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SIZE AND SHAPE VARIATION IN THE PAINTED TURTLE.[1] A PRINCIPAL COMPONENT ANALYSIS

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INTRODUCTION

The concepts of size and shape are fundamental to the analysis of variation in living organisms. And yet, as noted by Simpson, Roe and Lewontin (1960), there is at present no general agreement on practical definitions of size and shape. The adoption of a generally applicable method of measuring size and shape variation would be particularly timely as so much effort is being devoted to the study of morphological and physiological variation within and between plant and animal populations (Anderson, 1954; Prosser, 1955).

Parting biometrical variation into size and shape components is often highly desirable as the size of most organisms is more affected than their shape by fluctuations of the external environment; size variation is also more likely to reflect heterogeneity of samples with respect to age-composition. Shape tends thus generally to provide more reliable indications than size on the internal constitution of organisms; this makes the analysis of size and shape a basic step in the study of biometrical variation.

The present study of the Painted Turtle (*Chrysemys picta marginata*) is an attempt to evaluate the applicability of principal component analysis to size and shape variation in groups of living organisms. The beginnings of principal component analysis are probably to be found in the works of Karl Pearson (1901). The statistical properties of principal components were investigated in detail by

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Hotelling in 1933. Anderson (1958) has given the most comprehensive recent exposition. Principal component and related forms of multivariate analysis have been used by a number of authors (Blackith, 1960; Teissier, 1955; Wright, 1954) in attempts to describe complex growth patterns in terms of a minimum number of basic trends. Recent biometrical studies of character-complexes (Bailey, 1956; Kraus and Choi, 1958; Olson and Miller, 1958) have made increasingly clear that, whenever the discovery of genetical, developmental and functional relationships is contemplated, joint consideration of all characters becomes indispensable and multivariate statistical techniques are indicated. However, the relationships of principal components with the concepts of size and shape do not appear to have been ever examined in detail. This is the main purpose of the present note. A comparative analysis of sex dimorphism in several species of turtles will be presented later.

Among the vertebrates, turtles are perhaps those that are most readily suitable to studies of variation in overall size and shape. Due to a rigid bony carapace, consistent measurements of body dimensions can be obtained. Further, interesting changes of proportions occur in the shell during growth (Mosimann, 1958). Sexual dimorphism in body size and proportions is common. Finally, for aquatic species like the one studied here, shape is probably of major adaptive significance because of the importance of streamlining for locomotion in a dense fluid medium.

Material and Data

Eighty-four specimens of Midland Painted Turtles (*Chrysemys picta marginata*) were collected in a single day (August 2, 1956) from a small stagnant pond of the St. Lawrence Valley, at Coteau Landing, 35 miles southwest of Montreal, Canada. This material can therefore safely be assumed to represent a single local population. Specimens are preserved in the Department of Biology of the University of Montreal. Only individuals for which the sex was externally discernible are included in the present analysis, one abnormal male being excluded. Carapace dimensions were measured in three mutually perpendicular directions of space: length, maximum width, and height. More detailed definitions of these measurements have been given before (Mosimann, 1958). Thus each specimen is represented in this study by a set of three measurements

$$(\text{length, width, height})$$

hereafter designated

$$X = (X_1, X_2, X_3)$$

for convenience. Measurements rounded to the nearest millimeter are listed in Table 1. Several facts are explicit from examination of the data. (1) In general, long individuals are also wide and high, and inversely, short individuals are narrow and low. Clearly this reflects the fact that length, width and height are influenced by one general factor of variation, size. (2) However, some individuals of the same length show different widths or heights and these differences of proportions constitute shape variation. (3) In addition it can be seen that females attain a larger size than males and also (4) that they tend to be higher relative to length.

TABLE 1
CARAPACE DIMENSIONS OF PAINTED TURTLES (*Chrysemys picta marginata*) IN MM.

24 Males			24 Females		
length	width	height	length	width	height
93	74	37	98	81	38
94	78	35	103	84	38
96	80	35	103	86	42
101	84	39	105	86	40
102	85	38	109	88	44
103	81	37	123	92	50
104	83	39	123	95	46
106	83	39	133	99	51
107	82	38	133	102	51
112	89	40	133	102	51
113	88	40	134	100	48
114	86	40	136	102	49
116	90	43	137	98	51
117	90	41	138	99	51
117	91	41	141	105	53
119	93	41	147	108	57
120	89	40	149	107	55
120	93	44	153	107	56
121	95	42	155	115	63
125	93	45	155	117	60
127	96	45	158	115	62
128	95	45	159	118	63
131	95	46	162	124	61
135	106	47	177	132	67

BIVARIATE ANALYSIS

Whereas the preceding points can be detected by inspection of the data, they are brought out more clearly by plotting pairs of measurements of the various individuals as dots in cartesian coordinate systems. In the resulting bivariate scatter diagrams (Figures 1 and 2), the facts noted above are now graphically evident: (1) dots are spread along the diagonal of each diagram according to size differences and (2) scattered about it because of shape variation. (3) In both diagrams females extend further to the right than males since they grow larger and (4), in the first diagram, they tend to be above males of equal length because of greater relative height.

These phenomena have been made considerably more obvious by outlining the clusters of dots with ninety-five per cent equal frequency ellipses. The equation of the latter can be written in matrix notation as:

$$(X - \overline{X})\ W^{-1}\ (X - \overline{X})' = c^2$$

where $X = (X_1, X_2)$, the pair of coordinates of the locus of the ellipse; $X' = \begin{bmatrix} X^1 \\ X^2 \end{bmatrix}$, the column-vector obtained by transposing X; $\overline{X} = (\overline{X}_1, \overline{X}_2)$, the pair of coordinates of the center of the ellipse and the row-vector of sample means; $W = \begin{bmatrix} W_{11} & W_{12} \\ W_{21} & W_{22} \end{bmatrix}$, the inverse of the matrix of the equation of the ellipse and the covariance matrix of the sample. The value of c^2 is equal to that of chi-square with two degrees of freedom (Anderson, 1958: 54), which is 5.99 at the 95 per cent level. The elements of the bivariate mean vectors and covariance matrices for Figures 1 and 2 are all included in the trivariate statistics (Table 2).

To determine an equal frequency ellipse, the direction cosines $U = \begin{bmatrix} U_{11} & U_{12} \\ U_{21} & U_{22} \end{bmatrix}$ of its principal axes and the diagonal form $\Lambda = \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{bmatrix}$ of its covariance matrix are calculated, the subscripts in U and Λ always being ordered by convention so that $\lambda_1 > \lambda_2$. In this study, the elements of matrix $U = \begin{bmatrix} \cos\theta & \sin\theta \\ -\sin\theta & \cos\theta \end{bmatrix}$ were obtained from 5-place trigonometric tables after evaluating angle θ from $\tan 2\theta = \dfrac{2\ W_{12}}{W_{11} - W_{22}}$ and Λ was then calculated as $\Lambda = UWU'$, where

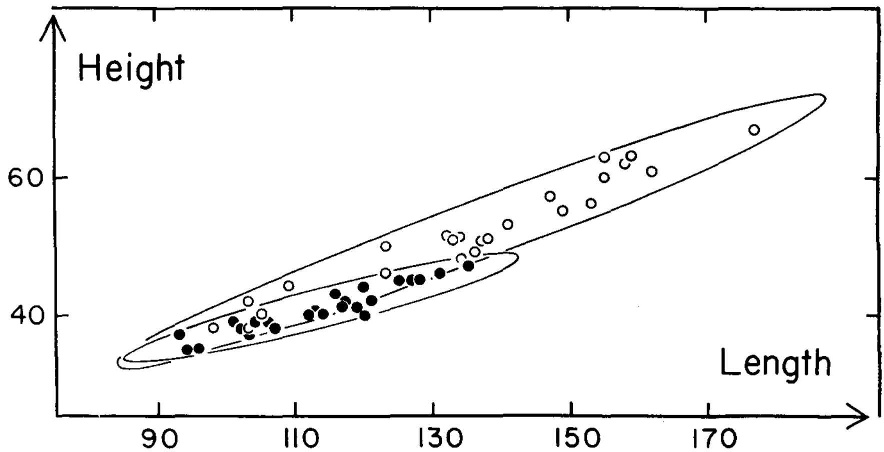

FIGURE 1
Bivariate scatter diagram of carapace height and length. Males, solid circles; females, hollow circles.

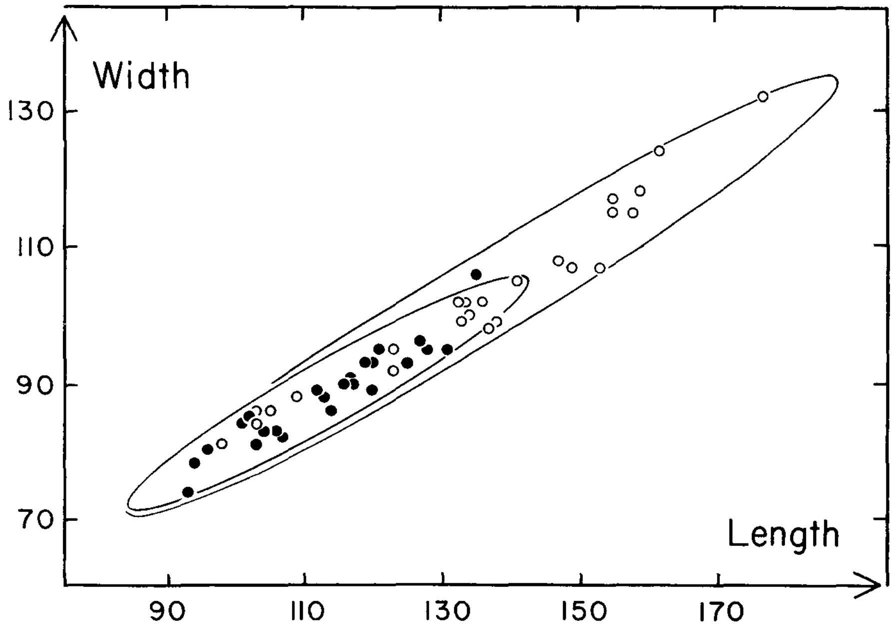

FIGURE 2
Bivariate scatter diagram of carapace width and length. Males, solid circles; females, hollow circles.

U′ is the transpose of matrix U. The principal components of the covariance matrix W are the variances λ_1 and λ_2 of the observations along the principal axes of their equal frequency ellipses, the direction cosines of these axes being (U_{11}, U_{12}) for the first and (U_{21}, U_{22}) for the second.

Providing the coordinate axes are graduated in the same scale, the extremities of the principal axes of a 95 per cent equal frequency ellipse are determined by the following vector equations:

$$\text{major axis} \qquad (X_1, X_2) = (\overline{X}_1, \overline{X}_2) \pm \sqrt{5.99\lambda_1}\,(U_{11}, U_{12})$$
$$\text{minor axis} \qquad (X_1, X_2) = (\overline{X}_1, \overline{X}_2) \pm \sqrt{5.99\lambda_2}\,(U_{21}, U_{22}).$$

The above equations lay bare the analogy of bivariate with univariate confidence intervals. After these extremities have been plotted, the ellipse can be graphed either by means of an ellipsograph (such as the one made by Riefler) or following a standard drafting procedure.

Were the parameter mean vector and covariance matrix known, and were the distribution of our observations exactly bivariate normal, then equal frequency ellipses would be true confidence intervals. Although this is not the case, our ellipses are estimates of true confidence intervals. Moreover, their main raison d'être in the present study is their descriptive validity, and the latter is confirmed by visual comparison with the clusters of dots of the data. On the other hand, with small samples, the effect of extreme observations is considerable and equal frequency ellipses should be used with caution. Their biometrical utilization has been thoroughly discussed by Defrise-Gussenhoven (1955).

Trivariate Analysis

While bivariate scatter diagrams with equal frequency ellipses have brought out size and shape differences rather satisfactorily, the present problem is basically trivariate. The well-justified popularity of bivariate techniques stems no doubt largely from the relative simplicity of bivariate computations as well as from the ease of preparation of bivariate scatter diagrams. Graphing is considerably more difficult in three than in two dimensions, and it becomes geometrically impossible when more than three variables are analyzed jointly. Algebraically and numerically, however, multivariate statistical techniques remain identical in pattern beyond the bivariate level.

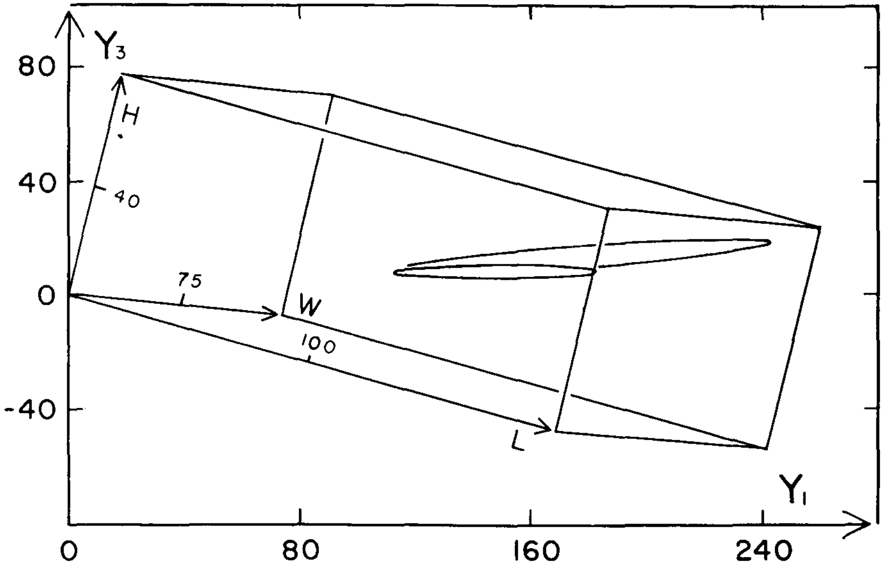

FIGURE 3
The trivariate scatter diagram of carapace length, width and height viewed perpendicularly to the first and third principal axes of males.

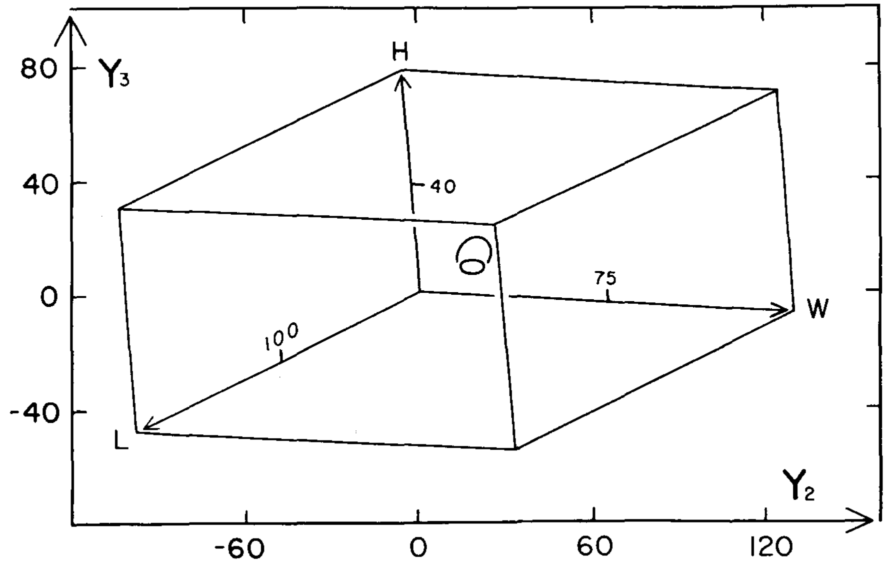

FIGURE 4
The trivariate scatter diagram of carapace length, width and height viewed perpendicularly to the second and third principal axes of males.

Inasmuch as the frequency distribution of observations is approximately multivariate normal, a sample can be summarized by its mean vector $\overline{X}$ and covariance matrix W. In the trivariate case,

$$\overline{X} = (\overline{X}_1, \overline{X}_2, \overline{X}_3) \text{ and } W = \begin{bmatrix} W_{11} & W_{12} & W_{13} \\ W_{21} & W_{22} & W_{23} \\ W_{31} & W_{32} & W_{33} \end{bmatrix}$$

The trivariate statistics relative to (length, width, height) in the present study are listed in Table 2. The elements of the mean vector of females are greater than those of males, reflecting the greater size of the former sex. The elements of covariance matrices are also greater in females, which reflects a greater range of size variation.

Earlier in this paper the analysis was restricted to that of the marginal distributions of the variables two by two. All components of $\overline{X}$ and W were perforce ignored at any one time except those corresponding to two of the variables. Thus the components of $\overline{X}$ other than $(\overline{X}_1, \overline{X}_3)$ and those of W other than $\begin{bmatrix} W_{11} & W_{13} \\ W_{31} & W_{33} \end{bmatrix}$ were automatically discarded in the bivariate analysis of (X_1, X_3). In other words, carapace length and height were analyzed as if width had not been measured, etc. Multivariate techniques alone can take all variables into account jointly and thus provide a unified analytical approach.

TABLE 2

MEAN VECTORS $\overline{X}$ AND COVARIANCE MATRICES W

	24 Males			24 Females		
	length	width	height	length	width	height
X	(113.38	88.29	40.71)	(136.00	102.58	51.96)
W	138.77	79.15	37.38	451.39	271.17	168.70
	79.15	50.04	21.65	271.17	171.73	103.29
	37.38	21.65	11.26	168.70	103.29	66.65

With the present trivariate data, a joint scatter diagram of all variables is fortunately still possible. Slanted views of the tridimensional scatter diagram have been calculated and illustrated (Figures 3 and 4), the clusters of male and female dots being represented by ellipsoids.

Analogously with bivariate principal components, multivariate principal components are the variances of observations along the principal axes of multidimensional equal frequency ellipsoids. In the present case, with three variables, the latter are tridimensional ellipsoids. The evaluation of the direction cosines $U = \begin{bmatrix} U_{11} & U_{12} & U_{13} \\ U_{21} & U_{22} & U_{23} \\ U_{31} & U_{32} & U_{33} \end{bmatrix}$ of the principal axes and of the corresponding covariance matrix $\Lambda = \begin{bmatrix} \lambda_1 & 0 & 0 \\ 0 & \lambda_2 & 0 \\ 0 & 0 & \lambda_3 \end{bmatrix}$ is an eigenvalue and eigenvector problem. Its best general solution is probably the Jacobi method of matrix diagonalization (White, 1958: 395), a generalization of the procedure already described for bivariate covariance matrices. The results of principal component analysis of our data are given in Table 3.

TABLE 3
COVARIANCE MATRICES Λ AND MATRICES OF DIRECTION COSINES U OF THE PRINCIPAL AXES

	24 Males			24 Females		
Λ	195.28	0.00	0.00	680.40	0.00	0.00
	0.00	3.69	0.00	0.00	6.50	0.00
	0.00	0.00	1.10	0.00	0.00	2.86
U	.84012	.49190	.22854	.81263	.49549	.30676
	—.48811	.86938	—.07696	—.54537	.83213	.10062
	—.23654	—.04690	.97049	—.20540	—.24907	.94645

TYPES OF VARIATION CORRESPONDING TO THE PRINCIPAL COMPONENTS

The types of variation occurring in the directions spanned by the principal axes can best be judged from the equations of the latter. Thus the equation of the first principal axis of males is

$$\frac{X_1 - \overline{X}_1}{U_{11}} = \frac{X_2 - \overline{X}_2}{U_{12}} = \frac{X_3 - \overline{X}_3}{U_{13}} = Y_1 - \overline{Y}_1$$

or

$$\frac{X_1 - 113.38}{.84012} = \frac{X_2 - 88.29}{.49190} = \frac{X_3 - 40.71}{.22854} = Y_1 - 147.99$$

upon substitution of the numerical values given in Table 3. The value of Y_1 is obtained by rotation of X as explained later. In fact, for a given set $X = (X_1, X_2, X_3)$, the value of Y_1 is equal to that of the linear compound $U_{11}X_1 + U_{12}X_2 + U_{13}X_3$. It is noteworthy that the direction cosines of the Y_1-axis are all positive. Because of this, the equation of the major axis corresponds to a simultaneous increase (or decrease) of all variables. For instance, a positive deviation of 100 units in Y_1 corresponds approximately to deviations of (+84, +49, +23) millimeters in (X_1, X_2, X_3), that is in carapace (length, width, height). For this reason, and since growth is generally defined as the increase in size of an organism, the first principal component is interpreted as a growth trend. The use of a linear compound like $Y_1 = U_{11}X_1 + U_{12}X_2 + U_{13}X_3$ as a size measure should be very practical in many types of studies, although it calls for careful distinction from the usual volumetric or ponderal definition of size. Size was for instance defined as a volume estimate from a non-linear compound ($Y_1 = k\ X_1\ X_2\ X_3$) and compared with direct volume measurements by Mosimann (1958).

A feature of special significance is the difference in relative magnitude of the direction cosines of male and female major axes, particularly those corresponding to carapace height. U_{13} equals .22854 and .30676 in males and females respectively. A positive deviation of 100 units in size thus corresponds approximately to a deviation in height of +31 mm. in females, but only to +23 mm. in males. This expresses the lower relative growth rate of carapace height in males, a phenomenon noticeable in Figure 1 and brought out previously by regression analysis (Mosimann, 1958).

The second principal axis of males has the equation

$$\frac{X_1 - \overline{X}_1}{U_{21}} = \frac{X_2 - \overline{X}_2}{U_{22}} = \frac{X_3 - \overline{X}_3}{U_{23}} = Y_2 - \overline{Y}_2$$

or

$$\frac{X_1 - 113.38}{-.48811} = \frac{X_2 - 88.29}{.86938} = \frac{X_3 - 40.71}{-.07696} = Y_2 - 18.28$$

with numerical values. The direction cosines of this second axis differ in sign, and this trend of variation corresponds to a joint increase of one variable and decrease of others. A positive deviation of 100 units in Y_2 would correspond approximately to deviations of (—49, +87, —8) millimeters in carapace (length, width, height). This second principal component is thus a trend of shape variation. The direction cosines of the third principal axis also differ in sign, and the third principal component is similarly interpreted as shape variation.

The results of the analysis of size and shape variation of the present data are summarized in Table 4. It is seen that females are much more variable than males in size and slightly more so in shape.

TABLE 4
SIZE AND SHAPE VARIATION

	24 Males			24 Females		
Principal axes	1st (major)	2nd (intermediate)	3rd (minor)	1st (major)	2nd (intermediate)	3rd (minor)
Magnitude of variance	195.28	3.69	1.10	680.40	6.50	2.86
% of total	97.61	1.84	0.55	98.64	0.94	0.41
Nature of variation	*Size* joint variation of all dimensions	*Shape* contrast of length vs. width mostly	*Shape* contrast of length vs. height mostly	*Size* joint variation of all dimensions	*Shape* contrast of length vs. width mostly	*Shape* contrast of length and width vs. height

SCATTER DIAGRAMS OF SIZE AND SHAPE

The principal axes of an ellipsoid are mutually perpendicular. The principal axes of equal frequency ellipsoids can therefore be used as new orthogonal coordinate axes. Heretofore the sets of measurements (length, width, height) have been interpreted as dots in the orthogonal coordinate system of variables $X = (X_1, X_2, X_3)$ or

$$X' = \begin{bmatrix} X_1 \\ X_2 \\ X_3 \end{bmatrix} \text{ in colum-vector notation.}$$

The new coordinates Y of the same dots on principal axes with direction cosines U are given by $Y' = UX'$

$$\text{or} \quad \begin{bmatrix} Y_1 \\ Y_2 \\ Y_3 \end{bmatrix} = \begin{bmatrix} U_{11} & U_{12} & U_{13} \\ U_{21} & U_{22} & U_{23} \\ U_{31} & U_{32} & U_{33} \end{bmatrix} \begin{bmatrix} X_1 \\ X_2 \\ X_3 \end{bmatrix}$$

in extended matrix notation. The operation transforming the X- into the Y-coordinates is commonly referred to as a rotation. The sets of values of the new variables have been represented in two-dimensional scatter diagrams (Figures 5 and 6). The latter constitute views of the tridimensional diagram (Figures 3 and 4) seen in the direction of principal axes.

To determine 95 per cent equal frequency ellipses of groups of dots in bivariate scatter diagrams of the elements of $Y = (Y_1, Y_2, Y_3)$, the covariance matrices of these new variables must be known. These could of course be calculated directly from the values of Y. However, it is much simpler to rotate the X-covariance matrices to the Y-axes. Thus a sample with covariance matrix W on the X-axes has covariance matrix UWU' on the Y-axes since $Y' = UX'$. Upon rotation to the male principal axes, the male covariance matrix assumes its diagonal form, Λ, while the female covariance matrix remains non-diagonalized to the extent to which it differs from that of males. The reverse situation occurs when rotating to female principal axes.

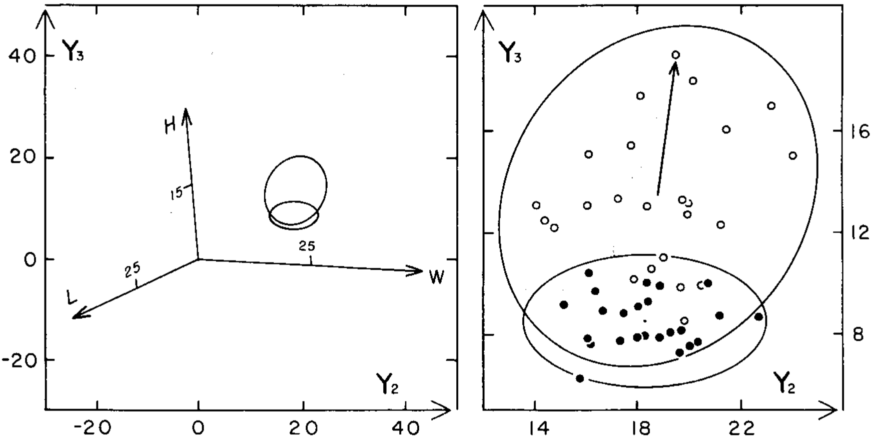

FIGURE 5
View perpendicular to the second and third principal axes of males; blown-up portion of Figure 4.

The cross sections of the male (Figure 5) and female (Figure 6) ellipsoids in the plane of (Y_2, Y_3) are both flattened in the direction of height. This suggests that there is less shape variation in carapace height than in carapace length and width. This may have no biological significance, however, since the order of magnitude of carapace height is smaller than that of length and width and all dimensions are expressed in millimeters. The influence of scales of measurement on principal components is discussed by Anderson (1958: 279). Standardizing variables (Teissier, 1955: 345) is certainly often preferable when only one group of observations is considered; the standard deviation of each variable is taken then as its unit and the covariance matrix becomes the correlation matrix. In the present case, however, this was not done as it would have led to different scales of measurement for males and females.

The cluster of female observations is clearly above that of males in Figures 5 and 6; this expresses the markedly greater carapace height of females. Although principal component analysis brings out well this difference of shape between the sexes, analyzing multivariate differences between groups of observations calls generally for discriminant functions. Discriminatory analysis leads to trends of maximum variation between groups of observations in the same way as principal components lead to trends of maximum variation within groups. The use of discriminant functions has been illustrated and discussed recently by Jolicoeur (1959). However, in the present study, the major interest lies in the nature and the magnitude of variation within local populations, and this calls for principal component rather than discriminatory analysis.

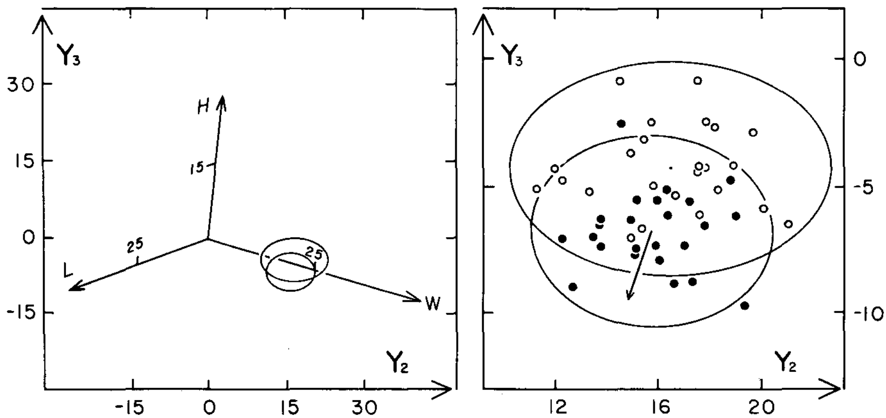

FIGURE 6
View perpendicular to the second and third principal axes of females.

Divergence in Shape During Growth

The major axis of each sex projects merely as a point on the plane of its own second and third principal axes (Figures 5 and 6). Correspondingly, size variation is absent in the scatter diagram of each sex with respect to its second and third principal components. On the other hand, male and female major axes are not parallel and the size variation of each sex is present with respect to the second and third principal components of the other sex. Thus large females tend to congregate upward from their mean in Figure 5 and large males downward from their mean in Figure 6.

The extent and the manner in which males and females diverge in shape as they increase in size can be judged from the projection of the major axis of each sex on the plane of the second and third axes of the other. These projections are indicated by arrows (upwards from the mean of females in Figure 5; downwards from the mean of males in Figure 6). Each arrow corresponds to a length of $\sqrt{5.99\lambda_1}$ units and its extremity can thus be visualized as the tip of an ellipsoid whose projections are the 95 per cent equal frequency ellipses represented. It is clear from this graphical analysis that there is a progressive divergence of relative carapace height between the sexes during growth. Also, carapace width appears to grow at a slightly higher rate in females.

CONCLUSIONS

Painted Turtles exhibit considerable variation in carapace dimensions. While the general nature and the magnitude of variation can be perceived by inspection of the data, they are made much more explicit by bivariate scatter diagrams and equal frequency ellipses. When considering multiple characters, however, multivariate statistical techniques are necessary to a unified analytical approach. Applied to carapace length, width and height, principal component analysis discloses three uncorrelated and mutually perpendicular trends of variation. The first principal component corresponds to a direction of size increase and can therefore be interpreted as a growth trend. The second and third principal components correspond to disjoint variation of the various characters and are consequently interpreted as trends of shape variation. Female painted turtles vary much more than males in size and slightly more in shape. While small turtles of both sexes are of comparable size and shape, females reach a greater size and their carapace becomes relatively higher than that of males.

The divergence in shape of males and females during growth is expressed by the difference in direction between the major axes of their covariance matrices. But covariance matrices are necessarily unequal when their principal components are not identical in direction and in length. The very fact that groups of living organisms have unequal covariance matrices can thus be of considerable biological significance since the way in which shape differences relate to size differences is of major importance in all biological disciplines directly or indirectly concerned with development and growth. Assuming covariance matrices of sets of data to be equal, as often done in theoretical statistics, would therefore frequently be unrealistic and misleading from the viewpoint of the biologist. Proper attention can be paid to growth divergences between groups of living organisms if principal component analysis is used. The latter seems the most promising method for the study of size and shape variation in complexes of biometrical characters.

The use of straight or curved lines is very common in relative growth studies and it has been customary to regard departures of data from growth curves as having little biological meaning. Such an attitude is difficult to maintain, however, when deviations of biometrical characters from growth curves are found to be correlated. The description of relative growth data in terms of several axes of variation, one of size and the others of shape, appears therefore more appropriate than their description in terms of a simple growth curve. The latter would generally constitute an over-simplification and would result in a loss of biological information.

At first, principal component analysis is most likely to be regarded by the non-mathematician as a highly arbitrary set of manipulations. Such a reaction should be readily dismissed, however, as soon as the geometrical meaning of the method is considered: principal component analysis merely leads to new angles of viewing data, angles best suited to disclose the nature and the magnitude of size and shape variation.

Summary

The applicability of principal component analysis to size and shape variation in living organisms is illustrated by a study of male and female painted turtles. Numerical and geometrical aspects are discussed in detail and it is concluded that principal component analysis of size and shape variation would be appropriate in relative growth studies whenever multiple biometrical characters are considered.

Acknowledgments

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