

Morphometric studies in inbred and hybrid House mice (*Mus* sp.): Multivariate analysis of size and shape

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Multiple group principal component analysis is used to investigate the relationship between morphometric characters in inbred and hybrid House mice. Weight is shown to be largely independent of linear size, and character relationships within inbreds are shown to be the same as those within hybrids. Multiple group principal component analysis is largely successful in defining general size and shape components in the osteometric characters. General size accounts for most of the within-group variation—in spite of the isogenicity, uniform rearing, and uniform age of the mice. Both size and shape are less variable in hybrids than in inbreds. Heterosis is apparent for general size and one component of shape, whilst dominance is widespread amongst the shape components. Canonical analysis is used to investigate inconsistency in the direction of dominance between individual components and the overall direction of dominance.

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Introduction

The separation and characterization of size and shape in linear proportions has long been attempted in fields such as macro and microevolution, taxonomy, palaeontology and anthropology although the reasons for wishing to separate size and shape vary. If one is studying racial variation (Thorpe, 1976; Thorpe, in press) between natural populations of organisms which exhibit continuous growth, e.g. mice, fish and reptiles, there may well be a bias in the growth stage between samples, that is, juveniles in one sample and adults in another. Since one does not wish this bias to distort the pattern of racial affinities, attempts may be made to take out the effect of growth-size, e.g. Thorpe *et al.* (1982). If the extent of growth varies between populations, i.e. some populations tend to have larger specimens, then size

varies both ontogenetically and racially. It can then be impracticable to separate ontogenetic and racial size if one does not know the age of the specimen. In this situation removing size not only removes the ontogenetic component of size, it also removes the racial component of size. However, this loss of information is generally of little importance in the context of assessing the pattern of racial variation.

If, on the other hand, one is dealing with organisms with terminal growth, e.g. birds, the rationale for separating size and shape differs. In this situation one may wish to separate size and shape to study their between-group variation separately. Excellent examples of this are the studies of geographic and temporal variation in House sparrows (Johnston & Selander, 1971; Fleischer & Johnston, 1982 and references therein) which show how natural selection works independently on the size and shape components.

When one is using adult specimens to assess the overall pattern of racial variation in a species with terminal growth there is no general reason to negate size, although one may still wish to characterize size and shape separately in order to investigate their relative contribution to the overall pattern. Some consider shape to be more useful than size as an indicator of relationships with the implication that size is less heritable (Gould, 1966; Corruccini, 1975). Only recently have serious attempts been made to consider this question (Leamy, 1977, 1981; Leamy & Sustarsic, 1978; Atchley & Rutledge, 1980; Atchley *et al.*, 1981; Leamy & Thorpe, in prep.) and it is emerging that size is highly heritable. This supports the inclusion of size in the above situation but does not overcome the need to negate growth-size when studying racial variation in organisms with continuous growth and unknown age (Thorpe, in press); neither does it negate the value of characterizing size and shape separately so that their contribution to the overall racial variation, or their independent variation in response to selective factors, can be investigated (Fleischer & Johnston, 1982).

This study uses inbred laboratory mice reared under standard conditions so the within-group variation is environmental whilst the between-group variation is largely genetic. In this situation the growth variation is minimized, but not negated, by using specimens of the same age. Other factors, such as between-group bias in growth and environmental effects are also minimized by the standardized conditions. Under these circumstances, if size and shape are characterized separately, their contribution to within- and between-group differences can be assessed as can their variability in inbreds and hybrids, and the extent and direction of their dominance.

There are various ways of statistically adjusting for size. Ratios are the simplest method, but they assume both that there is a linear relationship between the variables and that the axis describing this relationship passes through the origin. Since these conditions are seldom met, ratios are not a suitable way of adjusting for size except in very exceptional circumstances. A logarithmic conversion as suggested by Hills (1978) may straighten the regression line, but will not generally meet the second assumption. Regressing a size-dependent character against an "independent" size character such as body length (via an analysis of covariance) also may be used, but logarithmic conversion of both characters may be necessary to ensure a linear relationship. If there are several groups, the pooled within-group slope should be used, since pooling the samples irrespective of groups will result in confusion of within- and between-group differences (Thorpe, 1976). Size is perhaps best treated as a multivariate concept (Humphries *et al.*, 1981), since one measurement cannot encompass the various facets of length, width, etc. This use of multivariate analysis, however, entails some of the same assumptions as bivariate analysis. That is, the character

relationships should be linear (or transformed to become linear), and within-group relationships should not be contaminated by between-group differences and vice versa (Thorpe, in prep.). Hence to define multivariate size the pooled within group covariance or correlation matrix is used (Thorpe, 1981; 105).

Recently a genetical investigation of 18 morphometric traits in inbred and hybrid House mice was initiated, the first paper (Leamy, 1982*a*) in this series presenting tests of significance of various factors (sex, heterosis, lines, etc.) and the second (Leamy, 1982*b*) estimating the relative contributions of genetic and environmental components for the characters. In this paper, a multivariate approach is used in an attempt to characterize size variation in these inbred and hybrid samples. The approach features the use of multiple group principal component analysis (i.e. a principal component analysis of pooled within-group character relationships) in an attempt to define "size" and "shape" vectors, as well as canonical variate analysis to explore group differences.

Materials and methods

Three isogenic inbred strains of House mice were used in this study: C3H/FeHb (H), C57BL/6Hb (C), and AKR/Hb (A). These were crossed in all possible ways to yield three inbred and six hybrid classes.

The hybrids are designated HC, CH, HA, AH, CA and AC, where the first letter indicates the maternal, the second letter the paternal, parent. A total of 252 150-day-old mice were available for use, the sample size in each of the 18 (nine genetic \times two sexes) cells varying from nine to 29. Further details on husbandry and other matters are provided in Leamy (1982*a*).

Eighteen characters were used, 15 osteometric dimensions and two body proportions (expressed in millimetres), as well as body weight (grams). The characters, detailed descriptions of which are given in Leamy (1974), are listed in the order that they appear in the tables: skull length (SKL), palate length (PL), zygomatic fenestral length (ZFL), mandible length (ML), skull width (SKW), zygomatic width (ZW), interorbital width (IOW), innominate length (INL), ilium length (ILL), obturator foramen length (OFL), scapula length (SCL), femur length (FL), tibia length (TIL), humerus length (HL), radioulna length (RUL), tail length (TAL), body length (BL), and weight (W).

Prior to analysis, all variables were adjusted for the effects of two covariables, litter size and days (day of birth of each litter over the litter-bearing period), both of these covariables being used in the original analysis (Leamy, 1982*a*). Multiple group principal components analysis was then conducted to see if it was possible to isolate and define "size" and "shape" components of character variation, the precise procedure being as follows. All characters were logarithmically transformed to make their interrelationships linear. The covariance matrix was computed among the characters for each of the 18 groups, and these were pooled to produce a single within-group covariance matrix. From the matrix, the eigenroots and normalized eigenvectors were extracted using a high accuracy algorithm. Component scores were computed for each of the 252 individuals for every eigenvector. Means of these scores were then calculated for each group, the pooled within-group variance of the component scores simply being the associated eigenroot. Similar, multiple-group principal component analyses were also performed separately for inbreds and hybrids.

Within-group character relationships were interpreted by inspection of the sign and magnitude of the eigenvector coefficients for each character. Eigenvectors expressing a facet of shape have coefficients of different magnitude and/or sign whilst an eigenvector expressing general size should have coefficients of the same sign and "similar" magnitude. This is complicated by the fact that the magnitude of the coefficient for any character in an eigenvector extracted from a covariance matrix (as distinct from a correlation matrix) is a function of the variance of the character. Consequently, when the characters have identical variances, the eigenvector coefficients of a general size vector should be similar; but when the variances differ, this must be taken into account.

In this study, the characters were logarithmically transformed which resulted in the character variances being comparable. Nevertheless, differences in the variances were evident, and so when it was critical to compare the contribution of a character to a component, the effect of the variance was taken into account by computing the pooled within-group correlation between the character and the component score.

This is found as:

$$r_{ij} = \frac{a_{ij} \sqrt{\lambda_j}}{s_i}$$

where the coefficient r_{ij} is the pooled within-group correlation between the i th character and the j th component, a_{ij} is the coefficient for the i th character of the j th (normalized) eigenvector, λ_j is the eigenroot of the j th eigenvector (the pooled within-group variance of the component score), and s_i is the pooled within-group standard deviation of the i th character.

Correlation coefficients can be compared, and their significance tested, by utilizing z transformations. The standard normal deviate value for z is found as:

$$\frac{z}{\sigma_z}$$

where

$$\sigma_z = \frac{1}{k \sum_{i=1} (n_i - 3)} \quad \text{and} \quad z = \frac{1}{2} \log_e \left(\frac{1+r}{1-r} \right)$$

Here r is the correlation coefficient, k is the number of groups, and n_i is the sample size of the i th group. This tests the null hypothesis that there is no correlation between the character and the component score, but a similar test can be utilized to compare correlations (Snedecor & Cochran, 1967).

Group interrelationships were assessed by subjecting the component scores to canonical variate analysis as canonical variate analysis on component scores from a MGPCA gives identical results to using the original data. Size-in analyses used component scores for all eigenvectors whereas size-out analyses excluded the components for the vector expressing general size. Both principal components and canonical analyses are explained in standard texts whilst multiple-group principal components analysis and its relation to other methods is further discussed in Thorpe (in prep. and in press).

Results

Multiple group principal components analyses

Before an analysis over all groups was attempted, it first was decided to test whether character inter-relationships differed between inbreds and hybrids. Multiple group principal components analysis as previously outlined was therefore performed for all (pooled) inbreds, and separately for all (pooled) hybrids. For purposes of comparison, the percentage of the total variation accounted for by each vector in both analyses, as well as the correlations between comparable vectors, are given in Table I. The first three eigenvalues account for approximately 88 and 90% of the total variation, and are highly correlated between inbreds and hybrids. All of the hybrid vectors are significantly correlated with one or more inbred vectors, including even the last one which represents less than half a percent of the total variation. Since 20% of the variation is expressed by 15 vectors, the magnitude of these eigenvectors differs only slightly, with some being close or near coincident.

TABLE I

The eigenvalues of the 18 vectors derived from multiple-group principal components analysis of the morphometric traits in inbreds and hybrids in terms of correspondence of individual vectors, variance contributed by each vector, and correlations

Hybrid vector number	Equivalent inbred vector	Correlation	Variation hybrid eigenvalues (%)	Variation inbred eigenvalues (%)
1	1	1.00*	74.8	75.8
2	2	0.97*	11.7	7.7
3	3	0.94*	3.6	4.8
4	5	0.84*	2.4	2.6
5	6	0.83*	2.0	2.3
6	7	0.69*	1.1	1.4
7	4	0.55	0.9	1.3
8	9	0.73*	0.7	0.8
9	9	0.55	0.6	0.7
(9)	(11)	0.51		
(10)	(13)	(0.54)	0.5	0.6
11	8	0.79*	0.4	0.5
12	12	0.48	0.3	0.4
13	13	0.62	0.2	0.3
14	15	0.76*	0.2	0.2
15	17	0.68	0.2	0.2
16	14	0.84*	0.2	0.1
17	16	0.66	0.1	0.1
18	18	0.85*	0.1	0.1

Brackets indicate that although the correlation is significant one of the vectors is more highly correlated to another vector. The percentage variation for the hybrid and inbred eigenvalues are in order of magnitude. All the correlation coefficients are significant at $P < 0.05$.

*Significant at $P < 0.001$.

Almost all of the eigenvectors have direct single equivalents in the sister analysis, but some (e.g. vector nine in hybrids) are a compromise between two other vectors (e.g. nine and 11 in inbreds). Only vector 10 in the analysis of inbreds has no clear equivalent in the hybrid analysis. Consequently, 17 of the 18 eigenvectors for inbreds are significantly ($P < 0.05$) correlated with vectors from the hybrid analysis, these jointly accounting for fully 99.4% of the total variation. Therefore it is evident that there are no substantial differences between the character inter-relationships in inbreds versus hybrids.

Principal components analysis was therefore performed on the pooled within-group covariance matrix obtained from all 18 groups, the first two vectors from this analysis being plotted in Figure 1. As may be seen, body weight is largely, although not entirely, independent of the remaining linear variables. These coefficients show that only a small element of linear size is positively correlated with body weight. The second vector is largely a linear size vector since all linear measures have the same sign which in this case is contrasted to weight. Consequently, the inclusion of weight results in linear size being partitioned between the first two vectors such that the first is weight-correlated and the second is weight-uncorrelated.

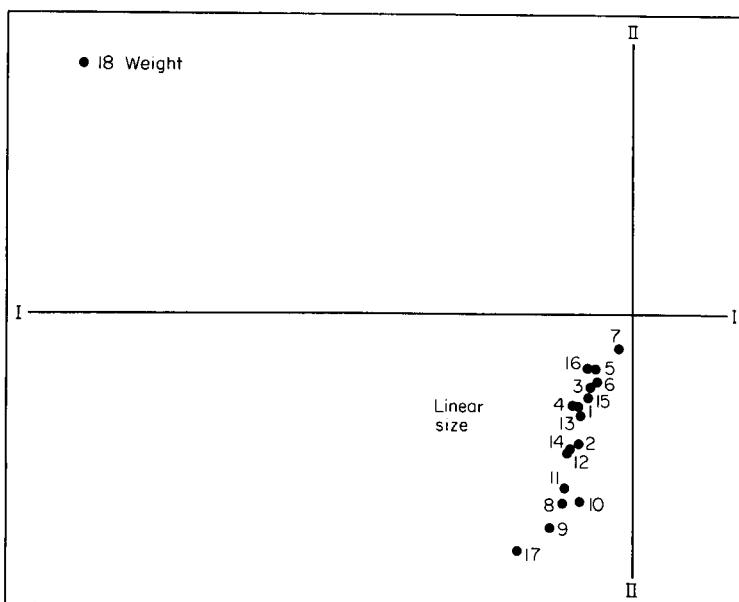


FIG. 1. Scatter of characters along the first two vectors of the pooled within-group covariance matrix between all 18 characters. Note that weight is largely independent of linear size. Character numbers reflect the order of the characters in the "Materials and methods" section.

It was decided to investigate the relationships in the 15 osteometric characters on their own, so that general osteometric size and shape could be more clearly defined. Table II(a) gives the loadings for all 15 vectors from such a principal components analysis, and Table II(b) gives the percentage variation they express as well as their morphological interpretations. The first vector (Table II(a)) is by far the largest (64%) as compared with the next largest (8%). Its coefficients are all of the same sign but they vary slightly in magnitude. The differences in magnitude of these coefficients are not solely due to differences in the variance of the characters. Nevertheless, all the correlations between the characters and the component are high except for inter-orbital width, and even this is significantly correlated with the first component (character seven, $r=0.24$, $P<0.001$). There is no clear shape comparison in the remaining characters for this vector even though the skull features (one to six) have coefficients of 0.57–0.85, these being slightly lower than those for the girdle (0.67–0.94) and limb features (0.83–0.91). Consequently, when viewed in proportion, the differences between the contributions of the characters (except seven) to this component are not great, and the first vector can be considered a general size vector, albeit equivocally.

The remaining 14 vectors are basically "shape" vectors, the sign and magnitude of the coefficients varying within each one. Since there is a minute element of shape in the size vector, it is possible that a minute element of "size" also exists in these 14 vectors, but even if so, it would have a trivial influence. The shape vectors (Table II(a)) do not generally show compact constellations of characters, although examples of several "types" of vectors are found. Vector 2 is basically a single character vector, for although the coefficients for all the pelvic measurements are similar, the magnitude of the coefficient for OFL is distinctly greater than all others. An example of a shape contrast is given by vector 14 in which the

TABLE II(a)
Multiple group PCA of osteometric characters

Pooled within-group correlation between character and first component given in parentheses
Eigenvectors in order of magnitude (coefficients $\times 100$)

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
(1) SKL	(0.85)24	-14	-24	-3	25	5	-10	-5	-13	-15	-9	-7	-84	5	19
(2) PL	(0.81)25	-13	-25	-9	31	29	-3	-5	-66	34	9	11	27	-6	-12
(3) ZFL	(0.57)18	-11	-60	-16	7	-67	23	-5	12	-8	12	-1	18	-1	-3
(4) ML	(0.76)24	-5	-14	-36	-54	32	14	-55	4	-15	-20	-4	4	-5	-3
(5) SKW	(0.63)16	-14	-1	-39	-4	1	-65	38	1	-42	-9	10	20	-3	-2
(6) ZW	(0.67)15	-7	-4	-30	-31	0	-11	30	27	72	16	7	-19	-1	14
(7) IOW	(0.24)7	-11	63	-55	23	-35	18	-16	-19	4	2	-10	-6	4	-1
(8) INL	(0.94)34	13	14	25	-9	-17	-14	-11	-13	0	3	-14	20	-28	75
(9) ILL	(0.92)40	3	17	38	-23	-31	-39	-22	-9	13	4	-8	-9	22	-48
(10) OFL	(0.67)30	89	5	-19	12	5	11	16	2	-4	-8	0	-4	7	-10
(11) SCL	(0.87)34	-22	13	-16	-31	2	50	57	-22	-17	-18	-7	-3	1	-8
(12) FL	(0.91)29	-9	15	12	18	1	10	-12	26	-2	-14	85	1	-8	2
(13) TIL	(0.87)23	-12	4	5	32	12	0	0	38	10	-21	-38	5	-62	-29
(14) HL	(0.90)28	-8	9	1	10	28	11	-1	23	-24	81	-9	4	13	-1
(15) RUL	(0.83)20	-16	-2	3	28	15	2	-2	29	12	-36	-24	25	67	19

TABLE II (b)
Percentage variations of principal component analysis and their morphological interpretations

Vector	Variation (%)	F of scores	Description
1	63.9	75	General size but with less emphasis on character 7
2	8.3	197	Obturator foramen length (10)
3	7.0	35	Skull shape (3 vs 7)
4	4.7	44	Skull widths and mandible length (4-7)
5	3.1	17	Mandible length (4)
6	2.7	61	Zygomatic fenestra length (3)
7	2.4	78	Skull width versus scapula (5 vs 11)
8	2.0	59	Mandible versus scapula (4 vs 11)
9	1.6	64	Palate length (2)
10	1.2	12	Skull shape, particularly zygomatic width (6)
11	0.9	52	Proximal versus distal bones of the front limb (14 vs 15)
12	0.8	91	Proximal versus distal bones of the rear limb (12 vs 13)
13	0.6	48	Skull length (1)
14	0.4	139	Distal bones front limb versus distal bones rear limb (13 vs 15)
15	0.3	29	Pelvis shape (8 vs 9)

The F of scores represents the F statistic derived from analyses of variance, of the component scores for each vector compared among all 18 groups. The numbers in parentheses in the description section are the character numbers (1-15, see "Materials and methods"). Descriptions are approximate and subjective. Note that the F ratio is not correlated to the magnitude of the eigenroot.

distal posterior limb (TIL) is contrasted with the distal anterior limb (RUL). On the other hand, vector 4 has high loadings on all three skull widths.

Although not shown here because of economy of space, means (and standard deviations) of the scores from all 15 components also were computed for each of the 18 different groups of mice. Means for the first (size) vector are plotted in Figure 2(a). If the inbred offspring are taken to be representative of their inbred parents, then "parents" can be compared with their hybrid offspring. For the size vector, it may be seen (Fig. 2(a)) that the hybrids are consistently larger than the midpoint between their two parents, and in most cases are larger than either (overdominance). This essentially is a multivariate indication of heterosis in size.

One additional vector, number three, also is depicted (Fig. 2(b)) since it is the only shape component which exhibits obvious overdominance. Dominance, however, is widespread in the shape components. The hybrid scores are rarely midway between parental scores, but generally show a bias toward one parent. The direction of the dominance in the various shape components tends to favour a particular strain, but is not consistent. For example, in the C × H crosses, the scores for males are biased toward the H strain in components one, three, nine, 10, 11, 14, and 15, but toward the C strain in components four, seven, and six. Clearly, the balance of dominance is in favour of the H rather than C strain.

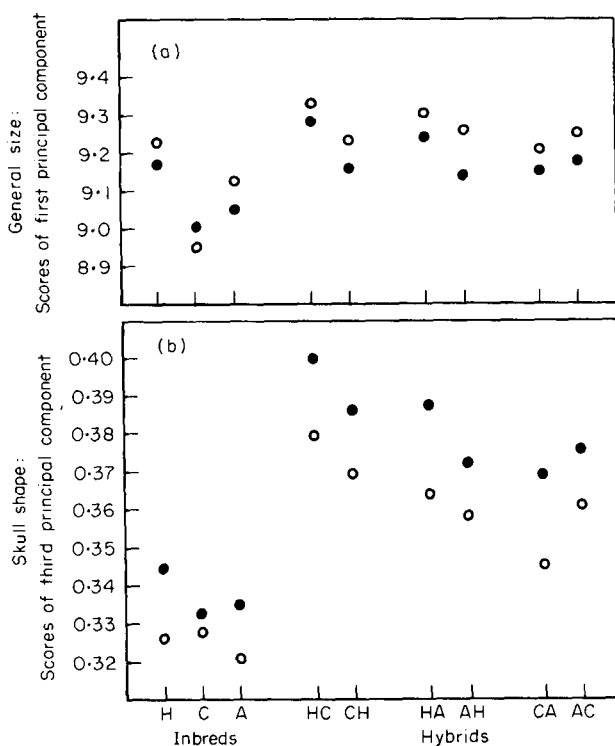


FIG. 2. Heterosis in osteometric components. Group means for the inbred and hybrid groups (closed circles ●, males; open circles ○, females) of component scores from the multiple group principal component analysis of 15 osteometric characters. Figure 2(a) indicates heterosis in general size (first component) whilst Figure 2(b) indicates heterosis in a component of skull shape (third component).

Inspection of the standard deviations of the component scores reveals that for the first (size) vector especially, they are smaller in the hybrids than in the inbreds. Thus even though these two breeding types show quite congruent patterns in their separate principal component analyses as previously detailed, the hybrids are less variable than the inbreds. The same is generally true for most of the remaining shape components, vectors eight and 14 being exceptions.

Canonical variate analyses

The overall relationships among the groups, including the patterns of "dominance", are more appropriately portrayed by canonical variate analyses. Such analyses were therefore performed on the scores previously generated from the multiple group principal components analysis of the osteometric characters. Figure 3(a,b,c), respectively, depict the results of these analyses for the $H \times C$, $H \times A$, and $C \times A$ sets of inbred and hybrid offspring. These canonical analyses were run for both size-in and size-out data. The pattern of inter-group relationships

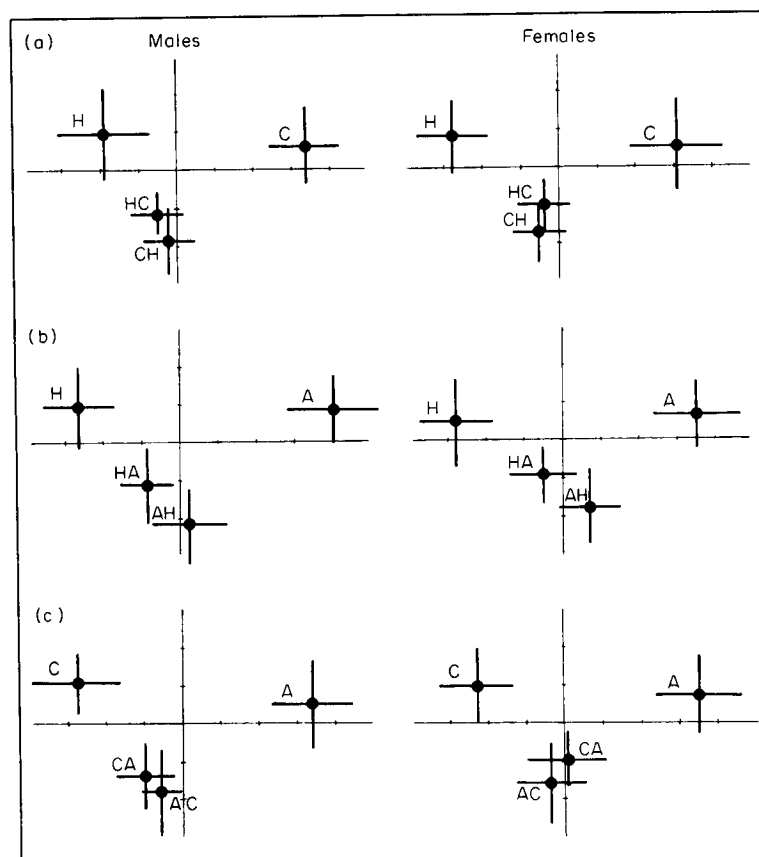


FIG. 3. Canonical variate plots of (a) $H \times C$; (b) $H \times A$; (c) $C \times A$ sets of inbred and hybrid offspring for the size-out analyses. Units of two pooled within-group standard deviations are marked on the first (horizontal) and second (vertical) canonical variates. Group means and two standard deviations either side of the mean are indicated for the groups.

is largely the same whether or not size is included. Since between group size is illustrated in Fig. 2a, only the size-out canonical variate scatters are illustrated. The overall within-group variance in shape is expressed by the dispersion around the centroids in the canonical analyses. The canonical variates are so arranged that the average within-group variance equals unity in each case. Thus any group with a variance less than one has less than average variability whereas those groups with a variance greater than one have greater than average variability.

As may be seen throughout the canonical variate analysis results (Fig. 3), the first canonical vector separates the two inbreds in each case from each other (with the hybrids invariably in between) whereas the second vector tends to separate the inbreds from the hybrids. These first two variates generally account for nearly all (over 97%) of the variation among the four groups. Both the size-in and size-out analyses confirm that the hybrids are generally less variable than the inbreds, this being particularly noticeable in the $C \times H$ crosses (Fig. 3(a)). Males are generally less variable insofar as size is concerned. This trend is far less obvious in the shape components, however, where there are from two to five groups contradicting this generalization for each component.

The overall balance and extent of "consistency" of dominance also is shown in the canonical variate analysis (Fig. 3). The hybrids generally are spatially removed from the midpoint between the two inbreds (although the degree of displacement of the two hybrids on the second vector is a measure of the extent to which the direction of this dominance is inconsistent). In the $C \times H$ crosses (Fig. 3(a)) for example, both hybrids are closer to the H strain, this being consistent with the patterns of the component scores already detailed. Similarly, the $A \times H$ hybrids (Fig. 3(b)) are closer to the H inbred, and the $C \times A$ hybrids (Fig. 3(c)) are closer to the C inbred. Thus the overall pattern among the three strains is H-C-A. Another pattern, albeit weak, is also evident. In nine out of 12 canonical analyses (size-in included), the hybrids are closer to that inbred serving as the maternal (rather than paternal) donor. Moreover, the degree of displacement of the hybrids along the second vector is always less for the hybrid in which the maternal donor is dominant (Fig. 3).

Discussion

It is evident that even though the mice were reared under standardized laboratory conditions, were all isogenic within a group, and were all the same age, general size dominates the variation within a group (i.e. 64%) so that the mice could not strictly be considered as being of the same growth stage. Consequently, when dealing with natural populations age cannot be taken as a flawless indication of growth stage.

Even though the first vector in the osteometric principal component analysis largely expresses general size, it is clear that it involves a very small element or phenotypic shape because the contribution of interorbital width is less than the other characters. The definition of general size is marginally sub-optimal because the spectrum of growth, although present, is limited in range. This can also be observed in studies of natural populations where a narrow growth spectrum has been deliberately selected as for example in Riska's (1981) study of *Limulus* variation.

Since the variances of the characters were not uniform and a covariance matrix was used, the character-component correlations proved to be useful in assessing the relative contributions of the characters to the size vector. The eigenvector coefficients for the first

vector are higher for the girdle characters (Nos 8–11) than say limb characters (Nos 12–15). The correlations show that this is due to differences in character variance, because the girdle characters ($r=0.67-0.94$) do not contribute more than limb characters ($r=0.83-0.91$).

Having largely separated size and shape, it was possible to test the hypothesis that the inclusion of (growth-dependent) size influences the assessment of group interrelationships. It is clear that in this data set size is not altering these inter-relationships; the size-in and size-out analyses are so similar that it is not worthwhile figuring both. When this occurs it can be for two reasons. First, the between-group variation in size could be congruent to the pattern of between-group variation in shape. Second, the contribution of size to the between-group variation could be low. In the analyses used in this study the contribution of size is measured by the F ratio of the between-group divided by within-group component scores from the MGPCA. For any one component, e.g. size, to be important its F ratio would have to be large compared to the sum of the F ratios for the other components. When all groups are considered the F ratio for the size component is 75 (Table II(b)) but this is only 7.5% of the total between group variation. In this case size is so inconsequential to the between-group differences that its congruence to between-group shape is of little importance in influencing the overall similarity between groups.

The value of using multivariate methods in biometrical genetics is apparent. Multiple group principal component analysis can reveal within-group character relationships that can subsequently be compared between breeding types. Variances, heterosis and dominance also can be investigated in these individual components. Moreover, once these multivariate components of size and shape have been defined, their heritability can be estimated (Leamy & Thorpe, in prep.). Canonical analysis in turn may be used to assess overall dominance, inconsistency in the direction of dominance, variability, and maternal effects.

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