Copeia, 1993(4), pp. 987–1002

Quantitative Genetics of Scale Counts in the Garter Snake *Thamnophis sirtalis*

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This study addresses the quantitative genetic basis of phenotypic variation and covariation for a series of meristic traits in the garter snake *Thamnophis sirtalis fitchi* (six head scale counts: loreals, supra- and infralabials, pre- and postoculars, temporals; three body scale counts: ventrals, subcaudals, dorsal scale rows at midbody; two derived traits: umbilical scar size and position). Each trait was scored on approximately 540 offspring and their 47 dams captured in the wild while gravid. Correlations of the meristic traits with body mass at birth, dam's snout–vent length and body mass, litter size, and number of days each dam was held under laboratory conditions prior to giving birth were removed by computing residuals from multiple regression equations. Narrow-sense heritabilities (estimated by restricted maximum likelihood) of residuals were high for temporal scale counts (0.59), moderately large for ventral (0.29) and subcaudal scale counts (0.41), and low (in the range 0–0.12) for the other five traits. Probably as a consequence of the low statistical power of significance testing under restricted maximum likelihood, only the heritability for temporal scales was significantly different from zero. Phenotypic ($r_p = 0.25$) and genetic ($r_g = 0.67$) correlations between ventrals and subcaudals were positive and significant. Phenotypic correlations between the head scale counts were generally low; however, the genetic correlations were larger, suggesting relatively tight integration at the genetic level. Phenotypic correlations between the head and body scale counts were generally low, but several genetic correlations were large (e.g., $r_g = -0.59$ for ventrals and infralabials, $r_g = 0.59$ for subcaudals and supralabials). These data indicate that scale counts from different regions of the body are not evolutionarily independent characters, despite their different spatial and temporal relationships during development. Overall, genetic correlations were not strongly correlated with either phenotypic ($r = 0.42$) or environmental correlations ($r = 0.16$).

EPIDERMAL scales are among the most distinctive features of living Reptilia. The functional significance of variation in reptilian scale counts is generally unclear (but see Hecht, 1952; Bennett and Licht, 1975; Regal, 1975), although numbers of ventral and subcaudal scales [which correspond directly to body and tail vertebrae (Alexander and Gans, 1966; Voris, 1975)] or their ratio may correlate with locomotor performance in garter snakes (Arnold and Bennett, 1988; Jayne and Bennett, 1989; unpubl.), and the number of head scales may affect cranial kinesis during ingestion of prey (S. J. Arnold, pers. comm.). Several early (Dunn, 1915, 1942; Inger, 1942, 1943; Hecht, 1952) and more recent studies (Fox, 1975; Arnold, 1988) have proposed or presented evidence suggesting that natural selection acts on scale counts, although the selective agents generally are not apparent; other authors have suggested that scale counts are often selectively neutral (Snell et al., 1984; Travis, 1989).

Studies of variation in scalation are prominent among evolutionary investigations of snakes, particularly for studies of geographic variation (Fitch, 1940, 1949; Klauber, 1941; Benton, 1980) and systematics (Ruthven, 1908; Thorpe, 1975; Rossman, 1979). The utility of reptilian scale counts as characters for systematic analyses and for classification has usually been assessed by relative phenotypic variation. In general, scale counts that differ among species while also exhibiting low within-population variation are favored over those that fail to show distinct taxonomic or geographic differences (e.g., see discussion in Ruthven, 1908; Fitch, 1940; Thorpe, 1975). For some scale counts, however, the magnitude of variation among individuals within a single population may exceed that existing among species (e.g., Ruthven, 1908). Most studies of geographic variation and systematics have implicitly (e.g., Kluge, 1969) or explicitly (e.g., Lee, 1985) assumed that scales on the head are evolutionarily independent of scales on the body. In part, this assumption seems reasonable based on the observation that scales over different regions of the body develop at different times (Maurer, 1895, cited in Mad-

erson, 1985; see below). Reptilian scalation would, therefore, seem appropriate for analysis of the relationship between developmental variability and evolutionary divergence (see discussion in Atchley, 1987).

When selection acts on single traits, those with substantial additive genetic variance (narrow-sense heritability, h_n^2) should be relatively labile evolutionarily, because they can respond rapidly to selection. When selection acts on multiple traits, the pattern of evolutionary response is more complicated (e.g., Lande, 1979, 1980, 1988), and theoretical models indicate how the genetic variance–covariance matrix may constrain the multivariate response to selection (see also Arnold, 1988; Zeng, 1988; Houle, 1991). Patterns of within-population genetic covariation may also lead to correlated character divergence by genetic drift, even in the absence of correlated selection (Lande, 1979; Lynch and Hill, 1986; Lynch, 1989). Moreover, it is widely claimed that "developmental constraints" may influence the course of evolution (Maynard Smith et al., 1985), and one way to attempt quantification of such constraints is at the level of the genetic variance–covariance matrix (Cheverud, 1984; Maynard Smith et al., 1985; Charlesworth, 1990).

Although estimates of narrow-sense heritabilities and of additive genetic correlations are of key importance for understanding multivariate evolution (e.g., Arnold, 1988; Boake, 1994; Brodie and Garland, 1993), we lack basic information about the inheritance of continuous or semicontinuous traits that are of general interest to morphologists and systematists (Atchley, 1983). For example, only two published studies have examined the genetic basis of phenotypic variation in reptilian scale counts (Beatson, 1976; Arnold, 1988), and none has examined the genetic relationships of scale counts within a single region as compared with between different regions of the body (e.g., head versus trunk). Several studies document the inheritance of scale counts in fishes (Lindsey, 1988), but none has reported genetic correlations. We suggest that the additive genetic variance–covariance matrix can be used to test the hypothesis that external scale counts constitute developmentally integrated traits.

The integument of snakes is a developmentally complex organ system, consisting of a superficial epidermal layer derived from the embryonic ectoderm plus adjacent dermis derived from mesoderm (Maderson, 1985). Each scale develops as an "outpushing" of epidermis containing a papilla of mesodermal tissue; the broad upper surface of the papilla cornifies, resulting in the formation of a scute. Reptilian scale counts are thus "composite traits," being the product of interactions among genetic effects and developmental pathways (after Riska, 1989). Considerable variation in the form and timing of development both among the regions of the body and within and among populations and species has been observed in reptiles (Maderson, 1985). Body scales appear earlier in development than do head scales. Series of embryos showing all stages of early scale development are available for a few species of reptiles, including the common garter snake, *Thamnophis sirtalis*. Zehr (1962) recognized 37 stages in the development of garter snakes. Ventral and subcaudal scales appear at stages 30–31, whereas head scales appear at stage 35. Scales around the eyes and mouth appear prior to the appearance of the temporals and other head scales. Because Zehr worked with embryos from wild-caught pregnant females, information about the absolute timing of these stages is not available. From limited data provided by Zehr (Table 1, 1962), it appears that stage 30 occurs at the beginning of the third month of development, whereas the head scales appear about a week later. A plausible interpretation of these events is that head and body scales constitute separate developmental units. In addition, Olson and Miller's (1958) concept of "morphological integration" predicts that functionally or developmentally related characters should tend to evolve as a unit. We, therefore, predicted that genetic correlations—to the extent they evidence developmental interactions—would be relatively stronger for pairs of head scale counts or for pairs of body scale counts than for pairs of head-body scale counts. As a null hypothesis, this prediction is consistent with some simple models of development [e.g., as described by Riska (1986) and Zelditch (1987); both of these are for predictions of phenotypic covariation]. Because *T. sirtalis* is one of the few reptiles for which an embryological series relating stages of development is available (Zehr, 1962), we have been able to compare our estimates of correlations with predictions based on developmental considerations.

Materials and Methods

All specimens used in this study were born to 47 female garter snakes (*Thamnophis sirtalis fitchi*) collected from the vicinity of Eagle Lake, Lassen County, California between 9 June and 4 July 1984 (Garland, 1988). The gravid females were taken by car to the University of California, Irvine, on 5 July 1984 and housed singly

in an environmental chamber on a 12-h photophase (30 C day, 20 C night) until parturition. The 47 dams gave birth to 563 offspring (271 male, 280 female) between 2 Aug. and 6 Sept. 1984 (mean litter size = 12.09 ± SD of 5.103, range = 1–26). At birth, offspring were weighed to the nearest 0.01 g, and progeny were divided into two groups (mean total litter mass = 29.94 ± SD of 13.022, range 2.88–53.18 g; 16 progeny were not weighed; total litter mass was obtained in these cases by substituting the mean sibling mass). Up to six progeny per family (n = 246) were selected randomly for use in studies of the quantitative genetics of activity metabolism (Garland, 1988, 1994; Garland and Bennett, 1990; Garland et al., 1990); the others were sacrificed by freezing immediately after weighing. Additional details of the maintenance conditions are described in Garland (1988). The important point for this study is that all progeny experienced at least one month of development time under standardized conditions of temperature and photoperiod (mean number of days = 49 ± SD of 7.6 days). As discussed earlier, limited evidence suggests that this period may coincide with scale formation in garter snakes; scale counts do not change after birth. Dams and all progeny were later preserved in formalin, then stored in 70% ethyl alcohol and shipped to the University of Wisconsin–Madison in 1987.

Scale counts.—A total of five body and six head scale counts (see Table 1) were chosen for study (Ruthven, 1908). Scales were counted under a binocular dissecting scope (8–10× magnification) for up to 545 offspring and 44 dams, only by the senior author (Lee, 1990). Three adult females and 18 progeny were either missing or could not be reliably scored. The head scales counted were loreals, pre- and postoculars, supra- and infralabials, and temporal rows. For populations of *T. sirtalis*, preoculars and loreals are usually an invariant one per side, whereas from two to four (typically three) postoculars occur (Fitch, 1949). On each side of the head, there are 6–9 (usually seven) supralabials, from 8–12 (usually 10) infralabials, and typically five temporals arranged in three rows. Counts for left and right sides of the head were summed for subsequent analysis. Ventral and subcaudal scale numbers were counted according to standard techniques (Dowling, 1951), as were dorsal scale rows at midbody. Two derived traits were also recorded: number of ventral scutes from the anal plate to the caudal end of the umbilical scar (UMBPOS); number of ventral scutes spanned by the umbilical scar (UMBSIZ). Such derived traits are common in the systematic literature (e.g., Thorpe, 1975; Rossman, 1979; Benton, 1980). UMBPOS and UMBSIZ were chosen because they were readily scored as the ventral scutes were counted and because individual variation for similar traits has been reported in snakes [e.g., *Nerodia* (formerly *Natrix*) *sipedon* (Dunn, 1915)].

Quantitative genetic analyses.—We estimated genetic parameters (additive genetic variances and covariances) using restricted maximum likelihood (REML) and Shaw's (1987) program. Traditional quantitative genetic methods based on analysis of variance or regression methods are restricted to limited sets of relatives and, therefore, do not use all of the information available for parameter estimation (Shaw, 1987; Falconer, 1989). Both dam–offspring covariance and full-sib covariance are used jointly in parameter estimation under REML, providing more precise estimates as compared to an analysis based solely on either relationship. The maximum likelihood method has additional advantages (Shaw, 1987). First, it does not require balanced designs; litter size of our garter snakes ranged from 1–26. Second, it allows tests of significance for genetic and environmental correlations that are not available for least-squares estimates, although the significance levels are conservative and may have low power (Shaw, 1987).

Point estimates of variance components were based on analyses of single characters. Estimates of genetic covariances were based on analyses of four character subsets, because we were unable to execute Shaw's (1987) program with all eight characters. In addition, genetic parameters were estimated for 44 sets of dams and offspring rather than the full data set because data were lacking for three dams. Thus, 25 offspring were excluded. Again, this was necessary to run the program. If estimates for any variance components were negative, these were constrained to zero, along with all covariances for that component, and new estimates were obtained. For significance testing, the likelihood of a further-constrained model was compared to that of the less-constrained model. Twice the difference in log likelihoods is distributed approximately as a chi-square with the number of parameters constrained to zero taken as the degrees of freedom (Shaw, 1987).

The head scales and one of the derived traits (UMBSIZ) exhibited relatively few classes and thus discontinuous distributions. Estimation of quantitative genetic parameters from discontinuous traits should be interpreted using a threshold model (Gianola, 1982; Falconer, 1989). An

TABLE 1. DESCRIPTIVE STATISTICS FOR BODY AND HEAD SCALES. Head scales are reported as the sum of left and right sides. Mass was measured at birth for all neonates and postparturition for adult females. Acronyms for the two derived traits are also given.

Trait	n	Mean	SD	Min	Max	Skewness	Kurtosis
Body mass (g)							
Dam	47	60.01	2.017	20.69	94.40	0.224	0.064
Offspring	547	2.48	0.385	1.15	3.57	−0.240	0.253
Dorsal scale rows at mid-body							
Dam	44	19	—	19	19	—	—
Offspring	543	19.00	0.096	17	20	−14.56	368.1
Ventrals							
Dam	44	161.23	2.972	155	169	0.025	0.276
Males	269	165.20	3.592	154	173	−0.484	0.165
Females	276	160.78	3.034	152	168	−0.096	−0.078
Subcaudals							
Dam	23	78.22	2.430	74	83	0.181	−0.619
Males	268	87.59	3.445	69	97	−0.617	3.025
Females	270	78.54	3.412	68	84	−0.653	−0.095
Position of the umbilicus relative to the anal plate (UMBPOS)							
Dam	42	13.02	1.615	10	16	−0.259	−0.584
Males	266	14.54	1.820	10	21	0.118	0.549
Females	271	14.15	1.722	10	20	0.491	0.532
Number of ventrals adjacent to the umbilicus (UMBSIZ)							
Dam	42	4.29	0.554	3	5	0.037	−0.445
Males	266	3.76	0.669	3	8	1.160	5.287
Females	271	3.64	0.593	3	6	0.648	1.235
Supralabials							
Dam	44	14.66	0.834	13	16	0.475	0.834
Males	267	14.14	0.464	12	16	1.606	8.705
Females	275	14.30	0.605	12	16	1.132	1.865
Infralabials							
Dam	44	19.68	0.829	18	21	−0.872	0.271
Males	267	19.37	0.850	17	21	−0.819	−0.476
Females	275	19.51	0.771	18	21	−0.983	−0.301
Loreals							
Dam	44	2	—	2	2	—	—
Offspring	544	2	—	2	2	—	—
Temporals							
Dam	44	10.07	1.437	5	14	−0.075	4.486
Males	266	9.48	1.716	4	15	−0.424	0.949
Females	275	9.02	1.931	4	17	0.116	0.795
Preoculars							
Dam	44	2	—	2	2	—	—
Offspring	544	2.01	0.096	2	4	18.8	368.4
Postoculars							
Dam	44	6.32	0.771	4	8	0.011	1.460
Offspring	544	6.09	0.747	2	10	0.254	4.980

underlying, continuously distributed liability for expression is assumed to exist for the expression of the trait; the observed phenotypic discontinuity is the expression of both genetic and environmental variation that has "mapped" onto a set of fixed thresholds (Gianola, 1982). When the phenotypic distribution is discontinuous, successful application of conventional quantitative genetic methods based on a multifactorial model depends greatly on the scale of measurement or transformation employed (Gianola and Norton, 1981; Gianola, 1982). However, it has been observed that, if the phenotypic scores are distributed over several categories (Self and Leamy, 1978) and if the categories are approximately symmetrically distributed (Gianola and Norton, 1981), unbiased estimates of heritability can be obtained by the parent–offspring regression and maximum likelihood methods employed in this study. Moreover, the maximum likelihood parameter estimates for the head scale traits are likely to be adequate (although significance tests have low power) because ML methods generally perform well even when the assumption of an underlying normal distribution is violated (see discussion in Shaw, 1987).

Suitability of garter snakes for quantitative genetic analyses.—Newborn garter snakes used in this study are presumed to represent sets of full siblings, consistent with previous studies and based on a variety of empirical evidence (references in Arnold, 1981a, 1981b, 1981c; Garland, 1988; Schwartz and Herzog, 1992). However, the assumption of single paternity may be invalid for some garter snake populations. Schwartz et al. (1989) have documented multiple paternity in some midwestern populations of *T. sirtalis*. Undisclosed multiple paternity (see also references in Brodie and Garland, 1993) in our population would reduce the resemblance among offspring within a family, because half siblings share only one-fourth of the additive genetic variance, whereas full siblings share one-half. Thus, estimates of heritability based on the presumption of purely full-sib relationships would be conservatively biased if families contain many maternal half siblings. However, heritability estimates from offspring-on-dam regressions would not be biased by the presence of undisclosed multiple paternity and thus can be considered to estimate true narrow-sense heritability (assuming that additive-by-additive epistatic variance, genotype-by-environment variance, and genetic or nongenetic maternal effects are absent; Falconer, 1989). If, however, litters were a mixture of full and half siblings, the standard errors of the heritability estimates would be inflated and, thus, may bias significance tests conservatively. Moreover, estimates of additive genetic variances and covariances will not be biased by undisclosed multiple paternity based on dam–offspring regression but may be conservatively biased in full-sib estimates.

Additive genetic variances and covariances were estimated from phenotypic scores of both dams and offspring. Although the inferences apply to the natural population from which the dams were obtained, the critical environmental circumstances for scale development certainly differ between the dams and offspring (Riska et al., 1989; Schwartz and Herzog, 1992). The offspring experienced a minimum of 28 days of development under laboratory conditions, whereas the adult female counts were the result of life-long development in nature. Several potential confounding issues need to be considered. For example, if specific environmental differences between the laboratory and nature affect genotypes differently, substantial genotype-by-environment interaction may be present. Thus, the genetic correlations reported in this paper would be lower than the actual "natural" genetic correlations (Falconer, 1989; Riska et al., 1989). Selection on the dams would also complicate inferences.

Nongenetic maternal effects contribute to the covariance of full siblings, thus inflating estimates of heritability (Willham, 1963) and genetic correlation (Lande and Price, 1989). In addition to developmental temperatures, nongenetic maternal effects mediated through maternal size (e.g., dam's age, nutritional status) might affect scale counts of the progeny (see discussion in Garland, 1988, 1994). For example, temperature can affect mean values, and temperature extremes experienced during development may cause skeletal and scute anomalies. Temperature-induced variation in meristic counts has been documented in snakes (e.g., Fox, 1948; Fox et al., 1961; Osgood, 1978; S. J. Arnold and C. R. Peterson, pers. comm.), amphibians (e.g., Peabody and Brodie, 1975), and fishes (e.g., Fowler, 1970). Thus, any thermoregulatory differences among dams in nature potentially may have affected progeny scale counts and, thus, biased upward our estimates of heritability. It is unknown to what extent nutritional status or stress experienced by dams may affect scale counts of their offspring. All progeny experienced from 28–63 days of development under standardized conditions of temperature in the lab (DAYS). Therefore, prior to genetic analyses, we used stepwise multi-

TABLE 2. RELATIVE VARIATION FOR OFFSPRING AND DAM MERISTIC TRAITS, RELATIVE VARIATION FOR RESIDUALS, AND TRANSFORMATIONS USED IN ESTIMATING QUANTITATIVE GENETIC PARAMETERS.

Trait	Dam	Offspring			
	CV (%)	CV (%)	SD of logs	SD of residuals	Transform
Ventrals	1.8	2.5	2.5	2.1	None
Subcaudals	3.1	4.2	6.9	4.1	Z^2
UMBPOS	12.4	12.4	12.4	12.0	$\log_{10}$
UMBSIZ	12.9	17.2	16.6	16.1	$\log_{10}$
Supralabials	5.7	3.8	3.7	3.7	Z^3
Infralabials	4.2	4.2	4.4	4.1	Z^4
Temporals	14.3	20.0	21.6	20.0	$Z^{1.5}$
Postoculars	12.2	12.9	12.9	12.9	$Z^{1.5}$

ple-regression analyses of each scale count on a series of potential covariates [offspring mass at birth, dam's mass, dam's SVL, litter size, DAYS, and $DAYS^2$ (the last standardized prior to squaring to reduce correlation with DAYS)] in an attempt to statistically remove maternal effects (Garland, 1988, 1994; Garland and Bennett, 1990; Garland et al., 1990). Sex-related variation was removed from the trait values by including sex as a dummy variable in the multiple regression of potential maternal effects. After determining which covariates were statistically significant, we computed residuals from multiple-regression equations to use in genetic analyses.

We also examined the distribution of each character and used procedures described in Sokal and Rohlf (1981) to test for significant deviations from normality. The transformations that best approximated normality (e.g., log, square, z^3, z^4) were then used in the genetic analyses of raw characters and for computing residuals, which were also checked for normality. For a comparative measure of variability of all meristic traits, we $\log_{10}$-transformed each trait, regressed them on significant covariates (see Results), then compared standard deviations of residuals (multiplied by 2.3026 because the variables were $\log_{10}$-transformed). This quantity is approximately equivalent to a coefficient of variation (Lewontin, 1966; Garland, 1984). Phenotypic correlations were calculated as Pearson product moment correlations between traits for progeny only, because this represents the population before any survivorship selection that may have occurred in nature (Lande and Arnold, 1983). SPSS/PC+ (Norusis, 1988) was used for most computations.

RESULTS

Descriptive statistics and variability of characters.—Descriptive statistics for the 47 dams, 280 female offspring, and 271 male offspring are reported in Table 1. Consistent with other reports (e.g., Ruthven, 1908; Fitch, 1949), the number of scale rows along the dorsal midbody was virtually invariant (two of 543 offspring had 17 and 20 rather than 19 scale rows). Loreals were also invariant and preoculars almost so (two of 544 offspring had four rather than two preoculars). These three characters were excluded from all subsequent analyses.

Coefficients of variation were lowest for ventrals and subcaudals and considerably greater for the two composite body scale traits, UMBPOS and UMBSIZ (Table 2). Relative variation for the head scales ranged from a low of 3.8% for supralabials to 20.0% for temporals (Table 2). The relative variability of characters was essentially unchanged after computing residuals (Table 2). Adults were either less variable or similar to offspring in variability, after accounting for sex differences.

Results of t-tests and Mann-Whitney U tests indicated that all of the body scale traits and three of four head scales differed significantly between the sexes (Tables 1). Sexual dimorphism for ventrals and subcaudals is well known in garter snakes (Fitch, 1949; Arnold, 1988) but is generally not observed for head scales.

Sex-corrected ventrals (subtracting the mean sex differences from the male's score) were slightly kurtotic (coefficient of kurtosis, $g_2 = -0.451$, $t_k = -2.16$, $P < 0.05$) but were not skewed (coefficient of skewness, $g_1 = -0.003$, $t_s = -0.03$, $P > 0.9$), so this trait was not transformed (Tables 1–2). Sex-corrected subcaudals were not appreciably skewed ($g_1 = -0.127$, $t_s = -1.21$, $P > 0.1$) but were kurtotic ($g_2 = -0.608$, $t_k = -2.90$, $P < 0.05$). Residuals (see below) were also approximately normally distributed for both ventrals and subcaudals, although the distributions became somewhat more skewed (Fig. 1). The raw scores for UMBPOS were positively skewed and leptokurtotic but were normalized with a $\log_{10}$-transform, and residuals were approximately normal (Fig. 1). The distribution of UMBSIZ was also positively skewed; the best transform ($\log_{10}$) improved normality, but residuals became noticeably discontinuous (not shown). Among the residual head scale characters, only temporals approximated a normal distribution (Fig. 1).

Among-family variance and attempts to reduce maternal effects.—Prior to calculating residuals from

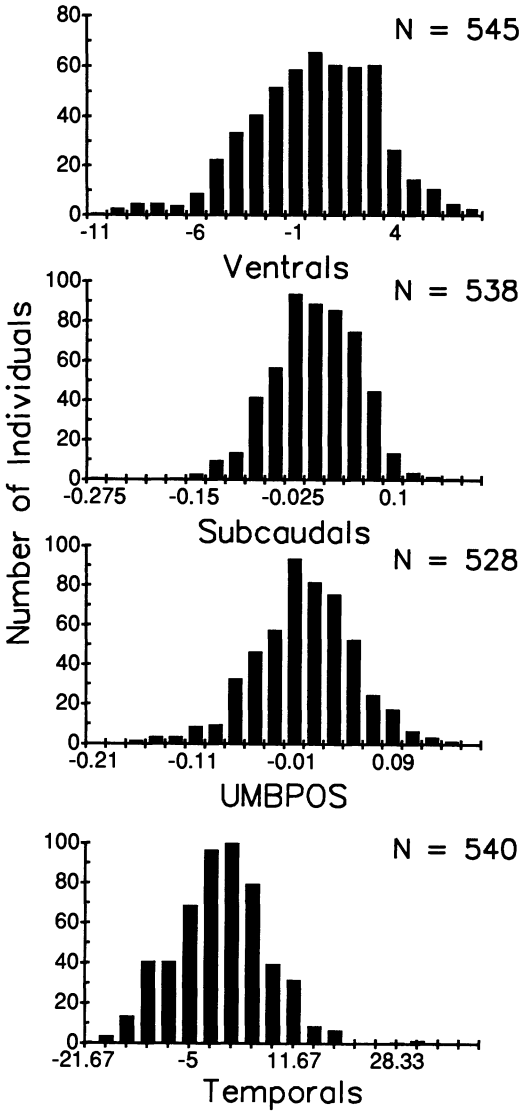

Fig. 1. Distributions of residuals from multiple-regression equations for offspring temporal (range −21.67 to 31.67), UMBPOS (range −0.21 to 0.05), subcaudal (range −0.275 to 0.175), and ventral (range −11.02 to 7.96) scale counts. Independent variables were log(body mass at birth), log(dam's mass), log(dam's snout–vent length), litter size, number of days dams were held in captivity prior to giving birth (DAY), and DAY² [the latter standardized to remove correlation with DAY (see text and Table 5)]. Both raw traits (using best transform) and residuals were used for estimates of quantitative genetic parameters.

TABLE 3. ESTIMATES OF HERITABILITY FOR RAW (BEST TRANSFORM) AND RESIDUAL MERISTIC COUNTS USING AMONG-FAMILY ANOVA OF OFFSPRING VALUES AND OFFSPRING-ON-DAM WEIGHTED REGRESSION (SIMILAR HERITABILITY ESTIMATES WERE OBTAINED FROM THE UNWEIGHTED REGRESSIONS). Approximate standard errors of the ANOVA estimates were calculated from equations in Becker (1984:52).

	ANOVA*	Regression	
Trait	h^2 (SE)	h^2 (SE)	P
Ventrals			
Raw	0.32 (0.086)	0.51 (0.140)	0.0008
Residual	0.26 (0.078)	0.54 (0.140)	0.0015
Subcaudals			
Raw	0.67 (0.115)	0.61 (0.354)	0.1847
Residual	0.56 (0.109)	0.58 (0.324)	0.1164
UMBPOS			
Raw	0.66 (0.114)	0.52 (0.210)	0.0188
Residual	0.59 (0.111)	0.48 (0.162)	0.0019
UMBSIZ			
Raw	0.21 (0.072)	0.01 (0.159)	0.6359
Residual	0.16 (0.065)	0 (0.166)	0.9271
Supralabials			
Raw	0.16 (0.063)	0.14 (0.088)	0.1112
Residual	0.12 (0.059)	0.11 (0.073)	0.1819
Infralabials			
Raw	0.47 (0.100)	0 (0.179)	0.1836
Residual	0.44 (0.098)	0.01 (0.172)	0.2614
Temporals			
Raw	0.76 (0.117)	0.66 (0.251)	0.0037
Residual	0.69 (0.115)	0.64 (0.206)	0.0031
Postoculars			
Raw	0.24 (0.075)	0 (0.143)	0.8941
Residual	0.20 (0.070)	0 (0.139)	0.8874

* P-values for all ANOVA were <0.0001.

the multiple regression equations, we calculated full-sib heritabilities (see Garland, 1994; Brodie and Garland, 1993) for the transformed scale counts (Table 3). Variation among families was highly significant for all meristic traits; however, these components of variance may be inflated by maternal effects, which we attempted to remove by regressing the characters on appropriate covariates and taking residuals. For example, estimates of birth mass heritability are greater than one (not listed in Table 3), which suggests that resemblance for birth mass within families is strongly influenced by maternal effects, in addition to any genetic effects (the among-family component of variance was 73.0%; $P < 0.0001$).

Of the potential covariates (see Materials and Methods), dam SVL and body mass (measured after parturition), offspring birth mass, and litter size were significantly correlated (Table 4), as reported previously (Garland, 1988). Days in captivity were positively correlated with dam's SVL but negatively correlated with dam's mass

TABLE 4. CORRELATIONS AMONG POTENTIAL COVARIATES OF MERISTIC CHARACTERS.

	Dam's mass	Dam's SVL	Litter size	Days in lab
Birth mass	0.565*	0.247*	−0.082	−0.095*
Dam's mass		0.805*	0.420*	−0.125*
Dam's SVL			0.516*	0.179*
Litter size				−0.054

* Pairwise 2-tailed $P < 0.05$.

and offspring mass at birth (Table 4). These negative correlations with body mass probably reflect the fact that many dams refused to eat while in captivity and, hence, lost mass.

Although all meristic trait variation showed some covariation with combinations of the potential maternal covariates, none of the covariates explained more than a few percent of the variation, other than that attributable to sexual dimorphism (Table 5). A small but significant amount of variation in all traits except subcaudals and postoculars was accounted for by the number of days in the laboratory experienced by the dam prior to birth (DAYS or DAYS^2). Offspring body mass at birth accounted for a small portion of the variation in the two derived traits (UMBPOS and UMBSIZ) but was not a significant covariate for any of the other traits. The dam's size (as indicated by either her mass or snout–vent length) had little effect on scale count variation. Interestingly, temporal scale variation was correlated with all of the potential covariates except body mass at birth, although the total explained variation was still small (11% in Table 5).

Heterogeneity of variances among families may partly reflect major gene effects on the phenotype (review in Mitchell-Olds and Rutledge, 1986). With the exception of the subcaudals (Cochran's C = 0.050, $P = 0.340$; Bartlett-Box F = 1.199, $P = 0.170$), UMBPOS (Cochran's C = 0.0619, $P = 0.057$, Bartlett-Box F = 1.175, $P = 0.196$), and infralabials (Cochran's C = 0.0539, $P = 0.167$, Bartlett-Box F = 2.176, $P < 0.001$), most of the residual characters showed significant heterogeneity of variances among families. This was confirmed using Levene's test, an ANOVA of absolute deviations of each individual's score from its family mean (Schultz, 1985; Garland, 1988). Levene's tests indicated significant among-family differences in variability for all eight meristic traits, with the among-family component of variance averaging 20%.

Heritabilities.—Restricted maximum likelihood estimates of additive genetic, nonadditive genetic (plus some possible maternal), and environmental variances are reported in Table 6. Because maximum likelihood provides the best parameter estimates for meristic traits, only results from the maximum likelihood estimates will be discussed here, unless otherwise specified. In most instances, both ANOVA and regression estimates for residuals (Table 3) were similar to maximum likelihood estimates.

Maximum likelihood estimates of narrow-sense heritabilities were moderate to high only for ventral (0.29), subcaudal (0.41), and temporal (0.59) scale counts, with only the last judged significant by likelihood ratio tests (Table 6). Regression estimates were similar for these three traits, but all were significantly different from zero (Table 3). The low heritabilities of the other five traits are not a simple function of low relative variation (see Table 2 and Discussion). All of the ANOVA estimates were significantly different from zero (Table 3).

TABLE 5. RESULTS FROM MULTIPLE REGRESSION ANALYSES OF OFFSPRING SCALE COUNTS ON OFFSPRING MASS AND MATERNAL TRAITS. All meristic counts were transformed prior to analyses (see Table 2). Partial r^2 reported are for sex-corrected residuals (asterisks denote significant sexual dimorphism, see Results). NS indicates no significant covariation ($P > 0.05$).

			Maternal trait								
	Sex	Offspring mass	Mass	SVL	Litter size	Day	Day^2	F	df	Multiple R^2	S.E.E.
Ventrals	*	NS	NS	NS	NS	NS	0.012	6.4	1534	0.01	3.319
Subcaudals	*	NS	NS	0.011	0.040	NS	NS	10.8	2525	0.04	552.530
UMBPOS	*	0.052	NS	NS	NS	0.010	NS	18.3	2525	0.06	0.052
UMBSIZ	*	0.024	NS	NS	NS	0.022	NS	11.2	2525	0.04	0.070
Supralabials	*	NS	0.035	0.024	NS	0.013	NS	6.6	3528	0.04	342.800
Infralabials	*	NS	NS	NS	NS	0.024	0.019	7.3	2529	0.03	22,340.010
Temporals	*	NS	0.013	0.029	0.027	0.013	0.049	13.3	5525	0.11	7.847
Postoculars	NS	NS	NS	NS	0.018	NS	NS	9.7	1530	0.02	2.780

* $P < 0.05$.

Nonadditive genetic variance (confounded by possible maternal effects) accounted for almost all variance in the two derived body traits, UMBPOS and UMBSIZ, and for most of the variance in infralabials (Table 6; zeros have been entered where negative variance components were estimated). The sums of the additive and nonadditive genetic columns in Table 6 set upper limits on broad-sense heritabilities and would equal broad-sense heritability if maternal effects were absent. Thus, the majority of the phenotypic variation appears to be genetic in origin for three of the four body traits and for two of four head scale counts. In contrast, environmental sources accounted for most of the variation in ventrals, supralabials, and postoculars.

Phenotypic, genetic, and environmental correlations.—Eleven of the 28 phenotypic correlations were significant in pairwise tests (Table 7), whereas only 1–2 would be expected to appear significant by chance alone. In general, however, the phenotypic correlations were small. For example, the phenotypic correlation between ventral and subcaudal residuals was only 0.25, and, perhaps surprisingly, the correlations between ventral and UMBPOS residuals, the latter a derived trait expressed by the number of ventrals from the anal plate, was only 0.08. Our estimate of the phenotypic correlation between ventral and subcaudal scales is within the range of values estimated by Arnold (1988) for several populations of *T. elegans*. All phenotypic correlations among the head scales were positive, but none exceeded 0.23.

Principal component analysis of the correlation matrix (not shown) illustrates the weak phenotypic correlation structure: PCI accounts for only 18.7% of the total variance and shows strong loadings only for the four head scales; PCII (15.6% of variance) shows strong loadings for ventrals and subcaudals only; PCIII (13.8% of variance) shows a strong loading for UMBPOS; PCIV (12.4% of variance) shows a strong loading for UMBSIZ. Thus, no PC indicates strong correlations between body or head scales.

Restricted maximum likelihood estimates of additive genetic, nonadditive genetic, and environmental correlations are presented in Table 7. [Regression estimates of additive genetic and environmental correlations were generally quite similar (Table 8).] Five of the additive genetic correlations were quite large in magnitude, and three of 28 were statistically significant by chi-square tests. Not surprisingly, those between ventrals and caudals and between infra- and supralabials were positive and significant. Surprisingly, temporals were positively genetically correlated with ventrals and negatively genetically correlated with both labial scales. Owing to the large number of zero genetic and environmental correlations, both matrices were ill-conditioned for principal component analysis. Significant negative nonadditive genetic correlations existed between subcaudals and four other traits, between UMBPOS and UMBSIZ and between temporals and postoculars. The environmental correlation between infra- and supralabials was significantly negative and, thus, opposite of the genetic correlation. Infralabials and ventrals showed a significant positive environmental correlation, again the opposite of the genetic correlation. In general, phenotypic correlations approximate the average of the additive genetic, nonadditive genetic, and environmental correlations, although covariances are additive, not correlations; exceptions occur where some variance components and, hence, covariances have been constrained to zero (see Table 7).

TABLE 6. RESTRICTED MAXIMUM LIKELIHOOD ESTIMATES OF ADDITIVE GENETIC (V_A), NONADDITIVE GENETIC (V_D), AND ENVIRONMENTAL (V_E) VARIANCES FOR RESIDUAL MERISTIC TRAITS. All values have been scaled as percentages of total phenotypic variance; thus, they sum to one and the first column equals the narrow-sense heritability. If estimates for any variance components were negative, they were constrained to zero and new estimates were obtained (see text). Chi-square is for V_A; critical value at $P < 0.05$ for 1 df is 3.841.

Trait	V_A	V_D	V_E	χ^2
Ventrals	0.29	0	0.71	2.324
Subcaudals	0.41	0.30	0.28	2.655
UMBPOS	0	1.00	0	—
UBMSIZ	0	1.00	0	—
Supralabials	0.12	0	0.87	0.360
Infralabials	0.12	0.68	0.20	0.372
Temporals	0.59*	0.13	0.29	9.872
Postoculars	0	0.41	0.59	—

* $P < 0.05$.

DISCUSSION

Our most general findings are as follows: (1) Only one of eight meristic traits shows significant narrow-sense heritability, although ventral and subcaudal scales probably would have been significant with more families. (2) Nonadditive genetic effects account for essentially all of the phenotypic variance for the two derived body scale traits. (3) Significant additive genetic correlations exist between numbers of

TABLE 7. PHENOTYPIC CORRELATIONS (r_p, PEARSON PRODUCT-MOMENT, BASED ON OFFSPRING ONLY) AND RESTRICTED MAXIMUM LIKELIHOOD ESTIMATES OF ADDITIVE GENETIC (r_a), NONADDITIVE GENETIC (r_d), AND ENVIRONMENTAL (r_e) CORRELATIONS FOR MERISTIC TRAITS, BASED ON RESIDUALS FROM MULTIPLE REGRESSION EQUATIONS (SEE TABLE 5). If estimates for any variance components were negative, they were constrained to zero, along with all covariances for that component, and new estimates were obtained (see text).

		Body scales			Head scales			
		Subcaudals	UMBPOS	UMBSIZ	Supralabials	Infralabials	Temporals	Postoculars
Ventrals	r_p	0.246*	0.082*	0.047	−0.020	−0.051	0.089*	0.018
	r_a	0.670*	0	0	−0.422	−0.594*	0.450	0
	r_d	0	0	0	0	0	0	0
	r_e	0.344	0	0	0.391	0.589*	−0.472	−0.472
Subcaudals	r_p		−0.082	−0.039	−0.040	0.050	0.024	0.005
	r_a		0	0	−0.136	−0.141	0.410	0
	r_d		−0.936*	−0.878*	0	0.260	(−1.464)*	(−1.070)*
	r_e		0	0	0.136	−0.132	0.601*	0.457
UMBPOS	r_p			−0.088*	0.104*	−0.034	0.026	0.022
	r_a			0	0	0	0	0
	r_d			−0.837*	0	0.552	0.130	−0.782*
	r_e			0	0	0	0	0
UMBSIZ	r_p				−0.053	−0.061	−0.043	−0.059
	r_a				0	0	0	0
	r_d				0	−0.986*	0.134	−0.988*
	r_e				0	0	0	0
Supralabials	r_p					0.137*	0.104*	0.090*
	r_a					(1.350)*	0.208	0
	r_d					0	0	0
	r_e					−0.703*	−0.305	0.196
Infralabials	r_p						0.170*	0.168*
	r_a						0.125	0
	r_d						0.093	−0.405
	r_e						0.015	0.582
Temporals	r_p							0.223*
	r_a							0
	r_d							0.902*
	r_e							−0.150

* Two-tailed $P < 0.05$ (unadjusted for multiple tests).

ventral and subcaudal scales, between numbers of supra- and infralabials, and (surprisingly) between some body and head scale counts. Thus, the epidermal scale counts studied herein do not represent eight evolutionarily independent traits. (4) In general, none of the maternal characteristics (e.g., body size, litter size, time in captivity) explained more than a few percent of the variation in scale counts.

Maternal and nongenetic covariation.—Maternal effects may bias quantitative genetic estimates (Falconer, 1989; Lande and Price, 1989). Our knowledge of environmental and maternal effects on meristic counts in reptiles is largely restricted to temperature effects during development. In an extensive study with *T. elegans*, S. J. Arnold and C. R. Peterson (pers. comm.) found no effect of maternal temperature on preocular or postocular scale counts, whereas ventrals, subcaudals, and both supra- and infralabial scales showed a curvilinear response.

Although all meristic trait variation showed some relationship with combinations of the potential maternal covariates in our study, none of the covariates explained more than a few percent of the variation (other than that owing to sexual dimorphism; Table 5). For example, the number of days in the laboratory experienced by the dam prior to giving birth had a small but significant effect on variation in all traits except subcaudals and postoculars; this may be attributable to nutritional condition rather than to temperature effects. Maternal size (mass or SVL), which reflects both maternal age and nutritional status, accounted for a small,

TABLE 8. GENETIC AND ENVIRONMENTAL CORRELATIONS FOR MERISTIC TRAITS, BASED ON RESIDUALS FROM MULTIPLE REGRESSION EQUATIONS. Genetic correlations, calculated from the covariances and cross-covariances obtained from offspring-on-dam regressions, appear on the first lines, standard errors of the genetic correlations [equation 19.4 of Falconer (1989)] are reported on the second lines, and environmental correlations [as calculated from equation 19.1 of Falconer (1989)] appear on the last lines.

	Body scales			Head scales			
	Subcaudals	UMBPOS	UMBSIZ	Supralabials	Infralabials	Temporals	Postoculars
Ventrals	0.635	−0.128	0	0.131	−0.511	0.492	0
	(0.1606)	(0.2057)	—	(0.2883)	(1.103)	(0.1548)	—
	0.468	0.398	0.077	−0.230	0.153	−0.444	−0.021
Subcaudals		0.385	0	0.191	−0.334	0.209	0
		(0.2615)	—	(0.4148)	(1.947)	(0.5054)	—
		−0.305	0.018	0.040	0.066	−0.145	−0.020
UMBPOS			0	0.372	−0.203	−0.102	0
			—	(0.2883)	(1.633)	(0.6998)	—
			−0.086	−0.076	0.052	0.233	0.016
UMBSIZ				0	0	0	0
				—	—	—	—
				−0.066	−0.055	0.006	−0.064
Supralabials					0.714	0.420	0
					(1.171)	(0.2692)	—
					0.011	−0.067	0.086
Infralabials						−0.328	0
						(1.4848)	—
						0.732	0.160
Temporals							0
							—
							0.179

but significant percent of total variation for three of the meristic traits. Similarly, parental age and size affect meristic counts in fish (reviewed by Lindsey, 1988). However, progeny variation in scale counts is not strongly correlated with any of the maternal traits measured in this study (Garland, 1988; Garland and Bennett, 1990; Garland et al., 1990; on physiological traits).

Comparisons of genetic parameters with previous studies.—A major issue in evolutionary biology is the relative constancy of quantitative genetic parameters. Using the standard predictive models of quantitative genetics to extrapolate over more than a small number of generations is useful only if the genetic parameters remain approximately constant. This is true both for univariate predictive models (e.g., Response to Selection = h_n^2 × Selection Differential; Falconer, 1989) and for their multivariate equivalents (e.g., Lande, 1988; Zeng, 1988; Houle, 1991). As stated by Ayers and Arnold (1983): "No one expects genetic variances and covariances to remain unchanged for millennia, but they might evolve so slowly that constancy can be assumed in models for the differentiation of local populations, geographic races and sister species." One way to test this proposition is to compare genetic parameters estimated for different populations or for closely related species (see also Arnold, 1988; Garland, 1994; Brodie and Garland, 1993).

Our results may be compared with those of two published studies; in general, we obtained comparable heritability estimates for the limited number of traits measured. For example, variation in ventrals in a population of water snakes [*Natrix* (*Nerodia*) *sipedon*] was highly heritable (75%), based on analysis of variance of full-sib data (Beatson, 1976). Arnold (1988) reported heritabilities of 65–79% for ventrals and 46–64% for subcaudals for two populations of *T. elegans*, based on offspring-on-dam regressions, and a genetic correlation of 0.28–0.36. We estimated narrow-sense heritabilities of 29% for ventrals and 41% for subcaudals (Table 6) and a genetic correlation of 0.67 (Table 7). No estimates of heritabilities or genetic correlations of reptilian head scale counts have previously been published.

Morphological integration and genetic correlations.—The concept of morphological integration, as proposed by Olson and Miller (1958), provides a useful framework for considering patterns of variation among the meristic traits measured in this study. Morphological integration predicts that functionally or developmentally related characters should be correlated and hence evolve as a unit (Olson and Miller, 1958; Zelditch, 1987, 1988). In turn, functional and developmental interactions should be reflected in patterns of genetic variation and covariation (Cheverud, 1982; Riska, 1989).

Body scale formation in all reptiles studied to date begins in the neck region and proceeds rapidly caudally and ventrally; in snakes, the ventrals and subcaudals appear prior to the formation of the head scales. Based on the timing (as well as the physical proximity) of scale formation during development in garter snakes (Zehr, 1962), we had predicted that there would be little correlation between head scales and body scales. At the phenotypic level, this was largely true; correlations between the two regions of the body were remarkably low (Table 7). Genetic correlations, however, revealed a different pattern; some body and head scale counts did show significant additive genetic correlations, both positive and negative (Table 7).

Several, not mutually exclusive, interpretations are consistent with these findings. First, the relationship between developmental timing (Zehr, 1962) and the pleiotropic effects of genes may be less direct than expected. Charlesworth (1990) and Houle (1991) have noted that unless the genetic correlation between two traits is near ± 1, it may be difficult to infer by examination of the genetic variance–covariance matrix whether all variation is in fact constrained by pleiotropic effects. Second, the apparent genetic integration between head and body meristic traits observed in this population may be temporary and unstable, a consequence of genetic drift or of recently changed selective pressures (Cheverud, 1982, 1984; Atchley, 1987). In fact, Garland et al. (1990) have suggested that this population may not be at genetic equilibrium, because of recent environmental changes and possible consequent changes in selection pressures. Third, our understanding of the developmental processes that lead to the formation of scale counts is only rudimentary (Maderson, 1985). Therefore, our prediction of no genetic correlation between head and body meristic counts, based on a simple model of developmental timing (e.g., Zelditch, 1987, 1988), may have been misleading. Similarly, Garland (1988) found that, whereas a consideration of muscle physiology and comparative data suggests a trade-off between capacities for locomotor speed and stamina, the genetic correlation between these two traits is actually positive in these garter snakes (see also Tsuji et al., 1989; Garland, in press).

Are genetic and environmental correlations correlated?—Because genetic and environmental effects act through the same biochemical and developmental pathways, one might expect patterns of genetic and environmental correlations to be similar (Cheverud, 1984). Previous empirical studies, however, report both positive and negative relationships (Hegman and DeFries, 1970; Cheverud, 1982, 1984). In our study, the relationship between additive genetic and environmental correlations was moderately negative but insignificant (Fig. 2).

Figure 2 also indicates a generally positive relationship between the additive genetic and phenotypic correlations. The genetic correlations tended to be greater in magnitude (when estimable) than the phenotypic correlations, indicating tighter morphological integration at the genetic level. The "effective sample size" (Cheverud, 1988) in the present study was approximately 14 families [the product of the number of families ($n = 44$) and geometric mean heritability (approximately 0.32 using the ANOVA estimates; simple average of the REML estimates yields 0.23)]. Cheverud's (1988) survey of 41 empirical studies indicates that differences between phenotypic and genetic correlations are most evident when the effective sample size is of this magnitude. Cheverud concluded that genetic and phenotypic correlations were often similar, provided the genetic estimates were from large studies. Cheverud's conclusions have been criticized on statistical grounds and because of the types of traits represented (Willis et al., 1991). On the other hand, the maximum likelihood estimates used herein should be more precise than the traditional methods used in the studies considered by Cheverud (1988), and their generally close similarity to those from offspring-on-parent regressions (Tables 7–8), increases our confidence in them. Thus, phenotypic correlations may in fact be poor predictors of genetic correlations for scale counts in these garter snakes [see Brodie and Garland (in press) for other comparisons with snakes].

Quantitative genetic parameters and character weighting.—As noted by Neff (1986), character weighting is "... an unavoidable part of systematics in one or more of its guises." Character

weighting may be defined as a judgment implying that one character is a better indicator of phylogeny than another (Neff, 1986; Mayr and Ashlock, 1991). Although a number of character weighting approaches have been proposed, all currently used methods are based solely on phenotypic variation, with the assumption that this variation is genetically based (Archie, 1985). Recently, however, several authors have suggested that estimates of heritability and genetic correlation could be used directly to weight characters for use in phylogeny reconstruction (Atchley, 1983; Schaffer, 1986; Felsenstein, 1988; H. B. Shaffer and R. N. Fisher, pers. comm.).

With respect to single traits, most systematists would tend to assign low weight to traits with low heritability and high weight to traits with high heritability, on the assumption that the latter better reflect phylogenetic relationship (Underhill, 1969; Atchley, 1983; Shaffer, 1986; H. B. Shaffer and R. N. Fisher, pers. comm.). Additionally, traits with high heritability might appropriately be assigned high weight if they are presumed to be of little selective importance (Falconer, 1989; Garland et al., 1990). On the other hand, Felsenstein (1988) has suggested that it may be more appropriate to assign lower weights to traits with high heritability, because this indicates the direction on the fitness surface along which selection or drift could lead to the most rapid evolutionary changes, including adaptation and convergent evolution. These arguments involve assumptions about the action of selection on morphological traits. Systematists may prefer to "avoid" such assumptions (Kirsch, 1982; Felsenstein, 1988), but it is clear that traits differ in heritability. In our study, heritabilities range from zero to almost 0.6. Ignoring such information is equivalent to assuming that all traits are equally heritable or that the genetic basis of traits does not matter.

With respect to multiple traits, Schluter (1984) suggested that the additive genetic variance–covariance matrix could be incorporated into measures of Euclidean distance among populations, to account both for the correlations between traits and for the traits' susceptibility to change under directional selection. Shaffer (1986) proposed a qualitative approach using genetic correlations to help identify independent characters prior to phylogenetic reconstruction. This is important, because lack of independence among characters may inflate the confidence one has in a constructed tree (see discussion in Shaffer, 1986). Similarly, Eldredge (1979) suggested that functionally or developmentally integrated complexes might be considered and analyzed as a single character rather than as many attributes of what is actually one "composite" trait (Riska, 1989).

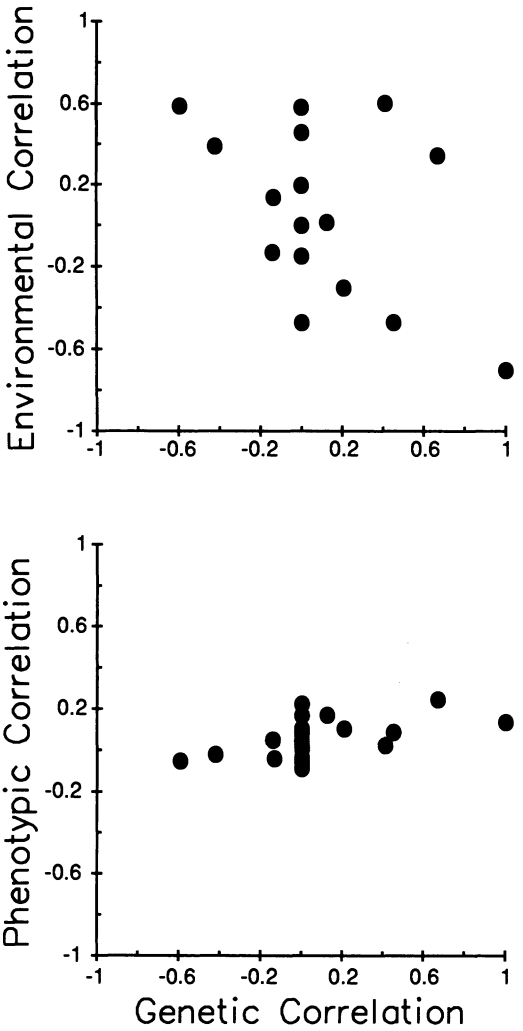

Fig. 2. Scatterplots of the bivariate distributions of phenotypic and genetic correlations (r = 0.47, two-tailed $P = 0.011$) and environmental and genetic correlations (r = −0.34, two-tailed $P = 0.078$). All correlations (n = 28) are from Table 7.

More recently, Lynch (1989) has proposed that the between-species variance be used as a "generalized distance measure" to construct phylogenetic trees under a neutral model of evolution. The measure could be weighted by the inverse of the within-population genetic variance. Lynch's proposal is similar to Schluter's in that both assign low weight to characters with high heritability. However, the difference is in the choice of an evolutionary model; Schluter's approach assumes that selection accounts for the mean divergence between two species,

whereas Lynch's model assumes that genetic drift accounts for the divergence between species (Lynch, 1989). In some cases, it may be possible to predict a priori which traits are more likely to have been subject to relative strong selection (e.g., organismal performance traits; Arnold, 1983; Garland et al., 1990; Garland and Losos, 1994).

Such approaches to character weighting would require knowledge of the additive genetic variance–covariance matrices for all taxa included in the study—an exceedingly unlikely situation. Nevertheless, even studies of genetic correlations in single species (Table 7) can suggest that some traits would provide largely redundant information for phylogenetic reconstruction, and a principal component analysis of a genetic variance–covariance matrix might be useful for identifying a smaller subset of independent characters.

Acknowledgments

We thank S. J. Arnold, M. R. Dentine, J. P. Hailman, and J. F. Kitchell for their comments on the manuscript and S. J. Arnold for helping to collect snakes and allowing use of his study sites. Partial financial support was provided by the University of Wisconsin Graduate School and by N.S.F. grants BSR-9006083 and BSR-9157268 to TG.

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