INDIVIDUAL VARIATION IN THE WHITE-NECKED RAVEN

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This paper is concerned with the quantitative aspect of individual variation in the skeleton of the White-necked Raven (*Corvus cryptoleucus*), but in addition it includes some consideration of variation in external characters and weight. Less work of this nature has been done with skeletal than with external characters because of the relative paucity of avian skeletal material in museum collections as compared with skins. I have been able to borrow an extensive series of skeletons through the generosity of Mr. E. R. Kalmbach, Director of the Wildlife Research Laboratory, U. S. Fish and Wildlife Service, Denver, Colorado. Mr. Shaler E. Aldous, Chief, Section of Wildlife Investigations, U. S. Fish and Wildlife Service, Washington, D.C., has lent me his personal field notebook, from which weight records and external measurements have been taken. Dr. Pierce Brodkorb and Dr. Arnold Grobman, Biology Department, University of Florida, have been most helpful with their encouragement and criticism. I am happy to express my sincere appreciation for the kindness all these gentlemen have shown me.

Throughout the paper the following abbreviations will be used: N = number of specimens; R = observed range; M = mean; σ = standard deviation; V = coefficient of variability; CD = coefficient of divergence in per cent. The formula for the coefficient of divergence (Klauber, 1940) is $200\ (M - M')/(M + M')$. In this paper, t-values of 3.00 or more are considered significant.

Aldous (1942) published measurements of White-necked Ravens taken in the flesh. These included weight in grams, tail length, wing length, total length, and extent of wings. Tail length was taken by bending the tail up at a right angle with the back and placing the ruler parallel with the tail, the end of the ruler touching the back of the bird at the base of the uropygium. Wing length was that of the chord. All of the linear measurements were recorded to the nearest eighth of an inch. Statistical calculations were made from Aldous's raw data.

WEIGHT

Variability demonstrated in body weight (table 1) was greater than in that of any linear external or skeletal measurement. Such factors as amount of food in the digestive tract at time of collection of the birds, age, sexual, and seasonal differences could contribute to the high amount of variation in this character. In the Fox Sparrow (*Passerella iliaca*), Linsdale (1928) found more variation in weight (V for ♂ 6.21; ♀ 8.41) than in linear skeletal measurements. Blanchard (1941) reported variability of similar magnitude in adults of *Zonotrichia leucophrys* (V of ♂ 6.54-8.75). The variability in weight of *Corvus cryptoleucus* is comparable to that of these species of fringillids.

Weight of females in *C. cryptoleucus* appears to be more variable than that of males (table 1). A statistical test was applied to determine if this sexual difference was real or might rather be attributed to errors of sampling. The values of V were found not to be significantly different ($t = 0.51$). Mean weights of the sexes differed significantly ($t = 6.10$), but the overlap of extremes prevents separation of the sexes by use of this character. The amount of sexual dimorphism is expressed by the coefficient of divergence. Males average 8.23 per cent heavier than females.

EXTERNAL MEASUREMENTS

Table 2 presents the external measurements. Greatest variation occurs in tail length; the least occurs in extent of wings. Behle (1950) reported that in males of several subspecies of *Geothylpis trichas* variability in tail length exceeded that of wing length (V of wing, 2.63-3.90; tail, 3.37-5.16). In the Canada Goose, *Branta canadensis interior,* however, which permits segregation of sexes by use of absolute measurements, since the extremes overlap in all cases. The differences between means of the sexes in all cases are statistically highly significant (t-values from 4.71 to 6.03).

Table 1

Weights of *Corvus cryptoleucus* in Grams

Sex	N	R	M	σ	V	CD
♂	76	442–667	556.08±5.00	43.60±3.54	7.84±.64	8.23
♀	68	378–607	512.14±5.18	42.69±3.66	8.33±.71	

Hanson's data (1951) show the same situation with large series of adults and juveniles of both sexes.

For all the external measurements of *cryptoleucus* the average V is 3.02 in males and 3.01 in females. Tests of significance for each external character show that in none is one sex more variable than the other (t-values range from 0.51 to 1.16). Males in every instance have larger mean dimensions than females. Coefficients of divergence range from 2.84 to 3.20 and average 3.07 per cent. There is no external measurement,

Table 2

External Measurements of *Corvus cryptoleucus* in Millimeters

Measurement	Sex	N	R	M	σ	V	CD
Tail length	♂	53	196.9– 228.6	214.4± .99	7.19± .70	3.35±.33	3.13
	♀	56	184.2– 222.3	207.7±1.06	7.93± .75	3.82±.36	
Wing length	♂	53	336.6– 381.0	359.2±1.56	11.33±1.10	3.15±.31	3.20
	♀	56	323.9– 362.0	347.9±1.32	9.88± .93	2.84±.27	
Total length	♂	53	463.6– 533.4	506.0±1.99	14.48±1.41	2.86±.28	2.84
	♀	56	457.2– 533.4	491.8±2.02	15.09±1.43	3.07±.29	
Wing extent	♂	52	997.0–1124.0	1063.0±3.98	28.71±2.82	2.70±.27	3.09
	♀	55	977.9–1066.8	1030.7±3.20	23.72±2.26	2.30±.22	

SKELETAL MEASUREMENTS

Fifty skeletons of *Corvus cryptoleucus,* 27 males and 23 females, were available for this study. Thirty-six measurements were made on various elements of each skeleton. Vernier calipers were used in all but two instances; for these it was necessary to use dividers, then lay off the measurement on a steel rule. Since skeletal measurements are frequently described in rather general terms, an attempt is made here to define them with more precision.

Skull length.—From tip of bill to most posterior point of cranium.

Basal length.—From tip of bill to posterior surface of occipital condyle.

Cranial length.—On midline, from most posterior point of frontonasal hinge to most posterior point of cranium.

Cranial depth.—From highest point on frontal bones in the midline to bottom of fossa just anterior to occipital condyle (dividers).

Culmen length.—From most posterior point of frontonasal hinge to tip of bill.

Frontonasal width.—Transverse distance across frontonasal hinge.

Postorbital width.—Distance between the two postorbital processes.

Ramus length.—Greatest length of a mandibular ramus, including symphysis of bill.

Ramus height.—Greatest height of a ramus at level of mandibular foramen.

Table 3

Skeletal Measurements of *Corvus cryptoleucus*

Measurement	Sex	N	R	M	σ	V	CD
Skull length	♂	21	91.0– 98.4	93.06±.46	2.10±.32	2.26± .35	3.28
	♀	14	85.5– 93.8	90.06±.62	2.32±.44	2.57± .49	
Basal length	♂	21	80.8– 88.7	83.91±.40	1.81±.28	2.16± .33	3.35
	♀	15	76.6– 85.7	81.10±.62	2.42±.44	2.98± .54	
Cranial length	♂	27	38.5– 43.4	40.92±.20	1.02±.14	2.49± .34	1.89
	♀	23	39.1– 41.4	40.16±.14	.66±.10	1.63± .24	
Cranial depth	♂	27	24.4– 27.2	25.82±.15	.76±.10	2.94± .40	1.09
	♀	23	24.5– 26.5	25.54±.13	.62±.09	2.42± .36	
Culmen length	♂	21	52.9– 59.5	55.16±.43	1.96±.30	3.54± .55	5.11
	♀	15	48.9– 56.4	52.42±.51	1.96±.36	3.74± .68	
Frontonasal width	♂	27	20.9– 24.8	22.97±.17	.86±.12	3.73± .51	4.10
	♀	23	20.9– 23.2	22.05±.13	.64±.09	2.88± .43	
Postorbital width	♂	27	36.7– 40.4	38.69±.17	.88±.12	2.27± .31	1.80
	♀	22	36.5– 39.2	38.01±.16	.76±.11	1.99± .30	
Ramus length	♂	20	73.1– 82.1	76.35±.53	2.37±.37	3.10± .49	3.31
	♀	12	70.1– 77.8	73.83±.60	2.07±.42	2.81± .57	
Ramus height	♂	27	8.5– 9.7	8.98±.06	.33±.04	3.64± .50	4.66
	♀	23	7.6– 9.1	8.57±.07	.32±.05	3.77± .56	
Basihyal length	♂	26	11.2– 14.5	13.24±.14	.73±.10	5.54± .77	5.47
	♀	21	10.4– 14.0	12.53±.19	.89±.14	7.11±1.10	
Keel length	♂	26	53.8– 63.5	57.37±.44	2.22±.31	3.86± .54	3.38
	♀	23	52.4– 60.5	55.47±.37	1.79±.26	3.23± .48	
Keel depth	♂	27	15.6– 18.8	17.53±.16	.81±.11	4.59± .63	4.63
	♀	23	15.0– 18.7	16.74±.19	.91±.13	5.42± .80	
Mid-sternum width	♂	27	26.8– 32.4	28.92±.25	1.31±.18	4.52± .62	.90
	♀	22	27.0– 30.8	28.66±.23	1.06±.16	3.69± .56	
Clavicle length	♂	26	43.0– 50.3	45.99±.27	1.38±.19	2.99± .42	4.70
	♀	21	41.3– 46.3	43.88±.31	1.43±.22	3.27± .50	
Coracoid length	♂	27	43.3– 49.4	46.73±.25	1.28±.18	2.75± .37	3.66
	♀	23	43.2– 46.6	45.05±.21	1.03±.15	2.28± .34	
Scapula length	♂	27	49.1– 56.7	53.53±.32	1.64±.22	3.07± .42	2.73
	♀	22	49.7– 53.7	52.09±.23	1.06±.16	2.03± .31	
Humerus length	♂	27	69.7– 79.0	73.84±.34	1.77±.24	2.40± .33	2.99
	♀	23	68.7– 75.0	71.67±.36	1.72±.25	2.40± .35	
Humerus shaft	♂	27	6.0– 6.9	6.48±.04	.21±.03	3.26± .44	3.49
	♀	23	5.8– 6.5	6.26±.04	.20±.03	3.12± .46	
Ulna length	♂	27	87.2–100.3	93.27±.50	2.61±.36	2.80± .38	3.21
	♀	23	85.7– 94.6	90.32±.48	2.29±.34	2.54± .37	
Radius length	♂	27	80.9– 91.9	85.92±.43	2.25±.31	2.62± .36	3.12
	♀	22	78.8– 87.5	83.29±.45	2.11±.32	2.53± .38	
Metacarpal III	♂	27	52.3– 58.9	55.52±.30	1.54±.21	2.77± .38	3.24
	♀	23	51.6– 56.2	53.75±.28	1.33±.20	2.48± .37	
Metacarpal II	♂	27	47.6– 53.6	50.73±.28	1.48±.20	2.91± .40	2.66
	♀	23	47.3– 51.7	49.40±.27	1.27±.19	2.57± .38	
Index, Phalanx 1	♂	27	23.7– 28.2	26.02±.20	1.01±.14	3.89± .53	3.27
	♀	23	23.1– 26.9	25.18±.20	.95±.14	3.77± .56	

Measurement	Sex	N	R	M	σ	V	CD
Index, Phalanx 2	♂	27	14.6– 18.0	16.13±.15	.75±.10	4.67± .64	3.39
	♀	23	14.0– 16.8	15.59±.14	.69±.10	4.39± .65	
Synsacrum length	♂	25	40.5– 47.8	44.33±.36	1.80±.25	4.05± .57	.51
	♀	22	39.9– 47.1	44.11±.38	1.77±.27	4.01± .61	
Mid-synsacrum width	♂	25	29.3– 35.5	33.51±.23	1.17±.17	3.49± .49	1.48
	♀	22	31.3– 35.4	33.02±.23	1.08±.16	3.28± .49	
Postilium width	♂	25	29.2– 36.0	33.68±.30	1.49±.21	4.42± .63	1.34
	♀	22	30.4– 35.9	33.23±.31	1.44±.22	4.34± .65	
Pelvic width	♂	25	21.9– 26.6	24.64±.20	.99±.14	4.01± .57	3.07
	♀	23	21.9– 26.1	23.90±.23	1.11±.16	4.65± .69	
Femur length	♂	27	49.3– 57.9	54.75±.30	1.54±.21	2.80± .38	3.32
	♀	23	50.6– 55.0	52.96±.21	1.01±.15	1.91± .28	
Femur shaft	♂	27	4.4– 5.0	4.60±.03	.16±.02	3.54± .48	2.29
	♀	23	4.2– 4.8	4.50±.03	.14±.02	3.18± .47	
Tibia length	♂	27	87.8–101.7	96.09±.60	3.13±.43	3.25± .44	3.08
	♀	23	87.4– 99.0	93.18±.52	2.49±.37	2.67± .39	
Tibia shaft	♂	27	4.1– 4.9	4.49±.05	.24±.03	5.32± .72	1.91
	♀	23	4.0– 4.9	4.40±.05	.25±.04	5.63± .83	
Tarsus length	♂	27	55.1– 65.3	60.86±.39	2.02±.28	3.32± .45	2.71
	♀	23	56.4– 61.9	59.23±.30	1.41±.21	2.39± .35	
Pygostyle length	♂	25	20.5– 25.1	22.82±.20	1.00±.14	4.38± .62	4.88
	♀	21	20.4– 24.4	21.73±.19	.88±.14	4.04± .62	
Hallux, Phalanx 1	♂	27	20.6– 23.7	22.40±.15	.76±.10	3.40± .46	5.49
	♀	22	19.2– 23.1	21.20±.20	.92±.14	4.33± .65	
Hallux, Ungual Phalanx	♂	26	16.2– 18.5	17.47±.18	.93±.13	5.34± .74	4.97
	♀	22	15.4– 18.3	16.62±.19	.87±.13	5.25± .79	

Basihyal length.—Length of basihyal, excluding cartilaginous processes.

Keel length.—From carinal apex to posterior border of metasternum.

Keel depth.—From dorsal base of manubrium to apex of carina (dividers).

Mid-sternum width.—Least distance between outer margins of each side of sternum at points just posterior to costal margins.

Clavicle length.—Length of one side of furcula; from ventral side of hypocleidium to apex of anterodorsal angle of epicleidium.

Coracoid length.—From head to tip of sterno-coracoidal process.

Scapula length.—From anterior tip of coracoid process to tip of blade.

Humerus length.—From head to most distal point of entepicondyle.

Humerus shaft.—Minimum transverse shaft diameter.

Ulna length.—From proximal point of olecranon process to distal point of external condyle.

Metacarpal II.—From most proximal point of carpometacarpus to facet for articulation of Digit II.

Radius length; metacarpal III; index digit, phalanges 1 and 2.—Greatest length of these elements.

Synsacrum length.—From middle of centrum of first vertebra incorporated into synsacrum to posterior surface of centrum of hindmost vertebra of synsacrum.

Mid-synsacrum width.—Distance between most lateral points of antitrochanters of each side.

Post-ilium width.—Width of postacetabular pelvis; distance between projections overhanging posterior edge of ilio-ischiatic foramina of each side.

Pelvic width.—From posterolateral angle of renal depression of one side of pelvis to corresponding point on opposite side.

Femur length.—From trochanter to distal point of external condyle.

Tibia length.—From proximal point of inner cnemial crest to distal point of internal condyle of tibiotarsus.

Femur shaft; tibia shaft.—Minimum transverse shaft diameter.

Tarsus length; pygostyle length; hallux, phalanx 1 and ungual phalanx.—Greatest length of these elements.

VARIATION IN THE SKELETON

The statistical constants of skeletal measurements are presented in table 3. Variability ranges from 2.16 to 5.54 in males and from 1.63 to 7.11 in females, with average V's of 3.50 and 3.37, respectively. However, in neither sex do the means and modes of the V's coincide. The modes fall in the class with values from 2.5 to 3.0, and hence below the means.

No statistically significant difference was found on comparing V's of the sexes for each character. The closest approach to significance was in length of cranium ($t = 2.07$). Thus, in no skeletal measurement was one sex more variable than the other.

Means of males are greater in every instance than those of females. Overlap in extremes between the sexes for each skeletal measurement obtains; hence, no absolute measurements can be utilized to effect separation of the sexes. Divergence coefficients range from 0.51 to 5.49, and average 3.18 per cent. The modal class of CD's is that with values from 2.5-3.5 per cent. To provide an approximate index of sexual divergence in the skeleton, it may then be said that the skeleton of male *cryptoleucus* is about 3.0 per cent larger than that of females. Significance of difference between males and females in the means of any given measurement has been demonstrated for all except the following, which have extreme t-values of 0.04 to 1.41: cranial depth; mid-sternum width; index finger, phalanx 2; synsacrum length; mid-synsacrum width; post-ilium width; pelvic width; femur shaft and tibia shaft.

VARIATION IN SCLEROTIC RING

Intact sclerotic rings were preserved with thirty-eight of the skeletons examined. Variation in these rings was studied to the extent of counting the plates comprising them. Nothing was done with variation in the ring pattern. The results summarized in table 4 represent counts on 30 pairs of rings and eight single rings. In only two individuals was there a difference between right and left eye rings in number of plates. Thus, one specimen (male) had rings of 12 and 14 plates, another (female) had 13 and 14 plates.

Table 4

Variation in Number of Plates in the Sclerotic Ring

Number of sclerotic plates	Males	Females
12	1	1
13	5	3
14	23	30
15	4	1

The modal number of sclerotic plates was 14, with extremes of 12 and 15. This agrees with the findings of Curtis and Miller (1938) in nine species of corvids, except that their extreme counts varied only from 13 to 15.

DISCUSSION

A comparison of relative amounts of variability in external and skeletal characters reveals that the average variability coefficient of the latter slightly exceeds that of the former (by approximately one-half of one per cent). However, it should be recognized that the average of only four external measurements is compared with that of thirty-six of the skeleton, so the small difference is probably negligible.

In three of the four pelvic measurements (synsacrum length, mid-synsacrum width, and postilium width), the coefficients of divergence for the sexes are all less than 1.5 per cent. In the majority (23 out of 36) of the skeletal measurements, sexual divergence in size favors the males by 3 per cent or more. This indicates that the female pelvis is

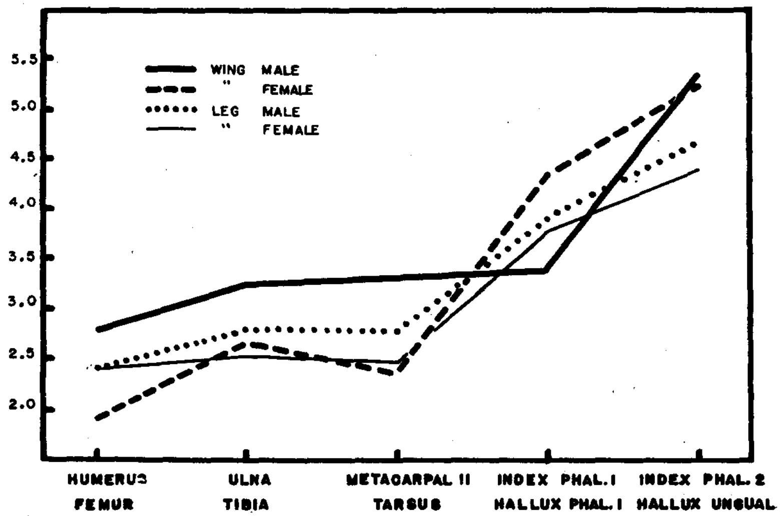

Fig. 1. Coefficient of variability of successively more distal elements of the limbs.

relatively larger than that of the male. Perhaps this is an adaptation to accommodate egg-laying.

Examination of variability existing in the wing and leg skeletal elements of *C. cryptoleucus* brings an interesting picture to light. In figure 1, the V's are plotted for each of the limb elements, which are arranged in order from most proximal to most distal. A trend is evident, with least variation in the proximal elements and greatest in the terminal ones. The gradation is slight, but it is striking that a similar condition prevails for both appendages.

It is noteworthy that other passerine species as well as species of three other orders of birds reveal this same increased variability of distal elements. This is brought out by Fisher's data (1947) on condors (*Gymnogyps*), Goodge's data (1951) on the Common Murre (*Uria aalge*), and Engels' data (1938; 1940) on the American Coot (*Fulica americana*) and the Mimidae. Engels (1940) thinks that in either reduction or lengthening of the wing skeleton, the chief parts involved are the distal ones. This hypothesis is supported by the greater variability of the distal elements in both the wing and the leg of *cryptoleucus*.

SUMMARY

Thirty-six measurements on each skeleton of 27 males and 23 females of *Corvus cryptoleucus* were taken. Standard statistical constants were calculated for these data, as well as for a series of external measurements and weights.

Variability of external measurements was about 3 per cent. Tail length was most variable and extent of wings least variable.

Average skeletal variability was about 3.5 per cent. The skull was somewhat less variable than any other part of the skeleton.

Greater variability was demonstrated in body weight (V about 8) than in any linear external or internal measurement.

A count of the sclerotic plates of the eye ring revealed that the modal number was 14, in agreement with that in other corvids.

In none of the characters considered was either sex significantly more variable than the other. Mean values of the males were significantly larger than those of females for weight, external measurements, and all but nine skeletal measurements. Sexual divergence was about 3 per cent for the skeletal and external characters, and approximately 8 per cent for weight; however, no absolute measurement was discovered by use of which sexes could be distinguished.

A relatively larger pelvis was indicated for females than for males.

In both the fore and hind limb skeletons there was noted a gradation in variability from least in the proximal elements to greatest in the distal elements.

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