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ADAPTIVE RADIATION ALONG GENETIC LINES OF LEAST RESISTANCE

DOLPH SCHLUTER
Department of Zoology and Centre for Biodiversity Research, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada
E-mail: schluter@zoology.ubc.ca

Abstract.—Are measurements of quantitative genetic variation useful for predicting long-term adaptive evolution? To answer this question, I focus on $\mathbf{g}_{max}$, the multivariate direction of greatest additive genetic variance within populations. Original data on threespine sticklebacks, together with published genetic measurements from other vertebrates, show that morphological differentiation between species has been biased in the direction of $\mathbf{g}_{max}$ for at least four million years, despite evidence that natural selection is the cause of differentiation. This bias toward the direction of evolution tends to decay with time. Rate of morphological divergence between species is inversely proportional to θ, the angle between the direction of divergence and the direction of greatest genetic variation. The direction of greatest phenotypic variance is not identical with $\mathbf{g}_{max}$, but for these data is nearly as successful at predicting the direction of species divergence. I interpret the findings to mean that genetic variances and covariances constrain adaptive change in quantitative traits for reasonably long spans of time. An alternative hypothesis, however, cannot be ruled out: that morphological differentiation is biased in the direction $\mathbf{g}_{max}$ because divergence and $\mathbf{g}_{max}$ are both shaped by the same natural selection pressures. Either way, the results reveal that adaptive differentiation occurs principally along "genetic lines of least resistance."

Key words.—Adaptive divergence, adaptive radiation, genetic correlation, genetic variance, heritability, natural selection, sticklebacks.

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Recent years have seen an increasingly wider appreciation that patterns of genetic (including developmental) variation constrain and direct the pathways of evolution (Bonner 1982; Maynard Smith et al. 1985; Futuyma 1988; Wake 1991). The promise of quantitative genetic theory was that it would enable precise predictions of such effects in natural populations for polygenic traits under natural selection (Lande 1979; Barton and Turelli 1989; Arnold 1992). This promise is being realized for evolutionary change across a single generation (Grant and Grant 1993, 1995).

The value of quantitative genetic theory for predicting long-term evolution is more doubtful. This is primarily because levels of genetic variance and covariance in evolving populations may not be sufficiently stable over time to permit prediction beyond a few generations (Lofsvold 1986; Turelli 1988; Barton and Turelli 1989; Wilkinson et al. 1990; Beniwal et al. 1992; Shaw et al. 1995). Second, a population in the neighborhood of a single adaptive peak will eventually climb the peak regardless of the pattern of genetic (co)variances (Lande 1979; Via and Lande 1985; Zeng 1988), in which case the role of quantitative genetics is only temporary. This second argument assumes that genetic constraints are not severe and that only a single fitness optimum is present. Quantitative genetic effects on the direction of evolution may endure when genetic variance in some directions is completely lacking (Gomulkiewicz and Kirkpatrick 1992) or when the selection surface has several local optima (Lande 1979; Arnold 1992; Price et al. 1993).

Here I take an empirical approach and ask whether, and for what period of time, the direction and extent of morphological diversification is influenced by genetic variances and covariances between the traits. I focus on a simple index of genetic variance and covariance within populations: the multivariate direction of greatest genetic variation. By "direction" I mean a vector of coefficients that describe a linear combination of the original morphological traits. The linear combination having maximum genetic variance within a population defines the genetic "line of least resistance" to evolutionary change by natural selection (Stebbins 1974; see Futuyma et al. 1993).

Three predictions are tested. The first is that populations and species very recently diverged from a common ancestor should differ in a direction close to the direction of greatest genetic variance (hereafter $\mathbf{g}_{max}$). This prediction stems from the fact that a population under the influence of a single fitness optimum does not evolve in the direction of greatest fitness increase (Lande 1979; Via and Lande 1985). Instead, progress toward an optimum should follow a curved trajectory that, in its initial stages, follows the direction of greatest genetic variance (Fig 1). Therefore, the direction of the line separating species means (herafter $\mathbf{z}$) should be biased toward $\mathbf{g}_{max}$ when species are very closely related. I quantify the bias using the angle θ between $\mathbf{g}_{max}$ and $\mathbf{z}$.

The predicted angle θ depends also on the location of the optimum, which is unknown. However, if the direction of selection is random with respect to the orientation of $\mathbf{g}_{max}$ then there should still be a tendency for initial divergence between populations and species to follow $\mathbf{g}_{max}$. In the Discussion I consider the possibility that optima are not randomly oriented with respect to $\mathbf{g}_{max}$. I also consider the consquences of multiple optima.

The second prediction is that this bias to the direction of evolution should be temporary and diminish with time. This is illustrated in Figure 1 by the tendency for the direction of difference between species, $\mathbf{z}$, to move farther away from $\mathbf{g}_{max}$ at progressively later stages of divergence. This decay in the value of θ with time is expected even if genetic covariances remain constant, but it may be hastened if the covariances change as well (for simplicity I will use "covariances" to refer to both genetic variances and covariances). The duration of the bias to the direction of evolution imparted by genetic parameters has not been previously estimated.

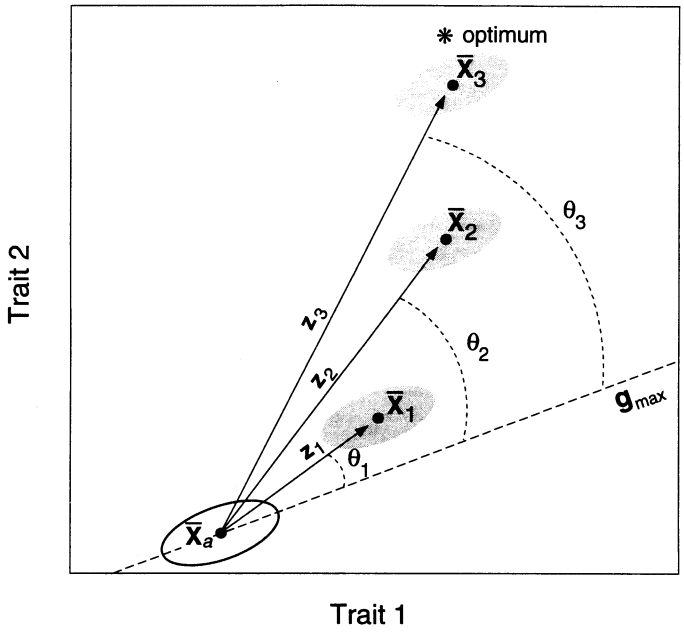

FIG. 1. The path of divergence between two species when traits are genetically correlated. Ellipses outline the additive genetic ("breeding") values of individuals within each population. The long axis of the ellipse is the direction of greatest genetic variance, $\mathbf{g}_{max}$. To simplify the illustration, the position of one of the species is assumed to be fixed at the ancestral value ($\bar{\mathbf{X}}_a$; unshaded). The second species (shaded) is diverging from the first because of continuous directional selection toward a new optimum. Three stages of divergence ($\bar{\mathbf{X}}_1 - \bar{\mathbf{X}}_3$) illustrate the curved path taken; $\mathbf{z}_1 - \mathbf{z}_3$ are directions of the difference between ancestor and descendant at each stage; θ measures the angle between $\mathbf{g}_{max}$ and the line separating species means, $\mathbf{z}$.

The third prediction is that progress should be relatively slow if selection favors divergence in a direction markedly different from that of $\mathbf{g}_{max}$, at least in the initial stages of divergence. This is because genetic variance is relatively low in directions other than $\mathbf{g}_{max}$, and this reduces the amount of evolutionary response expected from a given intensity of directional selection (Lande 1979). None of these predictions assumes that genetic covariances are constant through time and in all species. Indeed, malleable covariances may be an additional reason to expect that their influence will be temporary.

To test these predictions, I measured quantitative genetic variation in five ecologically important morphological traits in a threespine stickleback *Gasterosteus* sp. The species is part of a recent adaptive radiation of sticklebacks in freshwater lakes and streams of coastal British Columbia, Canada (Schluter and McPhail 1992; McPhail 1993; Schluter 1996; Taylor et al., in press). I compare $\mathbf{g}_{max}$ within the stickleback population to the direction of differences among populations in the same five traits. I then repeat this analysis on species in four other vertebrate taxa using data from the literature. This broader comparison was restricted to vertebrates because the ecological relevance of the morphological traits measured is known or suspected; this would increase the likelihood that natural selection (rather than drift) was the cause of evolutionary divergence. Finally, I quantify the resemblance between $\mathbf{g}_{max}$, the direction of greatest genetic variance, and the direction of greatest phenotypic variance within populations to determine whether the latter yields similar results.

METHODS

Threespine Sticklebacks

Genetic parameters were estimated in the "limnetic" species of threespine stickleback from Enos Lake (*Gasterosteus* sp.), Vancouver Island (McPhail 1984; Schluter and McPhail 1992). This freshwater species is one of many derived from the cosmopolitan marine species (*G. aculeatus*) that colonized newly formed lakes and rivers at the end of the Pleistocene (McPhail 1993; Taylor et al., in press). The Enos Lake limnetic is sympatric with and reproductively isolated from a second species, the "benthic" (McPhail 1984; Ridgway and McPhail 1984; Schluter and McPhail 1992). The two forms are morphologically distinct and exploit different habitats. The traits that distinguish them strongly affect feeding efficiency and growth rate in the different habitats (Schluter 1993, 1995).

Genetic parameters were estimated from measurements of wild-caught parents and their lab-reared offspring. Crosses were made in the field by extracting and mixing eggs and sperm from randomly paired adults captured in traps and nets. Parents were then fixed in 10% formalin and later stained with alizarin red and transferred to 37% isopropyl alcohol. Fertilized eggs from a total of 67 families were transported to the lab, where they were raised in 10-liter aquaria. Offspring were fed once daily infusoria culture, brine shrimp nauplii, and later, tubifex worms. After three months, one to five offspring from each family were selected at random, preserved, and stained in the manner of their parents.

Five morphological traits were measured as described in Schluter and McPhail (1992): body length, body depth, gape width, gill raker number, and gill raker length. Measurements were *ln* transformed and size-corrected as described in detail in Schluter and McPhail (1992). Measurements from sibs were then averaged to yield a single offspring mean per family. Additive genetic variances and covariances between traits were estimated as twice the observed covariance between trait values in offspring and midparents (Falconer 1989). This method yielded two estimates of genetic covariance between each pair of traits, which were then averaged. Because parents and offspring were raised in different environments, I cannot rule out the possibility that estimates of genetic covariance are biased by genotype-environment interactions (Riska et al. 1989).

The direction of greatest genetic variation ($\mathbf{g}_{max}$) is the major axis (first principal component or dominant eigenvector) of the resulting genetic covariance matrix (Pimentel 1979; Johnson and Wichern 1982). Figure 1 illustrates $\mathbf{g}_{max}$ in two dimensions as the longest axis of the ellipse describing the distribution of individual genetic values. The elements (coefficients) of $\mathbf{g}_{max}$ measure the contributions of each of the five traits to the most variable direction. For example, the coefficient for trait 1 in Figure 1 is greater than that for trait 2, because a unit change in the direction of $\mathbf{g}_{max}$ involves a greater displacement along the x-axis than along the y-axis. These coefficients were scaled such that $[\mathbf{g}_{max}]'[\mathbf{g}_{max}] = 1$

(where ′ indicates transpose). Total additive genetic variance in the population is the sum of the genetic variances of the five traits. Genetic variance among individuals in the direction $\mathbf{g}_{max}$ made up 71% of this total.

Populations included in the analysis were those presented in Schluter and McPhail (1992). In the other vertebrate data sets I analyzed, I calculated $\mathbf{z}$ as simply the direction of the line connecting species means (see *Other Vertebrates* for the calculation and Fig. 1 for an illustration). I modified this step in the sticklebacks to accommodate a large number of populations whose phylogenetic relationships are still obscure. Rather than calculate the direction of the difference between each pair of population means, I calculated $\mathbf{z}$ as the single major axis of variation among all the population means. This measurement is roughly the same as the average of the directions between all pairs of populations. The elements of $\mathbf{z}$ were scaled so that $\mathbf{z}'\mathbf{z} = 1$. The angle between $\mathbf{g}_{max}$ and $\mathbf{z}$ was calculated as $\theta = \cos^{-1}[(\mathbf{g}_{max})'\mathbf{z}]$ (Pimentel 1979). The major axis $\mathbf{z}$ accounted for 80% of the total variance among population means.

I tested the null hypothesis that in sticklebacks $\theta = 0$ using the following bootstrap procedure: (1) 67 families of sticklebacks (parents and offspring) were randomly sampled with replacement from the original pool of 67 families ("with replacement" results in some families being chosen more than once and other families not chosen); (2) a new value of $\mathbf{g}_{max}$ was computed from this "new" sample and its angle θ from the original $\mathbf{z}$ was computed; (3) steps 1–2 were repeated 1000 times. The fraction of iterations in which the new angle exceeded the original θ is an approximate *P*-value for a test of the null hypothesis that $\theta = 0$ (Efron and Tibshirani 1986). The standard deviation of the 1000 resampled vectors is the standard error of the estimated coefficients of $\mathbf{g}_{max}$. The reliability of the bootstrap method has not been evaluated in this context, but it is expected to behave well when, as in the present case, sample size is reasonable and the data are nearly normally distributed (Efron and Tibshirani 1986). This test assumes that the among-population direction is estimated without error. The null hypothesis that $\theta = 0$ would be more difficult to reject if sampling error in $\mathbf{z}$ were also incorporated.

Other Vertebrates

Published genetic covariances for ecologically relevant morphological traits were obtained for the Galapagos medium ground finch *Geospiza fortis* (Boag 1983), song sparrow *Melospiza melodia* (Schluter and Smith 1986a), collared flycatcher *Ficedula albicollis* (Merilä et al. 1994), and *Peromyscus* mice (Lofsvold 1986). (Co)variances were based on *ln*-transformed traits in most cases; in the remaining cases I used the squared coefficient of covariation instead.

In each taxon, the species for which $\mathbf{g}_{max}$ was measured was designated the focal species ("ancestral" species in Fig 1). The direction of difference $\mathbf{z}$ was then measured between the focal species and each species closely related to it. Each $\mathbf{z}_i$ was calculated as $\mathbf{z}_i = [\bar{\mathbf{X}}_a - \bar{\mathbf{X}}_i][(\bar{\mathbf{X}}_a - \bar{\mathbf{X}}_i)'(\bar{\mathbf{X}}_a - \bar{\mathbf{X}}_i)]^{-1/2}$, where $\bar{\mathbf{X}}_a$ and $\bar{\mathbf{X}}_i$ are the vectors of mean measurements for the focal species and the given related species *i*, respectively. The quantity between parentheses on the right-hand side of this equation is the inverse of the morphological (euclidean) distance between the pair of population means, which scales the direction so that each $\mathbf{z}'_i\mathbf{z}_i = 1$. The number of other species with which the focal species was compared was determined by the availabilities of morphological data and allozyme (or other molecular) measurements of relatedness.

Biochemical measures of relatedness were available for *G. fortis* and 10 other Galapagos finch species (Yang and Patton 1981). Five morphological traits were measured on these species (Grant et al. 1985): wing length, tarsus length, beak length, depth, and width. A species mean is the average of population (island) means. Natural selection occurs frequently on the five traits in every population that has been studied in detail (Boag and Grant 1981; Price et al. 1984; Gibbs and Grant 1987; Grant and Grant 1989) and species differences in morphology are strongly correlated with differences in diet (Grant 1986; Grant and Grant 1989). Natural selection was doubtless the main cause of morphological differentiation in this group.

Similar data were available for the song sparrow and its relatives. Allozyme distances between the song sparrow and nine species of *Melospiza*, *Zonotrichia*, and *Junco* were taken from Zink (1982). The same five morphological traits were measured in these species as in the Galapagos finches (Schluter and Smith 1986b; Schluter 1986, 1988a). Natural selection was observed to act frequently on these traits in a population of song sparrow studied intensively by J. N. M. Smith (Schluter and Smith 1986b; Schluter 1988b). This, along with the known association between these traits and feeding ecology in birds in general (Miles and Ricklefs 1984; Grant 1986; Miles et al. 1987; Richman and Price 1992; Suhonen et al. 1994), support the assumption that selection is the cause of their divergence.

In the collared flycatcher, $\mathbf{g}_{max}$ is compared with the line of differentiation between this species and the closely related pied flycatcher, *F. hypoleuca*. Seven morphological traits were measured in both species: beak length, depth, width, tarsus length, length of the wing, tail, and first primary feather (Merilä et al. 1994). There is no direct evidence of natural selection on these traits in the two flycatchers. However, most of these traits are known to be associated with feeding ecology and habitat in birds in general (Miles and Ricklefs 1984; Grant 1986; Miles et al. 1987; Richman and Price 1992; Suhonen et al. 1994), and I will assume that natural selection is responsible for morphological divergence between species (Merilä et al. 1994). Note that the number of traits measured in the flycatchers (seven) is two more than that available for sticklebacks, finches, and sparrows. This means that the results would not be directly comparable because the angle θ between $\mathbf{g}_{max}$ and $\mathbf{z}$ is expected to depend on the number of traits. To solve this problem, I computed θ for all subsets of five traits in the flycatchers and used the average. An allozyme-based measure of relatedness between the two species was found in Gelter et al. (1989).

Measurement means for two subspecies of *Peromyscus maniculatus* and one of *P. leucopus* were kindly provided by D. Lofsvold (unpubl. data). Two independent comparisons of means were therefore made: one between the two subspecies of *P. maniculatus* and the other between the average of these two subspecies and *P. leucopus*. The traits were head length, body length, tail length, ear length, several dimensions of the

skull, mandible length, and molar occlusal surface area. The functional basis of variation in these traits is not well known and the assumption that natural selection is responsible for differences between populations and species studied is therefore the least supported of my data sets. However, Lofsvold (1988) showed that covariances among population means were not proportional to genetic covariances within the populations, ruling out genetic drift as a cause of differentiation. Also, some associations between limb and tail measurements and resource use have been discovered (Horner 1954). I therefore decided to include *Peromyscus* in the present survey.

Estimates of genetic covariance of traits were available for all three populations of *Peromyscus* (Lofsvold 1986) and I pooled estimates of the forms involved in each particular comparison. Fifteen traits were measured. To compare findings with the other data sets, I carried out analyses on all subsets of five traits and averaged the results. Allozyme measurements of relatedness between the three forms were taken from Avise et al. (1979).

I used Nei's (1978) genetic distance calculated from allozyme frequencies to measure the time separating a pair of species. Rogers's (1972) distance was strongly correlated with Nei's in these same groups ($r = 0.99$, $t = 28.82$, df = 17, $P < 0.001$; tested using general least squares—see following section for explanation) and it led to identical results. For sticklebacks I used the average allozyme distance between freshwater populations in the region (Withler and McPhail 1985; McPhail 1984, 1992).

Statistical Analysis

I used linear regression to compare θ with other variables such as the amount of evolutionary differentiation between species and the time (allozyme distance) separating them. However, separate observations within the sparrow and finch clades are not statistically independent because of shared history. For example, the sparrows provide nine measurements of $\mathbf{z}$ (yielding nine measurements of θ), but each of them is calculated as the difference between the song sparrow and one of nine relatives. Similarly, $\mathbf{z}$ is measured between *G. fortis* and each of 10 other Galapagos finch species. The advantage of this approach is that every θ can be calculated using $\mathbf{g}_{max}$ of the focal species (the only species for which genetic parameters are known). An alternative approach based on independent contrasts (Felsenstein 1985; Harvey and Pagel 1991) would require the additional assumption that $\mathbf{g}_{max}$ of at least one of the species involved in each contrast is the same as $\mathbf{g}_{max}$ of the focal species.

I used general least squares (GLS) to solve the problem of nonindependent observations (Kendall and Stuart 1979; Draper and Smith 1981). This is a form of weighted regression that incorporates a matrix $\mathbf{V}$ whose elements $v_{i,j}$ are "correlations" specifying the degree of dependence between each pair of species i and j. The upshot of the approach is that a large value for an element of $\mathbf{V}$ assigns a low weight to the corresponding observation. The GLS model is:

$$\mathbf{Y}_c = \mathbf{X}_c\beta + \epsilon_c. \quad (1)$$

$\mathbf{X}_c$ and $\mathbf{Y}_c$ are transformed $\mathbf{X}$ and $\mathbf{Y}$ variables: $\mathbf{Y}_c = \mathbf{V}^{-1/2}\,\mathbf{Y}$ and $\mathbf{X}_c = \mathbf{V}^{-1/2}\,\mathbf{X}$. $\mathbf{V}^{-1/2}$ is the inverse of the "square root" of $\mathbf{V}$ (i.e., $[\mathbf{V}^{1/2}]'\mathbf{V}^{1/2} = \mathbf{V}$). ϵ_c is the vector of residuals. This transformation corrects $\mathbf{X}$ and $\mathbf{Y}$ so that they fulfill the regression requirement of independent observations and homogeneous variances of residuals. The regression coefficients β and their standard errors are then estimated in the usual way (least squares). GLS has been used in previous studies to correct measurements that are nonindependent because of phylogenetic relationships between species (Lynch 1991; Lynch and Jarrell 1993).

The matrix $\mathbf{V}$ was constructed as a series of submatrices representing individual clades in the data set. Within a clade the degree of dependence $\mathbf{v}_{i,j}$ between any pair of species i and j was calculated from branch lengths in the tree of phylogenetic relationships. For example, the phylogeny for sparrows (Zink 1982) was first redrawn such that the focal species (song sparrow) was the root of the tree, while retaining the original branch lengths. The expected dependence between observations for any two sparrow species i and j was then calculated as the branch length shared between these two species in the paths leading from each of them to the root of the tree. When $i = j$, branch length shared is simply the sum of branch lengths between the given species i and the root of the tree.

Because branch length is in arbitrary units of Nei's (1978) allozyme distance, I scaled values of $v_{i,j}$ by dividing them by the smallest value (summed branch length) in the given submatrix (dividing by the largest value instead gave virtually identical results). Submatrices for clades with only a single observation (sticklebacks and flycatchers) or where different values are independent (mice) were given 1s along the diagonal and 0s elsewhere. Submatrices were then arranged along the diagonal of $\mathbf{V}$. The dependence between observations from different submatrices (clades) was assumed to be zero.

GLS was also used to test whether the observed mean θ, based on all measurements combined, was significantly different from the random expectation of 1.18 radians (about 68°). This expected angle was calculated as the mean of angles between a large number of random vectors and an arbitrary fixed vector (I used the unit vector [0, 0, 0, 0, 1], but the result is the same with any other vector). I created each random vector by breaking a stick of length 1 into five pieces, with the break points drawn from a uniform random number generator. Each element of the random vector was the length of the corresponding piece of the broken stick. The angle between this vector and the fixed vector was then calculated. This procedure was repeated ten thousand times.

All calculations and statistical analyses were carried out using the computer program S-plus 3.1 (Statistical Sciences 1992).

RESULTS

Sticklebacks

The five morphological traits were heritable and genetically intercorrelated (Table 1). The direction of greatest genetic variance ($\mathbf{g}_{max}$; Table 2) showed that genotypes at one extreme of the population had relatively short, slender bodies; narrow mouths; and numerous, long gill rakers. Genotypes at the other extreme had the opposite set of features: relatively

TABLE 1. Estimates of genetic parameters for five morphological traits in limnetic sticklebacks from Enos Lake. Heritabilities (± SE) are listed in the first column. The remaining columns give genetic variances and covariances between traits (× 10^4 in bold) and genetic correlations. All traits were *ln* transformed and size corrected as described in Schluter and McPhail (1992).

Trait	Heritability	Length	Depth	Gape width	Raker number	Raker length
Length	0.37 (0.17)	**3.91**	−0.77	0.49	−0.24	−0.60
Depth	0.04 (0.18)	**−1.15**	**0.57**	0.67	−0.58	−0.31
Gape width	0.32 (0.14)	**3.19**	**1.69**	**10.88**	−0.36	−1.01
Raker number	0.36 (0.17)	**−1.37**	**1.29**	**−3.42**	**8.49**	0.46
Raker length	0.44 (0.15)	**−4.72**	**−0.94**	**−13.24**	**5.29**	**15.73**

long, deep bodies; wide mouths; and few, short gill rakers. This direction of maximum genetic variance within populations ($\mathbf{g}_{max}$) was surprisingly similar to the direction of differences among population means (Table 2). The angle θ between $\mathbf{g}_{max}$ and $\mathbf{z}$ was small (0.31 radians, about 18°, which was not significantly different from 0; Table 2). This θ is also well below the random expectation of 1.18 radians (bootstrap $P < 0.001$). These young stickleback populations and species have diverged mainly along $\mathbf{g}_{max}$, the genetic line of least resistance.

Overall Trends

Data from other available vertebrate groups confirms the pattern seen in the sticklebacks. The vast majority of evolution is in a direction closer to $\mathbf{g}_{max}$ than expected by chance (Fig. 2). The mean angle in this data set was estimated as $\bar{\theta}$ = 0.61 radians ± 0.13 SE, which is well below the random expectation of 1.18 radians (GLS; $t = -4.244$, df = 22, $P = 0.0002$). The results confirm the expectation that evolution is biased toward $\mathbf{g}_{max}$ among species that have diverged relatively recently. Values for θ are nevertheless highly variable and several values approach or exceed the random expectation (Fig 2). For example, divergence between the two species of flycatchers was in a direction very different from $\mathbf{g}_{max}$.

The smallest values of θ tended to occur between the most recently diverged species. This was true of species in four of five taxa whose date of divergence was less than about 0.07 allozyme distance units (flycatchers are the exception; Fig. 2). More distantly related species tended to differ in a direction closer on average to the random expectation. This tendency was also present within each of the three taxa represented by more than one observation (sparrows, Galapagos finches, and mice), though the trend is slight in the third case. These patterns hint that the genetic bias to the direction of evolution may decay with time. However, the positive overall relationship between θ and time was not significant (GLS; $\hat{\beta}$ = 1.27 ± 1.08 SE, $t = 1.157$, df = 21, $P = 0.13$, one-tailed test) because of the high variability.

The amount of evolutionary divergence between species was inversely related to θ (Fig. 3), in accord with the third prediction. That is, the greater the departure between the direction of evolution and the direction of greatest genetic variance, the smaller the amount of morphological change (GLS; $\hat{\beta} = -0.36 \pm 0.09$ SE, $t = -3.851$, df = 21, $P = 0.0005$, one-tailed test). The flycatchers exemplify the pattern: their direction of divergence was greatly different from $\mathbf{g}_{max}$ but their progress was small (Fig. 3). This analysis does

TABLE 2. Direction of greatest genetic variance $\mathbf{g}_{max}$ within the focal stickleback population and the direction $\mathbf{z}$ of highest variability among population means; $\mathbf{g}_{max}$ is the first principal component of the covariance matrix given in Table 1. SEs for the coefficients of $\mathbf{g}_{max}$ (in parentheses) were calculated by bootstrapping. Bootstrapping additionally showed that $\mathbf{g}_{max}$ is significantly different from all five unit vectors (e.g., [0,0,0,0,1]; all five $P < 0.01$) indicating that the five traits are significantly genetically intercorrelated. The angle between the two vectors (θ = 0.31 radians) was not significantly different from zero (bootstrap $P = 0.11$; tested assuming that the among-population direction is estimated without sampling error).

Trait	$\mathbf{g}_{max}$	$\mathbf{z}$
Length	−0.21 (0.07)	−0.14
Depth	−0.06 (0.09)	−0.35
Gape width	−0.59 (0.08)	−0.47
Raker number	0.72 (0.05)	0.75
Raker length	0.29 (0.12)	0.29

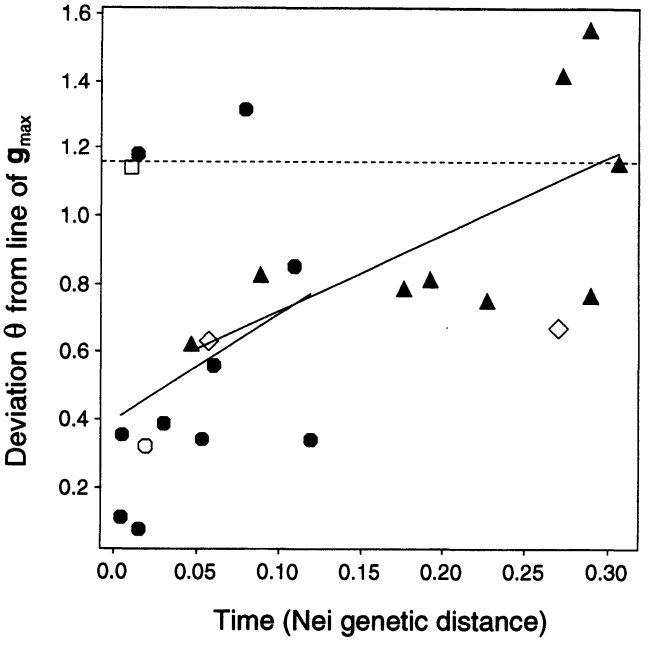

FIG. 2. The direction of evolution θ in relation to time and to the random expectation (dotted line). Each observation contrasts the focal species of a given clade with one of its relatives. Time is measured in units of Nei's (1978) allozyme distance. Symbols refer to different taxa: sticklebacks (○), Galapagos finches (●), flycatchers (□), sparrows (▲), and mice (◇). Solid lines are least squares regressions within the two largest clades (finches and sparrows).

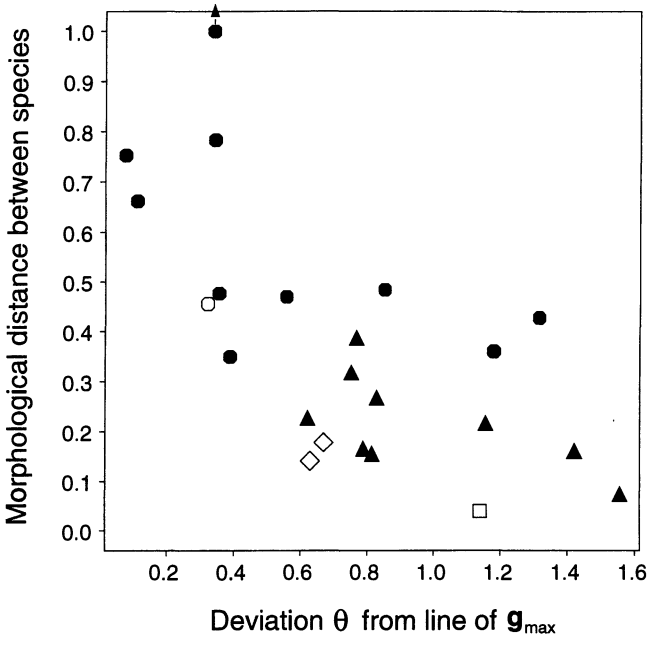

FIG. 3. Morphological (euclidean) distance between species in relation to the direction of their differences. Each observation contrasts the focal species of a given clade with one of its relatives. Symbols refer to different taxa: sticklebacks (○), Galapagos finches (●), flycatchers (□), sparrows (▲), and mice (◇).

not correct for the ages of the different species represented, but the result was similar when I used residuals from a regression of morphological distance on time instead (GLS; $\hat{\beta} = -0.52 \pm 0.16$ SE, $t = -3.333$, df = 21, $P = 0.0016$, one-tailed test).

Duration of Effect

These results demonstrate that the course of adaptive diversification is biased by genetic covariances within populations. The question I now address is: how long does this effect typically last?

The bias to the direction of evolution was strongest among the most closely related species and tended to decay with time (Fig. 2). If this tendency is real, then these data suggest that the bias endures until species are at least 0.3 units of Nei's distance apart. In passerine birds, 0.1 units of Nei's distance corresponds to roughly 3% sequence divergence in mitochondrial DNA, or about 1.5 million years (Zink 1991). An allozyme distance of nearly 0.3 between the two species of mice (*P. maniculatus* and *P. leucopus*) (Fig. 2) also corresponds to a mtDNA sequence divergence of roughly 10% (extrapolated from data in Avise et al. 1979 and DeWalt et al. 1993). On this scale, 0.3 distance units would represent over four million years. This estimate is conservative because the trend suggested in Figure 2 may be spurious (i.e., it is not statistically significant). The bias to the direction of evolution may therefore last longer than the four million years spanned by the present data.

The effect of $\mathbf{g}_{max}$ on the absolute amount of evolutionary divergence showed no tendency to weaken with time; absolute divergence was inversely related to θ across the full range of species ages (Fig. 3). The same was true of evolutionary rate (residuals from a regression of morphological distance on time). There were no examples in these data of a large amount of evolution in a direction markedly different from $\mathbf{g}_{max}$. Therefore, the influence of genetic variance and covariance on the rate and amount of morphological change endures for longer than four million years.

Phenotypic versus Genetic Lines of Least Resistance

Genetic covariances are difficult and costly to measure and published examples from vertebrates remain few—particularly of traits thought to have diverged by natural selection rather than genetic drift. This dearth limits the strength of some results, especially estimates of the temporal decay of θ. Here I ask whether the direction of greatest phenotypic variance, $\mathbf{p}_{max}$, is similar to $\mathbf{g}_{max}$, the direction of greatest genetic variance. If so, then it may be possible to substitute $\mathbf{p}_{max}$ for $\mathbf{g}_{max}$ in future analyses of this kind, greatly increasing the potential sample size. Similarity between $\mathbf{g}_{max}$ and $\mathbf{p}_{max}$ was measured by the angle between them (I used the average angle of all subsets of five traits when more than five traits were measured).

Similarity between $\mathbf{g}_{max}$ and $\mathbf{p}_{max}$ varied greatly among taxa. The difference between them was negligible in the Galapagos finch (0.08 radians, 4.5°) and small to moderate in the stickleback (0.28 radians, 16°), mouse (0.31 radians, 18°; calculated after pooling the three covariance matrices available), flycatcher (0.46 radians, 27°), and sparrow (0.60 radians, 35°). These angles between $\mathbf{g}_{max}$ and $\mathbf{p}_{max}$ are all well below the random expectation of 1.18 radians (68°). Data are not available in most cases to test whether these angles between $\mathbf{g}_{max}$ and $\mathbf{p}_{max}$ are significantly different from zero.

Despite these differences, $\mathbf{g}_{max}$ and $\mathbf{p}_{max}$ were nearly equally successful at predicting the direction of divergence between species. The average angle between $\mathbf{p}_{max}$ and the direction of species divergence was 0.63 ± 0.14 SE, which is hardly larger than $\bar{\theta}$ (0.61 ± 0.13 SE). The biggest difference between any individual value of θ (Fig. 2) and the same angle computed using $\mathbf{p}_{max}$ was 0.19 radians (11°). This suggests that $\mathbf{p}_{max}$ might be a reasonable substitute for $\mathbf{g}_{max}$ in many instances, for comparisons with directions of species divergence. This does not contradict Willis et al. (1991), who argued that phenotypic covariances are not good surrogates for genetic covariances when making precise predictions of evolutionary change across a generation. Phenotypic data may, however, be adequate for the coarser kinds of comparisons made here.

DISCUSSION

Despite widespread appreciation of the role of genetic (including developmental) constraints in evolution, quantitative tests are scarce. A few studies have shown that rate of evolution (but not necessarily its direction) is predicted by patterns of genetic variance. In an earlier study, I showed that the size of the morphological gap between Galapagos finch species was a poorer indicator of their phylogenetic affinity than was the net intensity of selection needed to cross the gap, which takes into account genetic covariances between traits (Schluter 1984); it follows that rates of divergence be-

tween species were limited by genetic covariance. Kluge and Kerfoot (1973) suggested that patterns of phenotypic variation within species, which might be a reasonable surrogate for genetic variation (Cheverud 1988; but see Willis et al. 1991), predicted amounts of morphological variation among species (see also Olson and Miller 1958; but see Rohlf et al. 1983).

Few studies have tested for an effect of genetic constraints on the direction of evolution. Futuyma et al. (1993, 1995) found that genetic variation in feeding response and survival of *Ophraella* leaf beetles on different host plants was frequently lacking and that this had partly limited the kinds of host shifts that occurred during the diversification of the genus. Phenotypic variation induced by manipulating amphibian development partly predicted the pattern of morphological differences seen among species (Alberch and Gale 1985). Theoretical models of morphogenesis and pattern formation have shown that relatively simple changes in development can produce observed patterns of species differences (Oster et al. 1988; Nijhout 1991; Price and Pavelka, in press).

The evidence presented here is therefore among the first to show that patterns of quantitative genetic covariance bias the direction of evolution over reasonably long spans of time. It also shows that amounts of morphological divergence in particular directions varies with the amount of genetic variance in those directions. The results provide a preliminary estimate of the duration of genetic constraints on morphological evolution. My study has been limited to functionally important traits in vertebrates on which selection has been directly recorded in some cases. The implication is that for at least four million years evolution in functionally important traits was most frequent, and evolutionary change greatest, along genetic lines of least resistance. Results also indicate that, for these data sets, the direction of greatest phenotypic variance is a reasonable substitute for $\mathbf{g}_{max}$, the direction of greatest genetic variance.

Genetic constraints on evolution is a reasonable explanation for these findings. Figure 1 illustrates how this may happen. The scenario is simplistic, however, because it implies that species are under continuous directional selection. In contrast, field studies suggest that stabilizing selection and/or oscillating directional selection is more common (Schluter and Smith 1986b; Gibbs and Grant 1987). An alternative scenario in which the adaptive landscape is contoured with many fitness peaks, rather than just one, and in which populations infrequently move between peaks may be more realistic than Figure 1. In this case the predicted trajectory will depend on the nature of the landscape, but the coarse features of divergence should be similar to those expected under the simple scenario. A population in a new environment temporarily under the influence of two (or more) adaptive peaks should tend to evolve toward that peak whose direction from the population mean is closest to $\mathbf{g}_{max}$ (Lande 1979; Bürger 1986; Arnold 1992; Price et al. 1993). This effect should also decay with time, as the number of adaptive peak shifts separating any two species increases. The qualitative effect of genetic constraints on evolutionary direction may be robust to features of the selection surface, provided that the location of available adaptive peaks is unbiased with respect to the direction of $\mathbf{g}_{max}$.

Two alternative explanations, however, may also account for the results. The first is that directional selection for species divergence is not random with respect to the orientation of $\mathbf{g}_{max}$, but instead tends to be strongest along it. Under this hypothesis $\mathbf{g}_{max}$ predicts the direction and rate of evolution because it is molded by these same natural selection pressures. For example, the presence of two resources (e.g., plankton and benthos in a lake) may subject a population exploiting them to correlational selection if each resource is best exploited by individuals having a distinct combination of trait values (e.g., many gill rakers and a narrow mouth, or few gill rakers and a wide mouth; cf. Table 1). Patterns of genetic covariance may then evolve to conform more closely to the pattern of selection (Lande 1980; Cheverud 1984; but see Turelli 1985). If species divergence then results in a partitioning of the two resources, morphological differences between the new species will match the genetic extremes of the prior populations, and hence will occur along the line of maximum genetic variance ($\mathbf{g}_{max}$). Low θ in this case is caused not by genetic constraint but by genetic "predestination."

This alternative hypothesis assumes that genetic covariances evolve in an adaptive way to conform to the shape of the selection surface. Whether this can happen is highly debatable (Wilkinson et al. 1990; Arnold 1992). A test of the assumption would require that $\mathbf{g}_{max}$ be compared among populations and species inhabiting different environments with contrasting patterns of selection; the assumption is rejected if $\mathbf{g}_{max}$ does not vary as predicted. I am aware of only one study that has compared genetic covariances between populations inhabiting environments with known differences in selection regime. Genetic correlations between eye and antennal characters in the amphipod *Gammarus minus* were stronger in both of two cave populations measured (where small eyes and large antennae are favored) than in two spring populations (where eyes are larger and antennae are favored) (Jernigan et al. 1994). This reveals that genetic correlations are somewhat malleable under selection, but it was not determined whether the differences in genetic correlations between cave and spring populations were adaptive.

A second alternative is that genetic covariances are shaped in part by gene flow between species and this causes $\mathbf{g}_{max}$ to conform to the direction of species differences. One way in which this might happen is through ongoing hybridization between species with different mean values for a suite of traits. Such hybridization maintains genetic variance in the direction of the difference between species by creating linkage disequilibrium (nonrandom associations) between alleles at the different loci responsible for species differences. Another way is through occasional movement from one species to another of alleles with pleiotropic effects on numerous traits. Linkage disequilibrium breaks down extremely rapidly once gene flow has ceased, but alleles with pleiotropic effects could potentially linger for some time after (T. D. Price, pers. comm., 1994).

I consider this second alternative less likely than the others for the following reasons. Not all species in taxa sampled hybridize currently, for example, the focal sparrow species does not (Schluter and Smith 1986a; gene flow between geographically differentiated song sparrow populations could,

however, produce the same effect if the morphological axis of population differentiation is similar to that between closely related species). The stickleback species used here (Enos Lake limnetic) possesses a unique allele that is not present in its sympatric congener (McPhail 1984), suggesting that gene flow is low (but unidirectional gene flow from the benthic to the limnetic is not ruled out by this observation). Hybridization also does not ensure that that $\mathbf{g}_{max}$ will be affected. For example, the two flycatcher species hybridize (Gelter et al. 1989, 1992; this may also have reduced the allozyme distance between them and hence their estimated age), but $\mathbf{g}_{max}$ remains very different from the line of difference between species means (Fig. 2). Finally, $\mathbf{g}_{max}$ in the Galapagos ground finches is similar to the line of maximum phenotypic variance ($\mathbf{p}_{max}$), which is an axis of general body size (Boag 1983; Schluter 1984). Yet $\mathbf{p}_{max}$ tends to be similar in all ground finch species whether they hybridize or not (Schluter 1984, unpubl. data; Grant et al. 1985).

These alternative explanations need further elaboration and testing. Nevertheless, despite uncertainty over causes, the results presented here show that estimates of quantitative genetic parameters are useful over extended periods of evolutionary time, even when change occurs by natural selection. Measures of genetic covariance are therefore valuable when the goal is to predict trends in the direction of adaptive differentiation.

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