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Changes in the components of phenotypic variance and covariance among traits during ontogeny in the sharp-snouted rock lizard (*Lacerta oxycephala*)

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Abstract. We estimated changes in the components of phenotypic variance and covariance among seven metric traits over the first 90 days of growth in the sharp-snouted rock lizard (*Lacerta oxycephala*). The broad-sense heritability estimated from the data representing mostly size components of the seven morphometic traits over four age periods was about 90%. The average broad-sense heritability for the shape components of the same traits and age periods amounted to about 42%. By using bivariate and multivariate statistical methods, ontogenetic allometry coefficients have been estimated. The average heritability estimated for the bivariate allometric coefficients was about 69%. Genetic correlation structures were highly integrated within each age period and this integration increased from newborn lizards to lizards aged up to 90 days. For absolute measurements, phenotypic correlation structures were less integrated than genetic correlation structures, while for size-free measurements the opposite trend was observed.

Introduction

Analyses of morphometric size and shape variations have been very popular in recent years among evolutionary biologists (e.g. Gould, 1977; Albrech et al., 1979; Albrech, 1982; Bookstein et al., 1985; Shea, 1985). This wide interest has been a primary consequence of the fact that size or shape are significantly modifiable within a single pattern of development, which can be a root of more than one adaptive design. Unfortunately, these studies have relied almost entirely on phenotypic analysis and few data exist as to the underlying genetic bases of morphometric size and shape variations. Knowledge of heritabilities of the traits, the patterns of genetic covariation among traits and changes in the components of phenotypic variation and covariation among traits during ontogeny are essential for complete evolutionary analyses of morphometric size and shape variations. It is this approach that we have adopted in the present paper, which relates to the sharp-snouted rock lizard (*Lacerta oxycephala*).

Lizards have very often been employed in tests of various hypotheses concerning the mechanisms of adaptation and speciation at the morphometic level (e.g. Schoener, 1967, 1969; Soulé, 1972; Rougharden, 1974). However, information on the extent of quantitative genetic variation of these traits is almost completely absent for natural populations of lizards. Assessment of the source of variation for polygenetically controlled metric traits in lizard populations is very difficult, due to problems associated with obtaining samples for which the genetic relationships between the individuals are known. Another problem is that quantitative genetic theory assumes that environmental deviations are independent, random, normal deviates. This implies that experiments must be carried out under controlled conditions. However, there has been disquiet about application of this methodology since there is a danger that inferences about genetic variation in the natural habitat may not be valid. Nevertheless, measuring genetic variation using quantitative genetic techniques in samples from wild populations grown in common environments can provide valuable information about the variation present in natural populations.

In this study we provide estimates of the components of phenotypic variance and covariance among seven metric traits by using a full-sib analyses of newborn lizards of the species *Lacerta oxycephala*. In addition, we have also attempted to detect the changes in these components over first 90 days of growth under laboratory conditions.

Material and methods

The lizards used in this study were the first generation descendants of gravid females captured at the island of Beška on Skadar Lake (Monte Negro). Among about one hundred females captured at the end of the reproductive season (May, 1991), we found 55 females which still carried eggs. These females were housed in separate cages in the laboratory. The cages were checked for eggs daily. After deposition, eggs were placed individually in plastic cups with moist vermiculite. These cups were kept in an incubator at 30 ± 1°C. We collected 197 eggs from 55 females (i.e. 3.58 per female).

The duration of development from deposition of eggs to emergence of young lizards was measured. Hatching success was only 28.93% under our laboratory conditions (i.e. from 197 deposited eggs we obtained only 57 newborn lizards). These newborns were placed singly in plastic cages with vermiculite and a small cup filled with water, and kept for the next three months (from early June to September) in a greenhouse. The lizards were fed every day with *Drosophila melanogaster*. Once a week vitamin D was added to the water offered to the lizards.

Seven body measurements were taken on each live lizard four times, at one day, 30 days, 60 days and 90 days after birth. Mass (W) was measured in grams, and six external morphometric traits were recorded to the nearest 0.01 mm on each individual using calipers. These were: L, total length; L_C, head length, from the tip of the snout to the posterior edge of the tympanic membrane; L_CD, tail length; L_TC, head width, the greatest width of the head behind the eyes; P_A, forelimb length; P_P, hindlimb length (limbs were measured on the right side). All measurements were always taken by the

same individual (I.A.) and repeatability of the measurements was checked sporadically throughout the study. Although there was only a slight sex difference among traits, all results are based on sex-corrected data. Cube roots of body weight were taken to render weight dimensionally equivalent to all other variables. All data were logarithmically transformed before any statistical analysis.

We assumed that the newborn lizards were of full-sibs (Arnold, 1981; Garland, 1988). Our heritability (h^2) estimates were based on analysis of variance within and among 16 sets of full sibs. The average number of progeny per family was 3.56. The most frequently occurring number of progeny per family (mode) was 3, and the number of progeny over families varied from 2 to 6.

Heritability estimates were based on full sib analyses and therefore include 1/2 of the additive genetic variance, 1/4 of the dominance and various amounts of the epistatic variance (Becker, 1984). In addition, these "broad sense" heritabilities (Falconer, 1981) are inflated by "maternal effects". It is important to note that the morphometric traits which we have analyzed here are related to hatchling size and that the maternal effects could heavily inflate our heritability estimates. Hatchling size in lizards is directly proportional to egg size, and later depends on the total amount of energy which a female invests in her clutch and/or on the pattern of allocation of reproductive investment into either many small eggs or few larger eggs. Bauwens (pers. comm.) has suggested that this counfounding factor could be removed by treating morphometric traits as relative measurements instead as absolute dimensions. He suggested that heritabilities could be estimated by taking regression residuals from the static allometric relations with some estimate of body size (here we have used regression of all traits except for head width against total length; we have regressed head width against head length). Following this suggestion we have estimated broad sense heritabilities on the two different sets of data: absolute and relative (based on the regression residuals) traits.

A genetic correlation (r_G) is defined as the genetic covariance between two traits standardized by the genetic variances:

$$r_G = \frac{cov_{G(xy)}}{[(var_{G(x)})*(var_{G(y)})]^{1/2}}$$

where $cov_{G(x}y_{)}$ is the genetic (full-sib) covariance of the traits X and Y, and $var_{G(x)}$ and $var_{G(y)}$ are the genetic (full-sib) variances of the traits. For unbalanced data set, unfortunately, standard errors of r_G are unknown (Sokal and Rohlf, 1981) and significance testing of this correlation from unbalanced data is not possible. According to Via (1984) a simple approximation to the genetic (full-sib) correlation can be made using the correlation of family means:

$$r_m = \frac{cov_{m(XY)}}{[(var_{m(X)})*(var_{m(Y)})]^{1/2}}$$

This is a Pearson product-moment correlation which contains, however, not only the variance and covariance among families but also a fraction of within-family error

variance as a contaminant. This correlation may underestimate the absolute value of the genetic correlation for the same breeding design. although, as pointed out by Via (1984), it is expected to converge to the true value as the number of individuals measured per family increases. The advantage of the family mean correlation is that it can be tested for significance even when the number of individuals per family varies. Since we have an unbalanced data set, both family mean correlations (r_m) and correlations constructed from the estimated genetic components of variance and covariance for analyzed traits were estimated. Phenotypic correlations (r_p) were also estimated.

Correlation pattern similarity was measured by a matrix correlation with Mantels test for statistical significance using NTSYS-pc (Rohlf, 1990). Matrix correlations reported here are Pearson product-moment correlations between the elements of different correlation matrices between different age periods, or between them within each age period. The significance test consists of repeatedly randomizing (1000 random permutations) the rows and columns of one matrix and correlating the randomized matrix with the unaltered target matrix. The matrix correlations obtained through this procedure are used to generate a distribution of matrix correlations based on the null hypothesis of no structural similarity among compared correlation matrices. The observed matrix correlation is then compared to this distribution, and the percentage of cases as extreme or more extreme than the observed one gives the probability of the observed correlation under a model of no similarity.

To get more information about genetic and phenotypic heterogeneity of different ontogenetic stages, multivariate principal component analyses (PCA) were performed separately for each age period. A series PCAs was carried out on the phenotypic correlation (r_p) and genetic correlation (r_m) matrices using SAS (proc. princomp). In order to estimate the heritability of the PCs (Cheverud, 1981), component scores obtained from phenotypic correlations were used.

The overall level of integration in the phenotypic and genetic correlation matrices within each age period could be measured using the index of integration (I; Cheverud et al., 1983). This index is defined as:

$$I = 1 - (\prod_{i=1}^{n} \lambda_i)^{1/n}$$

where λ_i is the ith eigenvalue and n is the number of analyzed traits. This index generally could take on values between O (no integration; i.e. very low or zero correlation) and 1 (perfect integration or all correlation coefficients equal one).

Since we have longitudinal or ontogenetic data, it is possible to estimate the ontogenetic allometry coefficients for analyzed sets of traits. Bivariate allometric analysis is generally made by using the simple allometric equation: $Y = aX^k$, or in logarithmic terms: $\log Y = k \log X + \log a$, where Y is the value for a trait, X is the value for another trait, log a is the Y-intercept and k is an allometric coefficient. The allometric coefficient is the ratio of specific growth rates for analyzed traits Y and X. Since Y is

conventionally taken as the size of the part, and X as the size of the whole, total animal length (acronym L) was chosen as the most appropriate independent variable. A regression analysis was carried out on each lizard for the six pairs of variables (i.e. L on W, L on L_C, etc.). Using these allometric coefficients we estimated the heritability of the ontogenetic allometry (Atchley and Rutledge, 1980).

To circumvent the limitation to two dimensions of the bivariate allometric equation, Jolicoeur (1963) proposes computing the principal components of the covariance matrix based upon the logarithmically transformed variables. The coefficient for each trait on the first eigenvector is then a multivariate allometry coefficient relative to a multivariate size vector (as pointed out by Mosimann, 1970, the Jolicoeur procedure implicitly chooses the geometric mean of all measurements as a size variable). The growth of traits is isometric, or in constant proportion with increasing in size, if the first eigenvector equals the reciprocal of the square root of the number of variables.

Results

The extent of the differences in the seven trait means over the 90 day period in the sharp-snouted rock lizard is shown in table 1. The broad sense heritabilities, estimated both from the absolute (h^2_1) and relative (h^2_2) measurements in each age period are also listed in this table. Estimations of heritabilities in different periods of the growing lizard are complicated because the means and variances of most morphological traits in increased with age. Not scaling the data for increasing body size when estimating variance components could have a strong effect on the magnitude of heritability estimates depending on the average size of the organisms (Atchley, 1984). The general method to remove such scale effects is logarithmic transformation of the data. Thus, log-transformation was applied to all data before heritability analyses.

As can be seen in table 1, broad-sense heritabilities (i.e. the upper limits of the true heritability of the traits) estimated from the absolute dimensions (h^2_1) are for all traits in each age period higher than those calculated from the regression residuals (h^2_2). In addition, most h^2_2 estimates are in the low range. The only significant h^2_2 value are observed for weight (but only in the 60 day old lizards), head width (first two age periods) and forelimb length (newborn lizards). Note also that seven out of the 24 h^2_2 estimates have negative signs, indicating the absence of any heritable variation. Thus, since the use of regression residuals has the advantage of removing the effect of body size (i.e. we have analysed some estimates of the shape variations), it is obvious that heritable variations for the shape dimensions in the lizards aged up to 3 months are very low. On the other hand, 18 out of 28 h^2_1 estimates (representing, mostly, genetic components of the size variations) are statistically significant (table 1). The only consistently low and insignificant h^2_1 estimates are observed for forelimb and hindlimb length. Note also that h^2_1 values for W, L and L_CD traits show a marked increase from the first to the 90th day of emergence. Similar trend could be seen when the average heritabilities of all seven traits are plotted against the four age periods (average heritabilities are calculated as:

$$h^2 = [\ \Sigma(h^2_i/S.E.^2_i)/\Sigma(S.E.^2_i)] \pm [1/\Sigma(1/S.E.^2_i)].$$

Table 1. Means ($\bar{X}\pm$ standard errors) and broad sense heritabilities (± standard errors) based on absolute (h^2_1) and relative (h^2_2) measurements over four age periods. Negative h^2 estimates are indicated by -0.00.

Traits	Age (in days)				Average h^2_1 ± S.E.
	1	30	60	90	
Total length (L)					
$\bar{x}$ ± S.E.	70.1897 ± 0.93	76.0345 ± 0.89	81.0600 ± 1.05	85.0000 ± 1.21	
h^2_1 ± S.E.	1.0777[b] ± 0.29	1.1148[b] ± 0.28	1.8959[c] ± 0.15	1.1233[b] ± 0.35	1.5594 ± 0.11
Weight (W)					
$\bar{x}$ ± S.E.	0.4589 ± 0.01	0.4510 ± 0.01	0.5728 ± 0.01	0.6679 ± 0.02	
h^2_1 ± S.E.	0.7723[a] ± 0.33	0.7203[a] ± 0.33	1.1557[b] ± 0.30	1.2701[a] ± 0.47	0.9498 ± 0.17
h^2_2 ± S.E.	0.3189 ± 0.34	0.5817 ± 0.34	0.8715[a] ± 0.35	0.2133 ± 0.39	0.5089 ± 0.03
Head length (L_C)					
$\bar{x}$ ± S.E.	7.5116 ± 0.07	8.2298 ± 0.04	8.3540 ± 0.05	8.3966 ± 0.06	
h^2_1 ± S.E.	0.5885 ± 0.34	0.7897[a] ± 0.33	0.7819[a] ± 0.34	1.0884[b] ± 0.33	0.8159 ± 0.17
h^2_2 ± S.E.	-0.00	0.1344 ± 0.32	-0.00	-0.00	0.1344 ± 0.32
Tail length (L_{CD})					
$\bar{x}$ ± S.E.	41.8966 ± 0.82	46.6035 ± 0.84	51.200 ± 0.90	53.977 ± 1.06	
h^2_1 ± S.E.	0.889[a] ± 0.31	1.1807[b] ± 0.29	1.1245[b] ± 0.32	1.0251 ± 0.15	1.0251 ± 0.15
h^2_2 ± S.E.	0.5137 ± 0.34	0.2426 ± 0.33	-0.00	0.1195 ± 0.39	0.3055 ± 0.04
Head width (L_{TC})					
$\bar{x}$ ± S.E.	2.7426 ± 0.02	2.7574 ± 0.02	2.9648 ± 0.02	2.9714 ± 0.02	
h^2_1 ± S.E.	0.7229[a] ± 0.33	1.0885[b] ± 0.28	0.4472 ± 0.37	0.3527 ± 0.41	0.7356 ± 0.17
h^2_2 ± S.E.	0.6520[a] ± 0.33	1.1092[c] ± 0.28	0.5996 ± 0.37	-0.00	0.8383 ± 0.03
Forelimb length (P_A)					
$\bar{x}$ ± S.E.	2.8441 ± 0.04	3.1447 ± 0.03	3.1656 ± 0.03	3.3452 ± 0.04	
h^2_1 ± S.E.	0.7259[a] ± 0.33	0.6939 ± 0.33	0.2653 ± 0.36	0.6215 ± 0.39	0.5871 ± 0.18
h^2_2 ± S.E.	0.6489[a] ± 0.34	0.3546 ± 0.34	-0.00	0.3114 ± 0.40	0.4512 ± 0.04
Hindlimb length (P_p)					
$\bar{x}$ ± S.E.	3.7543 ± 0.05	4.1035 ± 0.03	4.3210 ± 0.04	4.4522 ± 0.05	
h^2_1 ± S.E.	0.5033 ± 0.39	0.5404 ± 0.34	0.3641 ± 0.37	0.7818 ± 0.38	0.5452 ± 0.18
h^2_2 ± S.E.	0.3804 ± 0.34	0.1035 ± 0.31	-0.00	0.3574 ± 0.41	0.2596 ± 0.03
Average					
h^2_1 ± S.E.	0.7816 ± 0.12	0.8689 ± 0.12	1.2789 ± 0.10	0.9297 ± 0.14	
h^2_2 ± S.E.	0.5046 ± 0.02	0.4522 ± 0.02	0.7431 ± 0.07	0.2469 ± 0.04	

a-P<0.05, b-P<0.01, c-P<0.001

Such a trend, however, is not evident for the heritable variations of the shape dimensions (i.e. for the h^2_2 estimates; table 1). The grand mean over the all traits and the age periods suggested that about 41.6% of the shape variation in external morphology of young *L. oxycephala* is heritable. The corresponding grand mean for the h^2_1 estimates amounted to about 88.8%.

The results of the bivariate and multivariate allometric analyses are given in table 2. The regression estimates of allometry coefficients (k) range from 0.43 (for head width) to 1.33 (for tail length). Four traits (W, L_C, L_{TC} and P_A) exhibit statistically significant negative allometry, whereas tail length (L_{CD}) shows positive allometry. The multivariate allometric vectors (k'), estimated on the pooled data of the all four age periods, are also presented in table 2. Eigenvector loadings (i.e. allometric vector) are significantly

Table 2. Bivariate (k ± standard errors) and multivariate (k') allometric coefficients. Heritability estimates and their standard (h^2_k ± S.E.) for the bivariate allometric coefficients are also included.

Traits	k ± S.E.	k'	h^2_k ± S.E.
Total length (L)	-	0.4778	-
Weight (W)	0.6870^c ± 0.04	0.2005	0.8747^a ± 0.38
Head length (L_C)	0.6073^c ± 0.05	0.1680	0.0736 ± 0.39
Tail length (L_{CD})	1.3248^c ± 0.05	0.7324	1.1325^b ± 0.33
Head width (L_{TC})	0.4301^c ± 0.11	0.1423	0.1826 ± 0.41
Forelimb length (P_A)	0.8075^b ± 0.07	0.2802	0.8231 ± 0.41
Hindlimb length (P_P)	1.0378 ± 0.09	0.2609	1.0292^a ± 0.35

a-P<0.05, b-P<0.01, c-P<0.001

different from isometry (X^2 = 17.82; P<0.01). To measure relationships between eigenvector loadings (k') and bivariate allometric coefficients (k), Spearman's rank correlation was calculated. There was a significant rank correlation between allometric loadings for each trait on total length and eigenvector loading for PC1 (r_S = 0.94; P<0.05), which thus described variation in size among morphometric traits that was related to allometric growth.

Table 2 also shows heritability estimates (± their standard errors) for the bivariate allometric coefficients. As can be seen from this Table, three out of six broad-sense heritability estimates were significant (for W, L_{CD} and P_P).

The estimated phenotypic and genetic correlations among all analysed traits within each age period are presented in tables 3 and 4. The phenotypic correlations, calculated from the absolute dimensions, are generally moderate and show almost a stepwise increase from one day old to 90 day old lizards (table 3). However, the shift in the magnitude of the r_p must be interpreted carefully because it could be attributed to changes in the relative magnitude of the measurement errors. Measurement of morphometric traits in live lizards is a difficult task, especially in the newborn. Hence it is possible that the absolute amount of the error decreases as a lizard grows and, therefore, that r_p increases with lizard size. Interestingly, although the pairwise phenotypic correlations are highest in the 90 day old lizards, the trend mentioned above is not obvious in table 4. As can be seen in table 4, removing the effects of body size significantly changes the r_p pattern. Here, we have 26 out of the 60 r_p values (about 43.3%) which are significantly different from zero (in table 3 about 86% r_p values are significant). Moreover, eight of the significant phenotypic correlations are with negative signs (in table 3 we did not observe any significant r_p with negative sign).

The magnitudes of the estimated genetic correlations within each age period are generally higher than the phenotypic correlations and this is more pronounced in table 3 than in table 4. Again, we can see an increase in the magnitude of the genetic correlations with age. Generally, the correlations obtained usign family means (r_m) are lower than those constructed from estimated genetic components (r_G; we did not calculate r_G coefficients from the regression residuals because of the abundant negative genetic variance among traits). Out of the 60 r_m coefficients calculated from relative

Table 3. Phenotypic (r_P) and genetic (r_G and r_m) correlation coefficients within different age periods.

- -	Age (in days)											
	1			30			60			90		
Traits	r_P	r_G	r_m	r_P	r_G	r_m	r_P	r_G	r_m	r_P	r_G	r_m
W-												
L	0.77[c]	1.36	0.83[c]	0.55[c]	0.93	0.60[a]	0.72[c]	0.79	0.82[c]	0.55[c]	0.68	0.55[a]
L_C	0.51[c]	0.69	0.47	0.59[c]	0.77	0.66[b]	0.54[c]	0.67	0.65[b]	0.83[c]	0.95	0.83[c]
L_{CD}	0.65[c]	0.93	0.76[c]	0.49[c]	0.82	0.56[a]	0.64[c]	0.79	0.80[c]	0.51[c]	0.61	0.51[a]
L_{TC}	0.57[c]	0.89	0.55[a]	0.37[b]	0.94	0.49	0.46[b]	0.62	0.52[a]	0.57[c]	0.67	0.57[a]
P_A	0.64[c]	0.93	0.64[b]	0.38[b]	0.75	0.46	0.51[c]	1.03	0.68[b]	0.67[c]	0.90	0.67[b]
P_P	0.15	0.49	0.22	0.31[a]	1.98	0.69[b]	0.58[c]	1.11	0.81[c]	0.69[c]	0.89	0.69[b]
L-												
L_C	0.42[b]	0.53	0.41	0.67[c]	0.92	0.83[c]	0.57[c]	1.16	0.89[c]	0.64[c]	1.04	0.87[c]
L_{CD}	0.95[c]	1.00	0.98[c]	0.98[c]	1.00	0.99[c]	0.99[c]	1.01	0.99[c]	0.92[c]	1.02	0.98[c]
L_{TC}	0.52[c]	0.59	0.51[a]	0.11	0.33	0.17	0.24	0.41	0.32	0.60[c]	1.19	0.79[c]
P_A	0.59[c]	0.65	0.62[a]	0.51[c]	0.81	0.68[b]	0.52[c]	1.53	0.86[c]	0.67[c]	0.84	0.75[c]
P_P	0.20	0.62	0.41	0.46[b]	0.97	0.74[b]	0.49[c]	1.03	0.86[c]	0.41[b]	0.85	0.69[b]
L_C-												
L_{CD}	0.35[a]	0.72	0.46	0.64[c]	1.01	0.83[c]	0.49[c]	1.24	0.89[c]	0.59[c]	1.24	0.90[c]
L_{TC}	0.41[b]	0.19	0.24	-0.03	0.31	0.15	0.45[b]	0.23	0.36	0.66[c]	0.23	0.84[c]
P_A	0.38[b]	0.33	0.27	0.48[c]	0.81	0.68[b]	0.64[c]	1.08	0.83[c]	0.70[c]	1.07	0.81[c]
P_P	0.11	0.27	-0.09	0.35[a]	0.87	0.66[a]	0.62[c]	0.77	0.73[b]	0.74[c]	0.77	0.83[c]
L_{CD}-												
L_{TC}	0.45[b]	0.72	0.54[a]	0.05	0.22	0.10	0.17	0.46	0.30	0.56[c]	0.46	0.79[c]
P_A	0.51[c]	0.56	0.56[a]	0.46[b]	0.82	0.66[b]	0.44[b]	1.65	0.85[c]	0.61[c]	1.65	0.78[c]
P_P	0.06	0.63	0.33	0.37[a]	0.91	0.67[b]	0.41[b]	1.56	0.86[c]	0.44[b]	1.56	0.78[c]
L_{TC}-												
P_A	0.62[c]	0.98	0.70[b]	0.16	0.47	0.17	0.38[b]	-0.40	0.23	0.73[c]	-0.10	0.77[c]
P_P	0.21	0.05	0.08	0.15	0.52	0.21	0.38[b]	0.21	0.35	0.58[c]	0.21	0.77[c]
P_A-												
P_P	0.42[b]	0.75	0.55[a]	0.55[c]	0.72	0.67[b]	0.71[b]	0.72	0.72[b]	0.66[c]	0.72	0.73[b]
Mean	0.45	0.64	0.48	0.41	0.81	0.56	0.52	0.84	0.68	0.63	0.83	0.76
I	0.55		0.69	0.56		0.74	0.66		0.85	0.60		0.79

a-P<0.05, b-P<0.01, c-P<0.001

dimensions (table 4) only six (or about 10%) are significant (two of them are negative), while in the table 3 we can see 62 significant r_m coefficients out of the 84 coefficients (or about 74%). Considering statistical significance of these later r_m coefficients (table 3) we can observe (out of 21 pairwise combinations within each age period) the following number of significant genetic correlations: 11(or 52.4%), 14 (66.7%), 16 (76.2%) and 21 (100%) within respective age periods starting from one day old to 90 day old lizards. However, these changes in r_m coefficients could be simply a by-product of the increase in the heritabilities of the individual traits.

At the bottom of tables 3 and 4 the indexes of integration (I) are given. These indexes, measuring the overall correlation level of the correlation matrices within each age period, have only been calculated for r_p and r_m matrices (because the r_G matrices in several cases contain correlations greater than one, the index is indeterminate due to negative eigenvalue). The general impression from table 3 is that the genetic correlation

Table 4. Phenotypic (r_p) and genetic (r_G and r_m) correlation coefficients based on relative measurements.

	Age (in days)							
	1		30		60		90	
Traits	r_P	r_m	r_P	r_m	r_P	r_m	r_P	r_m
W-								
L_C	-0.44[b]	-0.42	-0.29[a]	-0.39	-0.58[c]	-0.69[b]	-0.00[c]	0.48
L_{CD}	0.33[a]	0.27	0.36[a]	0.32	0.23	-0.28	0.74[c]	0.64[a]
L_{TC}	0.15	0.09	0.39[b]	0.46	0.36[a]	0.55[a]	-0.11	0.28
P_A	0.37[a]	0.30	0.14	0.08	0.23	-0.07	0.49[b]	0.49
P_P	-0.01	-0.27	0.08	0.42	0.38[a]	0.33	0.61[c]	0.50
L_C-								
L_{CD}	-0.17	0.31	-0.11	-0.09	-0.53[c]	-0.03	0.04	0.59[a]
L_{TC}	-0.09	0.05	-0.28	0.54[a]	-0.31	-0.39	-0.01	-0.21
P_A	-0.19	-0.28	-0.27	0.18	-0.53[c]	-0.15	-0.02	0.26
P_P	-0.46[b]	-0.42	-0.46[b]	0.71[b]	-0.53[c]	-0.28	0.18	0.71[b]
L_{CD}-								
L_{TC}	-0.18	-0.42	-0.12	0.07	0.01	-0.12	-0.20	-0.10
P_A	0.18	0.04	0.21	0.29	0.49[b]	0.35	0.48[b]	0.42
P_P	0.03	-0.32	0.05	0.17	0.48[b]	0.03	0.68[c]	0.67[a]
L_{TC}-								
P_A	0.35[a]	0.41	013	0.11	0.13	-0.19	0.26	0.11
P_P	0.10	0.04	0.11	0.16	0.14	0.12	0.03	0.15
P_A-								
P_P	0.38[b]	0.35	0.42[b]	0.36	0.61[c]	0.01	0.57[c]	0.41
Mean	0.02	-0.02	0.02	0.05	0.04	-0.05	0.25	0.36
I	0.82	0.69	0.84	0.70	0.72	0.77	0.69	0.62

a-P<0.05, b-P<0.01, c-P<0.001

Table 5. Matrix correlations between phenotypic (r_P) and genetic (r_m) correlation matrices of different age periods. Comparisons between r_p and r_m within each age period are also included. Correlation matrices were obtained from absolute (1) as well as relative (2) data. Mantel's test was used for statistical significance.

Compared age periods	Matrices					
	r_P		r_m		r_P-r_m	
	1	2	1	2	1	2
1-					0.7155[b]	0.7871[b]
30	0.3707	0.8873[b]	0.1443	0.4410[a]		
60	0.3703	0.7991[a]	0.1706	0.1977		
90	0.4017[a]	0.5599	0.2581	-0.0429		
30-					0.4792[a]	0.9876[b]
60	0.7939[c]	0.8696[b]	0.9523[b]	0.7369[b]		
90	0.3261	0.5101	0.3044	0.1241		
60-					0.2887	0.6554[a]
90	0.4766[a]	0.6238	0.1988	0.0558		
90-					-0.0952	0.5996

a-P<0.05, b-P<0.01, c-P<0.001

Table 6. PC vectors for r_P and r_m matrices. EIG are eigenvalues while %V is the percent of the total variance explained by each PC Heritabilities (h^2) of each PC and their standard errors are also given.

	PC1		PC2		PC3	
Traits	r_P	r_m	r_P	r_m	r_P	r_m
Age: 1 day						
W	0.44	0.44	-0.12	-0.15	0.06	0.04
L	0.46	0.46	-0.22	0.00	-0.33	0.26
L_C	0.31	0.25	-0.05	-0.58	0.78	0.31
L_{CD}	0.42	0.45	0.35	-0.09	-0.39	0.23
L_{TC}	0.37	0.35	0.13	-0.06	0.27	-0.74
P_A	0.41	0.40	0.32	0.28	-0.03	-0.33
P_P	0.16	0.21	0.83	0.73	-0.23	0.34
EIG	3.90	4.10	1.09	1.19	0.78	0.80
%V	55.76	58.29	15.54	17.03	11.17	11.39
h^2	0.98[b]		0.44		0.94[a]	
S.E.	0.30		0.34		0.39	
Age: 30 days						
W	0.38	0.36	0.31	0.40	-0.37	-0.21
L	0.48	0.44	-0.18	-0.18	-0.16	-0.27
L_C	0.42	0.42	0.23	-0.13	-0.18	-0.21
L_{CD}	0.45	0.43	-0.25	-0.24	-0.22	-0.33
L_{TC}	0.11	0.14	0.86	0.84	-0.18	0.02
P_A	0.37	0.37	0.09	-0.12	0.51	0.79
P_P	0.32	0.40	0.14	0.02	0.68	0.32
EIG	3.69	4.56	1.15	1.13	0.89	0.46
%V	52.68	65.13	16.39	16.11	12.67	6.60
h^2	1.11[a]		0.84[a]		0.04	
S.E.	0.28		0.32		0.31	
Age: 60 days						
W	0.41	0.38	-0.07	0.24	0.31	-0.51
L	0.42	0.43	-0.46	0.13	0.09	-0.02
l_C	0.39	0.39	0.21	-0.12	-0.15	0.55
L_{CD}	0.39	0.42	-0.54	0.16	0.09	0.01
L_{TC}	0.26	0.19	0.55	0.91	0.71	0.29
P_A	0.38	0.38	0.26	-0.25	-0.45	0.32
P_P	0.38	0.39	0.29	-0.01	0.40	-0.50
EIG	4.19	5.26	1.13	0.93	0.70	0.39
%V	59.85	75.11	16.11	13.26	9.98	5.57
h^2	1.34[c]		0.70		0.19	
S.E.	0.25		0.37		0.36	
Age: 90 days						
W	0.38	0.38	0.32	0.12	-0.41	-0.37
L	0.38	0.38	0.54	-0.61	-0.14	0.08
L_C	0.41	0.39	-0.22	-0.02	-0.29	0.13
L_{CD}	0.36	0.39	0.56	-0.45	-0.20	0.23
L_{TC}	0.37	0.38	-0.02	0.24	0.73	-0.16
P_A	0.40	0.36	-0.05	0.23	0.37	-0.57
P_P	0.35	0.36	-0.48	0.56	-0.06	0.66
EIG	4.81	5.85	0.92	0.37	0.48	0.29
%V	68.75	83.49	13.17	5.33	6.85	4.17
h^2	1.32[c]		0.66		0.99[a]	
S.E.	0.27		0.40		0.35	

aP<0.05, bP<0.01, cP<0.001

structure is more integrated than the phenotypic correlation structure (the average I over four age periods is 0.76 *vs.* 0.59, respectively). Interestingly enough, it seems that the opposite is true for the relative measurements (table 4); the average I over four age periods are 0.69 (for the r_m coefficients) and 0.77 (for the r_p coefficients).

Matrix correlations among the phenotypic (r_p) and genetic (r_m) age-specific matrices are given in table 5. As shown by Mantels test, three out of the six comparisons in the both type of the age-specific phenotypic correlation matrices (i.e. calculated from absolute as well as regression residuals data) are significant. The average value of the matrix correlations among r_p coefficients obtained from the regression residuals is higher (0.71) than that obtained from the absolute measurements (0.46). The general impression from table 5 is that matrix correlations among the phenotypic age-specific correlation matrices are higher than those calculated for r_m matrices. Table 5 also contains matrix correlations between r_p and r_m matrices within each age period. It is noteworthy that these matrix correlations decreased markedly from one day to 90 day old lizards. The first two (for the absolute data) and three (for the regression residuals) matrix correlations are statistically significant, indicating moderate to high level of homogeneity between phenotypic and genetic correlation matrices.

Table 6 shows first three PCs extracted from r_p and r_m correlation matrices obtained from absolute dimensions. The first three components sum to average just over 84% and 90% of the total phenotypic and genetic variance, respectively, and we restrict our attention to these. The first eigenvalue represents 55.8% (for r_p matrices) and 58.3% (r_m matrices) of total variances in the one-day old lizards. At 30 days it drops to 52.7% for the r_p matrices but increases to 65.1% for the r_m matrices. At 90 days, the first eigenvalues extracted from r_p and r_m matrices increases to 68.8% and 83.5%, respectively (table 6). The loadings of the first PCs (for both r_p and r_m matrices) are strikingly similar from age period to age period. The first PC vector of the phenotypic correlation matrix has positive coefficients for all variables, and all coefficients are relatively large except that for hindlimb length (in one day old lizards) and head width (in 30 day old lizards). This vector could be interpreted as "size" vector. The first vector, respresenting overall body size, is most strongly inherited in young *L. oxycephala* lizards. The estimate of the broad-sense heritabilities for this vector varies from 0.98 (in one day old lizards) to 1.34 (at age 60 days). The first PC vectors of the genetic correlations have large unidirectional coefficients on all traits and over all age periods (table 6). This eigenvector can be interpreted as "genetic size" function (Atchley et al., 1981).

The second PCs of the r_p and r_m matrices can be interpreted as the generall phenotypic and genetic "shape" variable. The second eigenvalues of both types of matrices and at all age periods are consistently about 3 to 5 times smaller than the first, but subsequent components (from the third to the seventh) dwindle by much smaller increments. As can be seen in table 6, the second and third principal components exhibit little resemblance in eigenvectors over analysed age period. The broad sense heritabilities for all age periods for the third PC amounted to about 0.54, the estimated values of h^2 varied very broadly: from 0.04 in the 60 day old lizards to 0.99 in the 90 day old lizards (table 6).

Discussion

As in the few previous quantitative genetic studies with reptiles (e.g. Arnold, 1981; Arnold and Benett, 1988; Garland, 1988; Tsuji et al., 1989), the newborn sharp-snouted rock lizard (*L. oxycephala*) used in the present study are presumed to represent sets of full sibs. A limitation of full sibs analyses for estimating heritabilities is that they can yield only broad-sense heritabilities. Although our measures probably overestimate heritabilities, the results presented here indicate that natural populations of *L. oxycephala* may contain a considerable genetic variation for external morphometric traits. It should be kept in mind, however, that our results were obtained on a relatively small sample size (16 full sib families). Notwithstanding, since heritability estimates for any trait in *L. oxycephala* are entirely absent (which is true for almost all lizard species), our estimates are likely to be of broad interest for herpetologists.

According to animal breeding studies (Arnold, 1987; Mousseau and Roff, 1988), linear dimensions of vertebrates typically show heritabilities of 70% or higher. In *L. oxycephala*, external morphology (including body weight) appears to roughly confirm this generalization; the average broad-sense heritability based on the absolute data of the all seven traits and all age periods amounted to about 90% (table 1). However, the effect of the size-free data has been a decrease of the heritable variation in the external morphology of young lizards. The average broad-sense heritability from the shape variation is about 42%. Also, estimates of ontogenetic allometry relationships between total length and the six other traits are highly heritable for L*W, L*L_{CD} and L*P_P bivariate growth allometry (table 2). These results indicate that some traits at specific age periods or bivariate growth relationships should respond more rapidly to natural selection than others or at the other developmental stages. For example, both the total length and the weight should respond rapidly to selection at all analysed age periods by virtue of the high estimates of genetic variance for these traits (assuming, of course, that a portion of the genetic variance is additive), while the fore- and hindlimb length should respond slowly at all analysed age periods (table 1). The older age periods of the young lizards (i.e. 60 and 90 days old individuals) have generally higher estimates of heritability than the younger age periods. In addition, we might conclude, using the arguments from Fisher's Fundamental Theorem (Fisher, 1930; see also Falconer, 1981) that traits analysed here are loosely connected with fitness. Fisher's theorem concerning the nature of genetic variation within natural populations predicts that traits closely associated with fitness will have low heritabilities, since selection should consume any additive genetic variance for such traits. The most extensive compilation of data in support of this view was that recently presented by Mousseau and Roff (1988). However, this review as well as more complicated selection models (see e.g. Charlesworth, 1980, and Bulmer, 1980) indicate that inferences of a trait's selective value based on heritability estimates may not accurately reflect its contribution to the fitness of an organism. In addition, it is possible (although not likely) that our high heritability estimates are entirely the result of epistatic or maternal effects, since these are not distinguished by our design. It would therefore be highly desirable to know to what extent these values

overestimate true narrow-sense heritabilities. Unfortunately, no comparisons are presently available for lizards, and few exist for any natural populations of vertebrates.

It is well known (see e.g. Atchley, 1984) that variation in one trait during ontogeny and evolution produces parallel covariability in other traits and that the magnitude of this covariability is a function of the magnitude of the genetic correlation and the respective heritabilities. Although genetic correlations between seven analysed traits vary considerably within each age period (this is especially evident for the size-free variables; table 4), genetic correlation structures were, nevertheless, highly integrated within each age period and this integration increased from the newborn lizards to the lizards aged up to 90 days (again, this is less evident in table 4). For the absolute measurements the phenotypic correlation structures were less integrated than genetic correlation structures (table 3). However, when size-free measurements were used, the trend was the opposite. Studies with rhesus macaques (Cheverud, 1982), rats (Cheverud et al., 1983) and rats and mice (Kohn and Atchley, 1988) have shown that genetic correlation structures are better integrated than phenotypic correlation structures. Although these studies did not analyse size and shape variation separately (they used measurements which were labeled "absolute"), it could be that the size components of the morphological traits are more tightly integrated in the genotype than is indicated by phenotypic integration alone. Mantel's test shows somewhat higher congruence of the phenotypic correlations among different age periods than do genetic correlations (table 5). Interestingly enough, the phenotypic and genetic correlation matrices were significantly similar only within the younger developmental stages, indicating that phenotypic correlations could be a reliable guide to genetic correlations only for the younger animals. High congruence between phenotypic and genetic correlation matrices was found by Bailey (1956) and Kohn and Atchley (1988) but this was in contrast to the finding of Cheverud (1982).

Although we have estimated broad-sense genetic correlations (i.e. inflated by non-additive genetic variances and maternal effects), these correlations among morphometric traits reflect, until now to the unknown extent, associations arising from pleiotropy and linkage of the genes. Since the extent of genetic correlation due to linkage of genes is approximately inversely related to the number of linkage groups (*L. oxycephala* have a large number of linkage groups; 2n=38; Gorman et al., 1970) we can assume that pleiotropy of the genes is the main contributor to the genetic correlation patterns described in the present study.

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