

# Morphometric studies in inbred and hybrid house mice. Heterosis, homeostasis and heritability of size and shape

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One size (SIZE) and four shape measures (SHAPE 1–SHAPE 4) were derived from a multiple group principal components analysis of 15 osteometric variables in inbred and hybrid house mice. In both sexes, SIZE and two of the four SHAPE variables showed positive heterosis, the other two SHAPE variables exhibiting negative heterosis. SIZE showed a greater magnitude of heterosis (average of about 2.3 standard deviations) than all SHAPE characters except SHAPE 2, a skull length/width contrast. Inbreds were more variable than hybrids (positive homeostasis) for all characters, and there was a significant, positive correlation between heterosis and homeostasis in these characters. The reciprocals category in hybrids was more important for SIZE than for the SHAPE variables, presumably because maternal effects have a greater influence on growth characters. Broad-sense heritabilities for SIZE were 0.8 in inbreds and 0.6 in hybrids whereas they averaged only 0.4 for the SHAPE variables. It was postulated that there is a greater number of loci governing SIZE compared to SHAPE, and that this explains both the heritability and heterosis differences between these characters.

**KEY WORDS:**—Morphometrics – inbreds and hybrids – heterosis – homeostasis – heritability – multiple group principal components analysis.

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## INTRODUCTION

The partitioning of size and shape in morphometric characters in various organisms has been done in a variety of biological studies (Jolicoeur &

Mosimann, 1960; Gould, 1966; Thorpe, 1976; Humphries *et al.*, 1981). Taxonomists often adjust for size, for example, in order to reduce or eliminate age differences among samples which would otherwise obscure their proper discrimination. Shape characters often have been considered more useful than size as taxonomic indicators, and some have suggested this is because they are more heritable (Gould, 1966; Corruccini, 1975). In other cases, size and shape are separated so that they may be studied for their own sake (Johnston & Selander, 1971; Fleischer & Johnston, 1982). It also should be mentioned that a good part of the field of allometry, including its diverse applications, really has to do with size-related shape variation (Gould, 1966).

Given this considerable interest in size and shape, it is not surprising that a variety of methods has been suggested for their separation. Ratios are one such way of forming 'size-free' shape measures (Simpson, Roe & Lewontin, 1960), but have statistical (Atchley, Gaskins & Anderson, 1976) and interpretive (Gould, 1966) problems which detract from their usefulness. Regression may be used to partial out the effect of a given size covariate, but size is not always accurately represented by any single measure (Humphries *et al.*, 1981; Thorpe & Leamy, 1983). In recent years, principal components analysis has been widely used in size/shape analyses, primarily because the first component in many cases may be regarded as a 'size' vector, and the remaining ones, 'shape' vectors (Jolicœur & Mosimann, 1960). Related techniques for constructing size and shape variables recently have been proposed (Mosimann & James, 1979; Humphries *et al.*, 1981; Cherry *et al.*, 1982), including multiple group principal components analysis, (Thorpe 1983 and references therein), so the issue remains an active one.

In spite of the widespread interest in constructing and using size and shape variables, surprisingly little is known about the genetic properties of these variables. That is, what is the heritability of size and shape in a given population, and do they significantly differ? Some recent studies (Atchley *et al.*, 1981; Atchley, 1983), for example, have suggested that size is more heritable than shape, and for researchers in a variety of fields, it is important to know if this is generally true. The study reported in this paper was designed to provide estimates of heritabilities for size and shape, and also to characterize their differences, if any, with regard to properties such as heterosis and homeostasis. Inbred and hybrid lines of house mice are used as in previous studies in this series (Leamy, 1982a,b; Thorpe & Leamy, 1983), and size and shape measures are derived from a multiple group principal component analysis of 15 osteometric variables.

#### MATERIALS AND METHODS

The inbred and hybrid house mice used in this study were obtained from crossing three isogenic inbred lines—C3HeB/FeHb (H), C57BL/6Hb (C), and AKR/Hb (A). A total of 252 mice (69 inbred males, 70 hybrid males, 56 inbred females, and 57 hybrid females) were so produced, all being 150 days of age. Fifteen osteometric characters (previously described in Leamy, 1982a) were used here, these including four skull lengths, three skull widths, four girdle measures, and four limb lengths. Further details regarding the experimental design may be found in Leamy (1982a).

The precise multiple group principal components procedure for defining size and shape with these osteometric characters previously has been described in detail (Thorpe & Leamy, 1983), but may be summarized for convenience as follows. After adjustment first for the effects of two covariates, all 15 characters were logarithmically-transformed and covariance matrices were calculated for each of the inbred and hybrid male and female groups. A single within-groups covariance matrix then was calculated by pooling over all (18) groups, and this matrix was subjected to principal components analysis. Scores for all 15 components were calculated for each individual mouse, those for the first component representing a 'size' character, those for the remaining 14 components representing 'shape' characters.

Only the first five vectors were chosen for use in this study, for they collectively describe fully 87% of the total variation (Thorpe & Leamy, 1983). The remaining vectors (6–15) contributed less than 3% each, although are occasionally mentioned as appropriate in the discussion below. The first vector (hereafter designated SIZE) is a classical size vector which had moderate to high, positive loadings on all characters except interorbital width. The second vector (SHAPE 1) loaded most heavily on obturator foramen length, the third (SHAPE 2) contrasted a skull length and width, the fourth (SHAPE 3) was a skull width factor, and the fifth (SHAPE 4) primarily emphasized mandible length (Thorpe & Leamy, 1983).

Model I analyses of variance were conducted for the SIZE and SHAPE characters over all inbreds and hybrids to provide tests of significance for sex, heterosis, differences among the inbred lines, crosses, reciprocals within crosses, the interactions of sex with each of these and differences between litters. The basic design is precisely the same as that previously used for the raw osteometric variables themselves (Leamy, 1982a) except that the two covariates used originally (litter size and days) are not part of the analysis here because of the initial adjustment of their effects. This analysis therefore has two additional degrees of freedom not present in the previous analysis (Leamy, 1982a), and since values for the two covariates were identical within litters, the increase in degrees of freedom occurs in the between-litter (rather than within-litter) category. Further details regarding this experimental design are given in Leamy (1982a).

Model II nested analyses of variance also were used as before (Leamy, 1982b) to estimate variance components for the SIZE and SHAPE characters in the separate breeding types. Thus, within ( $\sigma_w^2$ ) and between-litter variances ( $\sigma_b^2$ ) were calculated in both inbreds and hybrids, the sum of these representing the total environmental contribution. The genetic contribution to each character was assessed by the 'strains' variance ( $\sigma_s^2$ ), this being equivalent to differences among lines (2 degrees of freedom) in inbreds, and differences among crosses and reciprocals (5 degrees of freedom) in hybrids (Leamy, 1982b). The strains variance in both inbreds and hybrids estimates both additive and non-additive genetic contributions, and when expressed as a proportion of the total variance, is a measure of broad-sense heritability (Falconer, 1981). The genetic variance among inbreds, but not hybrids, actually is expected to be twice that found in a hypothetical population from which the inbreds have been derived (Falconer, 1981). In any event, all three variances ( $\sigma_s^2$ ,  $\sigma_b^2$ ,  $\sigma_w^2$ ) were estimated over both sexes in each breeding type, the effects of sex (one degree of freedom) and the

sex by strains interaction (2 or 5 degrees of freedom) being taken out in the linear model.

## RESULTS

Before presentation of the results of the analyses of variance, the means and (pooled, within-group) variances of the SIZE and SHAPE variables in inbreds and hybrids of each sex are given in Table 1 for general inspection. Standardized measures of heterosis also are provided in the Table, these being calculated as the difference between the inbred and hybrid means divided by the square root of the between-litter mean square (Table 2) in each case. In both sexes, SIZE, SHAPE 2 and SHAPE 4 are larger in hybrids than in inbreds (positive heterosis), and the amount of heterosis is greatest for SHAPE 2 in males and SIZE in females. SHAPE 1 and SHAPE 3 actually show negative heterosis, although its magnitude is relatively low for both characters within each sex, and in fact does not even reach significance for SHAPE 3 (see Table 2 below). Inbreds are more variable than hybrids in all 10 instances, those differences for SHAPE 2 and SHAPE 4 in both sexes being especially pronounced. Nine of these comparisons also reach statistical significance, and

Table 1. Means ( $\bar{X}$ ) and variances ( $s^2$ ) of the SIZE and SHAPE characters in inbreds (I) and hybrids (H) of each sex. Variances are X 1000, and heterosis is expressed as the standardized differences between the inbred and hybrid means. \* =  $P < 0.05$ , \*\* =  $P < 0.01$  in  $F$  tests of significance of the variances

	Males						Females					
	$\bar{X}$		Heterosis	$s^2$		Heterosis	$\bar{X}$		Heterosis	$s^2$		
	I	H		I	H		I	H		I	H	
SIZE	9.090	9.197	1.86	2.23**	1.00	9.097	9.251	2.67	3.32**	1.56		
SHAPE 1	1.577	1.567	-0.51	0.30**	0.15	1.464	1.447	-0.87	0.31	0.26		
SHAPE 2	0.338	0.382	2.50	0.32**	0.09	0.325	0.362	2.10	0.32**	0.08		
SHAPE 3	1.578	1.577	-0.06	0.19**	0.10	1.557	1.547	-0.65	0.20**	0.08		
SHAPE 4	1.044	1.050	0.53	0.16**	0.05	1.052	1.059	0.61	0.12**	0.04		

Table 2. The complete analysis of variance for the size and shape characters. Mean squares are multiplied by 1000. \* =  $P < 0.05$ , \*\* =  $P < 0.01$

Source	d.f.	Mean squares				
		SIZE	SHAPE 1	SHAPE 2	SHAPE 3	SHAPE 4
Sex	1	153.26**	662.26**	14.40**	32.18**	4.96**
Heterosis	1	1190.04**	8.29**	98.35**	0.35	2.78**
Inbreds	2	536.09**	10.38**	0.64	26.64**	4.02**
Crosses	2	31.16**	5.03**	4.14**	3.67**	3.14**
Reciprocals	3	53.91**	0.28	1.15**	0.29	0.59**
Sex X heterosis	1	27.50**	0.27	0.59	0.70	0.04
Sex X inbreds	2	48.22*	2.36**	0.51	1.31**	0.72**
Sex X crosses	2	2.29	0.11	0.00	0.03	0.62**
Sex X reciprocals	3	2.89	0.17	0.16	0.27	0.10
Between litters	84	3.32**	0.38**	0.31**	0.24**	0.13**
Within litters	150	1.35	0.20	0.18	0.10	0.08

this is strong evidence for the presence of homeostasis in the SIZE and SHAPE variables.

The results of the complete analysis of variance for each of the five characters over both sexes and breeding types are given in Table 2. The between-litter mean squares are significant in all cases, and therefore are used as the most appropriate error terms for all tests of significance (Leamy, 1982a). Sex is a statistically significant factor for all five characters, especially for SHAPE 1, the obturator foramen shape component. The mean squares for heterosis reflect the standardized heterosis measures of Table 1—that for SHAPE 3 does not reach significance, and those for SIZE and SHAPE 2 are especially high. Differences among inbreds are significant for all characters except SHAPE 2, as are crosses for all characters, and reciprocals for SIZE, SHAPE 2, and SHAPE 4. The sex by inbreds interaction is significant for all characters except SHAPE 2, and only SHAPE 4 shows a significant effect for the remaining two sex interactions. In general, SIZE differs from the SHAPE variables in showing more heterosis, larger inbred and reciprocal, but smaller crosses differences, and greater sex by heterosis and sex by inbred interactions.

The percentage contribution of the within-litter ( $\sigma_w^2$ ), between-litter ( $\sigma_b^2$ ), and strains ( $\sigma_s^2$ ) components to the total variance in the five SIZE/SHAPE variables in inbreds and hybrids is given in Table 3. As may be seen for the inbreds, the genetical strains component (heritability) is quite high (81%), and exceeds the estimates for all four SHAPE variables. Only the  $\sigma_s^2$  estimate for SHAPE 3 approaches this level, for the average for the four shape variables is only 42%. The environmental within- and between-litter components for the shape characters in inbreds (average of 44% and 14%, respectively) also are therefore lower than those for SIZE, especially the  $\sigma_w^2$  value for SHAPE 2. The genetic and environmental components for hybrids generally show the same sort of trend as do the inbreds, except that  $\sigma_s^2$  for SHAPE 4 is slightly greater than the comparable value for SIZE. Thus the (broad-sense) heritability of the shape characters varies, but is generally lower than that for the SIZE variable.

Table 3. The percentage contribution of variances within litters ( $\sigma_w^2$ ), between litters ( $\sigma_b^2$ ) and among strains ( $\sigma_s^2$ ) to the total variance for the SIZE and SHAPE characters in inbreds and hybrids. The strains contribution is a measure of the broad-sense heritability, and the sum of the within and between litter components represents the total environmental contribution

	Inbreds			Hybrids		
	$\sigma_w^2$	$\sigma_b^2$	$\sigma_s^2$	$\sigma_w^2$	$\sigma_b^2$	$\sigma_s^2$
SIZE	13.1	6.1	80.8	21.3	18.4	60.3
SHAPE 1	42.5	19.8	37.7	53.8	11.9	34.3
SHAPE 2	82.8	15.8	1.4	54.1	15.3	30.6
SHAPE 3	15.4	7.9	76.7	42.6	20.0	37.4
SHAPE 4	36.4	10.7	52.9	32.5	5.6	61.9
Mean of SHAPE characters	44.3	13.6	42.1	45.8	13.2	41.1

## DISCUSSION

Although there is a variety of ways in which size and shape characters may be constructed (Gould, 1966; Thorpe, 1976; McMahon, 1973; Humphries *et al.*, 1981), multiple group principal components analysis of logarithmically transformed variables, as previously described, was used in this study. With this method, it should be realized that the loadings of the osteometric characters on the first component (Thorpe & Leamy, 1983) in fact represent multivariate allometric coefficients (Jolicoeur, 1963). As such, this first component reflects both size and any size-related shape variation (Cock, 1966). With reasonable homogeneity of variances among the characters, true isometry would obtain only if all of the 15 coefficients are approximately equal (Jolicoeur, 1963). Actually, application of Anderson's (1963) test clearly shows that they are not and therefore that significant multivariate allometry exists. As previously discussed (Thorpe & Leamy, 1983), however, the amount of allometric shape variation is small compared to the overall size variation captured in this component. It also is distinct from the 'size-free' shape variation depicted in the remaining 14 components (Thorpe & Leamy, 1983). All of these 14 shape components, incidentally, possess both positive and negative loadings as expected, and some (e.g., SHAPE 2) represent rather pronounced osteometric contrasts.

The significant, positive heterosis seen here for overall SIZE (average of 2.3 standard units) previously has been noted (Thorpe & Leamy, 1983), the individual hybrid means for this first component generally being greater than either of their inbred parents (overdominance). Only SHAPE 2 among the SHAPE characters also exhibited overdominance (Thorpe & Leamy, 1982), and its average heterotic effect here was in fact comparable to that for SIZE. This is not simply the result of SHAPE 2's low variance, incidentally, for its relative variability (assessed by the coefficient of variation) is the highest of all characters. Actually, SHAPE 2 contrasts the one character (zygomatic foramen length) which had the greatest individual amount of positive heterosis (about 3 standard units) with the only character (interorbital width) previously showing negative heterosis (Leamy, 1982a), so perhaps this at least partially explains why this combination was able to generate such a large inbred-hybrid difference. In any event, it is apparent that heterozygous loci in the hybrids are producing mice with significantly larger skull lengths, but smaller interorbital foramen widths, compared to their inbred parents. Interestingly, Leamy & Sustarsic (1978) have shown that black-and-tan heterozygotes (*a'a*) in congenic C57BL/6 house mice are smaller than either of their homozygous parents (*aa* and *a'a'*) with respect to interorbital width, but intermediate with respect to skull length.

SHAPE 1 and SHAPE 4 (but not SHAPE 3) also showed statistically significant heterosis (as did 9 of the 10 remaining shape components), although of a magnitude generally much less than that for SIZE (or SHAPE 2). Theoretically, heterosis ( $H$ ) in a given hybrid depends on both the magnitude of difference in gene frequency between the parents ( $y$ ), and on the degree of dominance ( $d$ ) of all relevant loci:  $H = \Sigma dy^2$  (Falconer, 1981). With isogenic parents,  $y$  is the same (1.0) for every locus heterozygous in the hybrid, so presumably heterosis is less for the SHAPE components because those loci which

act differentially on these bone measures either are fewer in number, or generally exhibit less dominance. Although it is not possible to distinguish between these two alternatives with the present data, the consistently positive genetic correlations among these osteometric traits in randombred house mice (Leamy, 1977) argue that the former is more likely. Also, previous studies (Leamy & Hrubant, 1971; Leamy & Sustarsic, 1978; Leamy, 1981b) have shown reasonable consistency in the effects of major genes across assorted morphometric characters, although single gene effects on shape are known (Leamy, 1981b).

The positive homeostasis of the SIZE and SHAPE characters (as well as 9 of the other 10 components) was expected, at least given its occurrence for the individual osteometric characters themselves (Leamy, 1982b). Precisely how the heterozygous loci in hybrids act to reduce the variation in assorted characters simply is not clear (Lerner, 1954; Mather, 1953; Falconer, 1981), but such homeostasis is widespread, especially for those traits showing considerable heterosis (Parsons, 1967; Hyde, 1973). To assess the relationship between heterosis and homeostasis here, Spearman's correlation of the  $F$  values from the variance ratios (Table 1) with the (signed) heterosis values for all 15 components in each sex was calculated. The value of this correlation was  $+0.52$  ( $P < 0.01$ ), which, unlike the case for the individual characters (Leamy, 1982b), indicates a significant, positive association between heterosis and homeostasis. Perhaps many or most heterozygous loci which affect quantitative characters are capable of producing both dominance and reduced variability, and we simply have not always been able to recognize or detect this. It is relevant in this regard that the black-and-tan heterozygotes in C57BL/6 house mice, previously cited as acting differentially on skull length and interorbital width, also were less variable than either homozygous parent (Leamy & Sustarsic, 1978).

The reciprocals category in hybrids largely reflects maternal effects (Leamy, 1982b), and it really is not surprising that these were more important for SIZE than for the SHAPE components. Growth and overall size in mammals long have been known to be sensitive to maternal influences, particularly during the lactation period (Tenczar & Bader, 1966; Leamy, 1974; Atchley & Rutledge, 1980; Falconer, 1981). Further, maternal effects seldom seem to act independently of overall body size (Tenczar & Bader, 1966). Thus Leamy (1981a) found that the average maternal impact for 15 osteometric characters (same as used here) in randombred house mice decreased from 25% to 5% when each was expressed as a ratio over skull length. Such ratios certainly do not eliminate all size and/or allometric variation (Gould, 1966; Leamy, 1981a), but nonetheless suggest that 'shape' may be less subject to maternal influences than is 'size'. Maternally important characters often are more affected by inbreeding depression (Falconer, 1981), and in this regard it is surprising that SIZE showed such a large amount of heterosis.

Beyond the differences between the SIZE and SHAPE variables already described, it was apparent for both inbreds and hybrids that the (broad-sense) heritability was higher for SIZE than for the SHAPE variables. The heritability was about 0.8 and 0.6 for SIZE in inbreds and hybrids, respectively, but averaged only 0.4 for SHAPE in both breeding types. Further, the means of the broad-sense heritabilities for the original osteometric characters themselves (0.71

for inbreds, 0.54 for hybrids) were closer to the values here for SIZE rather than SHAPE (Leamy, 1982a). Probably this implies that the bulk of the genetic variation for any given osteometric character primarily is reflecting size rather than shape differences in this character among individuals in the population.

It is easy to imagine that there is a greater number of loci influencing overall growth in most organisms as compared to specific (bone) shape contrasts, and this may very well account for the differences in heritability levels between the SIZE and SHAPE characters. This same hypothesis already has been invoked to explain the heterosis differences in these characters, as well as the significant, positive correlation found between heritability and heterosis values for the original osteometric variables (Leamy, 1982a). Spearman's correlation of the heritability (from inbreds) and heterosis values here was not significant, but differences among the size and shape characters are greater than are those among the osteometric characters themselves. Bryant & Turner (1978) have put forth the interesting suggestion that shape variables may be more subject to (non-additive) epistatic influences. Unfortunately, epistatic effects could not be assessed with the present design, but differences in their contributions between the SIZE and SHAPE characters, even if present, probably are small in comparison to those generated by additive genetic effects.

Whatever the reason(s) for the higher heritability in SIZE compared with SHAPE characters, this result is consistent with that of several recent studies involving osteometric characters in rats (Atchley, Gaskins & Anderson, 1981; Atchley, 1983; Leamy & Atchley, 1984). In randombred mice, narrow-sense heritabilities of ratios of various bone dimensions over body weight or body length—but not skull length—also were generally lower than the heritabilities of the individual dimensions (Leamy, 1981a). Of course all these laboratory strains are artificially derived and consist of individuals all of the same age, so there is the usual question of how well they serve as models for natural populations. Size most often is partitioned out in natural populations in order to reduce or eliminate age differences (Thorpe, Corti & Capanna, 1982), and the heritability of size in such instances may be low. Nonetheless, the evidence presented here suggests that size often has a significant genetic component, and size/shape partitions should not be done solely under the assumption that the shape characters so produced are more heritable (Gould, 1966, Corruccini, 1975).

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