

# Genetic and phenotypic correlations in a natural population of song sparrows

DOLPH SCHLUTER AND JAMES N. M. SMITH

Department of Zoology, University of British Columbia,  
6270 University Boulevard, Vancouver BC, Canada V6T 2A9

Received 17 February 1986, accepted for publication 19 March 1986

We estimated heritabilities, and genetic and phenotypic correlations between beak and body traits in the song sparrow (*Melospiza melodia*). We compared these estimates to values for the same traits in the Galápagos finches, *Geospiza* (Boag, 1983; Grant, 1983). Morphological variance is low in the song sparrow, and our results show that genetic and phenotypic correlations are considerably lower than correlations in the morphologically more variable *Geospiza*. Comparison using a larger sample of Galápagos populations confirms the existence of an association between variance and correlation for phenotypic values. We suggest two possible explanations for this association. First, most traits studied are functionally related, and the joint evolution of variance and correlation may have resulted from stabilizing selection about a line of optimal allometry between traits. Alternatively, introgression between populations and species could have caused correlation and variance to evolve jointly. Both selection and introgression were probably influential in producing the observed pattern, but it is not possible to estimate their relative importance with current data. Genetic and phenotypic correlations were correlated in the song sparrow, but heritabilities of traits varied greatly. As a result, the genetic variance-covariance matrix for traits is not simply a constant multiple of the phenotypic matrix. Evolutionary response to natural selection cannot, therefore, be predicted from the measurement of phenotypic characteristics alone.

**KEYWORDS:**—Allometry – genetic correlations – phenotypic correlations – heritability – song sparrow – morphological variation.

## CONTENTS

Introduction . . . . .	23
Methods . . . . .	24
Field study . . . . .	24
Analysis . . . . .	25
Results . . . . .	28
Phenotypic correlations . . . . .	28
Heritabilities and genetic correlations . . . . .	31
Discussion . . . . .	32
Acknowledgements . . . . .	35
References . . . . .	35

## INTRODUCTION

Evolutionary response to natural selection on a suite of traits depends on the genetic variances and correlations between traits. For example, selection on any one trait influences all others that genetically covary with it. Only when the

genetic parameters are known is it is possible to predict response to natural selection, or to infer from the observed response the selective forces which have acted (Lande, 1979; Lande & Arnold, 1983; Schluter, 1984; Price *et al.*, 1984a, b; Price & Grant, 1985; B. R. Grant, 1985). Observations of selection on traits in natural populations are becoming more common (Lande & Arnold, 1983; Endler, 1986), but there have been few attempts to estimate in addition the patterns of inheritance for these traits (especially genetic correlations). In a previous study (Schluter & Smith, 1986) we documented patterns of natural selection on beak and body size in a song sparrow population (*Melospiza melodia*) on Mandarte Island, British Columbia. Smith & Zach (1979) presented heritabilities for these same traits. Here we present revised estimates of heritability, and the first estimates of genetic correlations in the population.

Genetic variances and correlations may themselves evolve under natural selection. Grant & Price (1981) reviewed the hypothesis that differing levels of population variance result from differing ecological niche widths. Other studies have suggested a relationship between the strength of genetic correlations between traits and their degree of functional relationship (cf. Lande, 1980; Cheverud, 1982, 1984). Comparisons between species occurring in different environments provide a further means to evaluate whether genetic correlations are partly adaptive. Boag (1983) and Grant (1983) estimated phenotypic and genetic correlations between beak and body traits in three species of Galápagos finch, *Geospiza*. We compare our estimates of phenotypic and genetic correlations in the song sparrow to values for the same traits in these Galápagos finches. The song sparrow is less variable than *Geospiza* (Table 1), and we show that its phenotypic and genetic correlations are also considerably lower. This apparent association between levels of variability and correlation also holds among populations within the *Geospiza*. We suggest that this pattern may result from natural selection acting on functionally related traits, with the intensity of correlating selection depending upon the amount of morphological variation. However, an alternative non-adaptive mechanism (introgression) may also explain the trend.

## METHODS

### *Field study*

Mandarte is a 6 ha island located in the Haro Strait, 20 km north-northeast of Victoria BC Canada. Since August 1974, nearly all resident song sparrows have been captured in mist nests, measured, and individually colour-banded. The nests of banded pairs of breeding adults were located, and the nestlings were banded about 6 days after hatching. These nestlings were later measured when captured as independent young or adults. The sex of offspring was determined by their reproductive behaviour when they matured. Offspring of unknown sex were excluded. The resulting sample includes 232 offspring from 139 different broods and 84 families born between 1975 and 1978. Some families include young raised in different nests and years.

Six traits were measured on individual birds: weight, in grams, and wing length, tarsus length, beak length, beak depth and beak width, all in millimetres. These same six traits have been measured in the same way in

Galápagos finches (Abbott, Abbott & Grant, 1977; Boag, 1983; Grant *et al.*, 1985). Measurement procedures are described in Smith & Zach (1979). The measurements used in the present study are from birds at least 8 weeks old, by which time adult size has been essentially attained (Smith & Zach, 1979). Most individuals were captured and measured two or three times during the course of this study.

### Analysis

*Field measurements:* Some growth and/or wear in traits with age may occur after 8 weeks (Smith, Arcese & Schluter, 1986), and not all birds were measured at the same age. Measurements were therefore corrected for age before subsequent analysis, in the following manner. Individual measurements were grouped by the year of life in which they were taken: 1, 2, and 3 or more (birds rarely lived longer than 3 years; Smith 1986). Birds measured in both their first and second years were identified, and their average difference in measurement between the two years was subtracted from the second-year measurements of all birds. Similarly, the average difference between measurements taken at age 1 year and at age 3 or more years for birds measured at both these ages was subtracted from all the third-year measurements. In each bird we then averaged the two or three age-corrected measurements available.

Boag (1983) and Grant (1983) used log-transformed measurements in their analysis, and for this reason song sparrow measurements were  $\log_e$  transformed. This transformation is further useful in interspecific comparisons of population variation, in that it scales for differences between species in mean size (Table 1). However, the frequency distributions of character values in the song sparrow were approximately normal for both the transformed and untransformed measurements, and heritabilities and phenotypic and genetic correlations were virtually identical on both scales.

Male song sparrows are larger than females, particularly in weight and wing length (Smith & Zach, 1979). We therefore adjusted female measurements by adding to them the observed difference between male and female means. Boag

Table 1. Means and standard deviations  $\times 100$  (s.d. in parentheses) of morphological traits in the song sparrow and three species of *Geospiza*. Means are based on untransformed data, and are the unweighted averages of male and female means. s.d.s are based on  $\log_e$  transformed data. s.d.s for the song sparrow are values uncorrected and corrected for measurement error, respectively. *Geospiza* s.d.s are all corrected for measurement error. *Geospiza* figures are from Boag (1983) and Grant (1983), or from their original data.

Weight is in grams, and other measurements are in millimetres

Trait	Song sparrow	<i>G. scandens</i>	<i>G. fortis</i>	<i>G. conirostris</i>
Weight	23.9 (5.7, 4.5)	20.2 (6.9)	15.9 (6.7)	24.7 (6.8)
Wing length	65.2 (2.2, 2.0)	72.9 (2.7)	68.1 (3.1)	76.6 (3.4)
Tarsus length	19.8 (2.9, 2.6)	20.6 (2.8)	18.7 (2.8)	22.1 (3.5)
Beak length	8.7 (3.8, 3.3)	14.5 (4.0)	10.7 (5.9)	14.7 (5.6)
Beak depth	5.9 (3.4, 3.0)	9.2 (4.0)	9.6 (8.6)	10.6 (7.6)
Beak width	6.7 (3.1, 2.7)	8.6 (3.9)	8.7 (6.0)	9.8 (6.2)

(1983) and Grant (1983) did not adjust *Geospiza* measurements for sex differences, but these differences do not bias their estimates of heritabilities or genetic correlations (see Boag, 1983). However, failure to correct for sex differences produces inflated estimates of phenotypic variance and correlation, since the variance and correlation between male and female means are included. For this reason we did not use the estimates of phenotypic variance and correlation provided by Boag and Grant, but referred instead to their original data (provided by P. R. Grant and T. D. Price).

We estimated heritabilities of traits from the coefficients in an unweighted regression of offspring values on mid-parent values (Falconer, 1981):

$$h^2(X) = \text{cov}(X', X) / \text{var}(X'), \quad (1)$$

where  $\text{cov}(X', X)$  is the covariance between mid-parent ( $'$ ) and offspring values for trait  $X$ , and  $\text{var}(X')$  is the variance of trait  $X$  in mid-parents. Boag (1983) and Grant (1983) used the same procedure. We performed two analyses, one based on all offspring and another using family means. Heritability estimates and significance levels were similar in both cases, and we present results from the first analysis only. Significance tests for these heritabilities were based on values uncorrected for measurement error.

Genetic correlations between traits were computed from mid-parent-offspring covariances (Falconer, 1981; Boag, 1983), based on all offspring combined. Two estimates of genetic correlation are available for each pair of traits  $X$  and  $Y$ :

$$\begin{aligned} r_1(G) &= \text{cov}(X', Y) / \sqrt{[\text{cov}(X', X) \text{cov}(Y', Y)]}, \text{ and} \\ r_2(G) &= \text{cov}(X, Y') / \sqrt{[\text{cov}(X', X) \text{cov}(Y', Y)]}, \end{aligned} \quad (2)$$

where  $'$  refers to the mid-parent value. Since the two estimates should be the same, the extent to which they are similar can be used as a rough measure of their accuracy (van Noordwijk, 1984). Environmental correlations (Falconer, 1981) were calculated using  $r(G)$ , the average of  $r_1(G)$  and  $r_2(G)$ :

$$r(E) = (r(P) - r(G)h(X)h(Y)) / \sqrt{[(1 - h^2(X))(1 - h^2(Y))]}, \quad (3)$$

where  $r(P)$  is the phenotypic correlation between  $X$  and  $Y$ , and  $h$  is the square root of the heritability (Falconer, 1981). Standard errors for  $r(G)$  and  $r(E)$  were estimated using Reeve's (1955) formula.

*Museum specimens:* Our field studies, and those of the Galápagos finches, provide four populations with which to compare genetic correlations. We supplemented this information with a study of phenotypic variability and correlation in a larger sample of populations. Five of the six traits used here, weight excluded, have been measured for all available museum specimens of six *Geospiza* species (Grant *et al.*, 1985). We used all populations of these species where 50 or more individuals have been measured. Measurements were  $\log_e$  transformed to remove the effects of scale. Measurements were also corrected for sex within populations, as described above for the song sparrow.

*Measurement error:* Estimates of phenotypic variance are invariably inflated. This is because the observed size  $x'$  of an individual based on a single measurement is the sum of the 'true' size  $x$ , and a deviation  $e$  due to measurement error, assumed to be uncorrelated with  $x$ . Observed phenotypic variance for trait  $X$  is  $\text{var}'(X) = \text{var}(X) + \text{me}(X)$ , where  $\text{var}(X)$  is the true

phenotypic variance, and  $me(X)$  is the variance due to measurement error. When the average of several measurements for an individual bird is used,  $me(X)$  depends on the variance of the error  $e$  from the single measurement ( $var(e)$ ), and on  $n$ , the number of times each individual has been measured:  $me(X) = var(e)/n$ .

It is important to remove the effects of error when comparing populations or traits of different phenotypic variance, because when true phenotypic variance is low the effects of error on measured size are disproportionately large. We estimated  $var(e)$  for each character in the song sparrow as the mean square within individuals in a one-way ANOVA on the repeat measurements (age-corrected and log-transformed). These values were divided by the average number of measurements per bird to yield  $me(X)$ . Note that 'measurement error' here includes error due to the measuring process as well as to temporal fluctuations in measurement not associated with age (e.g. hourly fluctuations in body weight). Estimates of phenotypic variance in the song sparrow were corrected for measurement error by subtracting  $me(X)$  from the observed variance for each trait  $X$ , to yield  $var(X)$ . Estimates of phenotypic correlation were adjusted by dividing phenotypic covariance by the corrected standard deviations (square root of  $var(X)$ ). Observed heritabilities were similarly corrected (cf. equation 1).

Before employing the above methods we tested the assumption that measurement error was uncorrelated with sparrow size. For each individual sparrow we computed its error as the absolute value of the difference between its first and last measurement (age-corrected and log-transformed), and its size as the average of these two measurements. Error and size were uncorrelated for all six traits, supporting the assumption ( $r = -0.08-0.01$ ,  $P > 0.05$ ,  $N = 162$ ).

Estimates of the covariance between two traits are unbiased by measurement error, as long as measurement error in one trait is uncorrelated with error in the other. The assumption of uncorrelated error is valid when one of the two traits is from the mid-parent and the other is from their offspring. Hence, covariance terms in the equations for heritability and genetic correlation did not require adjustment for measurement error. Estimates of phenotypic correlation are computed from the covariance between two traits measured on the same individual, and errors in these measurements may be correlated. We tested for a correlation in the song sparrow by computing error in each individual and for a given trait as the difference between size at last measurement, and the average size at first and last measurement (age-corrected and log-transformed). Of 15 correlations between the errors in pairs of traits, only one was significant, that between beak depth and beak width ( $N = 162$ ;  $P = 0.01$ ). However, the correlation was not strong ( $r = 0.20$ ), and it is not significant when we account for the fact that 15 correlations were performed ( $P > 0.05/15 = 0.003$ ; Sokal & Rohlf, 1981). For this reason we did not adjust phenotypic correlations for correlations in measurement error.

Parameter estimates in the Galápagos finches were also adjusted for measurement error, using  $me(X)$  from the song sparrow. This adjustment can be done in two ways, depending on the source of measurement error. If error results solely from the measuring process, then error variance should be independent of species size only on the untransformed scale of measurement. Since we use log-transformed measurements,  $me(X)$  in song sparrows must be

adjusted for use in other species, and we use  $me(X)\bar{X}_1^2/\bar{X}_2^2$ .  $\bar{X}_1$  and  $\bar{X}_2$  are untransformed means for trait  $X$  in the song sparrow and the other species, respectively (Table 1). This adjustment follows from the fact that the squared coefficient of variation on the untransformed scale is approximately equal to the variance on a  $\log_e$  scale, when both are small (Lewontin, 1966). Alternatively, if measurement error results mainly from temporal fluctuations in size (e.g. weight change), then error should be proportional to size on the untransformed scale, and hence constant among species on a log scale. In this case, one can use  $me(X)$  for all species regardless of size. Both sources probably contribute to measurement error in our case, and so we adjusted measurement error in *Geospiza* using both  $me(X)$  and  $me(X)\bar{X}_1^2/\bar{X}_2^2$  in turn. The results were essentially the same for both adjustments, and we present values using only the former. Parameter estimates in the Galápagos finches were less affected by these corrections than the song sparrow, because of their greater phenotypic variance (Table 1).

*Comparisons involving ratios:* We compared heritabilities and genetic and phenotypic correlations among populations differing in total variability. Such comparisons are potentially tricky, because heritability and correlation are ratios which may include population variance in the denominator (e.g. equation 1). Spurious correlations are known to occur between a ratio and its denominator (Atchley, Gaskins & Anderson, 1976).

However, the associations we observed involving ratios are unlikely to be spurious. This is mainly because our results show that heritabilities and correlations tend to be positively associated with population variability, whereas spurious associations between a ratio and its denominator are invariably negative (Atchley *et al.*, 1976). To be safe, we tested for possible spurious associations using simulation. First, we randomly sampled individuals from four populations having different phenotypic variances but identical heritabilities, to see whether a spurious positive association between sample estimates of variability and heritability might result. Fifty observations were sampled in each population from bivariate normal distributions of mid-parent size and offspring size. Phenotypic standard deviations in the four populations were set to 0.03, 0.04, 0.05 and 0.06 to span the values for the four species compared in this study. Heritability was set to 0.6 in each population. Sampling was repeated 500 times, and in each sample we estimated the heritability (equation 1) and phenotypic standard deviation (offspring only). No spurious positive association between heritability and standard deviation was observed among populations (average  $r = -0.063$ ). In a second, similar simulation we tested for a spurious association between the phenotypic correlation between two traits and the average of their standard deviations. Again, no spurious positive association was found ( $r = -0.044$ ).

## RESULTS

### *Phenotypic correlations*

Phenotypic correlations between traits in the song sparrow were relatively low, ranging from near zero to a maximum of 0.47 (Table 2). Average phenotypic correlation was 0.23. In contrast, average phenotypic correlation in

Table 2. Observed phenotypic correlations between traits in the song sparrow (above diagonal), and correlations corrected for measurement error (below diagonal).  $N = 376$  individuals, parents and offspring combined. Values greater than 0.10 and 0.13 are significant at  $P < 0.05$  and  $P < 0.01$

	Weight	Wing length	Tarsus length	Beak length	Beak depth	Beak width
Weight	—	0.17	0.16	0.09	0.20	0.18
Wing length	0.23	—	0.19	0.18	0.05	0.21
Tarsus length	0.22	0.24	—	-0.04	0.00	-0.06
Beak length	0.13	0.23	-0.05	—	0.35	0.36
Beak depth	0.28	0.06	-0.05	0.44	—	0.35
Beak width	0.27	0.27	-0.08	0.47	0.44	—

the more variable *Geospiza* species ranged from 0.48 in *G. scandens* to 0.69 in *G. fortis* (Table 3). Among all four species there was a positive association between the mean standard deviation of traits within populations, and mean phenotypic correlation ( $r = 0.96$ ,  $N = 4$ ).

A useful way to describe differences in the average correlation between traits is to compare populations in the variance along the principal axis of variation (PC1), relative to total population variance. The fraction of the total population variance along PC1 is high when average correlation is high, and it is low when average correlation is low. This method gives a better description than average correlation of how the joint distribution of traits differs among populations. The method was applied to the larger sample of *Geospiza* populations available from museum specimens. The song sparrow was also included in this comparison. In each population we extracted principal components from the five-variable covariance matrix. Total population variance was computed as the sum of the variances of principal components, which is identical to the sum of the variances of the original five traits. The relation between the PC1 fraction and total variance is shown in Fig. 1. *Geospiza* points are shown for populations of *G. fortis*, *G. scandens* and *G. conirostris*; the pattern is the same when the other three species are included.

Figure 1 shows that the song sparrow is less variable than any of the three *Geospiza* species, and intercorrelation among traits (PC1 fraction) is also the lowest. Among populations of all species, the relation between the PC1 fraction and total variability is strong and positive (arcsin $\sqrt{\quad}$  transformation;  $r = 0.90$ ,  $P < 0.0001$ ,  $N = 16$ ). The scatter of points is compared in Fig. 1 with the extreme case, when differences between populations in total variance result entirely from differences in variability along PC1. If we let the sum of the variances of components 2–5 be the same ( $k$ ) in a number of hypothetical populations, then  $Y = (X - k)/X$  describes the relation between the PC1 fraction ( $Y$ ) and total variance ( $X$ ) among these populations in the extreme case. Curves for two different values of  $k$  within the observed range are shown in Fig. 1. Actual points are well delimited by these curves, indicating that the observed association between morphological correlation and variance is very steep.

Such differences between populations in morphological correlation imply large differences among populations in their joint distributions of traits. Figure 2A illustrates these differences for the song sparrow and the three

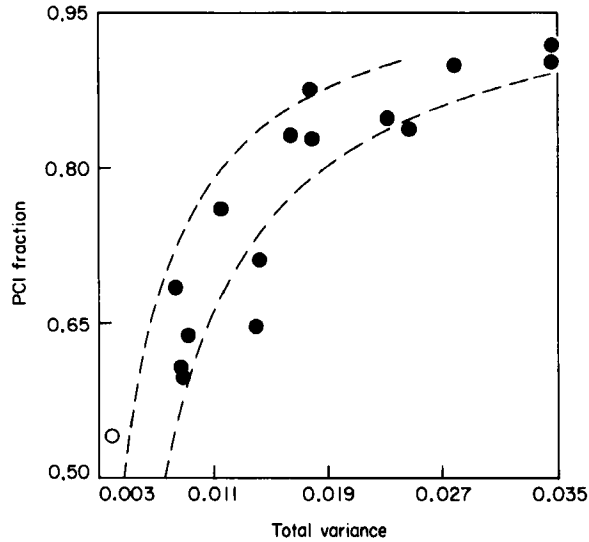


Figure 1. Relationship between morphological variance in populations and the fraction of the variance accounted for by the first principal component (PC1). Symbols indicate the song sparrow (○) and 15 populations of Galápagos *Geospiza* (●) (*G. fortis*, *G. conirostris* and *G. scandens*). The two curves indicate, for different starting values, the steepest possible relation between the PC1 fraction and total variance.

*Geospiza* species studied by Boag (1983) and Grant (1983). Ellipses of 95% frequency are shown for beak depth and beak width (Sokal & Rohlf, 1981). Ellipses contain approximately 95% of the individuals in a population, and hence they outline the joint distribution of two traits. Distributions in Fig. 2A vary from weakly elliptical in the song sparrow, to strongly elliptical in *G. fortis* and *G. conirostris*. Analogous differences between species exist for the other pairs of characters measured. Figure 2A illustrates the pattern detected in Fig. 1:

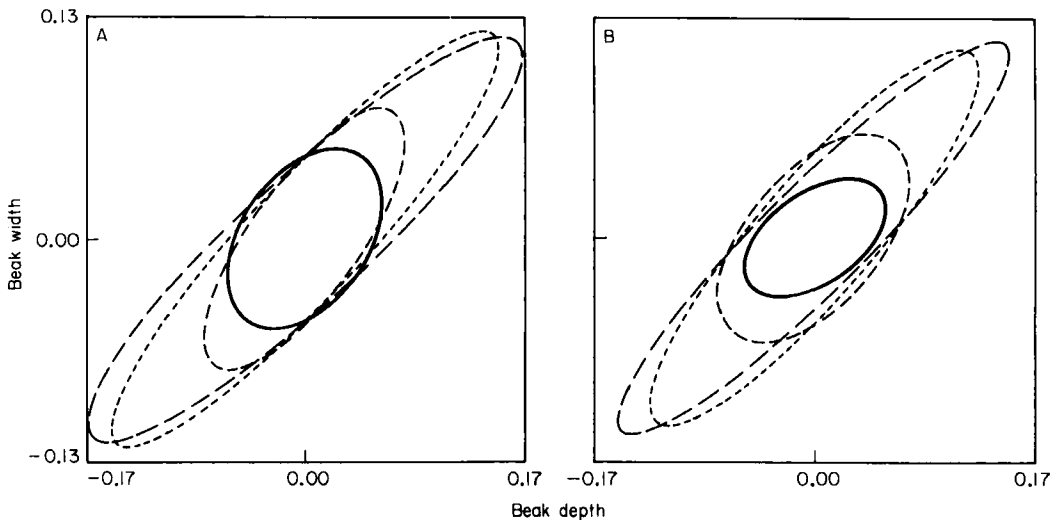


Figure 2. Bivariate distribution of phenotypes (A) and genotypes (B) in song sparrow (—) and three Galápagos finches: *G. scandens* (---), *G. fortis* (— — —) and *G. conirostris* (· · · · ·). 95% ellipses are based on variances corrected for measurement error, with means set to zero.



Table 3. Mean (corrected) standard deviations  $\times 100$  (s.d.), phenotypic correlations ( $r(P)$ ) and heritabilities ( $h^2$ ) in song sparrows and three *Geospiza* species. The latter are based on data in Boag (1983) and Grant (1983). Traits are given in Table 1

Species	Mean s.d.	Mean $r(P)$	Mean $h^2$
Song sparrow	3.0	0.23	0.44
<i>G. scandens</i>	4.0	0.48	0.43
<i>G. fortis</i>	5.5	0.69	0.88
<i>G. conirostris</i>	5.5	0.60	0.93

differences in variability among populations result almost entirely from differences in the variance along a single major axis. Widths of frequency ellipses perpendicular to the long axis differ very little, yielding large differences in phenotypic correlation between populations.

#### *Heritabilities and genetic correlations*

The phenotypic value of an individual is the sum of its additive genetic value and an 'environmental' deviation due to environment and non-additive genetic effects. Smith & Zach (1979) presented estimates of variance in the additive genetic fraction as a proportion of the phenotypic variance (the heritability) in the Mandarte song sparrows. Our revised estimates based on the larger sample are given in Table 4. Average observed heritability (0.35) was similar to the average given in Smith & Zach (0.30). Table 4 also shows estimates corrected for measurement error; these averaged 30% higher than observed values. Most heritabilities are significant, indicating a substantial additive genetic component to phenotypic variance despite low absolute levels of variance in this population.

While estimates of heritability in song sparrows are usually significant, they are lower on average than the equivalent estimates for at least two of the three *Geospiza* species (Table 3). The third species, *G. scandens*, probably also has higher  $h^2$  than the song sparrow; uncorrected estimates based on a larger sample of individuals in Price *et al.* (1984a) averaged 0.49 for four of the six traits. In

Table 4. Heritabilities ( $h^2$ , on left), genetic correlations (below diagonal of matrix), and environmental correlations (above diagonal) in the song sparrow. Heritabilities uncorrected for measurement error are given in parentheses. Estimates are based on 232 offspring in 84 families. No correlations are given for weight, since  $h^2$  is not significant ( $P > 0.05$ ). Significance levels are \* $P < 0.05$ , † $P < 0.01$

	$h^2$	Wing length	Tarsus length	Beak length	Beak depth	Beak width
Weight	0.12 (0.07)					
Wing length	0.31 (0.27)†		0.18	0.38†	0.68†	0.14
Tarsus length	0.49 (0.40)†	0.31*		0.03	0.15	-0.03
Beak length	0.44 (0.38)†	0.11	-0.03		2.31†	0.62†
Beak depth	0.95 (0.73)†	-0.08	-0.03	0.13		1.02†
Beak width	0.31 (0.24)†	0.55†	-0.08	0.26	0.45†	

the four populations whose phenotypic distributions are illustrated in Fig. 2A, mean  $h^2$  is positively associated with mean standard deviation ( $r = 0.94$ ,  $N = 4$ ). Note that a positive association between phenotypic correlation and variability could result from such differences in heritability, simply because a higher fraction of the phenotypic variance in low-variability populations is environmental, and environmental correlations may be weaker than genetic correlations (Cheverud, 1982; Boag, 1983). The actual relation between phenotypic and genetic correlations within and among populations is thus of interest.

Table 4 presents estimates of genetic correlations between traits in the song sparrow. Values shown are averages of the two estimates available for each pair of traits,  $r_1(G)$  and  $r_2(G)$ . Correlations were not computed for weight, since there was no evidence of significant additive genetic variance. Three of the 10 correlations are significant, and all were positive. As with the phenotypic values, genetic correlations are relatively low. This conclusion is supported by the low average values recorded for each of the two estimates,  $r_1(G)$  and  $r_2(G)$  (0.13 and 0.19). However, the two estimates were only weakly correlated with each other ( $r = 0.26$ ,  $N = 10$ ), indicating that the specific values for genetic correlation (and hence also environmental correlation) may be unreliable (Table 4).

Genetic correlations in Table 4 are related to the corresponding phenotypic values (Table 2) ( $r = 0.72$ ,  $N = 10$ ). Environmental correlations are also correlated with the phenotypic correlations ( $r = 0.65$ ), but not with the genetic correlations ( $r = 0.11$ ). Estimates of environmental correlation exceed the theoretical maximum value of 1.0 in two cases (Table 4). This can be attributed to sampling error;  $r(E)$  is computed from estimates of heritability and genetic correlation (equation 3), each of which is influenced by sampling error.

Low average genetic correlations in the song sparrow compare with higher averages for the phenotypically more variable populations of *G. fortis* (0.80; Boag, 1983) and *G. conirostris* (0.51; Grant, 1983). Genetic correlations for all five traits are not available for *G. scandens* (Boag, 1983), but average genetic correlation between the three beak characters was 0.45 (Price *et al.*, 1984a). This comparison indicates that the association noted between phenotypic variance and correlation among species must also be present in the genotype. Figure 2B illustrates bivariate frequency distributions of genetic values in two traits where estimates are available for all four populations. The *G. scandens* ellipse is based on heritabilities and genetic correlations given in Price *et al.* (1984a). Differences between populations in total variability are again associated with differences in the joint distributions of traits, from weakly elliptical in the song sparrow, to strongly elliptical in *G. fortis* and *G. conirostris*. Increases in genetic variance are largely restricted to a common major axis, with only small changes along the minor axis. For genetic as well as phenotypic values, morphological correlation increases with increasing morphological variance.

#### DISCUSSION

In this study we have measured phenotypic and genetic correlations between morphological traits in the song sparrow, and have shown that these differ in magnitude from correlations between the same traits in three species of

Galápagos finch. These differences are predictably and positively associated with differences in population variance, suggesting that morphological correlation and morphological variance have evolved jointly.

We can suggest two possible explanations for this pattern. First, the association between genetic correlation and variance may be the inevitable outcome of natural selection acting on functionally related traits. To see this, consider first the uncorrelated selection pressures which stabilize the variances of individual characters in a population. Such forces would be determined by environmental factors, such as food diversity. Ellipses in Fig. 3 illustrate the joint genetic distribution of two characters that might result from such forces alone. Two concentric ellipses are drawn, to indicate the effects of different intensities of selection on the total variance in two populations.

Next, consider the selection pressures which may influence the correlation between traits. In particular, if the two traits are functionally related, and hence must work in concert when carrying out functions, then an 'optimal' line of allometry should exist between them, with stabilizing selection perpendicular to this line (Fig. 3). For example in an individual finch, beak size and body size are functionally related traits, in that they are jointly involved in the efficient exploitation of food resources (Price *et al.*, 1984a; Schluter & Grant, 1984a, b). Optimal beak size in an individual finch should thus depend on its body size, and vice versa. Slope and position of the optimal line of allometry would be influenced by the particular environment, but the forces of selection favouring the correlation should be common to most environments. The joint genetic distribution of traits in two populations differing in overall variance will be differently affected when selection about a line of allometry is added (Fig. 3): the stabilizing forces acting perpendicular to the line of allometry have a proportionately greater effect on the more variable population than on the less

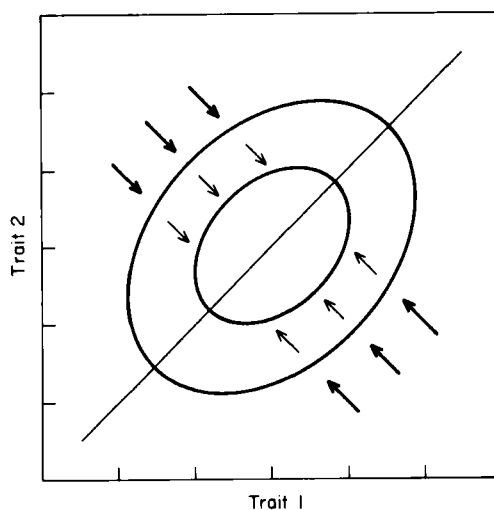


Figure 3. Joint distribution of traits in two hypothetical populations differing in total variability (ellipses). Straight line indicates a line of optimal allometry between traits, with stabilizing selection perpendicular to this line. Arrows indicate the magnitude and direction of selective effects on the joint distributions, heavier arrows indicating greater effects.

variable population, and hence the resulting correlation between the two traits should also be greater.

If the above hypothesis is correct, then the rapid rise in the fraction of total variance accounted for by PC1 as variance increases (Fig. 1) suggests that natural selection around the line of allometry is very strong. Total variance in a finch or sparrow population may be determined by a variety of ecological circumstances. Nonetheless, observed differences in population variance are due almost entirely to differences along a first principal axis (e.g. Fig. 2), indicating that deviations around this axis are selected against in many different environments. Consequently, the ecological environment that selects for a particular morphological variance within a population also indirectly determines morphological correlation, for functionally related traits.

A second possible hypothesis is that the joint evolution of morphological correlation and variance may be caused by immigration and hybridization (introgression). If the first principal axis within populations is the same as the one along which populations and species are separated, then introgression increases morphological variance predominantly along this one axis. When differences among populations in total variance result from differences in the amount of introgression, then correlations between traits will vary directly with total variance. This argument also assumes that there is selection about a line of allometry, since it requires a strong correlation between traits among populations. However, selection may be more effective in producing a correlation among populations than within (Grant & Price, 1981), and introgression will exaggerate within-population correlations.

*Geospiza* species occasionally hybridize on Galápagos islands, and exchange between differentiated populations of the same species may also occur (Grant & Price, 1981; Price *et al.*, 1984b). Hence, introgression is probably a factor in the comparison between the song sparrow and *Geospiza*. But the importance of introgression relative to selection is difficult to assess with our data. For example, immigration may not be a sufficient explanation of species differences in total variance; the possible importance of selection is indicated by an inverse relationship between observed population variance and the intensity of stabilizing selection recorded (Grant & Price, 1981). Also, morphological differences between species are not always a simple extension of morphological variance within populations: in *G. scandens*, hybridization would increase variance predominantly along the minor axes, yet this is not observed (Fig. 2A) (Schluter, 1984; Grant *et al.*, 1985).

Whatever the relative importance of introgression and selection, the association between genetic correlation and genetic variance should have evolutionary consequences. For example, low genetic variances should reduce the rate of divergence in morphological size between populations. Weaker genetic correlations between characters, will, however, facilitate the evolution of interpopulation differences in shape (Lande, 1979). Thus, if correlation and variance are generally associated in natural populations, patterns of morphological divergence in high- and low-variability species groups may be expected to differ qualitatively.

Similarity between genetic and phenotypic correlations is often noted (Falconer, 1981; Cheverud, 1982, 1984). This is not unexpected when heritabilities are uniformly high, as in *G. fortis* and *G. conirostris* (Boag, 1983;

Grant, 1983), since the correlations between environmental effects exert little influence on the phenotype (Searle, 1961; Cheverud, 1982; Boag, 1983). In the song sparrow, however, heritabilities average 0.44, and the environmental effects are therefore greater. Genetic and phenotypic correlations were related in this species, though the correlation was only moderate ( $r = 0.72$ ). Environmental correlations were weakly correlated with genetic correlations ( $r = 0.11$ ), a result of large differences between traits in estimated heritabilities (Table 4; Searle, 1961). A consequence of such differences between traits in heritability is that the genetic variance-covariance matrix in the song sparrow is not simply a constant multiple of the phenotypic matrix. This renders evolutionary response to selection unpredictable from the measurement of phenotypic characteristics alone (Lande, 1979; Leamy & Atchley, 1984), even when genetic and phenotypic correlations are similar.

While average genetic and phenotypic correlations between traits in the song sparrow are predictably related to population variance, there is considerable variability between traits in the strength of correlations (Tables 2 and 4). Clearly other factors may influence the evolution of phenotypic and genetic correlations (Cheverud, 1982; Grant, 1983). For example, in some situations a beak of fixed length may be favoured in a population regardless of body size, e.g. to extract nectar from a given flower type. In this situation an optimal line of allometry may not exist, leading to a lowered correlation between beak length and other morphological traits. Or, traits may vary in their degree of functional relationship. Such circumstances may explain the low correlation between tarsus length and beak characters in the song sparrow (Tables 2 and 4), although we are unable to identify the causal factors involved. One relevant observation is that there was significant directional selection associated with overwinter mortality in the song sparrow in two of four years (females only; Schluter & Smith, 1986). Individuals with longer beaks and shorter tarsi were favoured. It is difficult to predict the effects of directional selection alone on genetic correlations (Lande & Arnold, 1983). Nevertheless, these results show that tarsus length and beak length may not be functionally related in the song sparrow since they were not jointly favoured by selection.

#### ACKNOWLEDGEMENTS

We thank T. D. Price, P. R. Grant, P. Lavin and P. Arcese for comments and discussion, and I. Abbott, P. R. Grant and T. D. Price for the *Geospiza* measurements. R. Zach, A. A. Dhondt, J. R. Merkt, R. Moses and J. Russell helped in the field. The Tsawout and Tseycum Indian bands kindly allowed us to work on their island. This work was funded by NSERC University Research and Postdoctoral fellowships to D.S., and NSERC research grants to J.N.M.S.

#### REFERENCES

- ABBOTT, I., ABBOTT, L. K. & GRANT, P. R., 1977. Comparative ecology of Galápagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. *Ecological Monographs*, 47: 151–184.
- ATCHLEY, W. R., GASKINS, C. T. & ANDERSON, D., 1976. Statistical properties of ratios. I. Empirical results. *Systematic Zoology*, 25: 137–148.

- BOAG, P. T., 1983. The heritability of external morphology in Darwin's ground finches (*Geospiza*) of Isla Daphne Major, Galápagos. *Evolution*, *37*: 877-894.
- 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. *Journal of Theoretical Biology*, *110*: 155-171.
- ENDLER, J. A., 1986. *Natural Selection in the Wild*. Princeton: Princeton University Press.
- FALCONER, D. S., 1981. *Introduction to Quantitative Genetics*, 2nd edition. New York: Longman.
- GRANT, B. R., 1985. Selection on bill characters in a population of Darwin's finches: *Geospiza cinerostriis* on Isla Genovesa, Galápagos. *Evolution*, *39*: 523-532.
- GRANT, P. R., 1983. Inheritance of size and shape in a population of Darwin's finches, *Geospiza cinerostriis*. *Proceedings of the Royal Society of London, Series B*, *220*: 219-236.
- GRANT, P. R., ABBOTT, I., SCHLUTER, D., CURRY, R. L. & ABBOTT, L. K., 1985. Variation in the size and shape of Darwin's finches. *Biological Journal of the Linnean Society*, *25*: 1-39.
- GRANT, P. R. & PRICE, T. D., 1981. Population variation in continuously varying traits as an ecological genetics problem. *American Zoologist*, *21*: 795-811.
- LANDE, R., 1979. Quantitative genetic analysis of multivariate evolution, applied to brain : body size allometry. *Evolution*, *33*: 402-416.
- LANDE, R., 1980. The genetic covariance between characters maintained by pleiotropic mutations. *Genetics*, *94*: 203-215.
- LANDE, R. & ARNOLD, S. J., 1983. The measurement of selection on correlated characters. *Evolution*, *37*: 1210-1226.
- LEAMY, L. & ATCHLEY, W., 1984. Static and evolutionary allometry of osteometric traits in selected lines of rats. *Evolution*, *38*: 47-54.
- LEWONTIN, R. C., 1966. On the measurement of relative variability. *Systematic Zoology*, *15*: 141-142.
- PRICE, T. D. & GRANT, P. R., 1985. The evolution of ontogeny in Darwin's finches: a quantitative genetic approach. *American Naturalist*, *125*: 169-188.
- PRICE, T. D., GRANT, P. R. & BOAG, P. T., 1984a. Genetic changes in the morphological differentiation of Darwin's ground finches. In K. Wöhrmann & V. Loeschcke (Eds), *Population Biology and Evolution*: 49-66. New York: Springer.
- PRICE, T. D., GRANT, P. R., GIBBS, H. L. & BOAG, P. T., 1984b. Recurrent patterns of natural selection in a population of Darwin's finches. *Nature*, *309*: 787-789.
- REEVE, E. C. R., 1955. The variance of the genetic correlation coefficient. *Biometrics*, *11*: 357-374.
- SEARLE, S. R., 1961. Phenotypic, genetic and environmental correlations. *Biometrics*, *17*: 474-480.
- SCHLUTER, D., 1984. Morphological and phylogenetic relations among the Darwin's finches. *Evolution*, *38*: 921-930.
- SCHLUTER, D. & GRANT, P. R., 1984a. Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. *Evolution*, *38*: 856-869.
- SCHLUTER, D. & GRANT, P. R., 1984b. Determinants of morphological patterns in communities of Darwin's finches. *American Naturalist*, *123*: 175-196.
- SCHLUTER, D. & SMITH, J. N. M., 1986. Natural selection on beak and body size in the song sparrow. *Evolution*, *40*: 221-231.
- SMITH, J. N. M., 1986. Determinants of lifetime reproductive success in the song sparrow. In T. H. Clutton-Brock (Ed.), *Reproductive Success*. Chicago: Chicago University Press.
- SMITH, J. N. M. & ZACH, R., 1979. Heritability of some morphological characters in a song sparrow population. *Evolution*, *33*: 460-467.
- SMITH, J. N. M., ARCESE, P. & SCHLUTER, D., 1986. Song sparrows grow and shrink with age. *Auk*, *103*: 210-212.
- SOKAL, R. R. & ROHLF, F. J., 1981. *Biometry*, 2nd edition. San Francisco: W. H. Freeman.
- VAN NOORDWIJK, A. J., 1984. Quantitative genetics in natural populations of birds illustrated with examples from the great tit, *Parus major*. In K. Wöhrmann & V. Loeschcke (Eds), *Population Biology and Evolution*: 67-79. New York: Springer.