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HOMOGENEITY OF THE GENETIC VARIANCE-COVARIANCE MATRIX FOR ANTIPREDATOR TRAITS IN TWO NATURAL POPULATIONS OF THE GARTER SNAKE *THAMNOPHIS ORDINOIDES*

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Abstract.—Quantitative genetic models of evolution rely on the genetic variance-covariance matrix to predict the phenotypic response to selection. Both prospective and retrospective studies of phenotypic evolution across generations rely on assumptions about the constancy of patterns of genetic covariance through time. In the absence of robust theoretical predictions about the stability of genetic covariances, this assumption must be tested with empirical comparisons of genetic parameters among populations and species. Genetic variance-covariance matrices were estimated for a suite of antipredator traits in two populations of the northwestern garter snake, *Thamnophis ordinoides*. The characters studied include color pattern and antipredator behaviors that interact to facilitate escape from predators. Significant heritabilities for all traits were detected in both populations. Genetic correlations and covariances were found among behaviors in both populations and between color pattern and behavior in one of the populations. Phenotypic means differed among populations, but pairwise comparisons revealed no heterogeneity of genetic parameters between the populations. The structure of the genetic variance-covariance matrix has apparently not changed significantly during the divergence of these two populations.

Key words.—Antipredator behavior, color pattern, garter snake, genetic correlation, heritability, interpopulation variation, quantitative genetics, *Thamnophis ordinoides*.

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The application of quantitative genetic theory to phenotypic evolution has provided the tools needed to predict phenotypic change among suites of correlated traits (reviewed in Lande 1988). These methods can be used to isolate traits that are the targets of selection from those that change as a result of genetic coupling with traits under direct selection, when all the traits under selection are known (Lande and Arnold 1983). This approach has advanced our consideration of phenotypic evolution from questions about changes in single characters to queries regarding the developmental and functional integration of whole suites of traits.

This body of theory has been extended to predict the long term effects of selection on multivariate phenotypes and to reconstruct the past forces of selection necessary to produce observed phenotypic differences (Lande 1979; Lande and Arnold 1983; Price et al. 1984; Price and Grant 1985; Arnold 1988; Lofsvold 1988). Retrospective analyses of phenotypic divergence also provide the first opportunity to empirically evaluate the plausibility of random genetic drift as a differentiating force for specific natural systems (Lande 1976, 1977, 1979; Lofsvold 1988). Where available, information about divergence times can be coupled with reconstruction of the net selection gradients to calculate the minimum mortality per generation necessary to account for phenotypic differences among taxa (Lande 1979; Charlesworth 1984; Lofsvold 1988).

The application of these methodologies to natural populations requires a critical assumption. The pattern of genetic variances and covariances among traits must remain stable over the time that divergence is examined (Lande 1979; Lofsvold 1986, 1988; Turelli 1988; Barton and Turelli 1989). The importance of constancy (and the less rigorous criterion of proportionality) to conclusions drawn from retrospective analyses of the forces of divergence have been theoretically investigated (Turelli 1988). Without the assumption of at least proportionality of genetic variance-covariance matrices, little can be said about the importance of drift or selection in creating observed phenotypic differences.

Evaluation of the constancy of the genetic variance-covariance matrix (hereafter, **G**-matrix) over evolutionary time is an empirical issue (Turelli 1988). There is no doubt that **G**-matrices change over some period of time (all species do

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not share the same characters, let alone the same patterns of covariance) and in response to certain conditions (Bohren et al. 1966; Lande 1980, 1984; Zeng 1988; Wilkinson et al. 1990). The magnitude of this time scale and the frequency with which the necessary conditions for change occur are the current questions. The few studies that have attempted to assess the similarity of **G**-matrices among populations or species have produced ambiguous results (reviewed in Barton and Turelli 1989; and Wilkinson et al. 1990), implying that the dynamics of the **G**-matrix may depend on the types of traits and the taxa under consideration.

Most previous comparisons of **G**-matrices have concentrated on relationships among morphological traits (Lofsvold 1986; Kohn and Atchley 1988; Venable and Burquez M. 1990; Wilkinson et al. 1990). The temporal stability of genetic covariances within other categories of traits such as behavior (Arnold 1981) and life history (Platenkamp and Shaw 1992), and between traits of different categories (Billington et al. 1988; Shaw and Billington 1991) has been largely unstudied. I examined the **G**-matrix of a suite of morphological and behavioral traits that are important as antipredator mechanisms in two natural populations of the northwestern garter snake *Thamnophis ordinoides*. Color pattern and escape behavior are known to be genetically correlated in this species (Brodie 1989a) and this correlation is thought to be adaptive (Klauber 1931; Jackson et al. 1976; Brodie 1989a, 1992). Thus, this portion of the **G**-matrix is likely to be of some ecological significance.

Materials and Methods

A total of 203 pregnant female *Thamnophis ordinoides* were collected from two populations in coastal Oregon between mid-June and mid-August in 1987, 1988, and 1989. Seventy-seven females were collected from Clarence Creek Quarry (= CCQ) in Tillamook County (29 in 1987, 24 in 1988, 24 in 1989) and 126 females were collected from Tenmile Creek in Lane County (29 in 1987, 51 in 1988, 46 in 1989). These localities are approximately 120 km apart and are 12 km and 6.5 km inland from the Pacific coast, respectively The localities are separated by four major river drainages that run perpendicular to the coast line.

Females were brought into the laboratory in Myrtle Point, Oregon and maintained until parturition an a diet of earthworms (most females refused food during this period). Snakes were housed individually in plastic containers (35 cm × 17 cm × 9 cm) and kept on a 13:11 light : dark photoperiod. A thermal gradient between 25° and 30°C was provided during the light portion of the photoperiod. At all other times, the ambient temperature was 20°C (± 1°C).

Cages were checked daily for the presence of neonates from the end of August until all females gave birth. The mass and snout-vent length (SVL) of the mother and all offspring were recorded within 24 h of parturition. At this time, all neonates were separated and housed individually in circular plastic containers (12.5 cm diam × 6.5 cm deep). All individuals were maintained at 30°C during the light portion of the photoperiod and 20°C (± 1°C) at all other times.

Measurement of Color Pattern and Behavior

Maximum sprint speed over a 0.5-m interval (= speed), the distance crawled until antipredator display (= distance), and the number of reversals of direction during flight (= reversals) were assayed for each neonate using methods described by Brodie (1989a,b) except that sprint speed was timed using a stopwatch rather than electronic timers. The conditions and apparatus used followed these specifications throughout all phases of the study. Antipredator display (Arnold and Bennett 1984; Brodie 1989a,b) was also recorded but virtually no variation for this behavior existed in either population, so this trait was not analyzed.

Several color pattern components were scored and combined into an index describing the overall "stripedness" (= stripe) of an individual's color pattern (Brodie 1989a, 1992, 1993). The components scored included the completeness and contrast of the dorsal and lateral stripes [completeness was measured on a 0–4 scale, 0 = absent and 4 = present the entire length of the body (DS, dorsal stripe; LS, lateral stripe); contrast was scored on a 0 through 3 scale of increasing contrast (DC, dorsal stripe; LC, lateral stripe)]; and the presence or absence of dorsal and lateral rows of spots (= SPOT; 1, no spots; 2, 1 row of spots; 3, 2 rows of spots). The index used was [(DS × DC) + (LS × LC) + 1]/SPOT. The actual colors of the pattern components are not considered here.

All of the components of color pattern are probably controlled by one or two loci (S. J. Arnold unpubl. data for *Thamnophis couchi*) and some are strongly intercorrelated (Brodie un-

publ. data). The combination of these components into an index creates a quantitative trait more appropriate for quantitative genetic analyses and reduces the multicollinearity of the data and the dimensionality of the analyses. Additionally, the index describing overall stripedness of the color pattern is more readily interpretable in an ecological context (Brodie 1989a, 1992, 1993).

Behavior and color pattern scoring were conducted over a 4–5-day period beginning on the third day of postnatal life. On days 3 and 4, speed was measured twice each day (at least 4 h apart) for a total of four repeated measures of each individual. On days 5 and 6, distance and reversals were measured once each day for a total of two repeated measures. Stripe was scored on either day 6 or 7 and was scored only once for each individual.

Analysis of Phenotypic Data

Speed, offspring mass, offspring SVL, mother's mass, and mother's SVL were distributed normally and were not transformed for analysis. Distance was natural-log transformed to achieve normality. Stripe and reversals both showed right-skewed distributions and so were square-root transformed (Sokal and Rohlf 1981). No differences between males and females were detected, so both sexes were combined for all analyses.

Repeatabilities of the behaviors were calculated as intraclass correlations from a one-way ANOVA with individual as the main effect (Falconer 1981). The Type I sums-of-squares method of the VARCOMP procedure in PC-SAS release 6.03 was used to obtain these estimates (SAS 1988). To make the repeatabilites comparable to the genetic parameters, which were estimated based on averages of two or four measurements, the repeatabilites reported were adjusted for the appropriate number of measurements (Falconer 1981; Arnold and Bennett 1984; Becker 1984; Brodie and Garland 1993). Reports of heritabilities of behaviors that exceed repeatabilities (e.g., Brodie 1989a; Brodie and Brodie 1990) can result from a failure to scale both parameters to the same number of measurements. The repeated measures for each individual were averaged for subsequent analyses.

The GLM procedure of PC-SAS release 6.03 (SAS 1988) was used to test for differences in phenotypic means among years (one-way ANOVA with year as main effect). This analysis indicated differences among years within populations for most behaviors and for stripe. Pooling data sets with different means might inflate within population estimates of variance because of among year components of variance. Therefore, when data from three years were pooled for population estimates of phenotypic correlations, the means of each trait were set equal to the 1987 mean for that trait in that population. The use of corrected means eliminates the between-group component of variance and is often used when different sexes or ages are to be pooled for quantitative genetic estimates (e.g., Cheverud 1982; Arnold 1988; Dohm and Garland 1993).

Pearson product-moment correlations among phenotypic traits were calculated for each of the population data sets. Population comparisons of phenotypic correlations were conducted using a t-test of homogeneity of z-transformed correlation coefficients (Sokal and Rohlf 1981).

Because multiple tests of significance were made for each data set, significance levels were adjusted using a sequential Bonferroni adjustment (Rice 1989). Adjustments were made to control the Type I error rate for all estimates of a particular parameter (phenotypic correlations, heritabilities, etc.) within each population and for all tests of a particular parameter between populations. Each phenotypic correlation matrix included six correlations; thus, significance levels for tests whose correlations were different from zero were adjusted for the six tests conducted. Similar corrections were made for the tests of differences in correlations between the populations. Significance levels of population comparisons of phenotypic means were adjusted for the four tests performed. The P-values for repeatabilites were adjusted for the three estimates made in each population. All tests were judged significant at the adjusted 0.05 level.

Estimation of Genetic Parameters

All quantitative genetic parameters were calculated using least-squares estimation of covariances among full-sibs (Falconer 1981; Becker 1984). All offspring from a single female were assumed to be full-sibs. Recent electrophoretic work indicates that some degree of multiple paternity is present in at least two populations of another species of garter snake, *T. sirtalis* (Schwartz et al. 1989). Any incidence of multiple paternity will render genetic estimates based on full-sib assumptions conservative for two reasons. First, the average relatedness of full-sibs is

0.5 whereas that of half-sibs is only 0.25 (Falconer 1981). Multiple paternity in some litters decreases the average relatedness within litters to less than 0.5 (0.42 in *T. sirtalis*; Schwartz et al. 1989). Intraclass correlations are multiplied by the inverse of the relatedness within families to yield estimates of heritabilities or genetic correlations. Assuming too large an average relatedness will cause genetic parameters to be underestimates. Second, heritabilities and genetic correlations estimated from full-sib relationships include a fraction of dominance variance or covariance whereas those estimated from half-sibs do not (Falconer 1981). The inclusion of half-sib groups in a full-sib analysis will reduce the true contribution of dominance variance or covariance to the full-sib estimates obtained. In this way, unconsidered multiple paternity will cause full-sib quantitative genetic estimates to contain less contribution from dominance than expected and to underestimate the parametric full-sib heritabilities and genetic covariances (as based on actual average relatedness within families).

Quantitative genetic parameters estimated from full-sib groups may also include contributions from common family environments. Effects from common postnatal environments were experimentally reduced by splitting families at birth. Contributions from common prenatal environments (maternal effects) were statistically reduced by regressing behavior scores on potential indicators of maternal condition (Garland 1988; Brodie 1989a; Tsuji et al. 1989). Speed, distance, and reversals were each regressed on mother's mass, mother's SVL, offspring mass, and offspring SVL using a stepwise multiple-regression procedure (SAS 1988) to arrive at the model that explained the most variance in a particular trait. Separate regressions were performed for each behavior in each data set (all years in both populations, as well as pooled population data). No significant predictors ($P < 0.1$) were found for reversals, so the original trait values (square-root transformed) were used in subsequent analyses. Significant predictors of speed and distance varied among years and populations, but generally included offspring mass and SVL and only rarely included mother's mass. Residuals from the regression model significant for each trait and data set were substituted for speed and distance in all genetic analyses. This procedure statistically removes variation in speed and distance associated with maternal and offspring size at birth, thus reducing maternal effects associated with condition of the female (Garland 1988; Brodie 1989a; Brodie and Garland 1993).

Heritabilities and genetic covariances and correlations were obtained by least-squares estimation of variance and covariance components with a delete-one-family jackknife procedure. The ANOVA models used included year as a fixed effect to remove between-year components of variance from estimates of between-family variances. Previous simulations of jackknife procedures have indicated that this method of estimation of variance and covariance components has good statistical behavior for a variety of distributions and heterogeneous variances (Arveson and Schmitz 1970; Knapp et al. 1989; Mitchell-Olds and Bergelson 1990). The resulting quantitative genetic parameters are averages of all the jackknifed estimates for a particular data set and standard errors are approximately t-distributed (Knapp et al. 1989). A particular advantage to this form of estimation of heritabilities and genetic covariances is that well-defined significance tests exist even for unbalanced designs (Knapp et al. 1989).

The use of jackknife procedures to estimate quantitative genetic parameters and their standard errors also allows for simple t-tests of differences between estimates from two populations (Knapp et al. 1989). This method was used to test for differences between populations.

For each population, four heritabilities, six genetic correlations, four genetic variances, and six genetic covariances were calculated. The significance levels of these parameters were adjusted using the sequential Bonferroni technique for four, six, four, and six tests, respectively, in each population (Rice 1989). Comparisons of each of the parameters between populations were adjusted for the same number of tests.

Results

Population Parameters

All three behaviors were significantly repeatable in both populations (table 1). Repeatabilities were moderate to high, indicating consistent individual differences for each behavior.

Heritabilities were also large and significant for all traits in both populations (table 1). As expected from standard genetic models (Falconer 1981), the heritability of a trait was never larger than the repeatability.

Few genetic correlations were significantly dif-

TABLE 1. Phenotypic means, repeatabilities, and heritabilities (± standard error) for the Tenmile and CCQ populations. The number of families and individuals, respectively, for each population is shown in parentheses.

Population	Trait	Mean	Repeatability	Heritability
Tenmile (126,721)	Mass (g)	1.847 ± 0.012	—	—
	SVL (mm)	141.622 ± 0.409	—	—
	Stripe	12.862 ± 0.428	—	0.758 ± 0.097***
	Reversals	2.016 ± 0.066	0.734 ± 0.017***	0.649 ± 0.092***
	Speed (m/s)	0.270 ± 0.002	0.851 ± 0.008***	0.492 ± 0.101***
	Distance (cm)	338.164 ± 8.562	0.825 ± 0.012***	0.570 ± 0.089***
CCQ (77,393)	Mass (g)	1.608 ± 0.016	—	—
	SVL (mm)	137.578 ± 0.532	—	—
	Stripe	11.055 ± 0.530	—	0.866 ± 0.258***
	Reversals	1.609 ± 0.077	0.650 ± 0.029***	0.656 ± 0.111***
	Speed (m/s)	0.255 ± 0.003	0.796 ± 0.014***	0.514 ± 0.106***
	Distance (cm)	300.682 ± 10.297	0.805 ± 0.018***	0.539 ± 0.188**

** $P < 0.01$; *** $P < 0.001$.

ferent from zero in either population (table 2, 3). Speed and distance were positively genetically correlated in both Tenmile and CCQ. Stripe and reversals were negatively correlated, but this relationship was significant only in the Tenmile population. Genetic variances and covariances showed the same patterns of significance as the heritabilities and genetic correlations in both populations (table 4).

Phenotypic correlations were generally weak and positive, though many were significant because of the large sample sizes (table 2, 3). In both populations, speed and distance were positively correlated and each of these traits was weakly positively correlated with reversals. In the Tenmile population, stripe and reversals were negatively correlated.

The phenotypic and genetic correlations were estimated from the same data and could not be compared statistically because they were nonindependent. Qualitative comparison of the two matrices in each population indicated close agreement (fig. 1). Analogous phenotypic and genetic correlations were usually of the same sign and of similar magnitude, though the genetic correlations tended to be slightly larger than their phenotypic counterparts (table 2, 3; fig. 1).

Heterogeneity among Populations

Small but significant population differences were detected in the means of all four traits (table 5). The only phenotypic correlation that differed between the populations was that between stripe and reversals, which was negative for the Tenmile population and near zero for CCQ (table 5).

No differences between populations were detected for any of heritabilities, genetic correlations, variances, or covariances (table 5, fig. 2). Only the test statistics for population comparisons of heritabilities and genetic correlations are shown in table 5, but the same pattern (no differences) was true for comparisons of genetic variance and covariances (fig. 2). This was true even at the single-test significance level of 0.05. Qualitative inspection of the heritabilities and the genetic correlations, variances, and covariances (tables 1–4, fig. 2) reveal very similar point estimates for all parameters in the two populations.

DISCUSSION

Patterns of Variance and Covariance within Populations

Repeatability may be considered as a measure of stereotypy or individual consistency of be-

TABLE 2. Genetic and phenotypic correlations for the Tenmile population. Genetic correlations (± standard error, $N = 126$) are shown above the diagonal and phenotypic correlations (± standard error, $N = 721$) are shown below the diagonal. Correlations significantly different from zero are indicated by asterisks.

	Stripe	Reversals	Speed	Distance
Stripe	—	−0.328 ± 0.116*	−0.030 ± 0.161	−0.068 ± 0.136
Reversals	−0.230 ± 0.036***	—	−0.157 ± 0.236	0.195 ± 0.127
Speed	0.076 ± 0.037	0.101 ± 0.037*	—	0.418 ± 0.111**
Distance	−0.010 ± 0.037	0.102 ± 0.037*	0.435 ± 0.033***	—

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 3. Genetic and phenotypic correlations for the CCQ population. Genetic correlations (± standard error, $N = 77$) are shown above the diagonal and phenotypic correlations (± standard error, $N = 393$) are shown below the diagonal. Correlations significantly different than zero are indicated by asterisks.

	Stripe	Reversals	Speed	Distance
Stripe	—	−0.031 ± 0.200	−0.209 ± 0.247	0.061 ± 0.111
Reversals	−0.028 ± 0.051	—	0.226 ± 0.210	0.107 ± 0.188
Speed	0.000 ± 0.051	0.160 ± 0.050**	—	0.399 ± 0.157*
Distance	0.119 ± 0.050	0.167 ± 0.050**	0.340 ± 0.048***	—

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

havior (Boake 1989). All three behavioral traits considered in this study showed moderate to high repeatabilities. These estimates were roughly equal to those for the same traits reported for neonates (Brodie 1989a) and adult females (Brodie 1989b) from other populations of *Thamnophis ordinoides*. This result also indicates that the methodology used to score these traits is an efficient means of characterizing individual differences in escape behavior.

The heritabilities of all four traits were large and significant, suggesting that substantial additive genetic variance may exist in both populations for color pattern and antipredator behaviors. This conclusion is based on full-sib estimates of heritability, which may include a portion of dominance variance and contributions due to common family environments. Comparisons across a variety of taxa and traits indicate that full-sib estimates of heritability are not greatly inflated relative to estimates based on other relationships (Mousseau and Roff 1987; Roff and Mousseau 1987). For paired estimates of heritabilities from 11 independent studies, full-sib estimates exceeded parent-offspring regression estimates for the same traits by an average of only 0.073 (Mousseau and Roff 1987). This difference is less than the usual confidence interval that could be calculated from the standard errors obtained in most studies, suggesting that full-sib heritabilities often may be reasonably good estimates of additive genetic variance (though this depends on the specific characters examined).

The heritabilities of the behaviors examined here were larger than normally reported for such traits (Mousseau and Roff 1987; Roff and Mousseau 1987). This may be a partial result of using an average of two or four measures of each behavior to estimate the associated heritabilities in this study. Using multiple measures of a trait reduces the special environment variance that is responsible for variation within an individual (Falconer 1981; Arnold and Bennett 1984) and thus increases the heritability.

The heritability of stripe in both populations is very large, even for a morphological trait (Mousseau and Roff 1987; Roff and Mousseau 1987). Some of the color pattern components contributing to stripe are thought to be controlled by one or two loci with dominance effects in other species of the genus *Thamnophis* (S. J. Arnold unpubl. data), so it is possible that some of the genetic variation contributing to the full-sib heritability may be nonadditive. The potential importance of maternal effects cannot be evaluated based on our current knowledge of the embryonic development of snake color patterns, but it is difficult to imagine environmental contributions to the phenotypic variation in stripedness. Stripedness is known to change slightly over

TABLE 4. Genetic variances and covariances for the Tenmile and CCQ populations. Genetic covariances (± standard error) for the Tenmile population ($N = 126$) are shown above the diagonal and for the CCQ population ($N = 77$) below the diagonal. Genetic variances (G_{ii}) for both populations are shown at bottom. Parameters significantly different from zero are indicated by asterisks.

	Stripe	Reversals	Speed	Distance
Stripe	—	−0.169 ± 0.066*	−0.002 ± 0.008	−0.054 ± 0.106
Reversals	−0.028 ± 0.072	—	−0.002 ± 0.003	0.043 ± 0.028
Speed	−0.007 ± 0.010	0.003 ± 0.002	—	0.009 ± 0.003*
Distance	0.049 ± 0.098	0.023 ± 0.046	0.010 ± 0.005†	—
G_{ii} (Tenmile)	1.904 ± 0.291***	0.141 ± 0.027***	0.001 ± 0.0003***	0.339 ± 0.063***
G_{ii} (CCQ)	1.575 ± 0.665*	0.129 ± 0.027***	0.001 ± 0.0003***	0.504 ± 0.219*

* $P < 0.05$; *** $P < 0.001$.
† Single-test $P < 0.01$; adjusted P = NS.

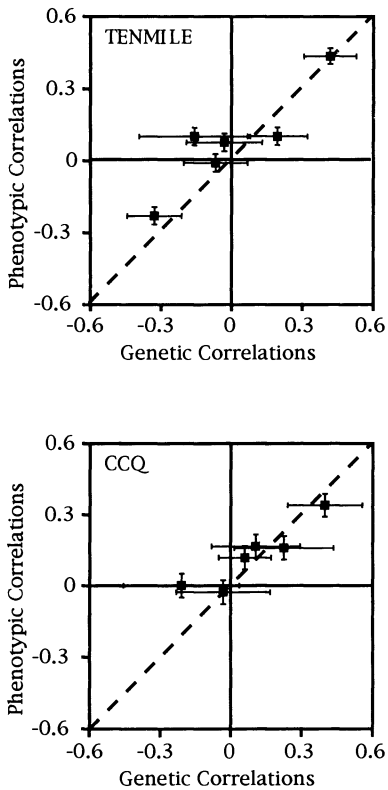

FIG. 1. Plots of phenotypic versus genetic correlations for each population (Tenmile above, CCQ below). Each point represents the genetic and phenotypic correlations between the same pair of traits. Standard errors of genetic and phenotypic correlations are indicated by the horizontal and vertical bars, respectively. The dashed line has a slope of one. If phenotypic and genetic correlations were identical within a population, they would lie on this line.

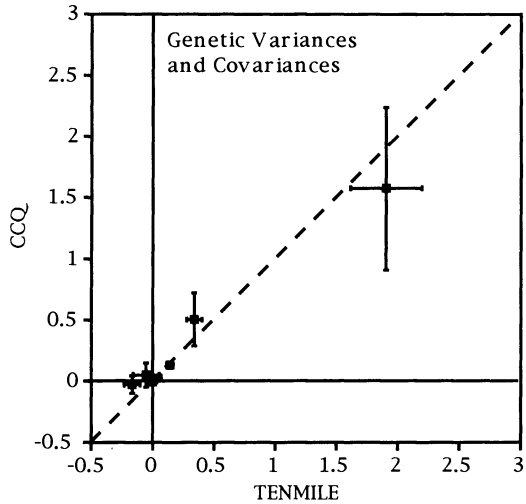

FIG. 2. Plot of the genetic variances and covariances in the CCQ population versus the Tenmile population. Each point represents the same genetic variance or covariance in the two populations. Standard errors for Tenmile and CCQ are indicated by the horizontal and vertical bars, respectively. The dashed line has a slope of one. If genetic variances and covariances were identical in the two populations, they would lie on this line.

the first few months of life, but all individuals change in a similar manner, becoming slightly more striped with age (Brodie 1993). The high heritability of stripe probably indicates that the unusual phenotypic variation in color pattern that is observed in natural populations of *T. ordinoides* is largely genetic in origin.

Reversals were negatively genetically correlated with stripe in the Tenmile population, supporting previous observations in this and one other population based on smaller sample sizes (Brodie 1989a). The corresponding phenotypic correlation means that individuals whose color pattern was linearly striped tended to flee without interruption until exhaustion, whereas snakes that were either unmarked or spotted crawled short distances and attempted to hide or change direction. This evasive form of escape is considered a behavioral component of crypsis that allows crypsis to be used as a defense even after

TABLE 5. Tests for differences between populations. *t*-statistics for population differences are shown for genetic correlations (df = 201) above the diagonal and phenotypic correlations (df = 1112) below the diagonal. *t*-statistics for population differences in heritabilities (h^2, df = 201) and phenotypic means ($\bar{x}$, df = 1112) for each trait are shown in the last two rows.

	Stripe	Reversals	Speed	Distance
Stripe	—	−1.382	0.632	−0.656
Reversals	−3.278**	—	−1.113	0.398
Speed	1.211	−0.954	—	0.104
Distance	0.039	−1.053	0.075	—
h^2	−0.457	−0.114	−0.142	0.164
$\bar{x}$	2.116*	4.102***	4.004***	3.030**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

initial detection by a predator (Pough 1976; Brodie 1989a,b, 1992, 1993). Interspecific correlations of escape behavior and color pattern among all species of North American snakes show similar combinations of pattern type and antipredator behavior (Jackson et al. 1976). This observation lends support to an adaptive explanation for the genetic correlation between reversals and stripe observed in the Tenmile population. To human observers, moving striped patterns create an optical illusion that obfuscates the detection of motion and the judgment of speed, whereas heterogeneous patterns provide fixed references points for the eye, allowing for better perception of movement (Brown 1931a,b). These effects of moving patterns are thought to be responsible for the selection by avian predators favoring certain combinations of pattern and behavior in juvenile *T. ordinoides* (Brodie 1992). Natural selection favoring a combination of traits could result in linkage disequilibrium among loci for each trait, which in turn is observable as a genetic covariance (Falconer 1981; Cheverud 1982, 1984; Lande 1984).

Negative genetic correlations between speed and stamina are expected because of the different physiological and morphological bases of these traits (reviewed in Garland 1988). Contrary to this expectation, positive genetic correlations between speed and distance were found in both populations of *T. ordinoides*. The distance crawled until antipredator display probably measures a behavioral component of a snake's willingness to crawl as well as its physiological endurance (see Jayne and Bennett 1990) and should therefore be interpreted cautiously as an indicator of stamina. Nonetheless, Garland (1988) also found positive genetic correlations between speed and a treadmill measure of endurance in *T. sirtalis*. A similar study of lizards failed to detect any genetic coupling between these traits (van Berkum et al. 1989). Together with empirical evidence of positive phenotypic correlations between speed and stamina in a variety of vertebrates, these results suggest a reevaluation of the theory predicting trade-offs between different measures of locomotor performance (reviewed in Garland 1988).

Phenotypic Heterogeneity between Populations

Large sample sizes in each population enabled the detection of small differences in the phenotypic means of all three behaviors and color pattern. Several differences were so slight as to be of questionable biological significance. The difference between the average speed of each population was only 1.5 cm/s, or approximately 6% of the pooled mean. The average distance crawled was 37.5 cm greater in the Tenmile population, or less than 12% of the pooled mean. Both of these differences in locomotor performance may be correlates of larger body size in the Tenmile population (table 1; mass: $t = 8.53$, df = 1112, $P < 0.001$; SVL: $t = 4.30$, df = 1112, $P < 0.001$). The differences between populations in reversals and in stripe are proportionally larger and are unlikely to be related to overall size differences (regressions of reversals on body size variables revealed no significant predictors, see methods).

The most obvious difference in the average phenotypes of the two populations was the negative covariance of reversals with stripe at Tenmile but lack of any relationship between these traits at CCQ. If correlational selection is responsible for the negative coupling of color pattern and antipredator behavior at Tenmile (Brodie 1992), then the independence of these traits at CCQ might imply spatial variation in the form of selection. Alternatively, selection on this combination of characters may be similar at the two localities, but other factors may break down any linkage disequilibrium generated by selection at CCQ, or sampling effects may have prevented detection of a genetic correlation in this population.

Similarity of **G***-matrices*

The **G**-matrix for color pattern and escape behaviors is apparently similar in the two populations examined. Not a single genetic parameter differed statistically between the populations, and the point estimates were remarkably similar given the sampling variance normally associated with estimates of quantitative genetic parameters (fig. 2). However, the power of statistical tests to detect differences between quantitative genetic estimates is notoriously low (the power of the test used here has not been specifically examined) and decreases with the magnitude of the difference between the true parameters (Shaw 1991). Although the sample sizes reported here are moderately large, especially for natural populations of vertebrates, the populations are not dramatically divergent; thus, the current study is not expected to have great power to detect differences in genetic variances and covariances. The phenotypic correlation between stripe and reversals was detectably different between populations and the close correspondence between phenotypic and

genetic correlations in both populations suggest that more statistical power might be able to demonstrate differences between Tenmile and CCQ for the genetic correlation between stripe and reversals.

In this study, I have employed pairwise comparisons of individual genetic parameters to evaluate the similarity of a **G**-matrix between populations. Such pairwise tests are a rigorous means of establishing identity of two sets of genetic parameters, but are not an explicit test of the similarity of matrices. However, if none of the individual elements of two matrices differ, it is unlikely that the matrices themselves are different. It is also unclear how many elements must be different to declare two matrices divergent enough to violate the assumption of constancy.

An advantage of pairwise tests is their ability to identify the actual components of the matrix that might diverge. If some covariances differ, it may be possible and still of some interest to investigate the forces responsible for divergence of only those traits whose genetic covariance matrix remains constant. Identification of trait combinations whose covariances differ among populations or species may also generate hypotheses about the forces that are responsible for such differences. Pairwise comparisons of elements become intractable when many traits are included in a matrix or when more than two populations are being considered. In these cases, the number of statistical tests becomes large and adjustments to control the Type I error rate of all comparisons make rejection of the null hypothesis of homogeneity of the elements extremely difficult (e.g., Venable and Burquez M. 1990).

The results of this study agree with others that have found homogeneity of **G**-matrices between natural populations of the same species (Arnold 1981; Arnold 1988; Venable and Burquez M. 1990; Platenkamp and Shaw 1992). Strong tests of constancy have not been conducted across subspecies, but similarity of structure has been demonstrated both at this level and between species (Lofsvold 1986; Kohn and Atchley 1988). Finally, manipulative experiments have shown that the **G**-matrix can change substantially in as little as 23 generations under selection in laboratory populations, but the response to selection is asymmetrical and it is not clear how important such phenomena are in nature (Wilkinson et al. 1990).

The dynamics of **G**-matrices are also likely to depend on the types of traits involved. Differences in the amount of additive genetic variance commonly observed for morphological, behavior, and life-history traits (Mousseau and Roff 1987; Roff and Mousseau 1987) may predispose genetic covariances among some categories of traits to respond more quickly to external forces than others. Likewise, the proximate causes of genetic covariances might also differ among certain categories of traits if such covariances are more likely to result from selection or inbreeding rather than pleiotropic effects (Lande 1984). Gametic phase disequilibrium created by selection will disappear quickly when selection is relaxed and if linkage is loose (Falconer 1981; Barton and Turelli 1989). If genetic covariances between categories of traits such as behavior and morphology are primarily due to correlations in allele frequencies rather than to physical linkages or pleiotropy, then genetic covariances between categories of traits may change much more rapidly than those within categories (Bohren et al. 1966).

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