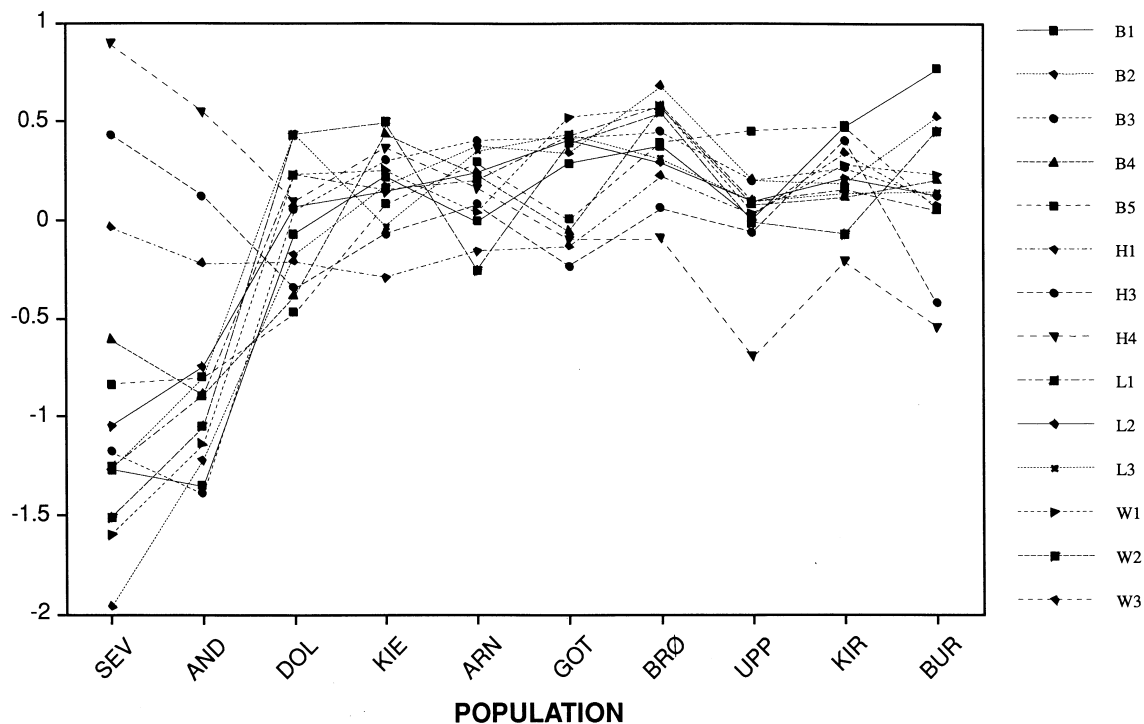


Fig. 1 Quantitative trait divergence in greenfinch skeletal traits across Europe showing discordant patterns of differentiation for different traits. The plotted values are standardized (mean = 0, SD = 1) population means.

1950; Lande, 1979). On the other hand, the 'adaptive' divergence models predict that the correlation of characters among populations can be independent of the within-population correlations because long-term evolution of populations is controlled by the underlying adaptive surface and not by genetic constraints (Zeng, 1988; Riska, 1989; Arnold, 1991).

Methods

Sample details and measurements

Samples of greenfinches were collected between 1992 and 1993 from the following 10 localities (abbreviation, country, n males/females, n total): Kirkkonummi (KIR, Finland, 32/15, 47), Bureå (BUR, Sweden, 25/24, 49), Uppsala (UPP, Sweden, 27/24, 51), Gotland (GOT, Sweden, 40/12, 52), Brønderslev (BRØ, Denmark, 24/27, 51), Arnhem (ARN, Netherlands, 11/12, 23), Kiev (KIE, Ukraine, 27/24, 51), Dole (DOL, France, 17/14, 31), Andujar (AND, Spain, 26/29, 55), Seville (SEV, Spain, 19/10, 29). A map, together with coordinates of locations, can be found in Merilä *et al.* (1996). From each individual, 14 linear skeletal measures representing four different body regions were taken. These were: Beak – Dentale length (H1), Internasal width (H3), Mandible width (H4); Body – Scapula length (B1), Coracoid length (B2), Keel length (B3), Keel depth (B4), Synsacrum width (B5); Wing – Humerus length (W1), Ulna length (W2), Carpometacarpus length (W3); Leg – Femur length (L1), Tibiotarsus length (L2) and Tarsometatarsus length (L3). All measurements were made by the same person using digital callipers to an accuracy of 0.05 mm. Per cent measurement error for each character was estimated from two repeated measures of the same 26 male greenfinches using one-way ANOVA (Bailey & Byrnes, 1990). Measurement error accounted for less than 10% (mean = 3.2%, range = 0.3–9.0%) of all variance in the traits, which was further reduced by averaging right- and left-side measurements for bilateral traits. Details of measurement landmarks and analysis of measurement error are given in Merilä (1997).

Statistical analyses

Preliminaries

The data from each population were first checked for multivariate outliers and possible mistakes that had occurred during the data entering using Hotelling's D^2 -tests. No outliers (>3.0 SD units from mean) were found and all measurements were ln-transformed to account for scaling of variances with the mean, to render covariances scale invariant and to enhance the normality of distributions (Bookstein *et al.*, 1985). To increase sample sizes we pooled the sexes after adjusting female trait values within each population to male equivalents

by adding the mean difference among sexes to female values (see Merilä, 1997). As the samples from Gotland, Bureå and Kiev included many first-year birds (Merilä *et al.*, 1995) which differed significantly from older birds in some of the trait means (variances and covariances equal), they were first adjusted to adult equivalents in the manner described for sexes. After this, all traits were tested for normality with Kolmogorov–Smirnov tests within each locality separately. All traits were approximately normally distributed.

Principal component analyses

All analyses were performed using correlation matrices because correlations are unitless and free from influences of sample mean, making intra- vs. interpopulational comparisons more reliable (Zeng, 1988), and because spectral decomposition separates size from shape better from a correlation matrix than from a covariance matrix (Somers, 1986). However, as the theoretical models are usually concerned with variance/covariance matrices, we also repeated all analyses of population differentiation by using variance/covariance matrices. We used principal component analysis (PCA) to obtain eigenvectors which summarize the directions of greatest variation in the matrices. Eigenvectors were calculated from correlation matrices enumerated (1) for each population separately, (2) for pooled population data (after standardization to zero mean) and (3) for data consisting of population means. The two first matrices will be referred to as 'within-population matrices' and the third as 'among-population matrix'. The significance of the eigenvalues (= amount of variance explained by a given eigenvector) of each within-population matrix was tested by subjecting each matrix to a bootstrap (500 replications) procedure and constructing 95% confidence limits from the bootstrap values (e.g. Gibson *et al.*, 1984). The standardization of eigenvector loadings (coefficients) was done by re-scaling to unit length, after which the loadings of the first eigenvector can be interpreted as allometric coefficients of general size (Strauss, 1990). If the loadings for different traits are unequal, this indicates that scaling of traits is allometrical. To investigate the importance of size-independent trait covariation, we used 'size-constrained' PCA (Somers, 1986), in which the variance due to isometric size (all loadings equal) is first partitioned out, after which the remaining vectors describe size-independent relations among different traits. Loadings (l) of a hypothetical isometric size vector for k trait case were obtained as $l = 1/\sqrt{k}$.

We used the variance of the eigenvalues of a correlation matrix ($V[\lambda]$) as a measure of morphological integration (I) (Wagner, 1984). If correlations are close to zero, all eigenvalues are almost equal and the variance becomes low. If correlations are high, the first eigenvector will account for most of the variance and the variance of eigenvalues becomes large. The significance of this index was tested against the expected variance of

a random correlation matrix given by $E([V(\lambda)]) = (M - 1)/(N - 1)$, where M = number of traits and N = number of individuals in the given sample (Wagner, 1984). To bring the eigenvalue variances to more intuitive scale, we further divided them with the maximum possible variance, which is obtained if the first eigenvalue equals M and the remaining eigenvalues are zero. For variance/covariance matrices, the index of intergration was derived in similar fashion as detailed in Björklund & Merilä (1993), but only values expressed as a percentage of the maximum are reported.

The similarity of correlation matrices was evaluated by means of vector correlations (r_v) and matrix correlations (r_M). Correlations among multivariate vectors were computed as the sum of the inner products of the unity normalized eigenvectors (Anderson, 1984). The vector correlation is the cosine of the angle between two vectors and provides an intuitive way of describing the similarity of orientation between two vectors. To test whether two vectors are parallel, the following procedure was undertaken. The null hypothesis is that the two vectors are parallel (drawn from the same population) and the observed difference is a result of sampling error. In other words, any two sample correlations from the same population will yield a difference equal to that observed. By using a bootstrap procedure, vectors were created from the same data set and compared to each other, and the number of times that this vector correlation was equal to or larger than the one observed was counted. This was repeated 999 times and thus the P value corresponds to the probability of getting a higher vector correlation than the one observed if they were drawn from the same population. The significance of matrix correlations (correlation coefficients computed using the corresponding elements of two matrices as paired observations) was determined by using a permutation (2000 runs) approach (Cheverud *et al.*, 1989).

The similarity of different within-population variance/covariance matrices was assessed with the method of Flury (1988) as implemented in the CPC-program of Phillips (1997). As a test of similarity, we used the Flury decomposition of χ^2 (Phillips, 1997) in which the hypothesis of matrix equality was tested against the hypothesis of matrix proportionality.

Assumptions

An implicit assumption we have made throughout this paper is that phenotypic correlations/covariances are at least qualitatively similar to the underlying genetic correlations. This assumption is founded on the fact that several studies, including an analysis of 41 pairs of phenotypic/genetic correlation matrices (Cheverud, 1988), have found high similarity between phenotypic and genetic correlations (Schluter & Smith, 1986b; Merilä & Gustafsson, 1993; Koots & Gibson, 1994; Roff,

1995). For example, a re-analysis of avian morphometric data indicated close to 1:1 relationship between phenotypic and genetic correlations (Roff, 1995). In fact, Roff's (1995) results suggest that phenotypic correlations may be as good, or even better, estimates of true genetic correlations as those estimated from small empirical data sets. Furthermore, our main conclusion remains unchanged even if the correspondence between genetic and phenotypic correlations is not perfect, given that they have a similar sign, which is likely to hold true (e.g. Cheverud, 1982; Schluter & Smith, 1986b; Merilä & Gustafsson, 1993; Roff, 1995).

Results

Correlation structure within populations

We first investigated whether there is any evidence of different populations having diverged in magnitude or pattern of correlation structure. The overall magnitude of correlations, as measured by index of integration (I), differed significantly from a random expectation in all populations ($P < 0.001$, in all tests). The mean index of integration was 2.23 (range: 1.54–2.92), corresponding to an average of 16.1% of the maximum possible, and none of the pairwise comparisons of integration indices between different populations was significant (Table 1). The results were very similar when variance/covariance matrices were used instead of correlation matrices (Table 1). Likewise, all possible pairwise matrix correlations between different within-population correlation matrices were significant, indicating that correlation structures among populations were similar (Table 2). Although some of the matrix correlations were low, this is to be expected when the number of matrix elements is large relative to the sample size (Cheverud, 1989; Cheverud *et al.*, 1989). This is illustrated by the fact that the lowest matrix correlations in Table 1 involve the population with the smallest sample size (Arnhem, $n = 23$). Furthermore, the comparison of different within-population variance/covariance matrices revealed also that character covariance structures in different populations were very similar: the hypothesis of equality was supported over the hypothesis of proportionality ($\chi^2_9 = 23.80$, $P = 0.0046$) and unrelated structure ($\chi^2_{945} = 1291.25$, $P < 0.0001$). From these, we conclude that the degree and pattern of trait correlations/covariances did not vary among populations. We therefore pooled the data from all populations to increase sample size and reduce sampling noise in the subsequent tests (in all subsequent tests, the within-population matrix refers to the pooled within-population correlation/covariance matrix). To avoid confounding the correlations/covariances by mixing samples with different means, we standardized all traits to zero mean within each of the populations before pooling.

Table 1 Index of integration (I = variance of eigenvalues) in 10 different Greenfinch populations. $I_{\%max}$ = the index expressed as percentage of the maximum possible. Confidence intervals (2.5% and 97.5% percentiles) were obtained with bootstrap.

Population	Correlation matrix				Covariance matrix	
	I	CI	$I_{\%max}$	CI	$I_{\%max}$	CI
KIR	1.54	1.2–2.4	11.0	8.6–17.3	7.52	5.41–19.37
BUR	2.92	2.2–4.3	20.9	15.4–30.7	15.69	6.67–46.48
UPP	2.00	1.5–3.1	14.3	10.7–22.1	8.30	4.89–20.78
GOT	2.92	2.2–4.2	20.9	15.7–30.3	16.00	6.43–47.41
BRO	2.32	1.7–3.4	16.6	12.6–24.1	12.23	8.18–26.74
ARN	1.78	1.7–2.9	12.7	12.2–20.6	9.39	6.86–27.79
KIE	2.21	1.6–3.2	15.8	11.8–22.6	10.43	6.38–25.71
DOL	2.66	1.7–4.6	19.0	11.9–32.8	14.32	5.90–47.42
AND	1.82	1.4–2.9	14.3	9.9–20.9	7.01	4.54–16.36
SEV	2.17	2.0–3.3	15.5	14.1–23.6	12.59	9.86–27.76
Pooled	2.17	1.9–2.5	15.6	13.6–17.9	9.46	7.84–14.20

Table 2 Pairwise matrix correlations (r_M) between different within-population correlation matrices. For population abbreviations see Methods.

Pop.	KIR	BUR	UPP	GOT	BRO	ARN	KIE	DOL	AND	SEV
KIR	1.000									
BUR	0.728	1.000								
UPP	0.651	0.775	1.000							
GOT	0.724	0.653	0.592	1.000						
BRO	0.716	0.715	0.729	0.509	1.000					
ARN	0.496	0.485	0.459	0.646	0.473	1.000				
KIE	0.709	0.778	0.809	0.662	0.735	0.532	1.000			
DOL	0.752	0.792	0.676	0.693	0.744	0.539	0.756	1.000		
AND	0.754	0.760	0.783	0.734	0.789	0.568	0.760	0.746	1.000	
SEV	0.674	0.718	0.568	0.684	0.630	0.431	0.560	0.698	0.712	1.000

All correlations are significant ($P < 0.05$) after Bonferroni adjustment at α – level = 0.05/47 (Rice, 1989).

Major axis of divergence

If the divergence among populations has occurred to dimensions predicted by within-population character correlations/covariances (allometries), then the greatest (major) dimension of the divergence, as summarized in the first eigenvector of the among-population matrix, should be collinear to the greatest dimension of variation within populations. The vector correlation between the first eigenvector of the among-population correlation matrix and the first eigenvector of the within-population correlation matrix was $r_V = 0.87$, corresponding to an angle of 30.1° between them. Although this correlation is high, it differs significantly from a perfect correlation ($P < 0.001$), showing that the divergence among different greenfinch populations has not occurred entirely, although largely, in the direction predicted by within-population correlations. The same result was borne out from the comparison of the within- and among-population variance/covariance matrices: the vector correlation between the first eigenvector of the among-population covariance matrix and the first eigenvector of the

within-population covariance matrix was $r_V = 0.77$, corresponding to an angle of 39.6° between them. The reason for the discordant orientation of within- and among-population variation patterns can be seen from the trait loadings on the first eigenvectors of within- and among-population matrices (Table 3). While the different traits load positively (though not equally) on the within-population vector, the among-population vector is bipolar, with large negative loadings on beak traits and large positive loadings on the remaining traits (Table 3). Consequently, while most of the variance within local greenfinch populations can be attributed to a latent general size factor (*sensu* Wright, 1932), divergence among populations has involved changes in beak–body size relationships. The mismatch between within- and among-population correlations is shown by the matrix correlation analysis: although the correlation between the two matrices is significant ($r_M = 0.56$, $P < 0.001$), it is clear that many elements of the among-population matrix are not predictable from the within-population correlations (Fig. 2). Taken together, these analyses indicate that within-population allometries do not

Table 3 First eigenvectors of within- and among-population correlation and covariance matrices with associated standardized trait loadings, and the second eigenvectors of within-population correlation matrices extracted with simple and size-constrained (sc) PCA (Somers, 1986). Eig. = eigenvalue. r_v = vector correlation.

Trait	Correlation matrix				Covariance matrix	
	Eigenvector I		Eigenvector II		Eigenvector	
	Within	Among	Within	Within _{sc}	Within	Among
B1	0.257	0.291	0.053	-0.047	0.256	0.396
B2	0.317	0.299	-0.024	-0.175	0.244	0.356
B3	0.227	0.294	0.189	0.081	0.221	0.323
B4	0.145	0.256	0.278	0.251	0.209	0.280
B5	0.181	0.256	0.127	0.112	0.260	0.253
H1	0.128	0.101	0.449	0.366	0.438	0.063
H3	0.128	-0.160	0.478	0.378	0.181	-0.078
H4	0.142	-0.240	0.532	0.394	0.221	-0.212
L1	0.331	0.296	-0.170	-0.277	0.266	0.230
L2	0.324	0.298	-0.195	-0.285	0.261	0.189
L3	0.308	0.286	-0.209	-0.273	0.293	0.259
W1	0.354	0.300	-0.114	-0.278	0.240	0.273
W2	0.362	0.284	-0.090	-0.269	0.246	0.259
W3	0.330	0.291	-0.149	-0.268	0.244	0.342
Eig	5.93	10.78	1.59	2.13	0.0041	0.0041
%	42.4%	77.0%	11.4%	15.2%	34.3%	84.7%

accurately predict among-population allometries, suggesting that the divergence among greenfinch populations cannot be satisfactorily accommodated by models that predict close similarity of within- and among-population correlations (Lande, 1979; Lofsvold, 1988).

Group size factors

After extracting the variation attributable to general size, we extracted the next largest eigenvector of the within-population matrix to unravel the major dimensions of size-independent trait correlations. The second eigenvector accounted for 11.4% of the variation in correlation structure, being bipolar with large negative and equal loadings on all wing and leg traits, and on some of the body traits (Table 3). However, the largest loadings were on beak traits and this vector can be clearly identified as a 'beak factor' (Table 3). As reflected in similar eigenvalues of original and size-constrained second eigenvectors (Table 3), the pattern of trait loading on this eigenvector is not greatly affected by the slight allometry in the first extracted factor. Of all the possible 12 subsequent factors, only the third was significant, and accounted for 6% of the variation, having large positive loadings on scapula and keel length, as well as on keel depth.

Examination of residual correlations, i.e. those remaining between two variables with effects of all other variables partialled out, provides an intuitive way of summarizing and identifying the important group size factors in the data. As it can be seen from Table 4, there are several large residual correlations (>0.20) mainly between traits belonging to the same *a priori* defined 'groups' (i.e.

beak, wing, leg, body). For example, the square of the residual correlation between Humerus and Ulna lengths indicates that 20% of the variation of either variable can be predicted (in the sense of linear regression) by the other variable but not by any other trait in the matrix. The pattern of residual correlations is summarized in Fig. 3. The residual correlations are generally highest within each of the 'body regions', but are an order magnitude lower between them (Fig. 3). Consequently, the pattern summarized in Fig. 3 is clear: after accounting for the variance attributable to size differences among individuals, most of the remaining (interpretable) variance is attributable to 'group' size factors. Hence, one of the major components of divergence (i.e. beak size) among greenfinch populations corresponds to one of the largest dimensions of size-independent within-population variation.

Discussion

We found that the pattern of character divergence among different greenfinch populations cannot be simply predicted from the knowledge of character correlations within local populations. In other words, as reflected in the nonparallel first eigenvectors of within- and among-population correlation matrices, the different greenfinch populations were not entirely, although mainly, differentiated along the dimension that was most variable within populations ('line of least resistance' Schluter, 1994). If the divergence among populations was a consequence of random genetic drift, or of selection on one particular trait, with the divergence in the rest of the traits being merely correlated responses, a pattern such as

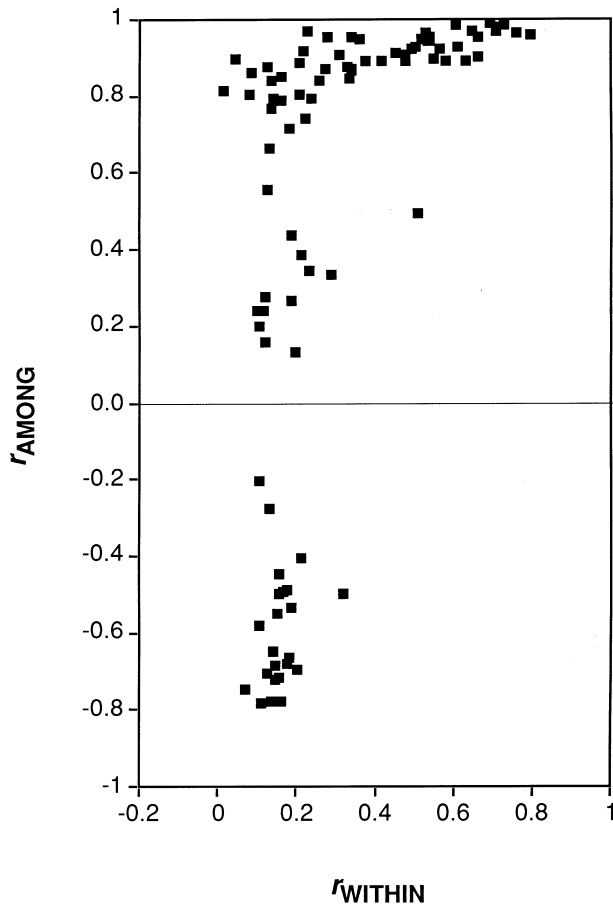


Fig. 2 Elements of the among-population correlation matrix as a function of homologous elements of the within-population correlation matrix. Note that the two axes are at the same scale although the negative region of the x -axis has been removed.

the one we have observed in this study is not to be expected (Lande, 1979). In other words, despite the low correlations between beak and the remaining traits, correlated response and drift models of population differentiation do not predict that weak positive intra-population allometry would result in a strong negative interpopulation allometry but rather the opposite (Zeng, 1988). This is assuming that genetic correlations between beak and body size traits are not negative (see Methods). If so, this would indicate that the divergence between local greenfinch populations has not followed the pathways predicted by 'null' models of population differentiation (Riska, 1989; Björklund, 1996), but that the divergence might be better accommodated by 'adaptive' models, such as the optimum-shift model (Lande, 1980), which predicts no necessary relationship between multivariate patterns of correlation within and among populations (Lande, 1980; Zeng, 1988). Hence, there are two good reasons to suspect that population differentiation in greenfinch morphology has been adaptive: first, the divergence has run in directions not to be expected under 'null' models (drift, correlated response) and, second, this discrepancy from expectations is mainly attributable to differentiation in beak size – a trait of obvious adaptive significance.

The results of this study, however, are not incompatible with the common finding that closely related taxa vary primarily in size and little in shape (e.g. Cheverud, 1989; Björklund, 1996). A large fraction of the variance in the among-population matrix indeed was in general size as most traits loaded about equally and positively. As the phenotypic correlations are likely to reflect underlying genetic correlations (see Methods), which are usually positive for morphometric traits (e.g. Cheverud, 1982; Merilä & Gustafsson, 1993), and most of the genetic variance in empirically estimated correlation matrices is

Table 4 Partial correlations (below diagonal) and squared multiple correlation (diagonal) between 14 skeletal traits in a sample of 436 greenfinches. Correlations >0.20 are shown in bold type. The squared multiple correlation gives the proportion of variance in a given trait that is common to all other variables in the matrix. For trait abbreviations, see Methods.

	B1	B2	B3	B4	B5	H1	H3	H4	L1	L2	L3	W1	W2	W3
B1	0.417													
B2	0.290	0.551												
B3	0.238	0.068	0.346											
B4	0.150	-0.019	0.238	0.194										
B5	-0.012	0.045	0.065	0.016	0.182									
H1	0.027	0.064	-0.022	0.125	0.055	0.178								
H3	-0.014	0.002	0.070	-0.034	0.080	0.084	0.244							
H4	-0.052	0.029	0.062	0.058	0.033	0.225	0.389	0.302						
L1	0.059	-0.002	-0.014	0.030	0.181	0.007	-0.033	-0.000	0.673					
L2	-0.036	0.101	0.003	0.024	-0.063	-0.032	0.068	-0.060	0.342	0.725				
L3	-0.008	-0.017	-0.042	-0.061	-0.003	0.015	-0.011	0.065	0.153	0.509	0.666			
W1	-0.015	0.197	0.054	0.003	-0.114	0.017	0.039	-0.028	0.400	-0.055	-0.106	0.776		
W2	0.122	0.064	-0.039	0.011	0.120	0.065	-0.036	0.114	-0.139	0.323	0.007	0.477	0.785	
W3	-0.012	0.090	0.154	-0.008	0.065	-0.084	0.012	-0.061	0.023	-0.202	0.346	0.215	0.291	0.661

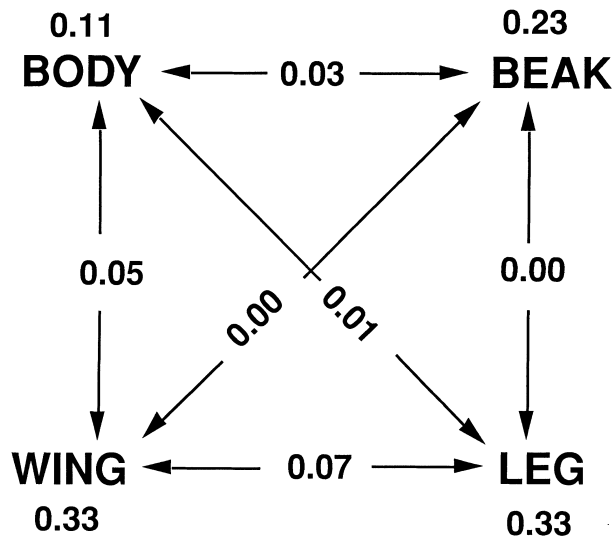


Fig. 3 Residual correlations within and between different functionally/developmentally homogeneous character complexes. Residual correlation is defined as the correlation that exists between a pair of variables with the effects of other variables partialled out.

orientated along the general size axis (Björklund, 1996), this pattern indicates that the divergence for most traits has in fact occurred along the 'line of least resistance', which is, in general, body size. However, we also identified several size-independent group size factors (Wright, 1932; Olsson & Miller, 1958), the most prominent corresponding to beak size. This is noteworthy because it means that beak traits are not strongly integrated with the rest of the body, and suggests that genetic correlations between 'beak' and 'body' are lower than those within them. Hence, the striking fact is that the largest dimension of the size-independent variance within greenfinch populations corresponds to one of the major components of divergence among populations. As the group size factors themselves are likely to be the results of natural selection favouring integration of traits performing important joint functions (Olsson & Miller, 1958; Cheverud, 1984), this might suggest that forces of selection which cause integration within populations are the same which cause divergence among populations.

The decoupling of beak and body size within greenfinch populations indicates that beak and body size have not been making any consistent joint contribution to individual fitness. If this were the case, we should expect that natural selection would have created a strong beak:body size allometry (Schluter & Smith, 1986b). In other words, if small individuals with large beaks and large individuals with small beaks are less fit than individuals showing more proportionality, then some 'optimal' line of allometry is expected to evolve (Cheverud, 1984; Schluter & Smith, 1986b). However, a weak allometry might be expected if the selection mainly acts on absolute beak size, irrespective of body size. For

example, it could be that there is a certain fixed beak size which is most effective in a given environment and that this size may differ between different populations. Moreover, suppose that growth in body and beak size were strongly integrated. Then the fact that body size is rather a labile trait, strongly influenced by nutrition in early life (e.g. Boag, 1983; Richner, 1989), would mean that individuals suffering from poor nestling growth would also end up with a beak under a certain 'minimum' threshold. Hence, low beak:body integration might have evolved as an 'insurance' against unpredictable environmental conditions during early growth.

The observed beak:body size decoupling is consistent with broader patterns of morphological evolution. For example, Darwin's finches and Hawaiian honeycreepers provide two of the best known examples of adaptive radiations (Raikow, 1977; Grant, 1986) and are characterized by an enormous diversity of beak forms (see Grant, 1986; his Figs 2 and 100). Hence, it seems possible that the decoupled beak body size integration is a widespread phenomenon, in other words, an ancestral 'character' state shared by a wide variety of species. To see whether beak:body size decoupling is widespread, we compiled information on phenotypic and genotypic correlations in other avian taxa. Indeed, the published phenotypic and genetic correlation matrices from different birds do provide some support for a generally low beak:body size integration (Table 5). For most of the species, especially to *Ficedula* and *Melospiza*, correlations between beak and body traits are much lower than those within either of these complexes. However, Darwin's finches provide a notable exception with no indications of relaxed beak:body size integration. We have no explanation for this difference between Darwin's finches and rest of the species, but it is worth noting that Darwin's finches have quite extraordinary levels of phenotypic and genetic variability as compared with other avian species studied to date (Schluter & Smith, 1986b).

Species level selection on emergent traits, such as variances and covariances, has been suggested to affect the extinction probability of different taxa. Species that are narrowly adapted have been proposed to be favoured by natural selection at a given time, but having sacrificed much of their plasticity, they might more frequently fail to track changes in the adaptive landscape (e.g. Dobzhansky, 1937; Lloyd & Gould, 1993). In this context, beak:body size integration clearly is a candidate for a trait which could become or could have been a target of species level selection. Low beak:body size integration might be a result of species level selection favouring taxa where beak traits to some degree evolve independently of rest of the body. Hence, it may be worthwhile to document macroevolutionary patterns of species survival and extinction, and attempt to relate this to the degree of integration in different clades. This would also shed light on an additional question, namely whether positive species level selection on phenotypic integration might

Table 5 Average phenotypic (P) and genetic (G) correlation between different traits within beak and body, as well as between them. n_i = number of individuals, n_T = number of traits. When data were available separately for both males and females, only male correlations were included. In all *Geospiza* correlations, the beak pointedness variable is excluded.

Species	Type	n_i	n_T	Average correlation (r)		
				Beak	Beak–Body	Body
<i>Parus caeruleus</i> ¹	P	64	6	0.43	0.13	0.16
<i>Corvus corone</i> ²	P	23–169	6	0.61	0.30	0.41
<i>Ficedula albicollis</i> ³	G	297–691	7	0.41	0.07	0.39
	P	1275	7	0.23	0.12	0.30
<i>Melospiza melodia</i> ⁴	G	376	5	0.45	0.06	0.24
	P	376	5	0.35	0.05	0.19
<i>Zonotrichia capensis</i> ⁵	P	971	6	0.40	0.06	0.24
<i>Carduelis chloris</i> ⁶	P	436	14	0.44	0.18	0.35
<i>Geospiza conirostris</i> ⁷	G	20	6	0.58	0.56	0.25
	P	20	6	0.65	0.51	0.47
<i>Geospiza scandens</i> ⁸	G	92	5	–0.32	–0.30	0.61
	P	92	5	0.50	0.43	0.36
<i>Geospiza fortis</i> ⁸	G	276	5	0.91	0.78	0.68
	P	276	5	0.82	0.57	0.56

¹Merilä, unpublished (adult males); ²Richner, 1989 (males); ³Merilä & Gustafsson, 1993; ⁴Schluter & Smith, 1986b; ⁵Handford, 1983 (males); ⁶this study; ⁷Grant, 1983; ⁸Boag, 1983.

be creating conservative patterns of morphological variability in higher taxonomic levels (Björklund, 1995).

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References

- Anderson, T.W. 1984. *An Introduction to Multivariate Statistical Analysis*, 2nd ed., Wiley, New York.
- Arnold, S.J. 1991. Constraints on phenotypic evolution. *Am. Nat.* **140S**: 85–107.
- Bailey, R.C. & Byrnes, J. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. *Syst. Biol.* **39**: 124–130.
- Björklund, M. 1991. Patterns of morphological variation among Cardueline finches (Fringillidae, Carduelinae). *Biol. J. Linne. Soc.* **43**: 239–248.
- Björklund, M. 1992. Selection of bill proportions in the common rosefinch (*Carpodacus erythrinus*). *Auk* **109**: 637–642.
- Björklund, M. 1995. Species selection on organismal integration. *J. Theor. Biol.* **171**: 427–430.
- Björklund, M. 1996. The importance of evolutionary constraints in ecological time scales. *Evol. Ecol.* **10**: 423–431.
- Björklund, M. & Merilä, J. 1993. Morphological differentiation in *Carduelis* finches: adaptive vs. constraint models. *J. Evol. Biol.* **6**: 359–373.
- Boag, P.T. 1983. The heritability of external morphology of Darwin's ground finches on isla Daphne Major, Galapagos. *Evolution* **37**: 877–894.
- Boag, P.T. & Grant, P.R. 1981. Intensive natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. *Science* **214**: 82–85.
- Bookstein, F.L., Chernoff, B.C., Elder, R.L., Humphries, J.M., Smith, G.R. & Strauss, R.E. 1985. Morphometrics in evolutionary biology. *Acad. Natural Sci. Philadelphia Special Publ.* **15**: 277pp.
- Cheverud, J.M. 1982. Phenotypic, genetic and environmental morphological integration in the cranium. *Evolution* **36**: 499–516.
- Cheverud, J.M. 1984. Quantitative genetics and developmental constraints on evolution by selection. *J. Theor. Biol.* **110**: 155–171.
- Cheverud, J.M. 1988. Comparison of genetic and phenotypic correlations. *Evolution* **42**: 958–968.
- Cheverud, J.M. 1989. A comparative analysis of morphological variation patterns in the papionins. *Evolution* **43**: 1737–1747.
- Cheverud, J.M., Wagner, G.P. & Dow, M. 1989. Methods for comparative analysis of variation patterns. *Syst. Zool.* **38**: 201–213.

- Cowley, D.E. & Atchley, W.R. 1992. Quantitative genetic models for development, epigenetic selection, and phenotypic evolution. *Evolution* **46**: 495–518.
- Dobzhansky, T. 1937. *Genetics and the Origin of Species*. Columbia University Press, New York.
- Falconer, D.S. 1989. *Introduction to Quantitative Genetics*. Longman Scientific and Technical.
- Flury, B. 1988. *Common Principal Components and Related Multivariate Methods*. Wiley, New York.
- Gibbs, H.L. & Grant, P.R. 1987. Oscillating selection on Darwin's finches. *Nature* **327**: 511–513.
- Gibson, A.R., Baker, A.J. & Moeed, A.J. 1984. Morphometric variation in introduced populations of the Common myna (*Acridotheres tristis*): an application of the jackknife to principal component analysis. *Syst. Zool.* **33**: 408–421.
- Grant, P.R. 1983. Inheritance of size and shape in a population of Darwin's finches, *Geospiza conirostris*. *Proc. R. Soc. Lond. B* **220**: 219–236.
- Grant, B.R. 1985. Selection on bill characters in a population of Darwin's finches: *Geospiza conirostris* on Isla Genovesa, Galapagos. *Evolution* **39**: 523–532.
- Grant, P.R. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton.
- Grant, P.R. & Grant, B.R. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* **49**: 241–251.
- Handford, P. 1983. Continental patterns of morphological variation in a south American sparrow. *Evolution* **37**: 920–930.
- Koots, K.R. & Gibson, J.P. 1994. How precise are genetic correlation estimates? *Proc. 5th World Cong. Gen. Appl. Livestock Prod.*, 18, pp. 353–356. Dept. Animal and Poultry Sci., University of Guelph, Ont., Canada.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30**: 314–334.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution applied to brain:body size allometry. *Evolution* **33**: 402–416.
- Lande, R. 1980. Genetic variation and phenotypic evolution during allopatric speciation. *Am. Nat.* **116**: 463–479.
- Lloyd, E.A. & Gould, S.J. 1993. Species selection on variability. *Proc. Natl. Acad. Sci. USA* **90**: 595–599.
- Lofsvold, D. 1988. Quantitative genetics of morphological differentiation in *Peromyscus*. II. Analysis of selection and drift. *Evolution* **42**: 54–67.
- Merilä, J. 1997. Quantitative trait and allozyme divergence in the Greenfinch (*Carduelis chloris*; *Fringillidae*). *Biol. J. Linn. Soc.* **61**: 243–266.
- Merilä, J., Björklund, M. & Baker, A.J. 1996. Genetic population structure and northward decline of genetic variability in the Greenfinch, *Carduelis chloris*. *Evolution* **50**: 2548–2557.
- Merilä, J., Björklund, M. & Bennet, G.F. 1995. Geographic and individual variation in haematozoan infections in the greenfinch, *Carduelis chloris*. *Can. J. Zool.* **73**: 1798–1804.
- Merilä, J. & Gustafsson, L. 1993. Inheritance of size and shape in a natural population of collared flycatcher, *Ficedula albicollis*. *J. Evol. Biol.* **6**: 375–398.
- Olsson, E.C. & Miller, R.L. 1958. *Morphological Integration*. University of Chicago Press, Chicago.
- Phillips, P.C. 1997. *CPC-Common principal component analysis*. A program distributed by P.C. Phillips, Biology Department, University of Arlington, Arlington, Texas.
- Raikow, R.J. 1977. The origin and evolution of Hawaiian Honeycreepers (Drepanididae). *Living Bird* **15**: 95–117.
- Reeve, E.C.D. 1950. Genetical aspects of size allometry. *Proc. R. Soc. Lond. B* **137**: 515–518.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* **43**: 223–225.
- Richner, H. 1989. Habitat-specific growth and fitness in carrion crows (*Corvus corone corone*). *J. Anim. Ecol.* **58**: 427–440.
- Riska, B. 1989. Composite traits, selection response, and evolution. *Evolution* **43**: 1172–1191.
- Roff, D.A. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. *Heredity* **74**: 481–490.
- Schluter, D. 1994. Adaptive radiation along 'genetic lines of least resistance'. *J. Ornith.* **135**: 357.
- Schluter, D. & Smith, J.N. 1986a. Natural selection on beak and body size in the song sparrow. *Evolution* **40**: 221–231.
- Schluter, D. & Smith, J.N.M. 1986b. Genetic and phenotypic correlations in a natural population of song sparrows. *Biol. J. Linn. Soc.* **29**: 23–26.
- Smith, T.B. 1991. Natural selection on bill characters in the two bill morphs of the African finch *Pyrenestes ostrinus*. *Evolution* **44**: 832–842.
- Somers, K.M. 1986. Multivariate allometry and removal of size with principal components analysis. *Syst. Zool.* **35**: 359–368.
- Strauss, R.E. 1990. Patterns of quantitative variation in Lepidopteran wing morphology: the convergent groups Heliconiinae and Ithomiinae (Papilionoidea, Nymphalidae). *Evolution* **44**: 86–103.
- Wagner, G.P. 1984. On the eigenvalue distribution of genetic and phenotypic dispersion matrices: evidence for a non random organisation of quantitative character variation. *J. Math. Biol.* **21**: 77–95.
- Wright, S. 1932. General, group and special size factors. *Genetics* **17**: 603–619.
- Zeng, Z.-B. 1988. Long-term correlated response, interpopulation covariation, and interspecific allometry. *Evolution* **42**: 363–374.

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