

# EFFECTS OF MIGRATION ON THE GENETIC COVARIANCE MATRIX

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In 1996, Schluter showed that the direction of morphological divergence of closely related species is biased toward the line of least genetic resistance, represented by  $\mathbf{g}_{\max}$ , the leading eigenvector of the matrix of genetic variance–covariance (the  $\mathbf{G}$ -matrix).  $\mathbf{G}$  is used to predict the direction of evolutionary change in natural populations. However, this usage requires that  $\mathbf{G}$  is sufficiently constant over time to have enough predictive significance. Here, we explore the alternative explanation that  $\mathbf{G}$  can evolve due to gene flow to conform to the direction of divergence between incipient species. We use computer simulations in a mainland–island migration model with stabilizing selection on two quantitative traits. We show that a high level of gene flow from a mainland population is required to significantly affect the orientation of the  $\mathbf{G}$ -matrix in an island population. The changes caused by the introgression of the mainland alleles into the island population affect all aspects of the shape of  $\mathbf{G}$  (size, eccentricity, and orientation) and lead to the alignment of  $\mathbf{g}_{\max}$  with the line of divergence between the two populations' phenotypic optima. Those changes decrease with increased correlation in mutational effects and with a correlated selection. Our results suggest that high migration rates, such as those often seen at the intraspecific level, will substantially affect the shape and orientation of  $\mathbf{G}$ , whereas low migration (e.g., at the interspecific level) is unlikely to substantially affect the evolution of  $\mathbf{G}$ .

**KEY WORDS:** Evolution, gene flow,  $\mathbf{G}$ -matrix, hybridization, multivariate selection, QTL.

Evolution by natural selection requires heritable variation. The most common way to represent the pattern and magnitude of the genetic basis of a series of traits is the genetic variance–covariance matrix, also known as the  $\mathbf{G}$ -matrix. This matrix shows the additive genetic variance for each trait down its diagonal, with the additive genetic covariance between each pair of traits shown off the diagonal.  $\mathbf{G}$  is extremely useful for predicting the response to selection over the short term. A population will evolve most rapidly along axes that have the most genetic variation, and more slowly in directions with little genetic variance. Because  $\mathbf{G}$  accounts for genetic covariance as well,  $\mathbf{G}$  can also help predict the indirect response to selection on one character from selection on another trait. If the genetic covariance between two traits is different from zero, selection on one trait will affect response to selection on the other.

If  $\mathbf{G}$  were roughly constant over time,  $\mathbf{G}$  and the divergence between closely related species could be used to infer the minimal

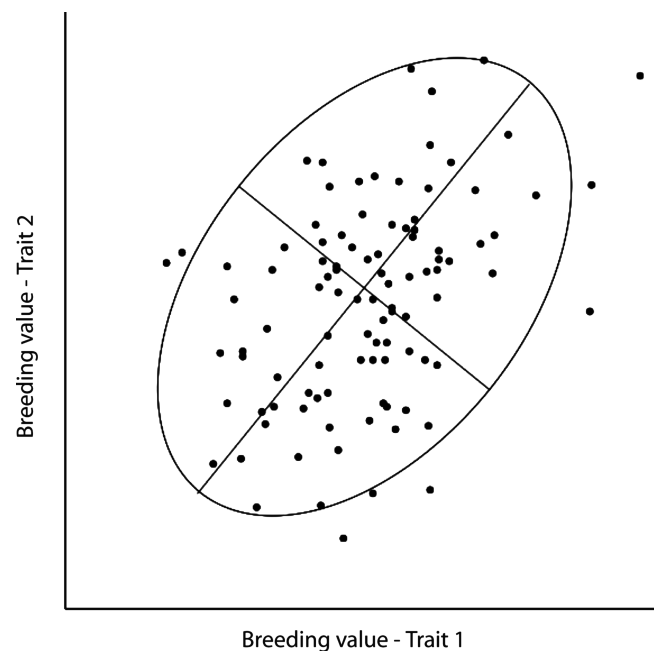
amount of selection that has caused the two species to separate (Lande 1979). Furthermore, if  $\mathbf{G}$  is roughly constant, the change in mean phenotype of a population in the future could be predicted from known patterns of selection. If  $\mathbf{G}$  is unpredictable, however, then we are greatly limited in our predictive or retrospective abilities; the pattern of evolution would be much more difficult to predict (Turelli 1988; Steppan et al. 2002).

$\mathbf{G}$  is known to not be perfectly constant, nor is it completely unpredictable over even short evolutionary time. Several studies comparing  $\mathbf{G}$ -matrices between distinct populations have found that  $\mathbf{G}$  stays relatively constant, sharing many features of eigenstructure and magnitude (Lofsvold 1986; Shaw and Billington 1991; Spitze et al. 1991; Platenkamp and Shaw 1992; Brodie 1993; Podolovsky et al. 1997; Roff et al. 1999; Waldmann 2000; Begin and Roff 2001, 2003, 2004). In contrast, however, several other studies, especially those that compare species, have found evidence of change in the shape of the  $\mathbf{G}$ -matrix (Lofsvold 1986;

Kohn and Atchley 1988; Paulsen 1996; Arnold and Phillips 1999; Roff and Mousseau 1999; Roff et al. 1999; Waldmann 2000; Begin and Roff 2001). These comparisons are complicated by the statistics; it is often unclear how different **G**-matrices are even when they are shown to not be equal or share a precise eigenstructure (Houle et al. 2002). Conversely, the statistics of **G**-matrix comparison lack power, so small studies can quite easily fail to reject the null hypothesis of equality, even with real differences between the **G**-matrices of different populations. Still, it seems clear that **G**-matrices change somewhat over time, but matrices of related species have much in common.

These conclusions from natural populations are supported by theoretical and experimental inferences as well. Turelli (1988) laid out the conditions required for stable **G**-matrices, and these conditions are unlikely to hold very often in nature. For example, genetic drift can change the amount of genetic variance (Lande 1979), but moreover drift can also change the shape of the **G**-matrix (Phillips et al. 2001). Selection has been shown experimentally to affect **G** (Wilkinson et al. 1990; Shaw et al. 1995). Gene flow also could potentially affect both the structure and the stability of **G**. In that respect, migration has not attracted much theoretical nor empirical attention yet, although it is a ubiquitous phenomenon of natural, fragmented populations, and is known to affect populations experiencing divergent selection in the wild (e.g., Boulding and Hay 1993; Lu and Bernatchez 1999; Taylor and McFail 1999; Hendry et al. 2001, 2002; Saint-Laurent et al. 2003; Hendry and Taylor 2004; Nosil and Crespi 2004; Nosil et al. 2006a,b). The present work aims to partially fill this gap for the case of migration between diverging populations.

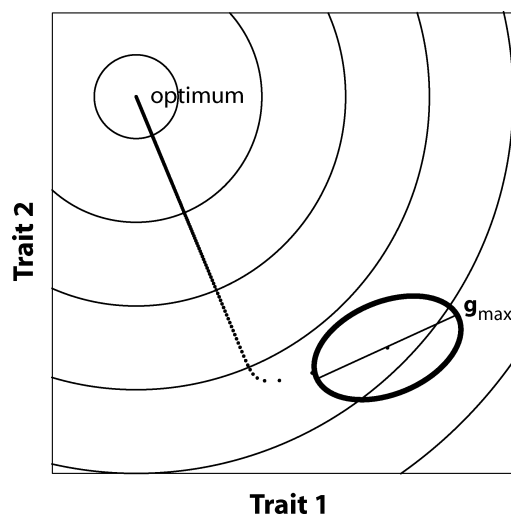
With **G** being dynamic, one question in particular becomes crucial: does the pattern of genetic constraint and opportunity measured by the **G**-matrix provide any information at all about the evolutionary process? In other words, if the **G** shown by a species at any one time is merely a snapshot providing little information about the past or future, can we use **G** to infer anything about evolutionary history or potential? One important attempt at addressing these questions was made by Schluter (1996). Schluter compared the direction of divergence of closely related species to the leading eigenvector of the **G**-matrix estimated from one of these species. This leading eigenvector of **G** is called  $\mathbf{g}_{\max}$ ; it is the direction in morphological space that has the most genetic variation (Fig. 1). If selection were applied consistently, but in a randomly chosen direction to a species with a fixed **G**-matrix, the response to selection would be biased on average toward the direction of  $\mathbf{g}_{\max}$ . (This bias would be seen on average, but not necessarily for all possible directions of selection, and its magnitude is expected to be proportional to the relative size of the eigenvalue associated with  $\mathbf{g}_{\max}$ . Therefore, depending on the amount of variance among the eigenvalues of **G**, this bias may often be small and go undetected. Also, although only the effects of the



**Figure 1.** A geometric interpretation of the **G**-matrix. Each point represents the genetic values for traits 1 and 2 for an individual, and the ellipse represents a boundary that encloses approximately 95% of the genetic values. The major axes of the ellipse lie along the first and second eigenvectors of the **G**-matrix, and the width along each axis is proportional to the eigenvalues of **G**. In this case the two traits are positively correlated, meaning that the major axis of variation in this population is along a line increasing from left to right. This major axis of **G**, its leading eigenvector, is often called  $\mathbf{g}_{\max}$ .

leading eigenvector of **G** have been explicitly tested, in theory the direction of evolutionary change is predicted to be affected by all axes of **G**.) Schluter (1996) found that the divergence between closely related species tended to fall more closely to the direction predicted by  $\mathbf{g}_{\max}$  than would be expected by chance. He called this “evolution along genetic lines of least resistance.” Hence, this is the first evidence that **G** actually helps predict the direction of evolutionary change. This pattern has been observed in other taxa in more recent studies (Begin and Roff 2003; Marroig and Cheverud 2005; Renaud et al. 2006).

We would like to interpret this evolution along lines of least resistance as evidence that **G** constrains, or at least directs, the course of evolution. If **G** were constant, then we expect relatively constant selection to engender a response biased toward  $\mathbf{g}_{\max}$  (see Fig. 2). Unfortunately, this is not the only available explanation for the relationship between divergence and **G**. As Schluter points out, the direction of divergence between two groups may correlate with  $\mathbf{g}_{\max}$  for a variety of reasons. He lists two alternatives: that selection molds **G** to be in the direction of dominant selection or that migration or hybridization between populations or taxa might increase genetic variance within populations along the lines of



**Figure 2.** Evolution on an adaptive landscape with a single optimum. The optimum (in the top left corner) is reached from a starting position (near the bottom right) by an indirect evolutionary trajectory, caused by a faster response to selection along the axis with greatest genetic variance,  $g_{\max}$ . Ultimately the evolving population reaches its optimum, but the initial divergence is biased in the direction of greatest genetic variance. The ellipse circling the starting position represents the range of genotypes present in the population, the dots represent the mean values of the population in successive generations, and the contour lines mark out regions of equal fitness.

divergence between populations. In addition, if divergence is due to genetic drift alone, then we would also expect divergence to occur most along the lines of the greatest genetic variance. The traits investigated by Schluter's paper, however, are mostly known to be under selection from more direct evidence.

If there is strong correlational selection (i.e., if certain combinations of characters are selected nonindependently), then selection will more rapidly eliminate alleles that cause divergence from the optimum in nonpreferred combinations of traits (Lande 1980; Arnold et al. 2001; Jones et al. 2003, 2004). As a result, the  $\mathbf{G}$ -matrix will tend to coalign with the axes of correlation in the strength of selection within a population. If the selective differences among populations tend to be along the same lines as correlational selection, then this would tend to bias  $\mathbf{G}$  in the direction of selective pressure. Thus,  $g_{\max}$  would coincide with the direction of divergence between populations, even if the direction of evolution were unconstrained by genetic correlations.

For example, the forelimbs and hindlimbs of quadruped organisms are plausibly under selection to maintain roughly the same relative length. If the whole organism were larger, then selection would favor genes for longer forelimbs and longer hindlimbs. In such a population, organisms with long forelimbs and relatively short hindlimbs (or vice versa) would be selected against, leaving a stronger positive genetic correlation in the population for limb

length. Moreover, if the population were in the future selected to be larger in size, both forelimbs and hindlimbs would likely be selected to increase in length. Thus, the physical basis of selection can result in a pattern of divergence that matches the pattern of correlation among genotypes, for reasons over and above the bias in response to selection caused by genetic architecture. This pattern has been shown to be very plausible by previous simulation research (Jones et al. 2003, 2004).

The other alternative proposed by Schluter has received less attention. Migration between evolving populations can potentially skew patterns of genetic variation substantially. Migration between populations of the same species and hybridization between closely related taxa is common (e.g., Grant and Grant 2002; Borge et al. 2005; Gow et al. 2006; Kronforst et al. 2006), and it is well known that migration can increase the amount of genetic variation within a population (Lande 1992; Whitlock 1999). Clearly, if genotypes are introduced into a population from another population, then the presence of these genotypes will skew the distribution of genetic effects toward the axis of divergence between the two populations. Moreover, migration ought to change the relative proportions of genetic variance for different traits, depending on the direction of differentiation between populations. Genetic variance ought to be increased by migration most along axes of greater difference between the two populations.

In this article, we want to explore the extent of the effects of migration on the  $\mathbf{G}$ -matrix. We chose to model an "island" population evolving toward a new optimum, distinct from the optimum in a "mainland" population. We allow unidirectional gene flow from the mainland to the island at varying rates, and we examine the effects on the size and shape of the distribution of genotypes on the island that result. We show that migration, in some circumstances, can substantially alter the orientation of the  $\mathbf{G}$ -matrix in the island population, and that this displacement from migration causes  $g_{\max}$  to change in the direction of the divergence between populations. We show that the shape of the  $\mathbf{G}$ -matrix can be greatly affected by strong migration, so that both the shape and orientation of  $\mathbf{G}$  are changed. Finally, we consider the question of how migration affects the stability of the  $\mathbf{G}$ -matrix. If migration is a strong and constant influence on the evolution of  $\mathbf{G}$  relative to other evolutionary forces, then  $\mathbf{G}$  should be more stable over generations with migration than without. We test these predictions with multilocus, quantitative genetic simulations of evolving populations connected by migration.

## The Model

We built a mainland-island population model with one-way migration in an individual-based, genetically explicit, stochastic simulation framework (Guillaume and Rougemont 2006). The populations were composed of dioecious individuals undergoing a

discrete generation life cycle. Each individual had two quantitative traits determining fitness in an additive genetic model. The genetic architecture of those traits consisted of 100 unlinked, diploid loci bearing pleiotropic mutations. Each new mutation was drawn from a bivariate Gaussian distribution with mean of zero, equal variances for both traits  $\sigma_1^2 = \sigma_2^2 = 0.05$ , and correlation  $r_\mu$ . The mutational correlation values were chosen to be 0, 0.5, and 0.9. Under the mutation model chosen, the new allelic value for each trait after a mutation occurred at a given locus was obtained by adding the mutation effects drawn from the previous distribution to the existing allelic values at that locus (i.e., continuum-of-alleles model; Crow and Kimura 1964). Each trait's phenotype was obtained by summing the allelic values across loci. As we assumed no environmental variance, the phenotypic value was equal to the genotypic value. Finally, the allelic mutation rate was  $\mu = 0.0002$ . Hence the mutational variance per individual was 0.002 per trait. The effects of lower values of  $V_m$  were also investigated by decreasing the per locus mutation rate by up to two orders of magnitude.

The fitness of an individual was obtained by computing the difference between the phenotypic value of each trait and its local optimum. Fitness decreased as a function of that difference and is determined by a bivariate Gaussian selection surface where the fitness  $W(\mathbf{z})$  of a phenotype  $\mathbf{z}$  was given by

$$W(\mathbf{z}) = \exp\left[-\frac{1}{2}(\mathbf{z} - \boldsymbol{\theta})^T \boldsymbol{\omega}^{-1}(\mathbf{z} - \boldsymbol{\theta})\right] \quad (1)$$

where  $\mathbf{z}$  is the vector containing the phenotypic values of the two traits,  $\boldsymbol{\theta}$  is the vector of the traits' local optima, and  $\boldsymbol{\omega}$  is the variance-covariance matrix of the bivariate Gaussian distribution (Lande 1979). (More generally, as we have assumed no environmental variance or covariance in these traits, the  $\boldsymbol{\omega}$  matrix is the sum of the selection matrix and the environmental variance-covariance matrix.) The elements of the selection matrix  $\boldsymbol{\omega}$  determine the curvature of the individual fitness surface with variance parameters  $\omega_{11}$  and  $\omega_{22}$  giving the intensity of stabilizing selection on trait 1 and trait 2, respectively; higher values represent weaker selection pressure on the traits. The orientation of the fitness surface is given by the correlation of selection,  $r_s = \omega_{12}/\sqrt{\omega_{11}\omega_{22}}$ . We chose a mild selection regime by setting  $\omega_{11}$  and  $\omega_{22}$  to 50 and varied  $r_s$  from 0 to 0.9 with an intermediate value of 0.5. Nonzero correlation values imply a nonisotropic fitness surface with a ridge of high fitness oriented at 45° in the phenotypic plane. Selection is then stronger when perpendicular to this ridge than along it. The selection and mutation parameters values were chosen to be close to the Jones et al. (2003) values.

The life cycle chosen was composed of the sequence: migration—reproduction—viability selection. Generations were nonoverlapping. The island population had exactly  $N = 1000$  individuals throughout that life cycle. Each new offspring created

during reproduction had a probability  $m(1 - m)$  to be descended from the pairing between a mainland immigrant and an island resident;  $m^2$  to be descended from two immigrants; and  $(1 - m)^2$  to be parented by two local island individuals,  $m$  being the one-way migration rate. The parents were randomly drawn from their respective population with replacement. The mating system is thus random, but selfing was not allowed. Mutations occurred during the creation of the offspring genotype. Each offspring then survived if a random number drawn from a uniform distribution was smaller or equal to its fitness as given by equation (1). To save on computing time, cases in which none of the first 500 offspring in a generation survived, relative fitness was rescaled by the maximum fitness of the previously created offspring. This rescaling was necessary only in cases of strong selection and in the first 10 generations of a run.

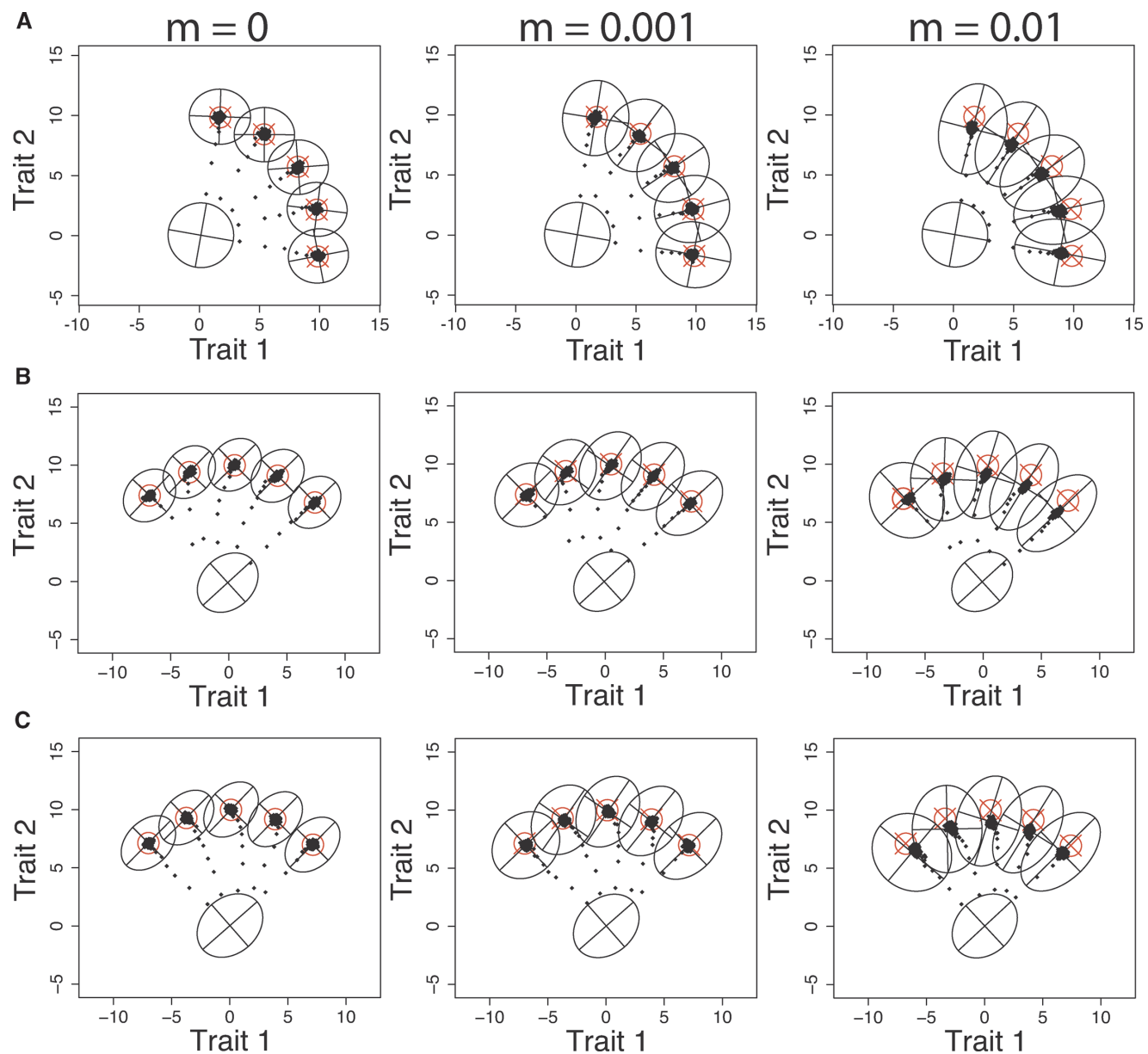
At the beginning of a simulation, each new island population is seeded with individuals randomly drawn from a mainland population. The selection and mutation parameters were equal in both populations, only the optimum values differed. The mainland trait optima were  $\boldsymbol{\theta}_{\text{mainland}} = \{0; 0\}$ . Island optima were set at one of five locations, placed relative to the eigenvectors of the mainland  $\mathbf{G}$ . On one type of island the optimum was set 10 units away from  $\boldsymbol{\theta}_{\text{mainland}}$  in the direction of  $\mathbf{g}_{\text{max}}$ . On another type of island,  $\boldsymbol{\theta}_{\text{island}}$  was set 10 units in the direction perpendicular to  $\mathbf{g}_{\text{max}}$ , defined hereafter as  $\mathbf{g}_{\text{min}}$ , the axis of lowest genetic variation. The remaining three types of islands had optima evenly spaced between the directions determined by  $\mathbf{g}_{\text{max}}$  and  $\mathbf{g}_{\text{min}}$ , at 22.5, 45, and 67.5 degrees away from  $\mathbf{g}_{\text{max}}$ . In each case the island optimum was 10 units away from the mainland optimum.

Migration was unidirectional from the mainland to the island, and the migration rate was varied from  $m = 0$  to  $10^{-2}$ . Each mainland population had 10,000 individuals and was first evolved over 20,000 generations to achieve stability in variances. Ten replicates of each set of mainland parameters were performed. The islands were seeded with a random set of  $N = 1000$  individuals from one of the 10 mainland replicate populations and evolved over 4000 generations for each of 100 replicates for each of the island optima. The statistics were computed over the last generation of each replicate, unless otherwise stated.

The effects of migration on the structure of additive genetic variances and covariances of the island populations were assessed by using three main statistics of  $\mathbf{G}$ : its orientation, eccentricity, and total variance. Orientation is the angle of the island's  $\mathbf{g}_{\text{max}}$ . Eccentricity ( $\epsilon$ ) is the first eigenvalue of  $\mathbf{G}$  divided by the second eigenvalue of  $\mathbf{G}$ . Total variance ( $\Sigma$ ) is the sum of the two eigenvalues of  $\mathbf{G}$ .

## Results

The genetic variance-covariance matrices of many populations evolving with and without migration are shown in Figure 3.



**Figure 3.** Effects of migration on the island  $\mathbf{G}$ -matrices in the case (A) without correlations in mutational effects and selection, (B) with intermediate selection correlation ( $r_s = 0.5$ ,  $r_\mu = 0$ ), and (C) with intermediate mutational correlation ( $r_s = 0$ ,  $r_\mu = 0.5$ ). The positions of the island optima in the trait space are represented by crossed circles. The elliptical representation of each  $\mathbf{G}$ -matrix of each island and mainland is centered on the population mean phenotypic value. The evolutionary trajectory of one replicate of each island population is represented by black dots, with one dot every 10 generations. The island  $\mathbf{G}$  ellipses are the average ellipses of 100 replicated simulations at generation 4000. The mainland ellipse is that of one replicate at generation 20,000.

Selection, mutation, and drift all affect the shape of the  $\mathbf{G}$ -matrix. In the absence of migration (left column of Fig. 3), the orientation of  $\mathbf{G}$  in the new island populations is roughly equivalent to that in the mainland population from which they originate and with which they share parameters of correlational selection and mutational correlation. With migration, however, the orientation of the island's  $\mathbf{G}$ -matrix is more similar to the line of divergence (LoD) between the island and the mainland. The effect of migration on  $\mathbf{G}$  is weak when migration is infrequent,

but the change in orientation can be quite large when migration is more common. Orientation is affected most when the other deterministic forces affecting  $\mathbf{G}$  (correlational selection and mutation correlations) are weak. In addition, migration affects the eccentricity of  $\mathbf{G}$ , with  $\mathbf{G}$  being stretched along the LoD between the two populations. Unsurprisingly, the total amount of genetic variance in the island populations is greatest in the presence of migration. We will explore each of these conclusions in turn.

### LINE OF DIVERGENCE AND $\mathbf{g}_{\max}$

In the great majority of cases, high migration rates are able to strongly bias  $\mathbf{g}_{\max}$  toward the LoD between the mainland and the island optima. This is especially true in the cases without correlated selection or mutational correlations, as pictured in Figure 3A. Without mutational or selection correlations to constrain the shape of the genetic covariance matrix,  $\mathbf{G}$  has low eccentricity and its orientation is evolutionarily labile. In this case,  $\mathbf{G}$  is very sensitive to introgression of mainland alleles (see Fig. 3A for  $m = 0.01$ ).

Mutational correlation and correlational selection are deterministic forces that act to constrain  $\mathbf{G}$  to a particular orientation and shape. Mutation or selection can overwhelm the effects of weak migration on the orientation and shape of  $\mathbf{G}$ . The strength of this effect depends on the difference between the LoD and  $\mathbf{g}_{\max}$  of the ancestral populations (i.e., on the position of the new optimum). With low levels of migration (e.g.,  $m \leq 0.001$ , see Fig. 3),  $\mathbf{G}$  does not change much in orientation because of migration, when other deterministic forces are present that affect  $\mathbf{G}$ 's evolution. When migration rates get high enough (see the column of graphs for  $m = 0.01$  in Fig. 3), then migration can significantly affect  $\mathbf{G}$  even in the presence of selection and mutation effects. (See Fig. 4 for comparisons.)

For most of the parameter values considered, the effect of migration is to "stretch"  $\mathbf{G}$  toward the mean of the ancestral population. For example, if the direction to the optimum on the new island population is along  $\mathbf{g}_{\max}$ , then the new population's  $\mathbf{G}$  will tend to have the same  $\mathbf{g}_{\max}$  as the ancestral population, but with a higher increase in variation along  $\mathbf{g}_{\max}$  relative to that on  $\mathbf{g}_{\min}$ .

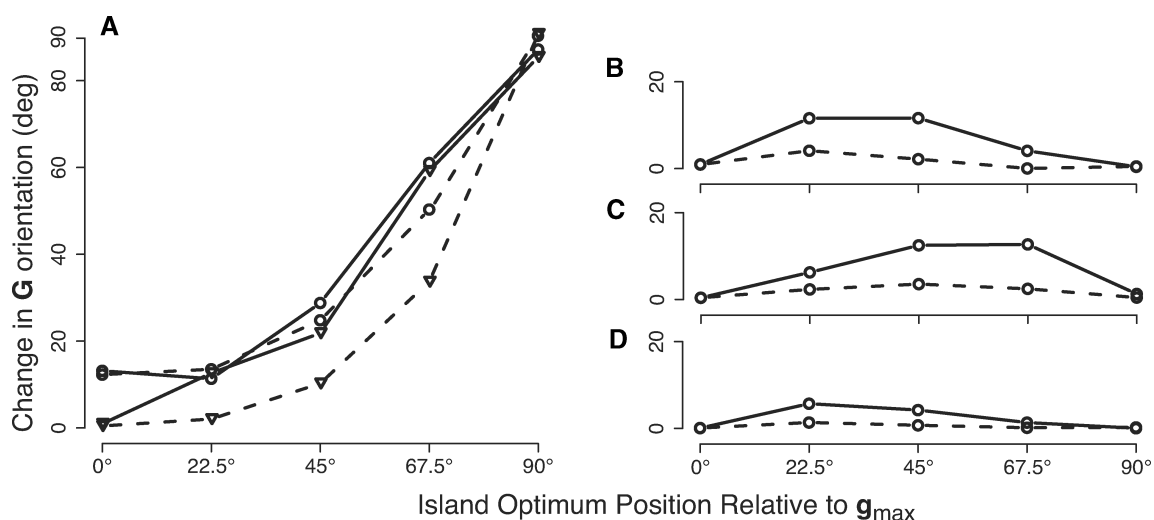
In contrast, when the optimum of the new population lies along  $\mathbf{g}_{\min}$ , strong migration ( $m = 0.01$ ) may cause a flip of the

rank order of the axes of the new population's  $\mathbf{G}$ ,  $\mathbf{g}_{\min}$  becoming  $\mathbf{g}_{\max}$  and vice versa (see Figs. 3B and C). The island  $\mathbf{g}_{\max}$  is then aligned with the LoD. However, with high mutation correlation or correlational selection, this flipping of the axes is less likely to occur. In this case the proportion of genetic variation that exists along  $\mathbf{g}_{\max}$  and that must be overwhelmed by the input of variance of migration along  $\mathbf{g}_{\min}$  is bigger (see Fig. 5). Note that the large amount of variance present on  $\mathbf{g}_{\max}$  may also be maintained by the gene flow from the mainland.

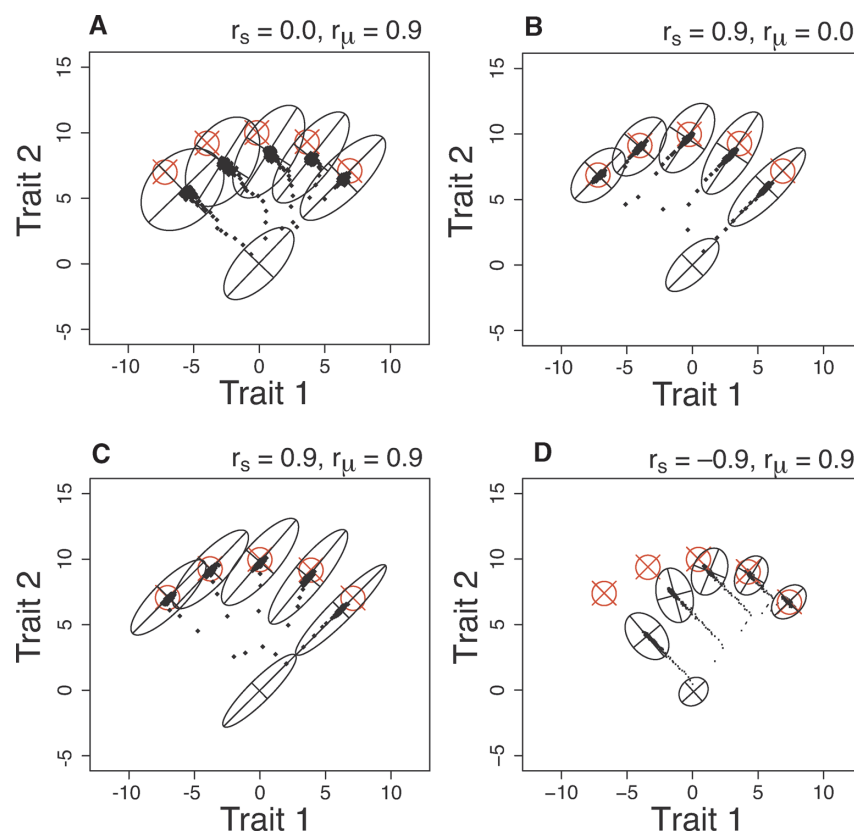
$\mathbf{G}$ 's orientation in island populations with optima between  $\mathbf{g}_{\max}$  and  $\mathbf{g}_{\min}$  is overall more affected by migration than when LoD aligns with a major axis of the ancestral  $\mathbf{G}$ . Intermediate-to-high migration rates will induce a rotation of  $\mathbf{G}$  toward the mean of the ancestral population. For intermediate migration ( $m = 0.001$ ), the rotation of  $\mathbf{g}_{\max}$  ranges from  $0^\circ$  to about  $10^\circ$ . For high migration ( $m = 0.01$ ), the rotation angle ranges from  $1.3^\circ$  to  $53^\circ$  (see Figs. 3 and 4), bringing  $\mathbf{g}_{\max}$  closer to the LoD.

It is useful to know how much of these effects are due to recent immigrants. None of these comparisons include migrants themselves, because the genetic assays were done after reproduction and selection. In general, only a small part of the rotation of the islands  $\mathbf{G}$  is due to the inclusion of the  $F_1$  individuals into the analysis, usually less than 10%. The observed bias of  $\mathbf{g}_{\max}$  toward the ancestral population is thus mainly due to the introgression of the mainland alleles over several generations. This introgression may be slow and required up to several hundreds of generations in our simulations to produce a significant effect on  $\mathbf{G}$ 's orientation (see below).

Stronger selection makes the introgression of foreign alleles into the island populations much more unlikely. In the case of strong selection on both traits ( $\omega_{11} = \omega_{22} = 5$ ), the  $F_1$  hybrids



**Figure 4.** Mean change in the orientation of the island G-matrices for two migration rates,  $m = 0.001$  (dashed lines) and  $m = 0.01$  (solid lines), relative to the case with  $m = 0$ . The deviation is given in degrees. (A)  $r_s = r_\mu = 0$  (circles) and  $r_s = -r_\mu = -0.9$  (triangles); (B)  $r_s = 0.9$ ,  $r_\mu = 0$ ; (C)  $r_s = 0$ ,  $r_\mu = 0.9$ ; (D)  $r_s = r_\mu = 0.9$ .



**Figure 5.** Effects of high level of migration ( $m = 0.01$ ) on  $\mathbf{G}$  orientation and shape with large correlations in selection and mutational effect. (A)  $r_s = 0.0$ ,  $r_\mu = 0.9$ ; (B)  $r_s = 0.9$ ,  $r_\mu = 0.0$ ; (C)  $r_s = r_\mu = 0.9$ ; (D)  $r_s = -r_\mu = -0.9$ .

rarely survive and thus migration has virtually no effect on the orientation and shape of the island's  $\mathbf{G}$  (results not shown). High correlation in selection also increases the strength of selection in populations with optima off  $\mathbf{g}_{\max}$  relative to the mainland population. In these cases, hybrids are very unfit along the axis of strong selection (orthogonal to the axis of correlational selection). The effective gene flow along that axis is then reduced compared to cases with equal selection in every directions (no correlational selection) and its effect on the islands'  $\mathbf{G}$  is consequently smaller. By contrast, introgression along the axis of correlational selection (i.e., close to  $\mathbf{g}_{\max}$ ) is more weakly opposed by selection and results in higher rotation angles (see Figs. 4B and C).

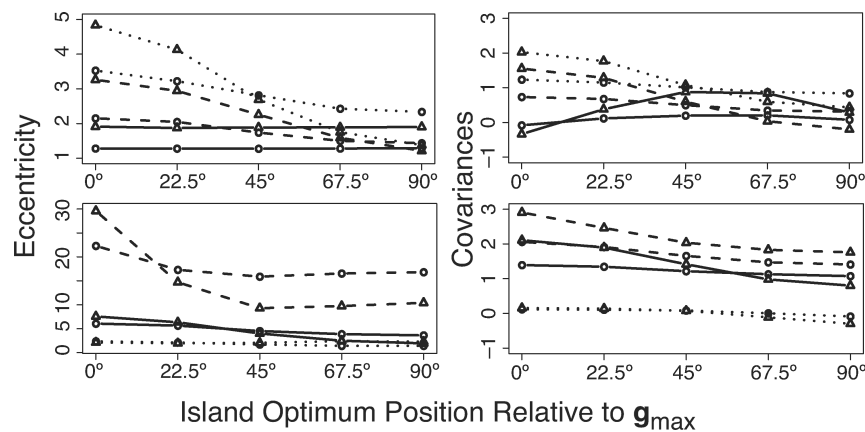
The amount of change in  $\mathbf{G}$ 's shape and orientation caused by migration depends on how much mutational variance is present in the population compared to that brought in by migration. So far, the total amount of mutational variance has been  $V_m = 0.002$ . By decreasing  $V_m$  by an order of magnitude or two, the power of migration to rotate the islands'  $\mathbf{G}$ -matrices is much increased, aligning them with the LoD in most cases (results not shown). However, with lower  $V_m$ , the lack of genetic variation increases the constraining effect of mutational correlation so that 5000 generations were not enough for some populations to reach their new optimum when it was far from  $\mathbf{g}_{\max}$ . Their phenotypic evolution-

ary path and  $\mathbf{G}$  orientation were constrained to follow the ancestral  $\mathbf{g}_{\max}$ .

#### THE EFFECT OF MIGRATION ON THE SIZE AND SHAPE OF $\mathbf{G}$

Aside from the effect on the orientation of  $\mathbf{G}$ , migration also affects two descriptions of  $\mathbf{G}$ : total variance ( $\Sigma$ : sum of eigenvalues) and eccentricity ( $\epsilon$ : ratio of eigenvalues). Unsurprisingly, the total amount of variance ( $\Sigma$ ) always increases as a result of introgression depending on the rate of migration and fitness of  $F_1$  hybrids. Migration rates lower than  $m = 10^{-3}$  did usually not increase the total variance by more than about 10% whereas higher migration rates ( $m = 10^{-2}$ ) caused as much as a threefold increase in variance (in the case in which  $r_\mu = 0.9$ ,  $r_s = -0.9$ ). Only a small part of this increase in variance is due to the presence of the  $F_1$  hybrid individuals in the dataset.  $F_1$  hybrids explain between 1.1% and 8.6% of the increase of variance due to migration.

Migration can affect the eccentricity of the  $\mathbf{G}$ -matrix substantially. The effect of migration on  $\mathbf{G}$ 's eccentricity ( $\epsilon$ ) depends on whether it increases variance along  $\mathbf{g}_{\max}$  (causing an increase of  $\epsilon$ ) or  $\mathbf{g}_{\min}$  (causing a decrease of  $\epsilon$ ), and thus it depends on the position of the island optimum (see Fig. 6). Without other deterministic forces strongly affecting  $\mathbf{G}$ , high migration may cause as



**Figure 6.** Eccentricity of  $\mathbf{G}$  and genetic covariances in the island populations as a function of the population optimum positions relative to  $\mathbf{g}_{\max}$ . Results for two migration rates are presented:  $m = 0.001$  (circles), and  $m = 0.01$  (triangles). Upper panels:  $r_s = r_\mu = 0$  (solid lines);  $r_s = 0.5, r_\mu = 0$  (dashed lines);  $r_s = 0.5, r_\mu = 0.5$  (dotted lines). Lower panels:  $r_s = 0, r_\mu = 0.9$  (solid lines);  $r_s = 0.9, r_\mu = 0.9$  (dashed lines);  $r_s = -0.9, r_\mu = 0.9$  (dotted lines)

much as a 50% increase in  $\epsilon$ , of which only 6.5% is due to the  $F_1$  hybrids. In that particular case, the change in eccentricity is independent of the position of the island's optimum.

With increased mutational correlation or correlational selection,  $\epsilon$  in the two islands diverging closest to  $\mathbf{g}_{\max}$  is increased by migration by a factor of up to 190% (for the case  $r_\mu = 0, r_s = 0.5$ , when the optimum is along  $\mathbf{g}_{\max}$ ) whereas  $\epsilon$  is lower in the three islands with optimum positions off the mainland  $\mathbf{g}_{\max}$  (see Fig. 6). The decline of  $\epsilon$  ranges 3% to 77%, of which 2% to 16% of the change is due to the  $F_1$ 's, for  $r_\mu = 0, r_s = 0.9$  and  $r_\mu = 0.9, r_s = 0$ , respectively. The largest decrease in  $\epsilon$  is seen when the island optimum position lies along  $\mathbf{g}_{\min}$  and when correlation in selection is low such that the two major axes of the island  $\mathbf{G}$ -matrix switch ranks and migration brings  $\epsilon$  close to one.

The covariance between the two traits is also affected by gene flow, and the general pattern of variation among the various island populations is similar to that of the eccentricity (see Fig. 6). Genetic covariance in the island populations diverging along directions close to the mainland  $\mathbf{g}_{\max}$  increases with gene flow whereas it decreases in population diverging close to  $\mathbf{g}_{\min}$  (see Fig. 6). The case without any correlation in selection or mutational effects is a notable exception that shows a reversed pattern (see Fig. 6). Note however that despite differences in covariances, all the island population's  $\mathbf{G}$ -matrices in that case have the same overall shape and only differ in their orientation. Therefore, the pattern of variation in covariances reflects that of the change in orientation of  $\mathbf{G}$  with migration. Overall, the highest changes in covariances are obtained when migration orients  $\mathbf{G}$  closest to  $45^\circ$  in the phenotype plane.

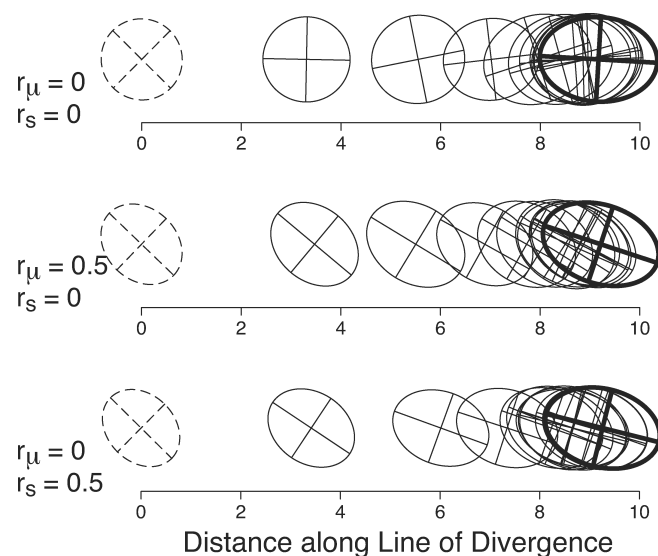
#### TRANSIENT CHANGES IN $\mathbf{G}$

The selective forces acting on a population may change as it evolves. Even if the selection function itself remains unchanged,

the direction to the optimum (and therefore the selection gradient experienced by the population) will change over time, for all cases in which genetic constraints cause the evolutionary trajectory to deviate from a straight line. Moreover, as the island population evolves, the phenotypic divergence from the mainland will increase, thereby making migrants more distinct from local individuals. Ultimately, reproductive isolation may reduce migration between the populations, and the effects of migration will become unimportant. As a result, the  $\mathbf{G}$ -matrix may go through successive changes in its structure. These transient changes in the shape and the orientation of  $\mathbf{G}$  are gradual as  $\mathbf{G}$  slowly rotates toward its new orientation and expands under the input of variance due to migration (see Fig. 7). Thus, changes in shape and orientation due to the introgression of the mainland alleles are slow and increase with time. The island population has usually gone about 80% of its way toward the new optimum before the effects of migration are detected (unless  $\mathbf{G}$  is not constrained by either mutational or selection correlations, see Fig. 7). As a consequence, the alignment of  $\mathbf{g}_{\max}$  with the LoD increases with time, as long as migration continues unabated.

#### EFFECTS OF MIGRATION ON THE STABILITY OF THE $\mathbf{G}$ -MATRIX

Finally, the stability of the orientation of the  $\mathbf{G}$ -matrix over time can be much affected by migration. We assessed this by looking at the standard deviation among replicates (SD) in  $\mathbf{g}_{\max}$  orientation. Overall, SD decreases with increased migration. This is especially true when  $\mathbf{G}$  is not under the influence of any of the two stabilizing forces, mutational correlation and selection correlation. Immigrant genotypes act here as anchor points for  $\mathbf{G}$ , providing it with a stable shape and orientation and decreasing SD from  $49^\circ$  for  $m = 0$  to  $4.9^\circ$  for  $m = 0.01$ . Migration may thus be a strong stabilizing factor of the  $\mathbf{G}$ -matrix (see Fig. 8). However,



**Figure 7.** Transient changes in  $G$  in the island populations on their way toward their new optimum. Ellipses are separated by 10 generations and the first 100 generations are represented here. The dashed ellipses on the right are the mainland  $G$ -matrices and the bold ones on the left represent the islands'  $G$ -matrices after 5000 generations. For these examples, the new population optimum is positioned  $45^\circ$  off  $g_{\max}$  and the migration rate is  $m = 0.01$ .

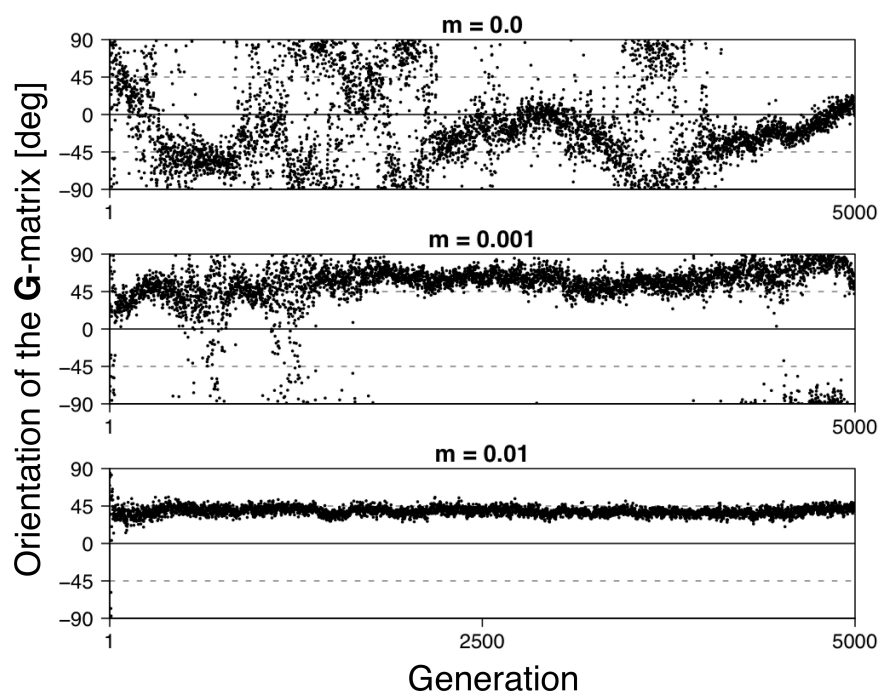
migration may increase instability when the island population is diverging along  $g_{\min}$  and correlations are of intermediate strength (i.e.,  $\leq 0.5$ ). In such cases, the variance brought to the population by migration may not always be enough to cause a flip of the axes

of  $G$  as described before. The between replicate SD is then as high as about  $30^\circ$  (for  $r_\mu$  or  $r_s = 0.5$ ). Stronger correlations reduce this effect, SD decreasing to  $3.0^\circ$  (e.g., for  $r_s = 0.9$ ).

## Discussion

The comparative study of the additive genetic covariance matrix  $G$  is still in early days. Closely related taxa tend to have similar  $G$ -matrices, but they are rarely identical (Steppan et al. 2002). All of the classical evolutionary forces—selection, drift, mutation, recombination, and migration—can affect the evolution of  $G$ ; in this article we have examined the role of the last of these most particularly. Gene flow from other populations of the same or different species can have a qualitative effect on the genetic covariance matrix, especially if migration rates are high and mutational and selection correlations are low. With low migration rates and strong correlational selection and/or strong mutational correlation, migration has little effect on the shape of  $G$ .

Our study was motivated by an important result by Schluter (1996): that the direction of divergence between new taxa is more likely to be near the direction of maximum genetic variance ( $g_{\max}$ ) than expected by chance. This result was shown in a variety of taxa, including sticklebacks, Darwin's finches, sparrows, and mice, but not in others, such as *Ficedula* flycatchers. One possible explanation for these results is that evolution is constrained by the genetic variation available in a population, and that divergence of populations or new taxa is sufficiently recent that deviations from optimal response to selection caused by the unequal genetic



**Figure 8.** Variation of the orientation of the  $G$ -matrix over 5000 generations for one replicate in the case without correlations in selection and mutation. The island population is diverging  $45^\circ$  away from  $g_{\max}$ . Migration is increasing from  $m = 0$  (top) to  $m = 0.01$  (bottom).

variation among traits still affect the pattern of divergence even after thousands of generations of evolution. Alternatively, genetic drift is expected to cause divergence most greatly in directions of greatest genetic variation. If either of these were the reason for the pattern of divergence being correlated with the maximum axes of **G**, then this would give support for the importance of the **G**-matrix in the study of medium-term evolution. If evolution does indeed proceed along “genetic lines of least resistance” and this pattern persists for more than a few generations, then understanding the evolutionary patterns and processes of the **G**-matrix itself becomes a topic of central importance in evolutionary biology. If the structure of **G** made no predictions about the course of evolution, then conversely we would have little reason to exert ourselves on the study of genetic variation.

Having said that, there are several reasons aside from constrained response to selection or drift that the divergence of new taxa may correlate with the major axis of **G**. Schluter (1996) lists two: (1) that **G** has been molded by the previous selection to align with the likely direction of future evolution and (2) that migration and/or hybridization between evolving taxa may expand the **G**-matrices of the taxa along the line of divergence. The first mechanism assumes that **G** will be affected by correlational selection, with the widest axis of variation along the lines of least selection; this has been demonstrated in the simulations of Jones et al. (2003) and recapitulated in our results as well. In order for **g**<sub>max</sub> to align most with divergence by this hypothesis, the optimum trait value of the new population must lie near the axis of weak selection. This is not unlikely if evolution proceeds along a ridge of phenotype space.

The second alternative hypothesis of Schluter forms the basis of the work presented in this article. The hypothesis is that migrants from one taxa will add genetic variation to another population and that this added variation will of necessity be most often in the direction of divergence between the two taxa. As a result, the **G**-matrix of the population receiving migrants will be expanded in the direction of divergence between the two taxa; statistically this implies that the direction of divergence is more likely to be a major axis of the variation in the recipient population. In this article we have seen that this scenario can in fact be true; migration between populations or taxa has the potential to rotate **g**<sub>max</sub> toward the direction of divergence between taxa. This is particularly the case when migration rates are high, but less so with low levels of migration. For the cases we studied, a migration rate of about one individual per generation was sufficient to cause substantial changes in the **G**-matrix, but lower levels of migration caused little effect in most cases. From these results, it is reasonable to conclude that in most cases hybridization between species is unlikely to cause a substantial change in the orientation of the **G**-matrix. However, migration between populations of the same species is quite likely to substantially affect **G**, aligning the

genetic covariance matrix along lines of divergence between the populations. The cases studied by Schluter represent incipient or actual new species likely separated by inconsequential levels of migration. As such we infer that hybridization is an unlikely explanation for the pattern of evolution along lines of least resistance observed by Schluter. However, if the rate of gene flow in these taxa is shown to exceed about one individual per generation, then hybridization may explain his results.

We predict that migration among populations of the same species is a dominant force in molding the **G**-matrices of local populations. Unfortunately, we have very little empirical evidence of the effects of intraspecific migration or gene flow on **G** evolution. The empirical studies studying the evolution of **G** at the intraspecific level have mainly focused on disentangling the effects of drift and selection (e.g., Brodie 1993; Arnold and Phillips 1999; Merilä and Bjorklund 1999; Roff and Mousseau 1999, 2005; Roff et al. 1999; Widen et al. 2002; Cano et al. 2004; McGuigan et al. 2005) or inbreeding (Phillips et al. 2001; Whitlock et al. 2002) in a context in which gene flow was most often absent.

There is good empirical evidence that adaptive differentiation in the presence of gene flow might be common in nature (e.g., Boulding and Hay 1993; Lu and Bernatchez 1999; Taylor and McFail 1999; Hendry et al. 2001, 2002; Saint-Laurent et al. 2003; Hendry and Taylor 2004; Nosil and Crespi 2004; Nosil et al. 2006a,b). From theoretical grounds, the genetic variance of a single polygenic trait in subdivided populations may be maintained at migration–selection balance if migration does not exceed a critical rate that may be low (Phillips 1996; Lythgoe 1997; Tufto 2000), much lower than that observed in most wild populations (e.g., Morjan and Rieseberg 2004). Above this threshold, the whole population becomes homogeneous. Drift and mutation are thus thought as being key in maintaining standing genetic variation in the face of uniform selection and migration in structured populations (e.g., Phillips 1996). In our model, the total variance in the island populations was always enhanced by migration, sometimes beyond that present in the mainland population (results not shown). Furthermore, a critical level of gene flow also exists, which favors local adaptation in sink (or marginal) populations by providing the necessary genetic variation, but too high gene flow, especially from a large central population, will swamp the local genetic variation and thus hinder local adaptation (Kirkpatrick and Barton 1997; Gomulkiewicz et al. 1999; Ronce and Kirkpatrick 2001; Lenormand 2002; Holt et al. 2003; Alleaume-Benharira et al. 2006).

Only one empirical study so far has focused on the effect of gene flow on the evolution of genetic covariances between quantitative traits. Nosil et al. (2006b) have shown, in a comparative and theoretical study, that the genetic covariance between host preference and a trait (cryptic coloration) affecting individual performance on two different host plant species

increases with migration between divergent host populations in a phytophagous insect species, *Timema cristinae*. They further show theoretically that migration between divergent habitats may generate the genetic covariances favored by selection. The **G**-matrices in different habitats should thus be parallel under symmetrical gene flow. Our model could be extended to include two-way migration between populations rather than having a one-way, strong effect on island populations only. In that hypothetical scenario, the effects of migration on **G** evolution should be enhanced.

Finally, it is interesting to note that the majority of the effects on **G** come through slow introgression over several generations and not from recent introgression from the first generation of immigrants descent—the  $F_1$  hybrids. Often researchers can identify new migrants and their  $F_1$ s with resident individuals (see, e.g., Grant and Grant 2002). In our analysis, the **G**-matrix was measured after reproduction and selection, so migrant individuals do not contribute directly to the measured **G**. If we measured **G** immediately after migration but before selection (as may occur in some empirical studies) the effect of migration on the orientation of **G** would be even more severe. The contrast would be especially great in cases of strong outbreeding depression, where a drastic change in **G**'s orientation due to immigrants could be observed but no hybrid offspring would survive (results not shown).

Over short time scales, **G** may be constant enough to predict response to selection. However, if evolutionary divergence is happening in the presence of gene flow, **G** may be constantly changing due to migration among diverging populations. As migration is reduced by evolution of reproductive barriers between groups, migration becomes less important in determining the shape of **G**, especially if other deterministic influences on **G**, such as correlational selection or mutation correlations, are present. If the pattern of influence on **G** from selection and mutation is similar in derived taxa as the ancestral taxon, then after migration and introgression halt, **G** may return to the ancestral state. **G** may help predict response to selection, but the present value of **G** will only approximate historical or future values.

Low gene flow ( $Nm < 1$ ), as commonly found in interspecific studies, is unlikely to affect the **G**-matrix enough to cause a correlation between the orientation of the **G**-matrix and divergence between populations. Therefore the patterns observed by Schluter (1996) are likely to be the result of genetic covariance influencing the response to selection or selection constraining the pattern of genetic covariance. For divergences among more closely related groups with higher levels of migration, though, **G** can be strongly affected by migration.

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