THE MEASUREMENT OF OVERALL BODY SIZE IN BIRDS

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ABSTRACT.—We compared a number of univariate and multivariate measures of body size used commonly in ornithological research, including eight multivariate measures (from principal components analyses), plus skull length, ulna length, tibiotarsus length, wing length, and weight. Analyses are based on 26 measurements on three randomly selected male and three randomly selected female Savannah Sparrows (*Passerculus sandwichensis*) from each of 53 different geographic localities throughout the species' range. Six of the eight principal components analyses provided essentially the same information about body size. Analyses based on the variance-covariance matrix of raw or log-transformed data provided first axes that varied most from the other multivariate estimates of size. Among the univariate measures, ulna length, wing length, and body weight contributed information that diverged from the multivariate measures of overall size. Weight better represents general size (i.e. PC I) than wing length, but because of variation in reproductive condition, weight is a far better measure in males than in females. Wing length is not a representative measure of body size. Inasmuch as each principal components analysis provides information about body size on PC I, we encourage researchers to choose among the various approaches according to analytical objectives rather than methodological simplicity or general utility. *Received 29 November 1988, accepted 18 May 1989.*

ORNITHOLOGISTS are frequently faced with the challenge of measuring body size in birds. A measure of overall size is required to test hypotheses predicting patterns of geographic variation (e.g. Bergmann's or Allen's rules; James 1970, Johnston and Selander 1971, Niles 1973, Fleischer and Johnston 1982, Handford 1983, Murphy 1985). An estimate of body size is also required to test hypotheses about the evolution of sexual dimorphism in body size (e.g. Hamilton and Johnston 1978, Johnston and Fleischer 1981, Fleischer and Johnston 1984, McGillivray and Johnston 1987, Rising 1987b). In addition, species must be ranked by body size to test models that predict size ratios among coexisting species in ecological communities (e.g. Ricklefs and Cox 1977, Ricklefs and Travis 1980, Haefner 1981, Sabo and Holmes 1983, Miles and Ricklefs 1984, Pulliam 1985, Brown and Maurer 1986, Miles et al. 1987). In physiology, standard measures of metabolic activity are frequently expressed as a function of body size, and it is often useful to examine the relationship of structures or organs *relative* to overall body size (e.g. Fisher 1947, Kendeigh 1976, Blem 1984, Calder 1984, Paladino 1985, Rising 1987a, Packard and Boardman 1988).

Body size, however, is difficult to measure. Perhaps the best measure of overall body size is total mass, but reliable information on mass is often difficult to obtain. Although recent compilations of data contribute much to our knowledge of the mass of birds (Clench and Leberman 1978, Dunning 1984), the available data on mass are all too often unsatisfactory because of seasonal and diet-related variability (e.g. Niles 1973). Consequently, ornithologists commonly use a measure of wing length as an estimate of relative body size (e.g. James 1970, Lack 1971, Snyder and Wiley 1976, Payne 1984, Jehl and Murray 1986, Zink and Remsen 1986). Wing length is measured easily on museum study skins and living birds; however, at least in some cases, it is a poor estimate of body size when compared with other, more precise measurements (Rising 1988). Even discounting measurement error, many factors that are difficult to quantify affect the wing length of a bird. First, wing feathers are subject to wear. Thus, the reliability of measurements of wing length decreases as the feathers progressively become more worn. This may be especially important in studies of sexual dimorphism, because in many species behavioral differences between the sexes lead to sexual differences in rates of feather wear. Second, the wing length of an individual varies from year to year—even though the bird's skeleton is completely ossified (and thus, in this sense, the bird is completely grown).

For example, Rising (unpubl. data) captured and measured (to the nearest mm) wild Savannah Sparrows (*Passerculus sandwichensis*) over many years. The average of the differences of measurements of wing length of males captured twice or more during the same year is −0.13 mm (range −4 to +2 mm, $n = 32$, SE = 0.24), but the average differences in wing length of males captured and measured during more than one year is +1.17 (range −2 to +6 mm, $n = 23$, SE = 0.43). A sign test shows that within seasons there are as many positive changes as negative changes in the measured wing lengths of individuals. Among years, wing lengths appear to increase more often from year to year than decrease ($P = 0.05$). Thus, wing length, to some extent, increases with age. Because of the difficulties of obtaining accurate information about body size from wing-length data, people have often used measures of individual bones (e.g. Johnston and Selander 1971) or of organ weight (e.g. Power 1970) as estimates of body size.

Alternatively, ornithologists have computed combinations of characters (e.g. the sum of many measures; McGillivray and Johnston 1987, Rising 1987b), or multivariate measures (such as principal component or discriminant function scores; Johnston and Selander 1971, Niles 1973, Zink 1986, Rising 1988) that account for the covariation among characters and extract a "size" axis. There has been considerable discussion concerning which of the models of principal components analysis best extracts a "size component" (Jolicoeur 1963, Mosimann 1970, Mosimann and James 1979, Bookstein et al. 1985, Somers 1986, Rohlf and Bookstein 1987). Here we empirically compare size axes from eight different principal components models and five univariate measures of body size, including mass (weight) and wing length, to determine the relative similarity of these estimates of overall body size.

METHODS

We selected two sets of 159 Savannah Sparrows to generate the various measures of overall size. One set consisted of three females from each of 53 different geographic localities, scattered throughout the species' range, and the other consisted of three males from each of the same 53 sites. Virtually the entire range of phenotypic variation in the species was represented in these samples, including relatively large individuals from Sable Island, Nova Scotia, and the Aleutian Islands, and relatively small individuals from the arid prairies, as well as large-billed birds from the coastal salt marshes of Mexico and small-billed birds from the interior of western North America (see Rising 1987b). The three individuals were selected at random from among larger samples assembled by Rising for studies of geographic variation. The 26 variables were measured (by Rising) for each individual (Table 1); only individuals for which all 26 variables could be measured were used in these analyses. The measurements include 24 skeletal elements, wing length (length of the chord of the longest unflattened primary wing feather), and mass (assessed in the field prior to preparation). The skeletal measurements are discussed in greater detail in Rising (1988).

Principal components analysis (PCA) summarizes covarying patterns of variation in morphometric data to produce independent composite variables that are loosely interpreted as size and shape axes (e.g. Pimentel 1979, Bookstein et al. 1985). A PCA of the variance-covariance matrix of logarithmically transformed data summarizes multivariate allometric size variation in the first eigenvector and associated component (Jolicoeur 1963). Slightly different versions of size and shape axes are produced by using different transformations of the data prior to PCA (e.g. Pimentel 1979, Reyment et al. 1984, McGillivray 1985, Somers 1986). Although the original models of PCA-based size and shape employed logarithms and the variance-covariance matrix (e.g. Jolicoeur 1963, Mosimann 1970), ornithological applications frequently use raw data because birds display determinant growth (e.g. Johnston and Selander 1971, Niles 1973, Johnston and Fleischer 1981).

In addition, Mosimann (1970) noted that variation in general size is summarized by the sum or mean of the log-transformed variables for each individual. This approach to measuring size reiterates the concept of isometric size where each variable contributes equally to the composite size estimate (see Jolicoeur 1963, McGillivray 1985). In PCA, an isometric size vector can be extracted through a number of manipulations, including size-constrained PCA (e.g. Somers 1986, 1989; McGillivray and Johnston 1987, Rohlf and Bookstein 1987).

For both males and females separately, we estimated overall size with eight multivariate approaches and five single variables. Traditional PCA using raw and log-transformed data was employed to estimate size with the first component (i.e. PC I) from variance-covariance (i.e. RCV and LCV) and correlation matrices (i.e. RCR and LCR). Because there is some debate as to the importance of the logarithmic transformation when using PCA (Reyment et al. 1984, see also Bryant 1986), we used an intermediate approach that incorporated Spearman's rank correlation matrix into the usual PCA (SPR; e.g. see Lebart et al. 1979). The use of ranks loses information on absolute scale, but it obviates the necessity to choose among various transformations (e.g. logarithms, square roots). Furthermore, the resultant rank correlations are resistant

TABLE 1. Means ($\bar{x}$), ranges (minimum to maximum), and coefficients of variation (CV) for 159 male and 159 female Savannah Sparrows.

Variable[a]	Females			Males		
	$\bar{x}$	Range	CV	$\bar{x}$	Range	CV
Skull length	27.2	24.9–30.5	3.3	27.7	25.7–31.0	3.6
Skull width	14.0	12.9–15.0	2.7	14.4	13.2–15.6	2.9
Premaxilla length	5.9	4.7–7.6	9.5	6.0	4.9–8.4	9.8
Premaxilla depth	3.4	2.9–4.2	7.4	3.5	3.0–4.3	7.7
Narial width	6.4	5.5–7.2	5.2	6.7	6.0–7.5	5.0
Premaxilla width	5.1	4.4–6.6	6.7	5.3	4.4–6.5	6.7
Interorbital width	2.5	1.9–3.1	9.0	2.6	2.0–3.6	9.3
Mandibular length	18.3	16.5–20.8	4.9	18.7	16.8–21.6	5.1
Gonys length	4.9	3.6–6.3	9.4	5.0	4.0–6.7	9.7
Mandibular depth	1.8	1.6–2.4	9.1	1.9	1.6–2.6	10.1
Coracoid length	16.6	15.3–18.4	3.2	17.5	16.2–19.2	3.1
Scapula length	19.0	16.8–21.7	4.1	19.9	17.9–22.3	3.7
Femur length	16.9	15.6–19.3	3.3	17.4	15.5–19.7	3.8
Femur width	1.2	1.1–1.4	5.6	1.3	1.1–1.5	7.1
Tibiotarsus length	28.0	25.3–31.2	3.9	28.8	25.2–31.9	4.2
Tarsometatarsus length	20.2	18.4–22.7	3.9	20.8	18.1–22.9	4.6
Humerus length	17.8	16.7–19.7	2.9	18.6	17.1–20.4	3.0
Ulna length	20.5	18.7–22.2	3.1	21.7	20.0–23.9	3.2
Carpometacarpus length	11.3	10.3–12.7	3.6	12.0	10.5–13.3	5.4
Hallux length	7.9	7.1–9.5	4.9	8.2	7.0–9.5	5.3
Sternum length	19.4	17.6–22.6	4.4	20.7	18.9–23.2	3.8
Sternum depth	8.8	7.6–10.3	5.5	9.4	8.2–10.7	5.1
Keel length	18.2	15.7–21.7	5.5	19.9	17.8–22.8	4.7
Synsacrum width	10.3	9.2–11.9	3.9	10.6	9.1–12.0	4.1
Mass	19.2	14.9–27.0	13.1	20.0	15.3–30.2	11.6
Wing length	66.3	59.4–72.2	4.1	70.2	61.4–82.7	4.0

[a] Measurements are in mm except for mass (g).

to problems because of outliers or curvilinearity that may bias estimates of covariances and correlations.

In addition, we extracted an isometric size vector using size-constrained PCA (SIZ; Somers 1986), and two isometric size analogues based on doubly centered PCA with raw and log-transformed characters and a correlation matrix (i.e. RDC and LDC; e.g. see Mosimann 1970, Darroch and Mosimann 1985, McGillivray and Johnston 1987, Somers 1989). This doubly centered approach to PCA is analogous to correspondence analysis (e.g. see Greenacre 1984, Lebart et al. 1984).

The five univariate estimates of overall size were body weight (WT), wing length (WING), skull length (SKLL), tibiotarsus length (TBTR), and ulna length (ULNA). We chose this subset of five variables because they represent various aspects of an entire bird. Body weight and wing length are traditional size approximations in spite of the problems described above. The remaining three osteological measures represent size variation in three distinct body regions—the skull (SKLL), wing (ULNA), and leg (TBTR)—that display patterns of size variation that may or may not covary with WT and WING (e.g. Power 1970, Johnston and Selander 1971, Niles 1973).

To evaluate similarities between the various size "components," a matrix of Pearson product-moment correlations was generated among the 13 size measures. Because the various size measures are not independent (i.e. each measure is based on all or part of the entire data matrix), the correlations between the size variables are biased. As a result, these correlations were not compared statistically (i.e. by inferring probabilities), but the resultant correlation matrix for each sex was summarized with principal coordinates analysis to spatially display the relative proximity of the various size measures (Gower 1966). The resultant two-dimensional configurations were compared with Procrustes analysis to identify where the male and female patterns differed (Schonemann and Carroll 1970, Gower 1975, Digby and Kempton 1987).

RESULTS

We obtained the means, ranges, and coefficients of variation for each of the 26 variables (Table 1). Mass (body weight) has the highest coefficient of variation among the variables. Mass also has the highest variance of the variables and will have the greatest influence of any single character on PC I in any analysis based on the variance-covariance matrix. The

TABLE 2. Percentages of total variance explained by each of the first three components of the principal components analyses.

	Percent variance explained					
	Males			Females		
Model	PC I	PC II	PC III	PC I	PC II	PC III
LCR	53.2	13.8	4.8	44.5	16.6	5.4
LCV	56.0	12.7	7.1	35.5	25.1	11.9
RCV	62.3	18.8	5.3	52.3	21.6	8.4
RDC[a]	—	36.5	20.0	—	33.0	19.4
RCR	53.5	14.2	4.7	45.4	16.6	5.2
SPR	49.4	12.5	5.1	40.6	15.8	6.1
LDC[a]	—	34.3	11.2	—	32.0	13.5
SIZ	52.0	13.9	5.6	42.5	16.6	6.4

[a] Size effects removed by subtraction before analysis; percentages are relative to remaining variation (i.e. shape alone).

large variance of this character underscores the difficulty of using mass as a measure of overall size. All of the birds used in these analyses were in breeding condition, and thus variation in mass due to seasonal differences in amounts of body fat is slight. However, the variance in female mass is increased because some were laying eggs, others incubating, and the presence of an egg affects mass considerably.

In these data, the measures of bill size (e.g. premaxilla length, width, and depth, gonys length, and mandibular depth; Table 1) also show relatively large coefficients of variation. This variation reflects the relatively large geographical variation in bill size and shape in this species. Different features might show relatively large variability in other species.

The relative proportion of the total variation summarized by the first three components of each PCA is given in Table 2. In all cases, the first or "size" axis for the males summarized a greater proportion of the total variation than in the females. As a result, PC II and PC III for the females are larger than those for the males (i.e. comprise larger proportions of the total relative variation). This implies that the females exhibit relatively more shape variation than the males. The logarithmic transformation results in little change in the relative variance in the first three components when the correlation matrix is used (i.e. RCR and LCR), but this contrasts with the results based on the variance-covariance matrix (i.e. RCV and LCV). PC I from the analysis using Spearman's rank correlation summarized less of the total variation than either the log-correlation or raw-correlation methods, whereas results from the size-constrained approach resembled those from the log-correlation analysis.

In doubly centered PCA, the row means as well as the column (character) means are subtracted from each observation. Consequently, size effects are removed and technically a PC I-size axis does not exist. As a result, PC I that we report for the doubly centered PCA (see Table 2) is a vector of row means and the percent variance explained by the shape components is proportional to the sum of the trace of the 26-variable correlation matrix based on shape effects alone.

Pearson's product-moment correlations among the PC I scores from the eight PC analyses, and five selected variables are summarized in Table 3. These correlations show that the first components from LCR, RDC, RCR, SPR, LDC, and SIZ are very highly correlated with each other (i.e. they give essentially the same information about body size). Of the selected univariate variables, the measure of leg length

TABLE 3. Correlations among various measures of size; 159 Savannah Sparrows of each sex from 53 localities (males above the diagonal; females below).

	LCR	LCV	RCV	RDC	RCR	SPR	LDC	SIZ	WT	WING	SKLL	TBTR	ULNA
LCR	—	0.95	0.89	0.98	1.00	0.98	0.99	1.00	0.85	0.54	0.85	0.89	0.75
LCV	0.90	—	0.79	0.90	0.95	0.93	0.98	0.94	0.83	0.40	0.91	0.82	0.58
RCV	0.84	0.73	—	0.96	0.90	0.85	0.86	0.90	0.88	0.84	0.69	0.78	0.76
RDC	0.97	0.86	0.94	—	0.98	0.95	0.96	0.98	0.87	0.68	0.80	0.87	0.78
RCR	1.00	0.90	0.84	0.97	—	0.98	0.99	1.00	0.86	0.55	0.85	0.89	0.76
SPR	0.97	0.90	0.80	0.93	0.97	—	0.97	0.98	0.83	0.49	0.83	0.87	0.73
LDC	0.97	0.97	0.81	0.94	0.97	0.94	—	0.99	0.85	0.50	0.88	0.86	0.69
SIZ	1.00	0.91	0.85	0.97	1.00	0.97	0.98	—	0.85	0.56	0.84	0.88	0.76
WT	0.66	0.74	0.79	0.74	0.66	0.65	0.71	0.67	—	0.55	0.73	0.74	0.60
WING	0.49	0.30	0.80	0.63	0.49	0.45	0.42	0.50	0.34	—	0.31	0.43	0.62
SKLL	0.78	0.85	0.57	0.72	0.78	0.78	0.80	0.78	0.52	0.24	—	0.75	0.44
TBTR	0.86	0.76	0.67	0.81	0.86	0.83	0.81	0.84	0.57	0.31	0.66	—	0.69
ULNA	0.74	0.47	0.69	0.75	0.74	0.69	0.62	0.73	0.40	0.55	0.32	0.63	—

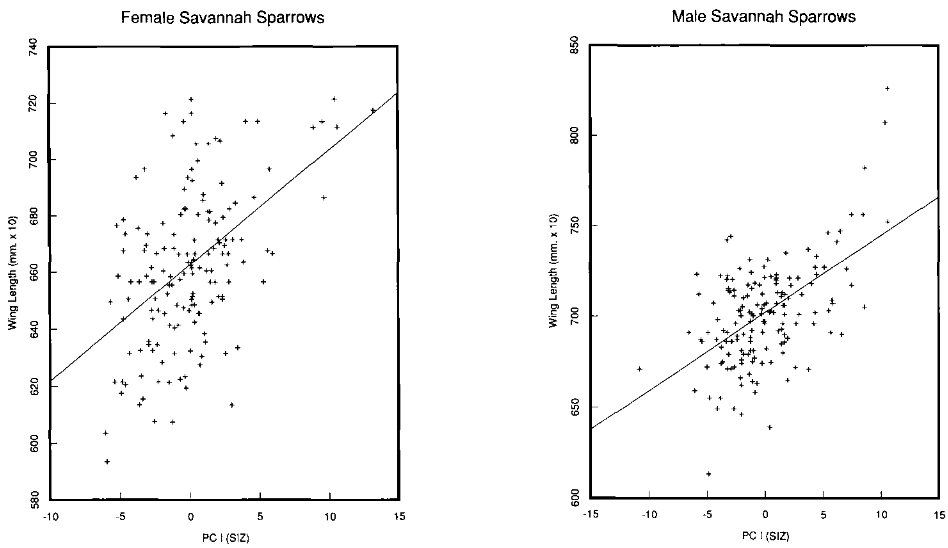

Fig. 1. Bivariate plots of wing length vs. PC I (SIZ: size-constrained PCA) for 159 male and 159 female Savannah Sparrows from 53 localities.

(TBTR, or tibiotarsus length) is the best approximation to multivariate body size. Ulna length, or possibly some other measure of wingbone length, might be better correlated with overall body size if we had included only individuals from migratory populations, but in these data sets there are several individuals from nonmigratory populations, and these nonmigratory birds have relatively small bones in the pectoral girdle.

Wing length, measured on museum study skins, is not particularly representative of overall body size (correlations with PC I scores range from 0.30 to 0.84 and are highest with scores from RCV, the most different multivariate measure of size). In plots of wing length vs. size (Fig. 1) considerable scatter is evident, and the correlation coefficients are inflated by outliers. For example, in males (Fig. 1), the correlation between wing length and SIZ falls from 0.56 ($n = 159$; Table 3) to 0.47 with the removal of three very large individuals from Sable Island, Nova

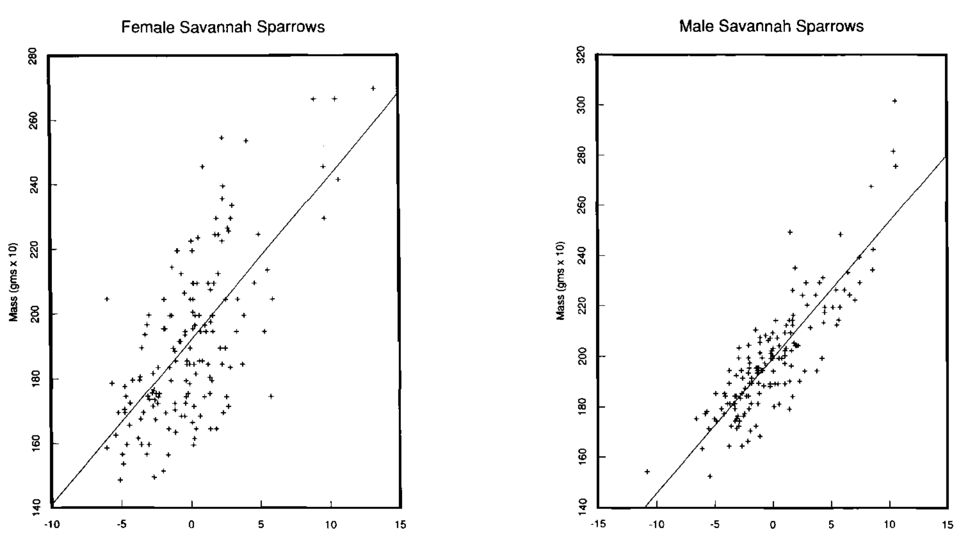

Fig. 2. Bivariate plots of mass vs. PC I (SIZ) for male and female Savannah Sparrows.

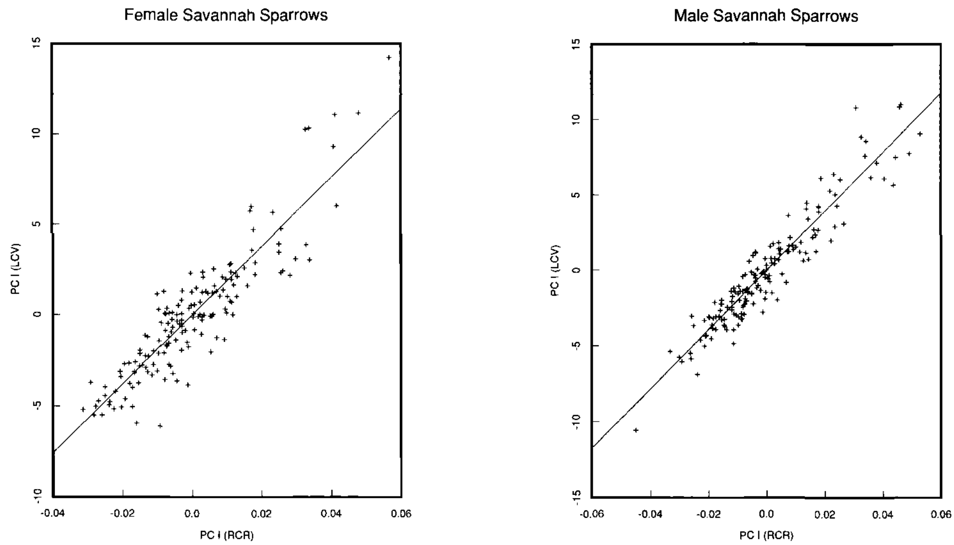

Fig. 3. Bivariate plots of PC I scores from variance-covariance matrix of log-transformed data (LCV) and from correlation matrix of raw data (RCR) for male and female Savannah Sparrows. These are the two most widely used PCA models.

Scotia. Rising (1988) similarly found wing length to be a poor estimate of body size among wintering Savannah Sparrows.

Overall, body weight is more representative of general size than wing length in these data (Fig. 2). Nonetheless, in females, variation in reproductive condition substantially decreases the correlation with multivariate size (Fig. 2; Table 3). The multivariate measures (e.g. PC I scores) seemingly are not sensitive to outliers (Fig. 3). Logically, the PCA based on Spearman's rank correlations should be the most resistant to outliers, and this likely explains why the variance summarized by the first three components is less in SPR (Table 2).

Patterns in the correlation matrix between the various estimates of size are summarized into two dimensions with principal coordinates analysis and the associated minimum spanning tree (Fig. 4). Of the variation in the male correlation matrix, 70% is represented by the first two axes. The univariate measures radiate out from the multivariate size measures. As might be expected, PC I for the raw variance-covariance matrix is most divergent among the multivariate size approximations. In contrast, the univariate measures of ULNA, WING, and WT exhibit more divergence, implying that these variables contain unique information relative to the multivariate size estimates and to the other univariate measures as well. By definition these univariate measures share less information with the multivariate estimates, but these correlation-based distances are compromised because the various size estimates are not independent (Mosimann pers. comm.). Statistical methods to disentangle this non-independence feature need to be developed to further evaluate these patterns.

The principal coordinates analysis of the correlation matrix for the female size measures summarized 65% of the variation in the first 2 axes (Fig. 4). The pattern based on the female results resembles that for males with the exception that SKLL and WT are displaced somewhat. The shift of female WT away from the cluster of multivariate size measures emphasizes the earlier statements that weight in females is more variable, and hence provides unique information, relative to the other size measures.

We used Procrustes analysis to identify points in the two configurations that spatially differ. Among the 13 points, ULNA, SKLL, WT, and WING were identified as the most different between the male and female patterns. As a result, TBTR is the only univariate measure that approximates the multivariate size measures for both males and females. In addition, the relative positions of the eight multivariate size measures are similar for males and females.

We found (Table 3; Fig. 4) that three of the principal component models give nearly iden-

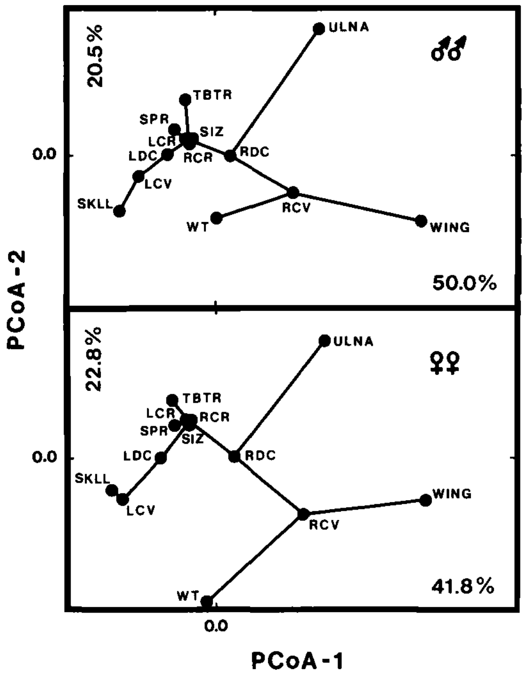

Fig. 4. Two-dimensional principal coordinate ordinations of estimates of size for male and female Savannah Sparrows. The points are connected by minimum spanning trees.

tical estimates of body size (i.e. RCR, LCR, and SIZ). Three other PC approaches (SPR, LDC, and RDC) provide similar size measures, whereas LCV and RCV diverge from these estimates. Of the five univariate measures, TBTR and SKLL resemble the multivariate size variables most, but SKLL varies between the sexes.

DISCUSSION

We suggest that the controversy surrounding the choice of PCA model to provide the best estimate of body size is somewhat misdirected. PC I from any of the widely used PC models gives essentially the same information about body size relative to any single variable. Thus, if an investigator is interested solely in extracting a multivariate measure of overall body size from a number of measurements, any principal component analysis will suffice. Perhaps the easiest to calculate is based on the RDC model where the average of all the measurements for a given individual approximates traditional multivariate size (e.g. see Mosimann 1970). This approach was used by McGillivray and Johnston (1987).

In selecting a PC model to analyze data, it is more important to consider the inherent aspects of the analysis, such as the usefulness of the shape information summarized by the other components (e.g. PC II and PC III). Rising (1988), for example, compared the results of RCR and LCV analyses and found (as we did here) that they gave similar information in PC I, but that PC II of RCR and PC III of LCV gave similar information. PC II of LCV, in that study, was greatly influenced by a single, relatively variable character (interorbital width) that was not highly correlated with the other measures. Thus, in that study, the RCR analysis gave more useful multivariate shape information in PC II and PC III. Our point is that analyses using the variance-covariance matrix are influenced by the variation of each character relative to the variation of all other characters. This may or may not be desired if shape differences are of interest.

When possible, univariate measures such as wing length and body weight should be avoided as estimates of overall body size. A great deal of variation *within any size range* in wing length is evident, and variables that are independent of body size (such as wear and age) doubtless contribute greatly to this variance. If a single variable is required to estimate overall body size, our results indicate that tibiotarsus length (or probably any other measure of leg length) approximates many of the multivariate measures, and this result is consistent for both male and female Savannah Sparrows.

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