TRIANGULATION-MEASUREMENT SCHEMES IN THE MULTIVARIATE ANALYSIS OF SIZE AND SHAPE

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ABSTRACT.—Skulls of seven rodent species were measured by a triangulation-measurement scheme and subjected to multivariate analysis. Results were compared to studies from the literature based on traditional measurements for the proportion of variance explained by overall body size, the number of shape factors, and the ease of interpretation of these factors. Principal-components analysis of triangulation measurements showed that size variation accounted for less than half of the variance within samples of Akodon, Gerbillurus, Chaetodipus, and Dipodomys. In contrast, size accounts for more than half of the variance in most studies in which traditional skull measurements were analyzed. Triangulation measurements appear to capture more information about variation in shape than do traditional measurements. In addition, shape factors extracted from these species can be interpreted in terms of variation in specific regions of the skull. Regional patterns of covariation maybe more amenable to explanations involving underlying biological processes than are results of multivariate analysis of more traditional measurements.

Morphometric data are analyzed to identify sources of variation (Straney, 1978), to examine patterns of allometry (Bookstein et al., 1985; Cock, 1966; Creighton and Strauss, 1986; Jolicoeur, 1963), and to identify patterns of integration in the mammalian skull (Atchley, 1984; Cheverud, 1982; Olson and Miller, 1958; Zelditch, 1988). Most commonly, analyses of morphometric data are used as a systematic tool to examine differences in morphology between populations and taxonomic units (Braun and Kennedy, 1983; Riddle and Choate, 1986; Schonewald-Cox et al., 1985). Common to all of these approaches is the analysis of differences in size and shape among individuals. Size and shape usually are studied with multivariate statistical methods, primarily factor analysis and principal-components analysis. These methods describe the complex associations of many characters in terms of relatively few composite variables that can be characterized as size or shape axes.

Size can be defined as the coordinated increase or decrease of the variables measured in a study. A size variable is viewed best as a particular linear combination of variables, such as a factor or principal component, positively and highly correlated with each of the measured variables. Perhaps the most informative size variable is one obtained by principal-component analysis of the variance-covariance matrix of log-transformed measurements; in this case, loadings (expressed as direction cosines) represent allometric coefficients for each measured variable (Jolicoeur, 1963). This multivariate definition captures more completely the intuitive meaning of size than does a univariate definition based on a single measurement such as body length. Longer animals are "bigger" than shorter animals only if other dimensions are larger as well.

Principal-component or factor axes independent of size usually are interpreted as shape variables, but in practice size and shape are partially confounded. Because skulls do not grow isometrically, change in overall body size also will be accompanied by change in shape. All of the composite variables, therefore, provide information about shape, but they may be divided into two categories: one axis that reflects only shape variation associated with general size, and the remaining axes that reflect shape variation independent of general size. When we discuss the "size" axis, we refer to the first category; when we discuss "shape" axes, we mean those in the second category.

In most systematics applications, size-independent shape differences are of primary concern; simple scaling differences among taxa must be identified to permit examination of other differences less likely to reflect variation in body size among individuals in the population. Because size appears to account for considerably more than half of the variation in most mammalian craniometric studies, it is desirable to increase the amount of variation explained by shape axes. Also, it is desirable to extract shape factors that can be interpreted in terms of changes in proportions of regions of the skull or as differences in relative proportions of specific skull bones. Unfortunately, shape axes identified in most cranial morphometric studies are notoriously difficult to interpret. Both of these aspects of a study are influenced directly by choice of original measurements.

Morphometric characters traditionally used by mammalogists are susceptible to the same criticisms as those applied by Strauss and Bookstein (1982) to traditional-measurement schemes used in studies of fish morphology. Traditional variables sample only orthogonal variation (length, width, and occasionally depth); oblique measurements rarely, if ever, are included. Furthermore, characters often overlap the same region of the skull and use the same endpoint repeatedly. Other regions in which significant shape variation may occur are sampled sparsely. Dimensions also are measured between points poorly defined by biological landmarks. For example, least interorbital width, a common character, is not defined by endpoints biologically homologous from one individual to another. Finally, when long dimensions are measured (such as greatest length of skull), variation within the regions spanned by the long measurements might be ignored. Truss measurements, and the related triangulation measurements (Fig. 1), were designed to eliminate exactly these shortcomings (Strauss and Bookstein, 1982). This triangulation-measurement scheme represents the shape of the skull more effectively than does a conventional measurement set.

With a truss- or triangulation-measurement scheme, variance within a population is spread more evenly across factors or principal components so that size variation does not dominate the results. Also, shape axes frequently are more interpretable in biological terms, because they represent differences in the proportions within and between well-defined regions of the skull. Herein, we focus on morphometric studies within populations; comparisons among factor-patterns extracted from different populations are more complicated (Meredith, 1964; Mulaik, 1972).

**Materials and Methods**

Skulls of 22 individuals of each of seven rodent species were examined: *Chaetodipus pencillatus, Apizolaya, Zacatecas, Mexico; Dipodomys merriami, Concepcion del Oro, Zacatecas, Mexico; Desmodillus auricularis, Gorrasis, Namibia; Gerbillurus paeba, Gorrasis, Namibia; Microtus pennsylvanicus, East Lansing, Michigan; Peromyscus melanophrys, Pinos, Zacatecas, Mexico; and Akodon azarae, Buenos Aires, Argentina. Specimens span a wide range of sizes and ages; all are housed in The Michigan State University Museum. Specimens were measured according to the triangulation-measurement scheme illustrated in Fig. 1. Biological landmarks, points presumed homologous across all specimens (Bookstein et al., 1985), were digitized from photographs that included a millimeter scale. We analyzed log-transformed Euclidean distances among landmarks.

General practice is to presume that the factor or component of either the correlation or variance-covariance matrix with the largest eigenvalue represents overall body size, when loadings are approximately equal and positive in sign. Other factors usually are interpreted as "shape," or are not interpreted at all. However, labeling the first component as size and the others as shape is arbitrary (Mosimann, 1970; Mosimann and James, 1979; Sprent, 1972). When size differences are not the principal source of variation within a population, the component that appears to represent size (because of its high positive loadings) may have a relatively small eigenvalue. Whether or not the size component is the first principal component, loadings on this component represent allometric coefficients for each of the original variates provided they are extracted from the covariance matrix of log-transformed measurements and expressed as direction cosines (Jolicoeur, 1963).

To study the effects of a triangulation-measurement scheme upon the amount of size and shape information extracted from these skull measurements, we considered the proportion of the variance explained by each unrotated principal component (the eigenvectors of the variance-covariance matrix) and the number of potentially significant components extracted by principal-components analysis. We compared the relative
Analyzing size and shape as factors requires use of factor analysis rather than principal-components analysis (Bookstein et al., 1985). Principal-components analysis is a technique for reducing the complexity of a large set of measurements by finding a small number of composite variables that account for variation in the less
parsimonious set of original measurements. We used principal-components analysis to compare the influence of general body-size differences in samples of triangulation and traditional measurements because it is used conventionally by mammalogists, and because it provides a unique solution. Factor analysis, although frequently used to find a parsimonious description of the variables, essentially is a method for explaining the covariance structure of observed measurements (Morrison, 1976). Because the factor model is appropriate to the study of interactions among observed measurements and the biological causes of covariation (Bookstein et al., 1985), we used factor analysis to study shape.

Covariance and correlation matrices of measurements were analyzed by both principal-component analysis and factor analysis with the factor procedure of the statistical program SAS (SAS Institute, Inc., 1985). Analyses were performed independently for each species.

RESULTS AND DISCUSSION

In the principal-components analyses of traditional measurements from several studies in the literature (Table 1), the first component is interpreted by the authors as a size variable. In all but two studies, this size axis accounts for over half of the total variance in the population, and the second component accounts for less than one-quarter of the total variance in each analysis.

In contrast, our principal-components analysis of the covariance matrix of triangulation mea-
measurements distributes variation more evenly across components (Table 2). In *Desmodillus* and *Akodon*, we extracted four significant components; in *Dipodomys*, we found five. In the remaining species, we found three components that accounted for at least the variation in a single character.

The first component explained considerably less than half of the variance in *Akodon* and *Dipodomys*. Only in *Desmodillus* does the first principal component account for more than half of the observed variation and represent a size component. Although the first principal component explained more than half of the differences among individuals in *Microtus* and *Peromyscus*, this component does not necessarily reflect size variation. In these two species, no single component of the covariance matrix can be interpreted unambiguously as an overall size component. Both the first and second principal components have several low positive loadings, and there are several high negative loadings on the first principal component. Low positive loadings do not, by themselves, preclude interpreting a component as a size variable; not all skull dimensions need respond to increasing overall body size by increasing in length. However, we cannot interpret the first component in these two species as a size component because of the high negative loadings. In *Chaetodipus* and *Gerbillurus* there is no ambiguity; the first principal component does not reflect size variation (Table 2).

The number of significant components is related to the number of original variables. However, several of the studies in Table 1 involved 19 or more characters; in none was four significant components reported. One potential explanation for at least some of the increase in the number of significant components is that we analyzed the variance-covariance matrix, whereas all of the studies listed in Table 1 (except that by Schonewald-Cox et al., 1985) used the correlation matrix. Principal-component analysis of the correlation matrix of triangulation measurements (Table 2) distributes the variation less evenly, even though the first principal component never accounts for >60% of the variance. As many as four factors were extracted with eigenvalues greater than one in three of the species. In addition, the first principal component of variation in *Perognathus* has high positive and negative loadings, thus it is unlikely to reflect variation in overall body size.

As evident in the principal-component analysis of correlations among truss measurements, the number of shape factors may diminish when the correlation matrix rather than covariance matrix is employed. Thus, use of different matrices explains some of the increase in the number of factors and it affects the amount of variance accounted for by general body size. However, not all of the increase in shape information obtained by triangulation measurements results from the choice of the matrix analyzed and the number of measurements used. A comparison of our results for *Dipodomys merriami* with the analysis of *Dipodomys agilis* by Best et al. (1986) suggests that triangulation measurements result in a more even distribution of variation across factors. Best et al. (1986) reported that one-half or more of the variation is a result of size, with <8% of the variation attributable to the third factor. In contrast, we found five factors, with size accounting for <40% of the total unstandardized variation and ≤51% of the variation extracted from the correlation matrix.

Although by factor analysis of the correlation matrix we found less variance related to shape than did our analysis of the covariance matrix, triangulation measurements still appear to yield more shape information than traditional measurements. The tendency for variance to be distributed more evenly across shape factors may justify using the covariance matrix for studies of variation. Further justification lies in the need to extract factors from the covariance matrix before comparisons between populations can be made (Mulaik, 1972). Finally, information about allometry is lost when the analysis is performed on the correlation matrix.

Any morphometric study depends upon the ability of the measurement scheme to capture information about size and shape. When size is the principal source of variation within a population, it follows that shape must account for a relatively small proportion of the total variance. Our results suggest that the triangulation-measurement scheme identifies more potentially significant components than a typical set of traditional measurements. Triangulation measurements, therefore, appear to provide more information about shape and also yield shape factors interpreted more easily.
Rarely are factor analyses subjected to thorough interpretation. In part, this is because factor analysis is known to be ambiguous and subjective (Harman, 1967), but another reason is that components independent of overall body size usually are more difficult to explain than a size component. For example, the second principal component in *Procyon lotor* (Table 1) was interpreted by Kennedy and Lindsay (1984) as reflecting an inverse correlation between the least postorbital width and the width of the foramen magnum. Although this second component represents a real source of variation, it is difficult to conceive of a biological process that might influence these two widely separated features without affecting intervening ones. Shape components may be interpreted more readily when the measurements involved are from the same region or functional complex of the skull. For example, the second principal component in elk, *Cervus elaphus* (Table 1), represents an inverse correlation between nasal and condylar breadths, and nasal and palatal depth (Schonewald-Cox et al., 1985); at least in the nasal region, width and depth are related inversely.
TABLE 3.—Correlations between variables and shape factors extracted from the covariance matrix by factor analysis. The variance explained is the proportion of the total variance explained by each factor. Only factors deemed significant by the minimum eigenvalue criterion are reported.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Chaetodipus Factor</th>
<th>Akodon Factor</th>
<th>Peromyscus Factor</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.41</td>
<td>-0.02</td>
<td></td>
</tr>
<tr>
<td>2</td>
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<tr>
<td>3</td>
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<td>-0.04</td>
<td></td>
</tr>
<tr>
<td>4</td>
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<tr>
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</tr>
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<tr>
<td>13</td>
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<td>19</td>
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<td>0.86</td>
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</table>

Variance explained: 55.72 7.91 21.84 9.14 6.05 17.06 6.20

Triangulation measurements reflect the regionalization of the skull, yielding a description of shape cast in terms of regional compartments of the skull. This allowed us to compare our interpretation against expectations. In particular, we expected the dorsal view of the skull to be bilaterally symmetrical, so that the right and left lengths of any compartment should covary strongly. Similarly, the oblique measure of a compartment should covary with lengths and widths of that compartment. Of 18 shape factors in our analysis, nine fit these expectations. For example, in Chaetodipus (Fig. 2a, Table 3), the first factor clearly reveals an inverse relationship between the posterior compartment of the rostrum and the anterior rostral compartment plus the interorbital compartment. In this population, individuals with relatively large posterior rostral regions possess relatively small anterior rostral and interorbital regions. The third factor in this species describes covariation among orbital, braincase, and occipital sizes. These three regions increase or decrease in size as a single unit, independent of their responses to general body size.

The second factor in Akodon (Fig. 2b, Table 3) accounts for almost 22% of the total variation and reflects an inverse relationship between size of the occipital and width of the posterior orbital region plus size of the posterior rostral compartment. In this population, individuals with relatively narrow and short occipital compartments also have relatively long and wide skulls in the posterior rostral and posterior frontal regions. In the third factor of Akodon (Fig. 2c), dimensions of the interorbital region and width of the anterior-most measure of the nasal bone covary; these measurements are associated negatively with lengths of the anterior rostrum and braincase.

In Peromyscus, the second factor (Fig. 2d, Table 3) accounts for 17% of the total variation. This factor reflects a contrast between dimensions of the orbital region, and dimensions of the anterior rostral compartment and length of the braincase. The third and fourth factors in Dipodomys, the third in Desmodillus, and the first factor in Gerbillurus are equally easy to interpret.

Four factors depart from symmetry expectations by a single measure. In the second factor of Microtus (Fig. 2e), only the left side of the occipital compartment covaries with the length of
the posterior rostrum. The second and fifth factors of Dipodomys, and the second factor of Desmodillus also deviate from the expected pattern by a single measure. The third factors in Peromyscus, Microtus, and Gerbillurus, and the fourth factor in Akodon differ from symmetry expectations by two measurements.

The fourth factor in Desmodillus (Fig. 2f) comprises length of the anterior rostral compartment on the left side, length of the posterior rostral compartment on the right side, and the oblique measure of this compartment all contrasted against length of the posterior rostrum on the left side, the oblique measure of the braincase, width of the posterior end of the braincase, and length of the occipital region on the right side. We find it difficult to find biological (or geometric) sense in this set of measurements. The pattern of loadings for this factor suggests an inverse correlation between measurements on the right and left sides of the same compartment. In this case, difficulties in interpretation caused by the sporadic pattern of loadings are magnified by the differences between observed and expected covariation among bilaterally symmetrical characters.

Deviation from expected bilateral symmetry may result, in part, from our small sample sizes. We analyzed 19 variables and our samples included only 22 individuals. Harris (1975) suggested that sample sizes for multivariate analysis should exceed the number of variables by $\geq 50$. Therefore, at least some of the correlations between variables and factors possibly are spurious, whereas other variables that we did not find to be correlated with a particular factor possibly are actually correlated. The geometry of the triangulation-measurement may result in spurious correlations among measurements within a single compartment because of errors in locating a common point shared by two measurements (Cheverud and Richtsmeier, 1986). Photographic and perspective errors thus may have created some correlations among measurements within compartments observed here. Thus, shape factors extracted from truss measurements should be interpreted as cautiously as those extracted from traditional measurement schemes.

Our study was designed specifically to identify shape factors. Biologists with other goals might have less reason to prefer a triangulation- or truss-measurement scheme. When the purpose of the study is to examine patterns of covariation among functionally interacting characters, a measurement scheme that focuses specifically on these characters might be preferred over a triangulation scheme. Thus, we are not arguing that triangulation invariably provides the best measurements for any analysis. Instead, we argue that triangulation measurements obtain general shape information more effectively than traditional mammalian skull measurements.

The ultimate goal of many cranio metric studies of mammals is to compare and discriminate among shapes in different species. We cannot compare shape factors merely by inspecting the patterns of loadings on these factors, because the factors must first be rotated to maximal similarity (Mulaik, 1972). Such comparisons may be most informative when shape factors account for relatively more of the variation than the size factor. Investigators have been reluctant to accept size differences as primary taxonomic distinctions because of the large influence that local environment may have on general body size (Patton and Brylski, 1987). Consequently, the literature on size-free morphometric discrimination is growing (Humphries et al., 1981; Somers, 1986). Because a triangulation-measurement scheme allows analysis of variation along dimensions excluded from traditional sets of measurements, it may reflect shape variation more effectively than a traditional approach to measurement.

**LITERATURE CITED**


BRAUN, J. K., AND M. L. KENNEDY. 1983. System-


