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Measurement Error of External and Skeletal Variables in Birds and Its Effect on Principal Components

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Assessment of measurement error is important for studies that use morphometric variables to make statistical inferences about biological phenomena (e.g. studies of adaptive radiation, taxonomic relationships, interspecific competition, age and sex determination, body condition, heritability, and growth). Use of variables with large measurement errors can result in Type II statistical errors (i.e. accepting false null hypotheses, see Toft and Shea 1983). The effect of measurement error, however, has been ignored in most morphometric studies. Those researchers that have assessed measurement error used techniques that identified interobserver or session biases (e.g. Nisbet et al. 1970, Zink 1983, Arendt and Faaborg 1989) or the absolute precision of particular measurements (e.g. Bortolotti 1984, Francis and Wood 1989). However, measurement error can be assessed properly only when it is evaluated *relative* to variation among individuals in a sample (Schluter and Smith 1986, Bailey and Byrnes 1990).

To assess relative measurement error of several external and skeletal measures in Rufous-collared Sparrows (*Zonotrichia capensis*), and external measures in American Coots (*Fulica americana*), we used repeated measurements and Model II analysis of variance (Schluter and Smith 1986, Lessells and Boag 1987, Bailey and Byrnes 1990). In addition, we examined the effects of such error on principal component analysis using morphological variables.

The specimens used represent subsets of larger collections of birds obtained for other research objectives. The morphological variables were selected for these research objectives and were not chosen specifically for a study of measurement error. Before conducting the present study of measurement error, we had intended that all variables be included in our respective studies. Hence, our data are typical of "real world" avian morphological data, except that we measured individual specimens more than once.

Twenty-one male Rufous-collared Sparrows were mist-netted in Belen, Catamarca Province, Argentina (27°39'S, 67°02'W). Thirteen skeletal characters were measured three times on each sparrow: skull width, partial skull length (from the base of the maxilla to the foramen magnum), coracoid length, width of the proximal end of the scapula, scapula length, sternum length, keel depth, synsacrum width (distance between acetabulae), width of proximal end of femur, femur length, tibiotarsus length, humerus length, and ulna length (see Robins and Schnell 1971 for detailed

descriptions). Measurements were collected using digital calipers (±0.01 mm), a TRS-80 datalogger, and the LESSOFT software package (Marcus 1986). We measured four external variables twice with dial calipers (±0.01 mm) on each prepared skin: length of unflattened wing, outer rectrix length, hind toe plus claw length, and tarsus length. Some sparrows had missing measurements because of specimen damage. Sparrows with one or missing variables were excluded from principal component analysis.

American Coots were shot near Minnedosa, Manitoba (50°16'N, 99°50'W). Thirteen external morphological characters were measured twice on each of 50 adult coot (26 males and 24 females; sex determined by dissection). We measured body length, wing length, wing chord, tarsus length, middle toe length, middle claw length, hind toe length, culmen length, bill length, bill height, bill width, head width, and head length (measurements were defined by Alisauskas and Ankney [1987] except bill length, which was defined by Petrie [1988]). Total body length and wing length were measured with a flat metal ruler (±0.5 mm), flattened wing chord was measured with a wing board (±0.5 mm), and the remaining characters were measured with dial calipers (±0.05 mm).

Each data set was collected by a single observer (Arnold for the coots and N. Howard for the sparrows). Measurements were taken on all birds in a sample before individuals were remeasured. Remeasurements were made without knowledge of previous measurements. We attempted to use the same level of care in measuring these specimens as in obtaining data from other birds measured only once; however, both observers were aware that measurement error was being assessed, and they may have subconsciously been more careful (e.g. Mills and Knowlton 1989).

Model II ANOVA (PROC NESTED; SAS Institute Inc. 1985) was used to estimate percent measurement error (%ME) for each morphological character in each of the three data sets. After estimating within- and among-bird components of variance (s^2_{within} and s^2_{among}), we calculated %ME using the following formula (Bailey and Byrnes 1990): $\%ME = [s^2_{within}/(s^2_{among} + s^2_{within})] \times 100$. We then employed principal component analysis (PCA) for each data set using the variance-covariance matrix from log-transformed data (PROC PRINCOMP; SAS Institute Inc. 1985). Principal components analysis is a multivariate technique that may be used for summarizing data sets combining large numbers of variables, and for detecting linear relationships among variables (Pimentel 1979, SAS Institute Inc. 1985). For each PCA axis, we obtained either two (sparrow and coot external data) or three (sparrow skeletal data) independent component scores for each bird. We again used Model II ANOVA to examine relative measurement error of these component scores.

In Rufous-collared Sparrows, percent measurement error (%ME) varied from 0.24% (tibiotarsus length) to 59.52% (scapula width) in skeletal measurements, and from 0.50% (hind toe length) to 19.11% (tarsus length) in external measurements (Table 1). Two of the three variables with high measurement errors (i.e. >10%ME), were width measurements from long, narrow bones (e.g. scapula and femur). Large %ME for tarsus length was due to one "glaring error" (made obvious only because of replication). If we excluded this value, %ME decreased from 19.11% to 6.40%. In general, the relative measurement errors in the sparrow data were small, despite the low amount of morphological variation among birds. All specimens were adult males collected from a single site over a 2-day period, and among-bird coefficients of variation were all less than 6% (Table 1).

TABLE 1. Simple statistics and percent measurement error (% ME) for 13 skeletal and 4 external characters of Rufous-collared Sparrows. Measurements are in mm. Sample sizes vary among variables because of specimen damage; n denotes number of birds measured for each variable. Each bird was measured 3 times (skeletals) or 2 times (externals). Mean and coefficient of variation (CV) were calculated from within-bird means for each variable.

Variable	n	$\bar{x}$	CV	% ME
Skeletal characters				
Skull width	21	15.82	1.80	0.57
Skull length	21	18.50	1.59	2.51
Coracoid length	20	16.69	2.56	3.64
Scapula width	21	3.69	4.51	59.52
Scapula length	19	19.07	3.08	0.85
Humerus length	21	18.99	1.99	1.00
Ulna length	19	21.14	3.13	1.04
Sternum length	21	19.26	2.36	0.64
Keel depth	21	6.58	5.81	2.67
Synsacrum width	21	9.03	2.62	3.55
Femur width	21	2.98	3.92	12.39
Femur length	21	17.69	1.36	0.98
Tibiotarsus length	19	29.49	2.35	0.24
External characters				
Wing chord length	21	75.30	1.91	0.54
Outer retrix length	20	69.67	2.49	7.76
Tarsus length	20	19.55	2.95	19.11
Hind toe length	21	13.23	4.53	0.50

Measurement errors for external characters of American Coots were relatively low for total length, wing chord, tarsus length, middle toe length, middle claw length, and culmen length, but high for total wing length, hind toe length, bill width, and head width (Table 2). Relative measurement errors were lower for the entire sample than within sexes because of greater average variation among birds in the pooled sample (Table 2). That is, coots are sexually dimorphic. Among variables, %ME of the male data was highly correlated with %ME of the female data (Table 2: $r = 0.81$, $P < 0.01$), which implies that it was consistently difficult, or easy, to measure certain characters with

TABLE 2. Mean, coefficient of variance (CV), and measurement error (% ME) of 13 external morphological characters of American Coots. Sample includes 26 males and 24 females. Each coot was measured twice. Means and standard deviations were estimated from the means of the two measurements. All measurements are in mm.

	Males			Females			Both		
Variable	$\bar{x}$	CV	% ME	$\bar{x}$	CV	% ME	$\bar{x}$	CV	% ME
Total body length	380.0	3.30	6.82	355.3	2.80	11.32	368.1	4.56	3.74
Total wing length	305.5	3.62	31.89	283.1	3.48	39.69	294.8	5.21	19.06
Wing chord length	204.6	3.13	3.82	188.6	3.28	4.29	196.9	5.17	1.59
Tarsus length	57.35	3.60	2.54	53.14	3.30	2.97	55.33	5.15	1.25
Middle toe length	77.52	3.39	2.38	72.00	3.57	2.06	74.87	5.07	1.05
Middle claw length	14.80	7.73	1.99	13.19	8.59	1.82	14.03	9.90	1.31
Hind toe length	25.20	6.39	19.29	23.71	5.08	21.54	24.49	6.55	16.10
Culmen length	51.85	3.30	1.92	48.46	4.09	4.61	50.22	4.98	1.88
Bill length	31.63	3.56	5.14	29.20	4.38	18.14	30.46	5.60	5.73
Bill height	13.18	5.08	14.47	11.89	4.72	14.29	12.56	7.12	7.12
Bill width	10.07	15.37	18.08	8.80	16.17	35.42	9.46	17.00	15.55
Head length	68.26	2.66	18.25	63.96	2.01	10.26	66.20	4.04	5.87
Head width	23.35	3.95	24.13	21.70	2.50	15.37	22.56	4.99	10.65

relative precision. Large apparent differences in %ME between sexes for bill length, bill width, and head width were due, at least in part, to "glaring errors" again made apparent only because of replicated measurements (e.g. high %ME for female bill length was due to one such error).

For sparrow and coot (sexes pooled) data combined, there were no obvious relationships between %ME and either the absolute length of particular structures ($r = -0.02$, $P = 0.91$, $n = 30$ variables) or the among-specimen coefficients of variation for each structure ($r = 0.20$, $P = 0.29$). Hence, structures of relatively large size, or with relatively high among-specimen variation, were as likely to have high %ME as were small structures or structures with little among-specimen variation. We suspect that the most important causes of high %ME for some of our variables were poorly defined landmarks, flexibility of structures, or both (e.g. Bailey and Byrnes 1990).

Visual examination of Scree plots (Cattell 1978) yielded 1–3 PCA axes from each data matrix as meaningful. That is, they represented real data structure rather than noise (Tables 3–5). The PCA of coot data indicated that as axis number increased, the proportion of data structure explained by that axis decreased (by definition). More importantly, relative measurement error tended to increase (Table 5). This trend was not as obvious in the sparrow data (Tables 3 and 4). The first principal components were little affected by measurement error (e.g. 0.59–5.32%ME; Tables 3–5). Nevertheless, by eliminating individual variables with high %ME from the PCA, %ME of PC1 may be

TABLE 3. Variable loadings and measurement error from principal component analysis of the variance-covariance matrix of skeletal data from Rufous-collared Sparrows. Percentage of total variation explained by each PC axis = % Variation. Percent measurement error associated with each PC axis = % ME. Asterisks indicate important axes as determined from a Scree plot (Cattell 1978).

Variable	PC1*	PC2*	PC3*	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13
Skull width	0.22	0.20	0.15	0.17	0.03	−0.01	0.20	−0.54	0.13	−0.35	−0.30	0.18	0.51
Skull length	0.21	0.13	0.08	0.13	−0.04	−0.06	−0.16	−0.56	−0.17	0.13	0.59	−0.40	−0.12
Coracoid length	0.22	0.15	0.03	−0.30	−0.10	−0.24	−0.20	0.40	0.32	−0.18	0.37	−0.17	0.51
Scapula width	0.22	0.10	0.46	−0.47	0.59	−0.13	0.02	0.03	−0.35	0.05	−0.08	0.06	−0.07
Scapula length	0.39	0.34	−0.08	0.33	−0.14	−0.51	−0.25	0.15	−0.11	0.34	−0.33	0.07	−0.10
Humerus length	0.23	0.21	0.02	0.05	−0.24	0.26	0.26	0.27	−0.37	−0.39	−0.20	−0.53	−0.10
Ulna length	0.15	0.23	−0.13	−0.13	−0.21	0.43	0.22	0.08	−0.33	0.49	0.18	0.33	0.34
Sternum length	0.20	−0.07	−0.12	0.05	0.13	−0.31	0.82	0.06	0.26	0.15	0.18	−0.06	−0.14
Keel depth	0.66	−0.64	−0.45	−0.19	−0.17	0.17	−0.13	−0.09	0.11	0.05	−0.15	0.02	−0.07
Synsacrum width	0.22	−0.11	−0.03	0.62	0.56	0.31	−0.11	0.29	0.022	−0.04	0.18	0.01	0.15
Femur width	−0.06	−0.04	0.83	0.22	−0.29	0.13	0.07	0.13	0.26	0.24	−0.01	−0.03	−0.04
Femur length	0.19	0.11	0.10	0.07	−0.21	−0.04	0.00	0.09	−0.10	−0.47	0.36	0.61	−0.38
Tibiotarsus length	0.18	0.51	−0.12	−0.20	0.14	0.41	−0.09	−0.07	0.56	0.07	−0.11	−0.02	−0.35
% Variation	35.28	16.37	15.60	8.17	6.53	5.40	4.10	3.40	2.38	1.46	0.90	0.28	0.11
% ME	0.76	2.80	20.67	14.21	31.08	4.72	1.56	5.40	27.08	10.68	9.09	35.45	47.43

TABLE 4. Variable loadings and measurement errors (% ME) from principal component analysis of variance-covariance matrix of external variables from Rufous-collared Sparrows (% variation, % ME, and asterisks as defined in Table 3).

Variable	PC1*	PC2*	PC3*	PC4
Wing chord length	0.21	−0.11	0.39	0.89
Outer rectrix length	0.95	−0.16	−0.22	−0.15
Tarsus length	0.22	0.85	0.46	−0.16
Hind toe length	0.03	−0.50	0.77	−0.40
% variation	52.24	22.67	18.17	6.92
% ME	0.59	18.30	6.78	5.93

reduced. For coot data, we deleted total wing length, hind toe length, bill width, and head width (e.g. Table 2) and recalculated PC1 for males, females, and both sexes combined. Percent ME of PC1 was reduced from an average of 3.40 in the earlier analyses to an average of 1.12 with the reduced number of variables. In addition, PC1 from the reduced variable analysis was more highly correlated with lean dry mass for both males and females (Arnold unpubl. data) (i.e. it was a better measure of overall body size). When scapula and femur widths were eliminated from the PC analysis of sparrow skeletal data (e.g. Table 1), %ME of PC1 remained similar (a change from 0.76 to 0.85%), but relative errors for second and third axes decreased (from 2.80 to 1.62 for PC2 and from 20.67 to 3.43 for PC3).

The first PC axis is widely used as a measure of overall body size, whereas subsequent axes are usually interpreted as indicators of body shape (Pimentel 1979, Rising and Somers 1989). In our analyses, relative measurement errors of these subsequent axes were substantially higher than for PC1 (Tables 3–5). This reflects the relatively greater measurement errors of variables important in defining these components. Gauch (1982) used simulated plant community data to illustrate that PCA selectively recovers structure from early axes, while deferring noise to later axes. Our analysis illustrates that, for morphometric studies, this noise is not simply unstructured phenotypic variation, but that the noise comprises a great deal of measurement error. Principal component axes based on variance-covariance matrices of log-transformed data were more obviously and predictably affected by variables with high relative error than were axes derived from correlation matrices of raw data (Lougheed and Arnold unpubl. data). Principal component axes with large %ME tend to have correspondingly high loadings for one or more variables with large %ME (Tables 3–5). For example, PC3 from the covariance matrix of the sparrow skeletal data explained 15.60% of the total variation in the data set and had been interpreted as meaningful, but it had a relative measurement error of 20.67% (Table 3). Scapula width and femur width had factor loadings of 0.46 and 0.83 on this axis, respectively, whereas loadings for the remaining 11 variables ranged from −0.20 to 0.33.

It could be argued that measurement error is un-

TABLE 5. Variable loadings and measurement errors (% ME) from principal component analysis of the variance-covariance matrix of external variables from American Coots; PCA loadings are given for pooled sample only (% variation, % ME, and asterisks as defined in Table 3). In both male and female samples, the first three PC axes are important.

Variable	PC1*	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13
Males and females													
Total body length	0.20	0.05	0.12	−0.03	−0.22	0.20	0.53	0.10	0.22	−0.64	0.17	−0.24	0.09
Total wing length	0.23	0.17	0.29	−0.16	−0.54	−0.24	−0.07	0.27	0.03	0.12	−0.53	0.10	0.29
Wing chord length	0.24	0.06	0.19	−0.08	−0.18	−0.39	−0.28	0.15	0.36	0.14	0.57	−0.17	−0.32
Tarsus length	0.24	0.14	0.17	0.02	0.41	−0.31	0.03	−0.45	0.17	0.06	0.02	−0.22	0.59
Middle toe length	0.23	0.24	0.12	0.19	0.12	−0.29	0.22	−0.36	0.03	−0.16	−0.33	0.25	−0.60
Middle claw length	0.46	0.22	−0.82	−0.23	−0.01	−0.09	0.00	0.06	−0.04	0.01	−0.02	−0.02	0.02
Hind toe length	0.21	0.40	−0.00	0.77	−0.01	0.29	−0.05	0.22	0.00	0.20	0.05	−0.09	0.07
Culmen length	0.22	−0.08	0.12	−0.29	0.09	0.45	0.37	−0.06	0.33	0.59	−0.09	−0.07	−0.16
Bill length	0.24	0.26	0.24	−0.27	−0.16	0.39	−0.36	−0.36	−0.48	−0.10	0.09	−0.22	−0.11
Bill height	0.33	−0.24	0.13	−0.06	0.49	0.18	−0.42	0.36	0.21	−0.30	−0.30	−0.03	−0.08
Bill width	0.42	−0.73	−0.06	0.33	−0.29	−0.03	−0.00	−0.26	−0.15	0.05	0.03	0.02	0.04
Head length	0.20	0.08	0.12	−0.08	0.05	0.17	−0.01	−0.01	0.03	−0.06	0.34	0.85	0.22
Head width	0.21	−0.05	0.22	−0.08	0.31	−0.24	0.37	0.42	−0.63	0.15	0.14	0.06	−0.03
% variation	61.91	12.49	8.05	5.15	2.83	2.42	1.89	1.77	1.09	0.86	0.77	0.43	0.34
% ME	1.36	15.89	3.89	27.54	31.08	9.00	12.90	27.72	36.15	39.73	49.11	42.44	41.40
Males													
% variation	34.25	25.97	13.27	6.89	5.10	3.69	3.05	2.85	1.48	1.26	1.03	0.74	0.43
% ME	3.53	11.50	10.45	16.99	15.76	32.00	8.18	30.01	33.38	38.08	51.70	72.64	32.66
Females													
% variation	40.88	18.68	13.63	6.85	6.05	4.12	3.37	2.30	1.49	1.23	0.85	0.34	0.22
% ME	5.32	21.83	5.57	21.90	23.25	50.58	20.20	30.45	39.04	54.28	51.15	68.53	79.47

important in morphological studies because such variation results in conservative hypothesis testing. We suggest that use of morphological variables with high relative errors increases the risk of accepting false null hypotheses (i.e. Type II error; Bailey and Byrnes 1990). Many investigators are as willing to make statistical inferences, whether implicitly or explicitly, from nonsignificant hypothesis tests as from significant tests (Toft and Shea 1983). This is incorrect if done without knowledge of statistical power, which depends not only on effect size, sample sizes, and levels of phenotypic variation (Toft and Shea 1983, Rotenberry and Weins 1985), but also on measurement error. We recommend that investigators who use morphological variables assess relative measurement error, preferably before initiating a major study. A pilot study could indicate possible modifications of measuring techniques, appropriate sample sizes, number of repeated measurements of each individual, and the appropriate choice of variables. In general, most morphometric characters we examined had low measurement errors, but we identified "problem" variables in each data set. We do not suggest that these particular variables will have high %ME in every avian study. Rules for exclusion of problem variables are necessarily subjective and will vary depending on the objectives of each study. The results of our assessment of measurement error led us to drop these problem variables from further statistical analyses, but in other studies a different approach may have been more appropriate depending on the availability of specimens, importance of particular variables, or ability to reduce %ME with a different measuring technique.

Because the first PC axis is commonly used as a measure of overall body size (e.g. Pimentel 1979, Alisauskas and Ankney 1987, Rising and Somers 1989), its apparent insensitivity to the effects of measurement error is an advantage (see also Gauch 1982). However, some investigators use every available variable in a PCA. Many of these variables may have large measurement errors and may have little relationship to structural size. Multivariate variables, such as PC scores, reflect properties of the univariate variables from which they were derived, and we recommend that investigators use analyses of measurement error to eliminate problem variables before employing multivariate techniques.

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