Evol Biol (2009) 36:323–326
DOI 10.1007/s11692-009-9062-y

ESSAY

Just How Much is the G-matrix Actually Constraining Adaptation?

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Received: 28 March 2009 / Accepted: 6 May 2009 / Published online: 22 May 2009

Abstract The genetic variance–covariance matrix (**G**) has long been considered to summarize the genetic constraints biasing evolution in its early stages, although in some instances, **G** can enhance divergence and facilitate adaptation. However, the effects of **G** on the response to selection might be of less importance than previously thought. In addition, it has been suggested that selection itself, under certain conditions, might rapidly alter the genetic covariance structure. If selection can indeed affect the stability of **G** to facilitate evolution, the overall structure of **G** might not be as important to consider as the past selective conditions that **G** was subject to. Thus, more empirical work is needed on the stability of **G** in the early stages of divergence before one can really assess to what extent **G** constrains evolution.

Keywords Adaptation · Constraints · G-matrix · Quantitative genetics · Selection

The genetic variance–covariance matrix (**G**) has been at the basis of many controversies ever since its importance on phenotypic evolution was formalized by Lande in 1979. It is predicted that **G** will constrain evolution in its early stages and bias its direction towards $\mathbf{g}_{\mathbf{max}}$, the genetic line of least resistance (Schluter 1996). **G** is therefore of interest for the study of phenotypic evolution and has been extensively investigated over the last decade, leading to the emergence of a new field of research named "comparative quantitative genetics" (Steppan et al. 2002). **G** encompasses the overall genetic constraints linked to phenotypic traits and deflects the response to selection towards the trait combinations that have the most genetic variation. As a consequence, in certain situations, **G** can potentially restrain evolution even with the presence of additive genetic variation in each trait if these traits are strongly negatively correlated. However, **G** might not necessarily reflect all constraining properties of an organism such as non-additive genetic effects or developmental constraints (Polly 2008). Another issue is whether **G** mainly is the result of ancestral and shared developmental pathways or past selective pressures (Cheverud 1984; Arnold et al. 2001; Arthur 2004). **G** has nonetheless been widely used to predict which kinds of evolutionary changes are most readily accomplished (Schluter 1996) and in retrospective selection analyses where the net differences between selection gradients of diverging populations were back calculated (Dudley 1996). However, both these types of evolutionary inferences rely on one major aspect of **G**: its stability (Arnold et al. 2008).

From a theoretical perspective, **G** has been shown to be prone to change under various conditions (Jones et al. 2003, 2004), but we still lack any simple and empirically testable forms of equations describing the dynamics of **G** on a generation time basis (Arnold et al. 2008). Most empirical work conducted in natural populations has found **G** to be stable over short periods of time but not over thousands or millions of years (Phillips and Arnold 1999; Cano et al. 2004; also reviewed in Arnold et al. 2008). Many of the studies on the stability of genetic covariances have led to the conclusion that often, most of the eigenstructure of **G** is conserved through time (Arnold et al. 2008). However, laboratory studies have also found that **G** could change very rapidly (Wilkinson et al. 1990; Shaw et al. 1995; Phillips et al. 2001). A limitation of these experimental assessments is that evolutionary forces

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specific to natural conditions promoting **G** stability might be absent with the experimental designs used (Arnold et al. 2008). But recently, a study on wild populations of nematodes (*Acrobeloides nanus*) has described very high dynamics of changes in **G** for three life-history traits under various environmental conditions (Doroszuk et al. 2008). This study was the first to show that over very short time frames (20 years), the genetic covariance structure of organisms could be altered due to divergent selection pressures. Another recent study on the phenotypic covariance structure of wing traits in different species of calopterygid damselflies has revealed that divergent selection on a single ecologically important trait could affect the overall stability of the covariance structure (Eroukhmanoff et al. 2009b), confirming that differences in integration patterns of traits serving multiple function can reflect different selective pressures (Eroukhmanoff and Svensson 2008). Moreover, the question of the stability of **G** is crucial because if selection can modify the covariance structure of certain traits, it also implies that selection might bias **G** to facilitate evolution as much as **G** has been considered to potentially restrain adaptation. Gould (1989) was among the first to introduce this idea of positive constraints, which facilitate adaptation by channeling variation in certain directions. Under the right conditions of size, eccentricity and orientation, **G** might just constitute such positive constraints in the adaptive landscape (Jones et al. 2003, 2004). Although this "positive side" of **G** is straightforward when considering the multivariate breeder's equation (Lande 1979), studies in the field of quantitative genetics have mostly regarded **G** as a negative constraint on adaptation (Steppan et al. 2002; Arnold et al. 2008). However, a recent meta-analysis of the literature on genetic covariance structure and selection has shown that **G** might in many instances have no effect on rates of adaptation, and sometimes even facilitated evolution (Agrawal and Stinchcombe 2009). It is possible these results indicate that selection might in many cases reshape or reorientate **G** to dampen its negative influence on adaptation.

Indeed, if **G** really is susceptible to selection, **G** may be prone, in certain selective conditions, to "store" ancient environmental pressures, which might weaken or strengthen its constraining effect on future selection pressures. In such situations, **G** is therefore both the constrained and the constraint, and the relationship between **G** and selection actually becomes a two-way interaction. The possibility that genomes might reflect their past environments, which might influence their response to new environmental pressures has been recently introduced under the label of "facilitated variation" (Gerhart and Kirschner 2007) and both theoretically (Parter et al. 2008) and empirically (Teotonio et al. 2009) tested. More empirical work is however needed to specifically determine to what extent **G** could accurately be used to predict future responses to selection, and to what extent selection could reorganize genetic variation by modifying the structure of **G** so that adaptation would be facilitated.

But the fact remains that the influence of **G** on evolution might be more limited than previously thought (Merila and Björklund 1999; Agrawal and Stinchcombe 2009). The hypothesis that phenotypic divergence proceeds along lines of least resistance due to the influence of the first eigenvector of **G** ($\mathbf{g_{max}}$) has been long tested and acknowledged (Arnold et al. 2008). But it might be also of interest to study under which conditions the path of divergence might depart more from $\mathbf{g_{max}}$ than the multivariate breeder's equation would predict, even in the early stages of evolution (Arnold et al. 2008; Hohenlohe and Arnold 2008) and what could be the consequences of such a process on the stability of **G** (Eroukhmanoff et al. 2009b). Of course, under sufficiently strong divergent selection and/or high mutation rates, the influence of $\mathbf{g_{max}}$ might be reduced (Mc Guigan 2005, 2006; Arnold et al. 2008; Eroukhmanoff et al. 2009b) and strong correlational selection might also alter the eigenstructure of **G** under certain conditions (Jones et al. 2003; Revell 2007).

If selection can really alter **G** over short periods of time (Doroszuk et al. 2008), it is possible **G** has less influence than expected on adaptation because selection has modified **G** to minimize its constraining properties in the early stages of divergence (Agrawal and Stinchcombe 2009). Indeed, most of the studies focusing on the genetic covariance structure have investigated populations which had been diverging for a certain amount of time. During this time, it is possible that selection had already reorientated $\mathbf{g_{max}}$ in the direction of the fitness peak and therefore there was little constraining effects to be found at the time **G** was estimated (Fig. 1). This possibility has already been discussed by Schluter (1996) when he suggested that patterns of divergence along lines of least resistance might only indicate that $\mathbf{g_{max}}$ and divergence may be shaped by selection into similar directions, and theoretically confirmed, e.g. by Jones et al. (2003).

In addition, very few studies have found evidence for rapid divergence of **G** in the wild. Of course, it might be impossible to consider the original covariance structure before divergence simply because the populations have already evolved when they are under scrutiny and it is too late to estimate **G**. But laboratory studies have the advantage of being more controlled, and therefore offer the possibility of detecting changes in **G** due to selection by using populations whose original covariance structures are known (Wilkinson et al. 1990; Shaw et al. 1995; Phillips et al. 2001). However, it has recently been shown that covariance structures estimated for lab-raised individuals might not reflect the real covariance structure that can be found in wild populations

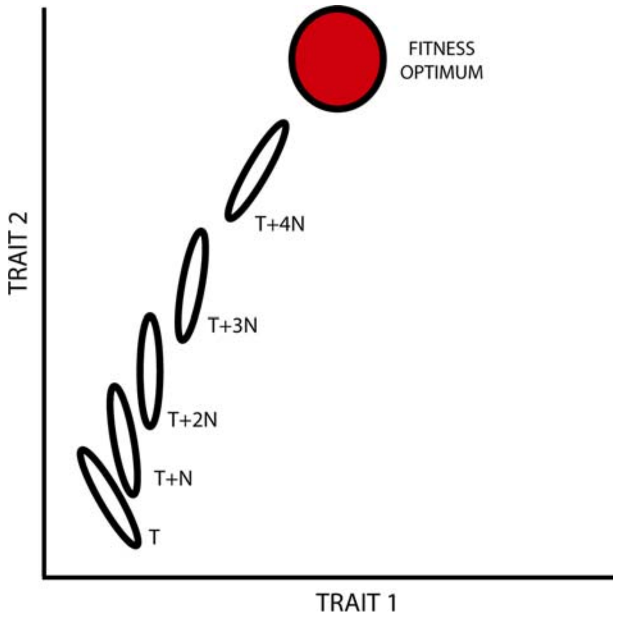

Fig. 1 The ellipsoids depicting **G** for two traits and at various times during divergence, starting from time T and showing different snapshots of **G** every N generations. At time T, there is a negative genetic correlation between trait 1 and trait 2. If selection can modify **G** to align $\mathbf{g}_{\mathbf{max}}$ in the direction of the fitness optimum under a short amount of time (N being small), then it will be difficult to capture the initially high constraining effects of **G** on selection (for instance if **G** is estimated after 3N generations)

(Jamniczky and Hallgrimsson 2009). As mentioned above, when studying wild populations which have been diverging for thousands of years, it is nevertheless unrealistic to assume that the initial genetic covariance structure of these populations could be estimated. Nevertheless, even in natural conditions, some systems involving colonization of novel environments by a known source population such as mainland-island radiations (e.g., Irschick et al. 1997) or ecotypic diversifications in lakes or marine systems (e.g., Schluter et al. 2004; Eroukhmanoff et al. 2009a) would provide good opportunities to study the stability of **G** under divergent selection and the role of historical and genetic constraints (Eroukhmanoff et al. 2009a). Moreover, such systems where it would be possible to compare **G** before and after colonization are often replicated independently in a parallel fashion (Schluter et al. 2004; Eroukhmanoff et al. 2009a). Thus, they offer not only a possibility to assess the constraining role of **G** during divergence of single traits (Schluter et al. 2004; Revell et al. 2007), but also to investigate how deterministic selection on covariance structures (or more simply on quantitative traits) can be (Schluter et al. 2004; Revell et al. 2007). Unfortunately, very few studies have so far capitalized on these opportunities (e.g., Revell et al. 2007).

In conclusion, both the stability of **G** (Doroszuk et al. 2008) and its negative effects on adaptation (Agrawal and Stinchcombe 2009) have recently been contested. Based on these results, it is clear that some of the assumptions that have been made on **G** need to be revised. Indeed, we still have many points to address empirically when it comes to issues such as the stability or the constraining effect of **G** in the context of divergence, but many opportunities remain to be pursued.

Acknowledgements I thank Erik Svensson's laboratory group for many intense discussions on issues related to the **G**-matrix, which have helped me clarifying some of the points treated here. This study was financially supported by the Ecole Normale Supérieure (ENS) and the Royal Physiographic Society of Lund (KFS).

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