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NEW STATISTICAL METHODS FOR ALLOMETRY WITH APPLICATION TO FLORIDA RED-WINGED BLACKBIRDS

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Allometry, the association of size and shape in populations of organisms, is the subject of an extensive literature (Reeve and Huxley, 1945; Gould, 1966, 1975; Spielman, 1973; Sprent, 1972; Thorpe, 1976). In this paper we present new statistical methods for the study of size and shape, and use these methods to study the morphology of red-winged blackbirds, *Agelaius phoeniceus*, breeding in Florida.

We use definitions of size and shape variables that permit the study of the entire statistical distribution of a given variable. We offer these methods as an alternative to classical methods based on the allometric equation in which relations are summarized in single coefficients reflecting at best the mean trend of shape with some size variables. Our alternative goal is to determine visually and geometrically meaningful size and shape variables which permit the direct study of the association of size and shape.

This paper is in two parts. In the first part we discuss definitions of size and shape variables and summarize statistical results which include exact tests for size-shape associations (Mosimann, 1970, 1975a, 1975b). In the second part we use these methods to study geographic variation in red-winged blackbirds in Florida.

Throughout we consider the following situation: N individuals are independently sampled from some population. For each individual there are k positive measurements, all in the same units, say millimeters. For the i-th individual we then

have the "data" vector $\boldsymbol{x}_i = (x_{i1}, \cdots, x_{ik})$. The distribution of these data vectors in the population is given by the positive random vector $\boldsymbol{X} = (X_1, \cdots, X_k)$. For the purpose of developing statistical tests we assume that $\boldsymbol{X}$ has a multivariate lognormal distribution. However, some general results where the positive random vector $\boldsymbol{X}$ has an arbitrary distribution are presented first.

THE SHAPE AND SIZE OF A DATA VECTOR

Our approach is to conceptualize each sample data vector $\boldsymbol{x}$ as a pair of variables: (1) a "shape vector" variable, $\boldsymbol{Z}(\boldsymbol{x})$, which identifies the positively-directed ray from the origin on which $\boldsymbol{x}$ lies, and (2) a scalar "size" variable which identifies how far from the origin $\boldsymbol{x}$ is found on that positively-directed ray. A *size variable* $G(\boldsymbol{x})$: (1) has as its value some positive real number and (2) exhibits the homogeneity property $G(a\boldsymbol{x}) = aG(\boldsymbol{x})$ for all positive $\boldsymbol{x}$ and all $a > 0$. If now we divide each element of $\boldsymbol{x}$ by $G(\boldsymbol{x})$ we obtain a *shape vector* $\boldsymbol{x}/G(\boldsymbol{x}) = \boldsymbol{Z}(\boldsymbol{x})$. Examples of size variables are x_i, Σx_i, $(\Pi x_i)^{1/k}$. Examples of shape vectors are ratios $\boldsymbol{x}/x_i$, proportions $\boldsymbol{x}/\Sigma x_i$ and $\boldsymbol{x}/(\Pi x_i^{1/k})$. The norm $(\Sigma x_i^2)^{1/2}$ is a size variable, and the direction cosine vector $\boldsymbol{x}/(\Sigma x_i^2)^{1/2}$ is a shape vector. Two data vectors $\boldsymbol{x}_i$ and $\boldsymbol{x}_j$ are said to have the same "shape" if one is a scalar multiple of the other; that is $\boldsymbol{x}_i = a\boldsymbol{x}_j$ for some $a > 0$. Since the direction cosine vector $\boldsymbol{x}/(\Sigma x_i^2)^{1/2}$ is a shape vector, then two data vectors have the same shape if and only if they have the same direction cosines; that is, if and only if they lie on the same positively-directed ray from the origin in k-dimensional Euclidean space. This is consistent with Huxley's (1932) and Reeve

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and Huxley's (1945) use of the allometric equation: $x_2 = ax_1^b$, where (x_1, x_2) are simultaneous measurements on two parts of an individual. When $b = 1$, there is "isometry" (Reeve and Huxley, op. cit.); that is, no shape change. In fact then any two points (x_{11}, x_{12}) and (x_{21}, x_{22}) which satisfy the equation must lie on the same ray, and therefore have the same shape.

IN THE POPULATION AT MOST ONE SIZE VARIABLE CAN BE INDEPENDENT OF SHAPE

The population is represented by the positive random data vector X, or equivalently by an associated random shape vector $Z(X)$ and size variable $G(X)$. The lack of association of size and shape in the population is the condition that $Z(X)$ be statistically independent of size $G(X)$. "Isometry with respect to size G" is the statistical independence of some (every) random shape vector $Z(X)$ and size $G(X)$. For example, if the ratio vector X/X_k is independent of $(\Pi X)^{1/k}$, the geometric mean, then we have isometry with respect to the geometric mean. We briefly state theoretical results whose exact statements and proof are given elsewhere (Mosimann 1970, p. 937; 1975a, pp. 209–210).

If size G is independent of some shape vector (say $X/\Sigma X$) then G is independent of every shape vector. Thus if $G = X_1$ is independent of the proportion vector $X/\Sigma X$ it must also be independent of ratios X/X_i, direction cosines $X/(\Sigma X^2)^{1/2}$, etc. Because of this result we can speak unambiguously of the independence of shape and size, G. On the other hand assume shape varies and suppose a size variable G is independent of shape. Then no other size variable can be independent of shape. Thus if X_1 is independent of shape then none of the size variables $X_2, \Sigma X, (\Sigma X^2)^{1/2}$, etc. can be independent of shape. The independence of G and shape implies that no other size variable is independent of shape, and the only exception is virtually no exception at all; namely, if H is a size variable such that for some $a > 0$,

$\mathrm{Prob}(H = aG) = 1$, then H is also independent of shape.

Since in the population, shape can be independent of at most one size variable, it will never be surprising to find associations of size and shape in biological studies and there is no necessary reason for shape to be related in a similar fashion to two different size variables.

BUT IN THE SAMPLE, SHAPE COULD APPEAR TO BE INDEPENDENT OF MORE THAN ONE SIZE VARIABLE

We add that one can construct theoretical distributions in which shape may be "almost" independent of more than one size variable. For example, suppose all positive probability is on a single ray from the origin, so that shape is constant and thereby independent of all size variables. Then let shape vary just a little about this single ray. Then shape is nearly independent of several size variables so that for biological purposes one could say that several size variables were unrelated to shape. Samples from such a population might show no significant association of shape with any of several size variables.

THE CHOICE OF A SIZE VARIABLE IS IMPORTANT

In allometric work prior to 1970 there was virtually no recognition that isometry depends critically on the choice of a size variable. One standard approach to testing isometry *implicitly* chooses the geometric mean as a size variable (Mosimann, 1970, p. 938). Historically isometry was defined in terms of the allometric equation with $b = 1$. Under this deterministic model with $b = 1$, all data vectors $x = (x_1, x_2)$ fall on the same ray from the origin, and shape is constant and independent of all size variables as just noted above. However in all biological studies, shape varies and the data vectors never all lie in the same ray. When this happens shape can be independent of at most one size variable. To discuss isometry one must speak of isometry with respect to a specified size variable.

The Independence of Shape and Size in a Lognormal Population

We now assume the random data vector X has a multivariate lognormal distribution. Let $Y_i = \log X_i$, $i = 1, \cdots, k$. Then the log data vector $Y = (Y_1, \cdots, Y_k)$ has a multivariate normal distribution. Now consider the shape vector X/X_k. Its log vector is $(Y_1 - Y_k, \cdots, Y_{k-1} - Y_k, 0) = Q^*$, say. Q^* is a linear transformation of Y, and therefore Q^* itself has a multivariate normal distribution (in turn implying that X/X_k has a lognormal distribution).

Now consider some size variable G. Shape (every shape vector) is independent of G if and only if X/X_k is independent of G, and this latter is true if and only if Q^* is independent of $\log G$.

Whenever $\log G$ is a linear combination of Y (that is $G = \Sigma a_i Y_i$) then $\log G$ is normally distributed and G is lognormally distributed. Then Q^* and $\log G$ jointly follow a multivariate normal distribution. In this case Q^* and $\log G$ are independent if and only if the multiple correlation coefficient of Q^* with $\log G$ is zero. Thus whenever $\log G = \Sigma a_i Y_i$, the hypothesis that shape is independent of G is equivalent to the hypothesis that the multiple correlation of Q^* with $\log G$ is zero.

Some remarks are appropriate. The independence of shape and size variables like X_i, or $(X_i X_j)^{1/2}$ or any geometric means $(\Pi X_i)^{1/s}$, where there are s coordinates in the product, may be tested exactly since in each of these cases $\log G = \Sigma a_i Y_i$. (Since G is a size variable, $\Sigma a_i = 1$ but some a_i's may be zero or negative.) Also, not every shape vector is lognormal (e.g. $X/\Sigma X$), but $X/\Sigma X$ is independent of G whenever X/X_k is.

How to Test for Isometry With Respect to a Lognormal Size Variable

Suppose that G is lognormal so that $\log G = \Sigma a_j Y_j$. Now consider N independently sampled data vectors $x_i = (x_{i1}, \cdots, x_{ik})$, $i = 1, \cdots, N$, of k measurements each, as in part 1. Each data vector is a realization of the random vector X which is assumed to have a multivariate lognormal distribution. Take logarithms of each measurement (base 10 or base e) obtaining $y_i = (y_{i1}, \cdots y_{ik})$, $i = 1, \cdots, N$. Each of these vectors is then a realization of Y which under the assumption has a multivariate normal distribution. For each y_i calculate $(y_{i1} - y_{ik}, \cdots, y_{i(k-1)} - y_{ik}, \Sigma_{j=1}^{k} a_j y_{ij})$, $i = 1, \cdots, N$. Each of these vectors is a realization of the random vector $(Y_1 - Y_k, \cdots, Y_{k-1} - Y_k, \log G)$. The sample multiple correlation coefficient R of the random vector $(Y_1 - Y_k, \cdots, Y_{k-1} - Y_k)$ with $\log G$ is then used to calculated the F statistic

$$F(k - 1, N - k) = [R^2/(1 - R^2)]/[(k - 1)/(N - k)],$$

to test the hypothesis that the population multiple correlation coefficient is zero (Anderson, 1958, pp. 89–92). This hypothesis is equivalent to "shape is independent of size G" or "X is isometric with respect to G." Furthermore this sample F-value occurs as standard output for multiple regression using the General Linear Models procedure of SAS, the Statistical Analysis System (Barr et al., 1976), when $\log G$ is used as the "dependent" variable, and $Y_i - Y_k$, $i = 1, \cdots, k - 1$, as "independent" variables. The F-value (mean square model)/(mean square error) is in fact the desired statistic for testing that the population multiple correlation coefficient is zero, and hence that shape is independent of the size variable G. The calculations are illustrated in the Appendix.

This Multiple Correlation Coefficient Measures the Relation of Shape and Size

More important than the test for association of shape with size is the measurement of the degree of such association. The multiple correlation coefficient above provides a measure which does not depend on the particular choice of log-shape vector used. Let $Q = (Y_1 - Y_k, \cdots,$

$Y_{k-1} - Y_k$). Any log-shape vector which is linear in Y will have the same multiple correlation coefficient of log shape with log size as Q. More generally, any invertible linear function of Q, say $U = QA$, also represents log-shape, since (1) $Q = UA^{-1}$ gives back Q, and (2) taking antilogs of the elements of Q gives the original shape vector and hence potentially any other shape vector.

The multiple correlation coefficient of Q with log G will be the same as that of U with log G since this coefficient is the ordinary correlation coefficient of log G with that linear combination of Q which has maximal correlation with log G. Since U is a linear combination of Q, and conversely, both have the same multiple correlation coefficient with log G. One consequence is that any such U may be used in place of Q in the test procedure of the previous section.

THE COMPLEXITY OF ALLOMETRIC HYPOTHESES

There is a great deal of complexity to the formulation of allometric hypotheses even apart from the choice of size variables (cf. Mosimann, 1975a, 198–199). The independence of shape and size in k dimensions does not imply the independence of shape and size in $(k - 1)$ dimensions, nor conversely. Let X be multivariate lognormal. Then of the two statements (1) k-dimensional shape is independent of $(\Pi_1^k X_i)^{1/k}$, (2) $(k - 1)$-dimensional shape is independent of $(\Pi_2^{k-1} X_i)^{1/(k-1)}$ both may be simultaneously true, both false, or either true while the other is false. To see this let Σ be the covariance matrix of Y, the logarithms of X, and denote by t_i the sum of the elements in the i-th column of Σ. Then statement (1) is true if and only if all column totals are equal: $t_i = t$, $i = 1, \cdots, k$ (Mosimann, 1970).

Next denote the first $(k-1)$ coordinates of X by X_1, with its logarithms, Y_1. Denote the covariance matrix of Y_1 by Σ_1. This comprises the initial $(k - 1)$ row and

column elements of Σ. Let s_i be the sum of the elements in the i-th column of Σ_1. Then statement (2) is true if and only if $s_i = s$, $i = 1, \cdots, k - 1$. It is possible to have Σ such that (1) and (2) are both false, true, or either is true separately.

Nor does the complexity of allometric hypotheses stop here. There are k different $(k - 1)$-dimensional shape vectors depending on the choice of a coordinate X_i which is dropped. The independence of $(k - 1)$-dimensional shape and size for one choice does not imply such independence for another choice.

For example consider male and female map turtles, *Graptemys geographica*, which were studied by Mosimann (1958, Fig. 2.9). (His conclusions are verified by retesting with the new methods here.) Carapace length (L) increases relatively faster than either width (W) or height (H), but width and height maintain the same ratio. Given the data vector (H, W, L), three-dimensional shape (H/L, W/L, 1) is not independent of "volume" $(LWH)^{1/3}$, since W/L and H/L decrease with increasing size. However for (H, W), two-dimensional shape (H/W, 1) is independent of "cross section" $(HW)^{1/2}$. On the other hand for (H, L), two-dimensional shape (H/L, 1) is not independent of "transverse section," $(HL)^{1/2}$.

SEPARATE STATISTICAL ANALYSES OF SIZE AND SHAPE VARIABLES

The association of shape with size is but one facet of studies of size and shape variables. In connection with such studies, it may be of interest to study variation in a log size variable (like Y_i) or a log shape variable alone (e.g. $Y_i - Y_k$). Under the lognormal assumption for X, both Y_k and $Y_i - Y_k$ are univariate normal variables. Standard statistical techniques (like the analysis of variance) may be applied to either. The advantages of the distinct definitions of size and shape variables used here are that they permit study of the entire distributions of the relevant random variables.

GEOGRAPHIC VARIATION IN SIZE
IN BIRDS, INTRODUCTION

In a study of geographic variation in wing length (size) in twelve species of birds over the United States, all showed an increase in wing length northward and westward from Florida (James, 1970). The twelve species, which included the downy woodpecker *Dendrocopus pubescens,* blue jay *Cyanocitta cristata,* white-breasted nuthatch *Sitta carolinensis* and meadowlark *Sturnella magna,* were of diverse morphology, habitat and diet. Thus the common geographic trend in size is not likely to be explained by factors which differ among these species.

In the eastern and central states the pattern of size variation even reflects topographic features such as the Appalachian Mountains, the Ozark and Edwards plateaus, and the valley of the Mississippi River. Most data were available for the downy woodpecker, and its wing length was correlated with climatic indices combining temperature and humidity, particularly wet-bulb temperature. Other species showed similar relations (James, 1970, Tables 7, 8). These observations, together with consideration of King and Farner's (1964) equilibrium model for heat loss in an individual bird, led to an empirical reformulation of Bergmann's Rule as

"Intraspecific size variation in homeotherms is related to a combination of climatic variables that includes temperature and moisture. Small size is associated with hot humid conditions, larger size with cooler or drier conditions."

This idea is an extension of the observations of Hamilton (1958, 1961) for vireos and is consistent with the findings and conclusions of Power (1969) for the red-winged blackbird in the Great Plains. While not proof of cause and effect, and not without exceptions (Niles, 1973), the relationships provide evidence that the thermoregulatory consequences of size are important determinants of species that exhibit geographic variation.

Others do not believe that climatic factors are very important in determining such geographic variation in size. For example, Rosenzweig (1968) found that mammalian carnivores tend to be larger at higher latitudes, in colder areas and in deserts, a result consistent with the above studies. However he interpreted the negative correlation of size with actual evapotranspiration in tundra and deserts to mean that the low productivity of the plants in these regions (and presumably the unpredictable supply of prey) made large size advantageous. McNab (1971) and Rosenzweig (1966) also reject the Bergmannian interpretation in favor of one based on predator size. MacArthur (1958), Schoener (1965), Cody (1973) and Hespenheide (1973) have championed the thesis that the size of a species is at least partly determined so as to maximize differences among related species coexisting in a given area, thereby reducing interspecific competition.

These explanations are not mutually exclusive. While we cannot test the various explanations here, we would like to state that any explanation for birds should be consistent with the following:

(1) Variation may change within a few decades at a single locality. Thus Power (1970a) shows changes in wing length and width of the lower mandible in breeding red-winged blackbirds at localities in central Canada and in the central United States over periods of about 20 years.

(2) A species may show rapid differentiation in the course of expanding its range. The house sparrow, introduced into North America in the middle of the 19th century shows the same degree of geographic variation in morphology as native species (Johnston and Selander, 1964, 1971, 1973).

(3) A number of North American species of diverse morphology and habits show gradual changes in wing length with the smallest extreme in the southeast and increases northward and westward. Secondary variations with-

TABLE 1. *Arithmetic means of measurements (mm) and weight (gm) for the 12 geographic blocks.*

Geographic block with block number*		Number in block		Bill depth X_1		Bill length X_2		Leg length X_3		Tail Length X_4		Wing length X_5		Weight (Grams)	
		Male	Fe-male	Male	Fe-male	Male	Fe-male	Male	Fe-male	Male	Fe-male	Male	Fe-male	Male	Fe-male
24-81	1	5	9	8.2	7.3	22.9	19.4	46.7	42.3	89.2	69.6	115.2	92.2	53.5	36.7
26-80	2	52	67	8.7	7.5	23.6	19.8	48.1	42.7	82.9	67.6	108.1	89.0	47.2	32.1
26-81	3	8	9	8.7	7.4	23.8	19.8	48.8	43.5	86.4	70.1	111.1	91.4	51.1	34.8
26-82	4	6	5	8.7	7.8	23.2	19.9	48.8	42.4	87.3	70.4	113.3	92.1	51.5	36.0
28-80	5	14	12	8.6	7.6	23.2	19.5	48.8	42.7	89.3	70.3	114.3	90.9	52.4	33.0
28-81	6	42	42	9.1	7.6	23.8	19.4	49.3	43.7	87.9	70.3	113.9	92.3	52.4	35.2
28-82	7	10	6	9.2	7.8	23.1	19.7	48.6	43.2	88.7	71.3	114.9	93.7	55.4	36.2
29-82	8	11	18	8.8	7.6	23.4	19.5	49.0	43.5	87.5	70.9	114.2	93.7	56.1	38.3
29-83	9	15	17	9.3	7.7	23.1	19.6	49.0	43.1	87.0	69.4	114.2	93.5	54.0	34.9
30-82	10	8	18	9.1	7.6	23.3	19.3	48.2	42.8	90.1	70.0	114.6	93.6	55.5	34.5
30-84	11	10	6	9.0	7.9	23.5	19.8	48.4	43.5	87.0	70.7	115.9	94.7	56.4	37.2
30-87	12	7	6	9.5	8.1	23.6	19.9	48.8	43.2	88.7	72.9	117.2	96.7	58.5	36.1

* Latitude and longitude of the southeastern corner of the 1-degree block followed by block number used in Figure 2

in this overall pattern conform to a surprising extent to changes in topography, such as the Appalachian Mountains, the Mississippi River, and the Ozark and Edwards plateaus (James, 1968, 1970).

Because of these three points we do not believe that interspecific competition and predation are prime sources of the observed geographic size variation in birds. At a minimum we believe that climatic sources warrant further study.

Whatever explanation is offered, our methods permit the study not only of size variation but of associated shape variation and hence offer more facts for interpretation than currently available.

RED-WINGED BLACKBIRDS IN FLORIDA

The red-winged blackbird, *Agelaius phoeniceus,* is one of the most abundant and widespread species of bird in North and Central America. In connection with a study of crop depredation, the U.S. Fish and Wildlife Service collected a number of them at 99 localities in Florida during the breeding seasons of 1964, 1965 and 1966. In an initial analysis presented by Howe, Laybourne and James (1977), the specimens were organized into seven geographic units, defined partly on the basis of Howell and Van Rossem (1928) who felt

that four populations deserved subspecific recognition, primarily based on a southward trend to paler females. Considering only morphological data, Howe et al. (op. cit.) described a pattern of gradually increasing size (wing length, weight) in the seven regions from southeastern to northwestern Florida. Weights and wing lengths of red-winged blackbirds published elsewhere (Ridgway, 1902; Amadon, 1956) indicate that this trend continues throughout the eastern and central United States. These findings are consistent with those of Power (1969, 1970a, 1970b), who applied multivariate techniques in a detailed study of morphological variation in red-winged blackbirds in the Great Plains. The pattern of variation in Mexico and Central America is currently under study by Dickerman and Hardy (Dickerman, 1965; Hardy and Dickerman, 1965).

ORGANIZATION OF THE DATA

Taking the Florida data set and dividing the state of Florida into 1-degree latitude-longitude blocks, we consider birds within a block together. Each block is approximately 65 miles on a side, but some contain little land mass. Blocks with fewer than five individuals of either sex are excluded, leaving 12 blocks (Table 1, Fig. 1) and a total of 188 adult males and 215
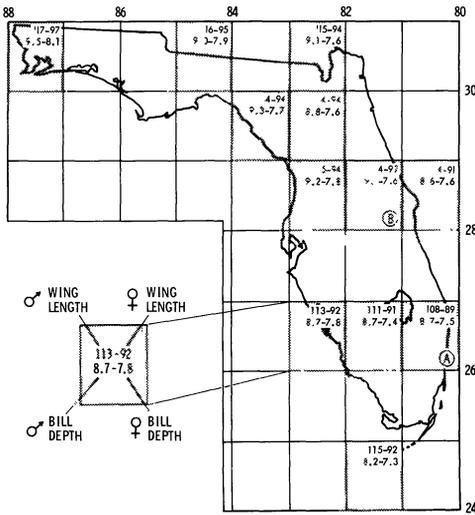
FIG. 1.—Means of wing length and bill depth for adult red-winged blackbirds for 12 one-degree latitude-longitude blocks in Florida. In tables, in other figures, and in the text, block A is referred to as "Eastern Everglades" and block B as "Central Florida."

adult females. Two blocks have sufficiently large numbers of birds of both sexes to permit a study of variation within them. The "Eastern Everglades" block (A in Fig. 1) has 52 males and 67 females collected between 26° and 27° north latitude and 80° and 81° west longitude. Most are from the vicinity of Fort Lauderdale. The "Central Florida" block (B in Fig. 1) has 42 males and 42 females collected between 28° and 29° north latitude and 81° and 82° west longitude. Most are from the vicinity of Orlando.

Measurements were made by Roxie Laybourne from museum study skins now held by the United States National Museum of Natural History. There are five measurements (in mm) for each bird: bill depth (at nostril), X_1; bill length (exposed culmen), X_2; toe plus tarsus length, X_3; tail length, X_4; and wing length (chord), X_5. We let $X = (X_1, \cdots, X_5)$ and denote the respective logarithms by $Y_i = \log_{10}X_i$, $i = 1, \cdots, 5$. In addition we have the weight of each bird.

The mean measurements for the blocks show that in both sexes wing length, tail length, and bill depth all increase regularly across Florida from southeast to northwest, with their smallest extreme (except for bill depth) in the Eastern Everglades (lat. 26, long. 80). The weight data show this same general pattern (Table 1, Fig. 1). Note also that mean wing length decreases from west to east at all latitudes and that birds of the southernmost block, in the Florida Keys (24, 81) are similar in weight and wing length to those of middle and northern Florida.

THE MULTIVARIATE LOGNORMAL ASSUMPTION

Our bird measurements are all positive variables, and it is natural to use a probability distribution for positive random variables, like the lognormal, in their analysis. In Figure 2, log (bill length/bill depth) is plotted against log wing length, and 95% ellipses are fitted to the data under the assumption of a normal distribution for these log variables. The ellipses describe the points rather well. In Figure 3, following the example of Jolicoeur and Heusner (1971), we briefly examine the consequences of choosing a bivariate lognormal, as opposed to normal, distribution for (tail length, wing length) = (X_4, X_5). Illustrated are the data for males from the Eastern Everglades and Central Florida blocks, together with 95% ellipses. Also drawn (dashed lines) are the antilog curves of the 95% ellipses fitted to the log data, (Y_4, Y_5). There is little difference due to either choice.

Our preference for the lognormal model is based on the following: (1) it is a model for positive measurements; (2) it affords considerable theory for allometry since ratios are lognormal if the original measurements are; (3) it allows the statistical procedures we have outlined, which are exact under the model; (4) it describes our data at least as well, perhaps better, than the normal model.

ANALYSIS OF VARIANCE OF SIZE AND SHAPE VARIABLES

Geographic variation in various log size and log shape variables was examined for
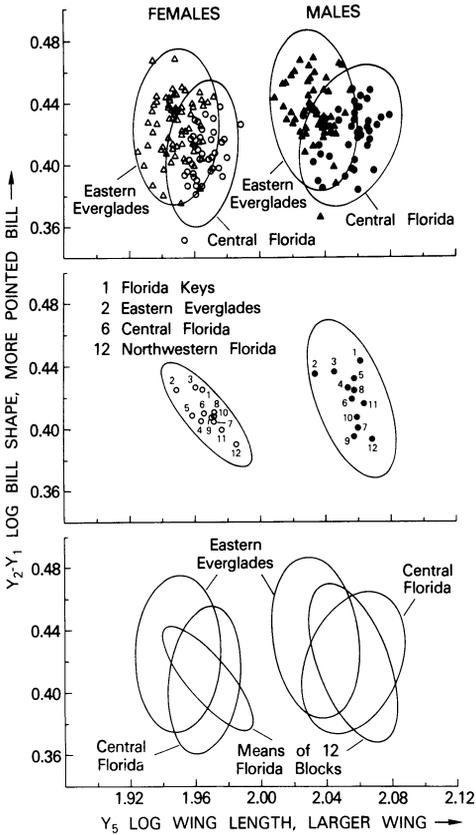
FIG. 2.—The relationship between size (log wing length, Y_5) and bill shape (log bill length/log bill depth, $Y_2 - Y_1$) for (a) the Eastern Everglades and Central Florida populations, (b) means of the 12 Florida blocks identified by block number in Table 1 and (c) both a and b, showing that the interlocality trend is not a reflection of the within-locality variation. Ellipses are 95% equal frequency ellipses calculated from the appropriate covariance matrices, using the appropriate values of Hotelling's T^2.

FIG. 3.—The relationship between tail length, X_4, and wing length, X_5, for males from the Eastern Everglades and Central Florida blocks. Solid-line ellipses are 95% equal frequency ellipses calculated from the covariance matrix of (X_4, X_5). Dashed line curves are the antilog of the 95% equal frequency ellipses calculated from the covariance matrix of the log measurements (Y_4, Y_5) using Hotelling's T^2. There is little difference in the respective curves.

each sex separately over the 12 Florida blocks (188 males, 215 females). For each variable, variance component estimates were obtained from a one-way analysis of variance (Table 2). The between-block component is an estimate of the variance of the means across blocks, and hence a measure of the geographic variation. Each analysis presupposes that the within-block error variance is constant over the 12 blocks, but major conclusions will not be disturbed by some departure from this as-

sumption. (Each variable in Table 2 is normally distributed whenever the data vector X is lognormally distributed.)

We first consider log size variables in Table 2. Most of these show considerable geographic variation in both sexes. However, the variation in log (toe plus tarsus) length, Y_3, is negligible, and there is no significant variation in log bill length, Y_2. Log bill depth, Y_1, shows considerable geographic variation. This is greater for males (between, 213; within, 222) than for females (between, 78; within, 230). For each sex, log wing length, Y_5, has a between component which is larger than its within component. This high between/within ratio supports the traditional use of wing length as a variable apt to show geographic variation. Log weight has a high between/within ratio for males, but a much lower ratio for females. This and the high within-block variance for females (1,315) show weight to be an unreliable indicator of size in breeding-season females.

Various log-shape variables are given in Table 2. Log (tail length/wing length), $Y_4 - Y_5$, shows no significant geographic variation in males, and only negligible such variation in females, even though

TABLE 2. *Variance components between and within localities for various log size and log-shape variables. Components estimated using one-way analysis of variance are given separately for males and females. For between-block components significance from zero is indicated by **, .01 level; and *, .05 level. All component entries must be multiplied by 10^{-6} to obtain the actual variance estimates.*

	Log Size Variables							
	Log bill depth Y_1	Log bill length Y_2	Log toe plus tarsus length Y_3	Log tail length Y_4	Log wing length Y_5	Log geometric mean $(Y_1 + \cdots + Y_5)/5$	Log geometric mean of bill $(Y_1 + Y_2)/2$	Log weight (gms)
Males								
Between 12 blocks	213**	13	19**	155**	148**	57**	60**	923**
Within block	222	232	144	335	127	66	129	580
Females								
Between 12 blocks	78**	9	15**	77**	113**	30**	19**	673**
Within block	230	227	146	244	86	65	150	1,315

	Log Shape Variables						
	Log (Bill length/ Bill depth) $Y_2 - Y_1$	Log (Toe plus tarsus length/Bill length) $Y_3 - Y_2$	Log (Tail length/Toe plus tarsus length) $Y_4 - Y_3$	Log (Bill depth/Wing length) $Y_1 - Y_5$	Log (Bill length/Wing length) $Y_2 - Y_5$	Log (Toe plus tarsus length/Wing length) $Y_3 - Y_5$	Log (Tail length/Wing length) $Y_4 - Y_5$
Males							
Between 12 blocks	212**	12	111**	135**	197**	108**	10
Within block	391	346	475	354	319	239	175
Females							
Between 12 blocks	99**	48**	39**	40**	180**	78**	13**
Within block	314	301	352	294	271	190	137

both log tail length and log wing length showed considerable geographic variation. A relatively constant wing/tail ratio may be important in flight. In contrast, log ((toe plus tarsus) length/wing length), $Y_3 - Y_5$, shows considerable geographic variation. Recall that log (toe plus tarsus) length showed only negligible geographic variation, while log wing length showed considerable such variation. Whatever adaptations to perching and hopping are reflected in toe plus tarsus length, variation in this length does not follow closely variation in wing length, and a range of ratios can occur. Finally, log (bill length/ bill depth), $Y_2 - Y_1$, shows considerable geographic variation which is associated with geographic variation in log bill depth, but not log bill length.

Briefly, geographic variation is considerable in wing length, tail length, bill depth, and weight, but absent or negligible in bill length and toe plus tarsus

length. Wing length is a good size variable to use in studying geographic variation, since it is easy to visualize and has a high between/within variance component ratio.

THE ASSOCIATION OF FIVE-DIMENSIONAL SHAPE WITH SIZE

Next we will consider the association of size and shape within the Central Florida and Eastern Everglades blocks and also geographically across the 12 blocks.

For each of the two within-block analyses the test procedure of part one is followed directly. For example, for females from the Central Florida block, there are 42 data vectors each with five measurements ($N = 42$, $k = 5$). For geographic associations of size and shape there is a between-block analysis for each sex. For each sex and each of 12 blocks the means of the log measurements ($\bar{Y}_1, \cdots, \bar{Y}_5$) are found. For each sex there are then 12 data vectors ($N = 12$, $k = 5$). The procedure

TABLE 3. *Five-dimensional size-shape associations in Florida red-winged blackbirds. Entries are the multiple* R^2 *of log five-dimensional shape* $(Y_1 - Y_5, Y_2 - Y_5, Y_3 - Y_5, Y_4 - Y_5)$ *with the given log size variable, as well as with log weight. Significance from zero is indicated by* *, .05 *level and* **, .01 *level.*

	Log geometric mean $(Y_1 + \cdots + Y_5)/5$	Log geometric mean of bill $(Y_1 + Y_2)/2$	Log wing length Y_5	Log bill length Y_2	Log weight
Males					
Between Florida Blocks N = 12	.73*	.89**	.87**	.65	.78*
Eastern Everglades N = 52	.28**	.71**	.51**	.79**	.07
Central Florida N = 42	.15	.50**	.66**	.71**	.05
Females					
Between Florida Blocks N = 12	.80*	.87**	.91**	.62	.51
Eastern Everglades N = 67	.12	.47**	.46**	.70**	.17*
Central Florida N = 42	.17	.76**	.40**	.84**	.21

of section 8 is followed with these 12 mean vectors as data vectors.

First consider the association of five-dimensional shape with the size variables: wing length, X_5; bill length (culmen), X_2; geometric mean of all measurements $(\Pi_1^5 X_i)^{1/5}$ and geometric mean of the bill measurements $(X_1 X_2)^{1/2}$. The squared multiple correlation of log 5-D shape $(Y_1 - Y_5, \cdots, Y_4 - Y_5)$ with the log of each of these size variables is given in Table 3.

Recall from part one there is no reason to expect similar size-shape associations for the different choices of a size variable. Table 3 confirms this. The squared multiple correlation coefficients of log shape with log size (see part one) demonstrate a variety of size-shape associations, both between and within blocks:

(1) Log wing length, Y_5, is very highly associated with five-dimensional shape both between blocks and within Eastern Everglades and Central Florida. The relationship is stronger between blocks than within them. Recall that log wing length shows considerable between-block variation.

(2) Log bill length, Y_2, shows sizeable but not significant size-shape association between blocks, but shows stronger significant size-shape association within the two blocks. Recall from Table 2 that bill length varies very little between blocks. Here, the within-block association of size and shape is higher than that between blocks.

(3) The log geometric mean of all measurements shows very little association with shape within blocks, but higher associations between blocks.

(4) The log geometric mean of bill measurements is significantly related to five-dimensional shape, both between and within blocks, with higher associations between blocks.

(5) Log weight is poorly correlated with log shape within blocks, but between-block associations are higher.

Two features of this allometric methodology are illustrated by these analyses. First, there are various shape associations with different size variables. Second, there is the possibility of associating shape with a size variable such as weight that was not included in the data vector.

THREE-DIMENSIONAL SHAPE OF BILL AND WING MEASUREMENTS

Since we have demonstrated geographic variation in bill shape as well as in wing

TABLE 4. *Some size-shape associations in the three-dimensional vector (bill depth, bill length, wing length) = (X_1, X_2, X_5). Log_{10} measurements are (Y_1, Y_2, Y_5). Log "bill shape" is log (bill length/bill depth) = $Y_2 - Y_1$. In the first column are squared multiple correlation coefficients of log three-dimensional shape $(Y_1 - Y_5, Y_2 - Y_5)$ with log wing length, Y_5. In the second, third and fourth columns are ordinary correlation coefficients of log bill shape, $Y_2 - Y_1$, with Y_5, Y_2 and Y_1 respectively. For Between-block components significance from zero is indicated by ** , .01 level; and *, .05 level.*

	Log shape, $(Y_1 - Y_5, Y_2 - Y_5)$ with log wing length Y_5 R^2	Log bill shape, $Y_2 - Y_1$		
		with log wing length, Y_5	log bill length, Y_2	log bill depth, Y_1
Males				
Between Florida blocks N = 12	.84**	−.52	.03	−.95**
Eastern Everglades N = 52	.30**	−.16	.53**	−.65**
Central Florida N = 42	.57**	.32*	.64**	−.67**
Females				
Between Florida blocks N = 12	.88**	−.80**	−.19	−.94**
Eastern Everglades N = 67	.43**	.05	.66**	−.70**
Central Florida N = 42	.30**	.20	.56**	−.55**

length we shall now analyze the association of the three-dimensional shape of the vector of bill and wing measurements (X_1, X_2, X_5) with wing length. First, however, consider associations of the log measurements (Y_1, Y_2, Y_5) themselves within the Central Florida and Eastern Everglades blocks. There is little to no correlation among these measurements. Of the 12 ordinary correlation coefficients among these Y's (three for each sex and block) only the two largest (.38, .30) are significant. Thus there is little within-block association of the logs of bill depth, bill length, and wing length in these adult birds.

We now look at size-shape associations among the bill measurements and wing length. In Table 4 we give squared multiple correlation coefficients of log three-dimensional shape $(Y_1 - Y_5, Y_2 - Y_5)$ with log wing length Y_5. The geographic association of size and shape across blocks is much stronger than the within-block association. Also in Table 4 we consider log (bill length/bill depth), $Y_2 - Y_1$, henceforth called log bill shape. Ordinary

correlation coefficients of log bill shape with the logs of bill length, bill depth and wing length are given. (Relationships with log wing length are pictured in Figure 2.) Log bill shape is related geographically to log bill depth, but not log bill length. This is consistent with the virtual lack of geographic variation in log bill length. Relatively stouter bills in larger birds are due to increased depth, not decreased length. This geographic association is not reflected within the Central Florida and Eastern Everglades blocks. There the associations of log bill shape with the logs of bill depth Y_1 and bill length Y_2 are consistent with the more or less independent variation of these measurements themselves just noted. The associations of $Y_2 - Y_1$ with Y_2 and Y_1 are nonetheless real. Longer bills are relatively narrower bills, and one can, for example, imagine possibilities for natural selection operating on either bill shape or on bill length. In any event the geographic association of bill shape with bill depth is not a reflection of an allometric trend within a given block.

Our between-block analyses are based

on means and seem relatively immune to possible unequal measurement error variances for bill depth and length. However, our within-block analyses might be affected by unequal measurement error variances. (Virtually all statistical analyses, regression and principal component analysis as well as size-shape, would be so affected.) We do not have repeated measurements on the same individual that would allow us to evaluate the effects of unequal error variances. But we have examined a simple error model and do not believe effects of unequal error variances could alter the conclusion that the geographic association of bill shape with either wing length or bill depth is not explained by the within-population allometric trend.

DISCUSSION

These allometric methods for the study of size-shape associations are applicable to N independently sampled vectors of positive measurements expressed in the same units (e.g. mm). They are not intended, nor suitable, for the study of shape change throughout the growth of a single individual. The choice of size variables is an important, but almost totally neglected, aspect of allometric studies. For example, Jolicoeur's procedure (Jolicoeur, 1963; Gould, 1975, p. 260) implicitly chooses the geometric mean of all measurements as a size variable (Mosimann, 1970). In the present study the geometric mean of all the measurements does not have a simple visual interpretation. However, wing length is easy to visualize, and has a high between/within variance component ratio. This latter renders wing length the best discriminator among populations of those size variables presented in Table 2. Our methods have permitted us to select among size variables and also to compare shape with a size measurement, weight, not derived from the data vector.

The usual use of the word "size," such as by Bonner (1965), involves some idea of total size. He considers three such measurements: weight, volume, and length,

and concludes that no one measure is ideal for all organisms. We believe, with Bonner, that no one size measurement is ideal. In fact, even within a single species no one size measurement answers all purposes, and allometric relations with respect to bill size may be as interesting as those with respect to wing length. The methods here allow such choices.

The relationship of our method with those of other allometric studies has been discussed elsewhere (Mosimann, 1970, pp. 942–944). Here we amplify some remarks made there concerning the use of discriminant (canonical) analysis and principal component analysis to define size variables. We shall assume that the analyses are based on the covariance matrix Σ of the logarithmic variables, or for a model with unequal measurement errors, are based on the model covariance matrix resulting after subtraction of the error matrix from Σ (Jolicoeur and Heusner, 1971; Hopkins, 1966; Mosimann et al., 1978).

In discriminant analysis, the random variable corresponding to the first canonical axis, say $\Sigma a_j Y_j$, has a maximal between/within variance ratio in the space spanned by the canonical axes. Sometimes this variable may be defined as size. However, the underlying variable $\Pi X_j^{a_j}$ is a size variable only if $\Sigma a_j = 1$. When this is not so then $\Pi X_j^{a_j}$ and $\Sigma a_j Y_j$ contain shape as well as size information. If another population is studied, new coefficients for the first canonical axis, $\Sigma b_j Y_j$ will likely result, and the geometric meaning of "size" will therefore differ. (Remarks directly analogous to these apply to defining the first principal component of Σ as "size.")

In our approach the aim is not to produce automatically uncorrelated "size" and "shape" variables as above. We first produce geometrically meaningful definitions of shape (proportionality) and size. Then whether or not shape and size are related is a matter of empirical observation, and a subject for statistical analysis.

Consider wing length, which has a fixed geometric definition across populations.

This measurement has traditionally been used by ornithologists. We have shown that wing length has the largest between/within variance ratio of the size variables considered. Within the set of geometrically meaningful, simply measured, size variables considered by us, wing length achieves the desirable maximization of the between/within ratio.

We have shown that geographic variation in the size of red-winged blackbirds in Florida is consistent with that observed by Power (1970a) for this species in the Great Plains, and with trends in other species observed by James (1970). Birds in the panhandle region of Florida are larger (longer-winged, heavier) and have relatively deeper bills. Bill length shows no geographic variation, so bills are deeper but not longer. The resulting geographic association of longer-winged birds with relatively deeper bills is not a reflection of size-shape associations within populations at single localities, since the two within-block analyses do not reveal a similar association. Therefore the geographic variation in shape is not a simple by-product of size variation. (This is consistent with Gould's remarks on scaling, 1971, 1975, p. 277.)

In their study of Galapagos ground finches (*Geospiza* spp.), Abbott et al. (1977, Fig. 11) consider 16 sympatric species pairs. There were three measurements for each pair: their "overlap in diet," their ratio of beak depths, and their ratio of culmen lengths. There was no correlation of "overlap in diet" with the culmen length ratio, but a significant negative correlation of overlap with the beak depth ratio. The authors do not find this surprising since "the main component of diet of finches is seeds and fruits . . . which are cracked; it is the depth and width components of the beak which chiefly determine its crushing strength." It is interesting to note that over a relatively small part of the range of a single species, the red-winged blackbird, we have found negligible variation in culmen

length but considerable variation in bill depth.

Bill shape is a feature of evolutionary importance within the blackbird family Icteridae. Beecher (1951) concluded that the family as a whole has undergone radiation from a seed-eating finch-like ancestor into fruit, nectar, and insect-eating forms. He emphasized the importance of the gaping motion (the forceful opening of the bill) in adaptations toward a more insectivorous or frugivorous diet.

Given the observations of Abbott et al. (1977) and Beecher's (1951) conclusions, it is tempting to think that the variation we have observed within a single species might reflect adaptation to diet, and that northwestern Florida blackbirds are larger because their relatively deeper, more conical, bills are better adapted for eating seeds. In such a case increase in size might follow a change in bill shape.

This explanation would not seem to account for the fine block-to-block gradations in wing length in Florida blackbirds, nor would it account for the large birds with shallow bills which occur on the Keys. Further, such an explanation would not explain the concordant increase in wing length observed by James (1968, 1970) for other species of diverse diet. Considering its whole range, the largest red-winged blackbirds are found on the hot-dry Mexican plateau (Dickerman, 1974) and in the Great Plains of the United States (Power, 1970a) and this is consistent with the notion that climatic variables underlie the observed geographic trend in size. We cannot select among hypotheses—themselves not necessarily mutually exclusive—here.

We do believe that simultaneous consideration of shape and size variation will be a considerable aid in the interpretation of size trends in North American birds.

SUMMARY

New methods for allometry are presented. The definition of random size and shape variables which are visually mean-

ingful is stressed. In contrast to classical methods which attempt to summarize size-shape associations with single coefficients, the methods here permit the study of the entire joint distribution of size and shape variables. The diversity of allometric hypotheses is revealed, and the choice of size variable is shown to be important. Under a multivariate lognormal assumption, exact statistical tests are presented.

The methods are illustrated by study of geographic variation in the red-winged blackbird in Florida. Bill depth and bill shape, but not bill length, show interesting covariation across Florida. The observed bill variation for the red-winged blackbird is suggestive of variation found across species of Darwin's finches, and is also consistent with size trends observed in a variety of bird species in eastern North America.

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APPENDIX

We give an illustration of allometric calculations with artificial data to allow ease of entry into the computer. The situation imagined is that of 10 individuals with four measurements on each. There are thus $N = 10$ data vectors with $k = 4$ variables

$X1$	$X2$	$X3$	$X4$
2	5	15	20
3	8	21	30
4	9	22	31
4	10	25	28
9	15	28	40
10	9	26	37
11	8	22	30
8	6	20	25
6	9	20	25
2	6	20	18.

The corresponding Y's (log base 10 of the X's) for the first two data vectors are

$Y1$	$Y2$	$Y3$	$Y4$
0.30103	0.69897	1.17609	1.30103
0.47712	0.90309	1.32222	1.47712.

Let $Z_1 = Y_1 - Y_4$, $Z_2 = Y_2 - Y_4$, $Z_3 = Y_3 - Y_4$. The values of "log shape" for the first two data vectors are then

$Z1$	$Z2$	$Z3$
-1.00000	$-.602060$	$-.124939$
-1.00000	$-.574031$	$-.154902.$

Values of the log size variables $M = (Y_1 + Y_2 + Y_3 + Y_4)/4$ and Y_4 for the first two data vectors are

M	$Y4$
0.86928	1.30103
1.04489	1.47712.

The squared multiple correlation of M with Z_1, Z_2, Z_3, with $F(3,6)$, is

F VALUE	PROB $> F$	R-SQUARE
8.47	0.014	0.809.

Hence four-dimensional shape is significantly associated with the geometric mean of all measurements $(X_1X_2X_3X_4)^{1/4}$. The squared multiple correlation of Y_4 with Z_1, Z_2, Z_3 again with $F(3,6)$, is

F VALUE	PROB $> F$	R-SQUARE
5.00	0.045	0.714.

Hence the association of four-dimensional shape with the fourth measurement, X_4, is significant, but not so strong as for $(X_1X_2X_3X_4)^{1/4}$. However, 2-D shape $(1, X_2/X_1)$, or simply X_2/X_1, is not significantly associated with X_2. The squared correlation of $Y_2 - Y_1$ with Y_2 with $F(1,8)$ is

F VALUE	PROB $> F$	R-SQUARE
0.03	0.877	0.003.

This also could have been tested using the ordinary correlation coefficient of $Y_2 - Y_1$ with Y_2 which is $-.056$.