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A FRESH LOOK AT THE TAXONOMY OF MIDCONTINENTAL SANDHILL CRANES

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Abstract: The midcontinental population of sandhill crane (*Grus canadensis*) includes about 500,000 birds and provides valuable recreational crane-watching and hunting opportunities in Canada and the United States. It comprises three subspecies, one of which (*G. c. rowani*) was of uncertain taxonomic status and another of which (*G. c. tabida*) merited protection from excessive harvest due to its small population size. We obtained measurements of cranes used by Johnson and Stewart (1973) and additional crane specimens to 1) evaluate the subspecies designation of midcontinental sandhill cranes and 2) to seek improved methods for classifying cranes from selected measurements. We found that the three named subspecies are in fact morphologically distinct, although there is a general gradient of smaller birds breeding in the far north to larger birds breeding at more southerly latitudes. We were not able to find better ways of identifying subspecies; in particular we could not find a reliable method that did not require knowledge of the sex of an individual crane.

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Migratory sandhill cranes (*Grus canadensis*) breed over an extensive area from the northern contiguous United States, Canada, Alaska, and northeastern Siberia. Three migratory subspecies are generally recognized, based on differences in morphology and plumage (Johnsgard 1983). The lesser sandhill crane (*Grus canadensis canadensis*), the most abundant subspecies, is distributed across the northernmost portions of the breeding range. The greater sandhill crane (*G. c. tabida*), which originally bred through much of southern Canada and the northern contiguous United States, declined in abundance and distribution but now has recovered in Michigan, Wisconsin, Minnesota, southern Ontario, and the northern Rockies; in addition, smaller populations exist in the Pacific Flyway. The Canadian sandhill crane (*G. c. rowani*) breeds in interior Canada (Walkinshaw 1965, Aldrich 1979, Meine and Archibald 1996), although the exact extent of its breeding range is uncertain. Biologists primarily use morphological measurements and sex to discriminate among these subspecies; however, there is considerable overlap in measurements between putative subspecies (Johnson and Stewart 1973, Tacha et al. 1985).

What has been termed the midcontinental "population" of sandhill cranes includes segments of all three migratory subspecies. Almost 500,000 cranes that breed in Canada from Manitoba and Nunavut, Alaska, and northeastern Siberia (Johnsgard 1983, Sharp and Vogel 1992) migrate through the Great Plains and winter in south-central United States and northern and central Mexico.

Management of midcontinental sandhill cranes provides valuable opportunities for recreational crane-watching (e.g., Lingle 1992) and hunting in Canada and the United States. Interest in crane hunting has heightened; the harvest of cranes has increased by 3.4% per year over the past 18 years (1982-2000), about twice the rate of population growth (1.6% per year) (Sharp et al. 2002). During 1990-2000 an average of 18,486 midcontinental sandhill cranes were harvested in the United States (Sharp et al. 2002). Because sandhill cranes have delayed sexual maturity and the lowest known recruitment rates of any hunted avian species in North America (Drewien et al. 1995), hunted populations must be carefully managed. Current management is based in part on information gained by the identification of subspecies within the harvest; that information has been used to try to limit the harvest of *tabida*, which has been in recovery throughout much of its breeding range. This strategy is based on the assumption that different subspecies, as identified by morphological measurements, derive from different portions of the breeding range. Some states assess the racial composition of harvested cranes by recording morphological measurements—lengths of primary wing chord, tarsus, and culmen—on a sample of the harvested cranes (e.g., Kendall et al. 1997, Schmitt and Hale 1997). Because females and males differ in measurements, the sex of each adult bird also must be determined, which is sometimes difficult in field situations because it requires examination of internal reproductive organs.

Oberholser (1921) noted that morphological measurements from some crane specimens were intermediate between those of *tabida* and *canadensis*, which at that time were considered two distinct species. Walkinshaw (1949:64) identified an area in central Canada where breeding cranes were intermediate in size between *tabida* and *canadensis*. Later, Walkinshaw (1965) described this intermediate subspecies and named it *rowani*. Walkinshaw (1965) based his definition of *rowani* on measurements and plumage coloration on 10 birds (7 males and 3 females) collected in Saskatchewan, Alberta, and southern Mac-

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kenzie District. Johnson and Stewart (1973) reexamined the measurements of those 10 cranes and determined that each of them (not just their average) was statistically distinct from both *tabida* and *canadensis* in terms of wing chord, tarsus length, and exposed culmen length.

Other researchers have questioned the validity of these subspecies, particularly the *rowani* subspecies. Stephen (1967) contended that attempts to differentiate subspecies by the criteria used at that time were not warranted, largely because measurements of adult males appeared to follow a normal distribution, which he erroneously concluded indicated a single population. Tacha et al. (1985) argued against the subspecies notion because migrant and wintering cranes did not form three distinct morphometric groups. Tacha et al. (1985) did not form that conclusion on the basis of breeding birds, however, which is essential for identifying subspecies. They also reported evident pairing between sandhill cranes presumably of different subspecies. They claimed that populations with a high degree of genetic interchange would be unlikely to persist as distinct subspecies.

Measurements of midcontinental sandhill cranes are consistent with a cline in size, in which the largest cranes (*tabida*) are in the southernmost areas and the smallest (*canadensis*) are in the northernmost areas (Walkinshaw 1949). Also, information on the morphology and distribution of *rowani*, the intermediate-sized species whose breeding range falls between *canadensis* and *tabida*, is very limited. Measurements from these birds have been the primary basis of studies assessing subspecies composition in various areas and seasons and in harvest assessments (e.g., Buller 1967, Stephen 1967, Lumsden 1971, Aldrich 1979, Guthery and Lewis 1979, Kendall et al. 1997). Further, recent studies of sandhill crane genetics indicated differences in mitochondrial DNA only between *canadensis* and 4 other subspecies (Rhymer et al. 2001) and a suggestion that *rowani* is a mixture or hybrid of *tabida* and *canadensis* (Petersen et al. 2003). Similarly, Jones (2003) examined microsatellite nuclear DNA and found no patterns concordant with a separation of the *rowani* subspecies.

Considerations about the validity of *rowani* as a subspecies, particularly the limited number of specimens from which the morphology has been described, and the difficulty in determining subspecies in operational surveys of hunter-shot birds led to this study. Our objectives were 1) to evaluate the subspecies designation of midcontinental sandhill cranes, particularly with respect to *rowani*, based on morphological characteristics; and 2) to develop improved classification methods for determining subspecies from selected measurements of hunter-shot cranes. We discuss our findings relative to recent results from genetic studies and the significance for the management of midcontinental sandhill cranes.

METHODS

We obtained measurements of sandhill cranes from several sources: 1) original notes provided to DHJ by L. H. Walkinshaw on numerous crane specimens from throughout North America that Walkinshaw had measured, which were used by Johnson and Stewart (1973); 2) additional museum specimens that had been collected in Alaska, British Columbia, Oregon, Alberta, and Saskatchewan; 3) cranes collected specifically for this study in the Northwest Territories, Alberta, Saskatchewan, Manitoba, Ontario, and Minnesota; 4) measurements of live cranes in Wisconsin under study by the International Crane Foundation; and 5) cranes measured along Lake Huron in Ontario (Urbanek 1988). All birds included in this study were of known sex and known breeding locality (except for a few migrant birds recorded where only *tabida* occur). It is possible, nonetheless, that some of the birds were non-breeders and might have wandered outside of the normal breeding range of their subspecies.

We tentatively assigned cranes to subspecies based on their breeding locality and the presumed breeding ranges of the 3 subspecies (e.g., Lumsden 1971, Aldrich 1979, Johnsgard 1983). That is, cranes breeding in the lower 48 states of the U.S. or in southern British Columbia were assigned to the *tabida* subspecies (Fig. 1). Birds from the central or northern parts of the Prairie Provinces, southern Northwest Territories, and central or northern Ontario were deemed *rowani*. Cranes from coastal Alaska and the northern portions of Nunavut, Northwest Territories, and British Columbia were assigned to the *canadensis* subspecies. Four cranes collected recently from extreme southeastern Manitoba were initially left unclassified.

We used 3 standard morphological measurements (recorded to the nearest 0.1 mm): culmen post-nares (from bill tip to proximal end of nares), total tarsus length (diagonal length from the most medial condyle of the tarsometatarsus where it articulates with the mid-toe to the rounded exterior portion of the distal condyles of the tibiotarsus; Dzubin and Cooch 1992), and wing chord (from carpal joint to tip of longest unflattened primary).

For some specimens, recorded culmen measurements were from the posterior of the nares; for others the entire exposed culmen length (from where integument meets the horny portion of the mandible) had been measured. Likewise there was some inconsistency in tarsus length measurements, sometimes involving the diagonal tarsus, other times involving the total tarsus. To obtain a complete set of comparable measurements, we developed conversion ratios. These values were determined from specimens on which both types of measurements had been recorded. To estimate culmen post nares length from exposed culmen length, we multiplied the exposed culmen length by the median ratio of culmen post nares length to exposed culmen length (0.767; mean = 0.769, SD = 0.035, N = 101). Diagonal tarsus measurements were obtained from total tarsus measurements by multiplying the latter quantity by the median ratio between the 2 types (0.919; mean = 0.919, SD = 0.022, N = 69).

To determine if certain linear combinations of the morpho-

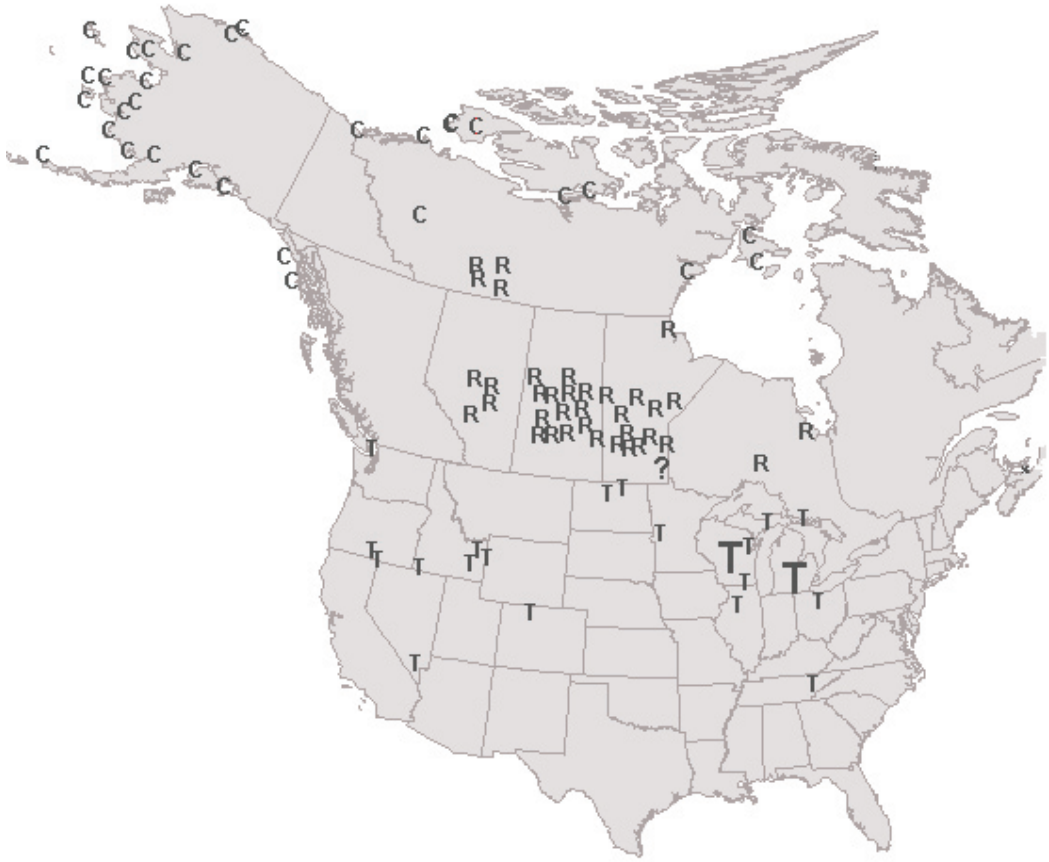

Fig. 1. Tentative assignment of sandhill crane specimens to subspecies, based on location; C denotes *canadensis*, R denotes *rowani*, and T denotes *tabida*. The large T's indicate large samples of birds from Wisconsin (N = 64) and lower Michigan (N = 17). Four cranes in southeastern Manitoba, denoted by ?, were not initially assigned to subspecies.

logical measurements usefully summarized the data, we performed principal component analysis on the 3 measurements. We examined differences in morphological measurements among putative subspecies by estimating orthogonal contrasts between means of *canadensis* and *rowani*, and between *rowani* and *tabida*. These comparisons were made for both the original measurements and the principal components with SAS Proc GLM (SAS Institute Inc. 1989).

We performed linear discriminant function analysis to determine if the 3 morphological measurements could reliably distinguish the 3 subspecies. Analyses were performed separately for each sex with SAS Proc DISCRIM (SAS Institute Inc. 1989). To estimate the misclassification rate, we used a cross-validation approach. That is, we classified each crane using discriminant functions computed from the data set, excluding the individual crane being classified, and determined how many cranes were assigned to the wrong subspecies. This leaving-one-out method is the most rigorous way to estimate the error rate (Lachenbruch 1975). Discriminant function analysis also generates for each crane "probabilities" that the crane is a member of each of the 3 subspecies.

We further considered the feasibility of classifying birds when certain information is lacking. We performed discriminant function analysis for pooled birds, without distinguishing sex. We also conducted analyses with subsets of one or 2 of the 3 available morphological measurements. We did these latter analyses both with and without using knowledge of the sex of each bird.

RESULTS

We had measurements of 240 sandhill cranes, including 65 presumed *canadensis*, 49 *rowani*, 122 *tabida* (Table 1), and the 4 cranes with undetermined subspecies. The 3 measurements were fairly strongly correlated; among all birds, correlation coefficients were 0.80 between culmen length and tarsus length,

Fig. 2. Deciles (by sex) of the first principal component of sandhill crane morphological measurements, indicating that largest birds typically are found in the 48 contiguous states, smallest birds are in northern Alaska, and birds of intermediate size are found in central Canada. The large numbers indicate median values of large samples of birds from Wisconsin (N = 64) and lower Michigan (N = 17).

0.67 between culmen length and wing chord, and 0.77 between tarsus length and wing chord. The principal component analysis yielded one principal component (PC1) that explained 83% of the variation in the three measurements. It reflected overall body size, with similar coefficients for each measurement: 0.60 for tarsus length, 0.57 for culmen length, and 0.56 for wing chord. When we grouped the PC1 values (by sex) into deciles (e.g., smallest 10%, next-smallest 10%, etc.), we found that larger birds were found mostly in the lower 48 states, smallest birds were in Alaska and the far north, and intermediate-sized birds were mostly in central Canada (Fig. 2).

Morphometric measurements, as well as the first principal component, varied among subspecies and between sexes (Table 1). Contrasts comparing *canadensis* with *rowani*, and *rowani* with *tabida* indicated that *rowani* was closer in average measurements to *tabida* than to *canadensis* for culmen length and tarsus length, but closer to *canadensis* for wing chord (Tables 1 and 2).

Discriminant functions reflected the same patterns, with greater differences between *canadensis* and *rowani* for culmen length and tarsus length, and between *rowani* and *tabida* for wing chord (Appendix). Discriminant function analysis assigned most birds to their putative subspecies (Table 3). All (63) *canadensis* were correctly classified. Two of the 46 (4.3%)

Table 1. Means, standard deviations, minimums, and maximums of morphological measurements (mm) of sandhill cranes, including the first principal component, by sex and putative subspecies.

	Females			Males		
Variable	*canadensis*	*rowani*	*tabida*	*canadensis*	*rowani*	*tabida*
Culmen length	68.9	84.5	94.0	70.9	90.7	100.5
SD	4.0	5.7	8.9	4.7	5.8	10.2
Minimum, maximum	63, 78	73, 98	76, 113	60, 78	76, 99	82, 120
Tarsus length	174.5	212.9	238.5	187.8	227.6	251.8
SD	13.8	12.2	11.3	14.4	8.9	13.6
Minimum, maximum	141, 198	189, 233	221, 278	158, 214	204, 243	226, 289
Wing chord	444.7	469.8	511.9	469.5	494.1	535.6
SD	19.9	16.6	20.0	21.7	16.3	19.1
Minimum, maximum	420, 490	435, 500	478, 575	418, 505	455, 524	490, 575
PC1	-2.58	-0.78	0.76	-1.82	0.17	1.68
SD	0.56	0.51	0.60	0.60	0.44	0.58
Minimum, maximum	-3.66, 1.68	-1.55, 0.10	-0.29, 2.47	-3.32, -0.90	-0.95, 0.96	0.19, 3.11
N	21	21	60	44	28	62

Table 2. *F* values associated with estimated contrasts between closest subspecies of original morphological measurements and principal components

Variable	*canadensis* v. *rowani*	*rowani* v. *tabida*	Degrees of freedom
Culmen length	148.01	51.08	1, 229
Tarsus length	271.97	136.83	1, 232
Wing chord	44.81	157.23	1, 222
PC1	307.68	235.43	1, 221
PC2	18.73	16.41	1, 221
PC3	5.31	1.37	1, 221

Table 3. Most sandhill cranes were assigned to the correct putative subspecies (based on breeding location) by linear discriminant functions (based on morphological measurements and sex), as measured by cross-validation error rates.

		Classified into		
Sex	Classified from	*canadensis*	*rowani*	*tabida*
Female	*canadensis*	21	0	0
	rowani	0	18	1
	tabida	0	3	52
Male	*canadensis*	42	0	0
	rowani	0	26	1
	tabida	0	5	53

presumed *rowani* specimens were assigned to *tabida*. Eight of the 113 (7.1%) putative *tabida* specimens were classified as *rowani*. No *rowani* or *tabida* were assigned to *canadensis*. Overall, then, if cranes were equally likely to belong to any of the 3 subspecies and either sex, the discriminant functions would misclassify about 3.8% of them.

For 8 of the 9 misclassified cranes, the classification probabilities for the presumed subspecies and for the assigned subspecies were very close; that is, the cranes were nearly intermediate between averages for the two subspecies. The single misclassified specimen for which assignment probabilities were not close, and 4 other misclassified birds, were from Wisconsin; these were measured as live birds and were classified as *rowani* rather than *tabida*. Two other misclassified cranes were from Michigan and Ohio, presumably *tabida* but classified as *rowani*. Two putative *rowani*, both from central Saskatchewan, were classified as *tabida*.

Of the 4 cranes from extreme southeastern Manitoba, to which we did not initially assign a subspecies, two were classified as *tabida* and two as *rowani*. These cranes did not appear to be intermediate in size between the 2 subspecies; the discriminant function assigned each of them with posterior "probabilities" between 0.96 and 0.98.

When we treated sex as unknown and tried to classify cranes into subspecies based on the three morphological measurements, error rates increased dramatically (Table 4). A few (3 of 63) *canadensis*, all males, were called *rowani*. Two (females) of 46 *rowani* were classified as *canadensis* and 4 (males) were grouped with *tabida*. Nineteen (18 females, 1 male) of 113 *tabida* were misclassified as *rowani*. The overall error rate tripled, to 11.5%, versus 3.8% when sex-specific discriminant functions were used.

Discriminant functions based on subsets of the 3 morphological measurements tended to have higher error rates than those based on the full set, except that tarsus length and wing chord performed as well as the full set (Table 5). Tarsus length was the single best discriminating variable, but error rates based on only that measurement were much higher than error rates based on two or more measurements.

DISCUSSION

We found that the 3 putative subspecies of midcontinental sandhill cranes are morphologically distinct, in that specimens from breeding ranges described for the subspecies are distinguishable. The *rowani* subspecies, which is intermediate both in terms of breeding latitude (approximately) and in morphological measurements, differed most markedly from *tabida* in wing chord, and from *canadensis* in culmen length and tarsus length. Although subspecies appear distinct, all measures of body size demonstrate a size gradient, with larger birds found at more southern latitudes and smaller birds at more northern

Table 4. When the sex of individual cranes was treated as unknown, more birds were misclassified by linear discriminant analysis.

Sex	Classified from	Classified into		
		canadensis	*rowani*	*tabida*
Female	*canadensis*	21	0	0
	rowani	2	17	0
	tabida	0	18	37
Male	*canadensis*	39	3	0
	rowani	0	23	4
	tabida	0	1	57

Table 5. Error rates (estimated probabilities of misclassification, as percentages) for discriminant functions based on various sets of morphological measurements, with or without sex known.

Sex	Classified from	Classified into		
		canadensis	*rowani*	*tabida*
Female	*canadensis*	21	0	0
	rowani	2	17	0
	tabida	0	18	37
Male	*canadensis*	39	3	0
	rowani	0	23	4
	tabida	0	1	57

latitudes. The trend toward smaller body size in the north is similar to that found among Canada geese (*Branta canadensis*; Bellrose 1980, Dunn and MacInnes 1987), a species that also breeds from southern latitudes to the Arctic.

The cranes from southern British Columbia, initially assigned to *tabida*, indeed turned out to be large and ultimately were assigned to *tabida* by the discriminant functions. Those birds had been collected between 1947 and 1964. Recent observations of sandhill cranes from that area have generally been consistent with measurements of *rowani*, although uncertainty is considerable because the sex of individual birds was not known (Ivey et al. 2004). Both *tabida* and *rowani* have been recorded in southwestern British Columbia (Ivey et al. 2004), so the assignment of *tabida* to the cranes included in our analysis is sensible.

It seems reasonable to speculate that the breeding range of sandhill cranes was once contiguous, but that, possibly due to reductions in numbers, breeding populations became constricted and fragmented into more-or-less discrete ranges, including those inhabited by non-migratory birds in Mississippi, Florida, and Cuba. As populations have grown in recent decades, breeding ranges have expanded dramatically. Conceivably, areas that once separated breeding ranges have become occupied, and the distinctions between subspecies are becoming blurred. This conjecture is consistent with the 4 cranes reported from southeastern Manitoba, which included 2 evident *tabida* and 2 vident *rowani*. The occurrence of cranes classified as *rowani* or *tabida* outside of their expected ranges in this study and inconsistencies in classification to subspecies between genetic and morphological approaches (Glenn et al. 2002) is consistent with the possibility of interbreeding across subspecies (Tacha et al. 1985).

Regardless of the genetic distinctiveness of what have been called subspecies, the populations of birds differ in a variety of ways, including morphology (Aldrich 1979, this study), migrational timing and pathways (e.g., Johnson and Stewart 1973), rates of development (Baldwin 1977), onset of homeothermy (Baldwin 1977), and other characteristics. Further, the distributions (this study) of the 3 subspecies indicate that generally they breed in different areas: most *canadensis* breed in the arctic regions of Alaska and northern Canada; *rowani* in subarctic, boreal, and parkland ecoregions of Canada; and *tabida* in various regions of the United States and southernmost Canada. Indeed, it is not necessary to accept the division of sandhill cranes into the 3 subspecies in order to recognize the distinctiveness of the birds based on body size and the consistency of the association between body size and breeding area (Fig. 2). Hence, it may be desirable to manage these regional breeding populations individually.

For our second objective, we were not able to develop more effective methods for classifying cranes into the 3 subspecies. The discriminant functions we developed performed well, nonetheless, with a 3.8% error rate. We did find that, in our samples, discriminant functions that used only tarsus and

wing chord, along with sex, performed as well as those that also used culmen length. Because culmen length is readily measured, however, we recommend that it be included. Wing chord has traditionally been used as a measure of wing length, but it is affected by wear of the longest primaries, which likely contributed to its high error rate even when sex was known. A more precise measure of wing size, e.g., midwing (measured ventrally from proximal end of ulan to distal end of radius, proximal to spur; Rasmussen et al. 2001) could be considered as an alternative to wing chord.

Although it would be desirable to have effective classification rules that do not require knowledge of the sex of individual birds, we found that such discriminant functions performed much more poorly than those that used knowledge of the sex. Error rates tripled for the most effective discriminant functions when information about sex was not used. Nesbitt et al. (1992) also found that determinations of subspecies when sex was unknown were not accurate.

Whereas knowledge of the sex of a crane is valuable for ascertaining its subspecies, it may be reasonable to consider the subspecific composition of groups of birds, rather than individuals. That is, it may be feasible to estimate the subspecific composition of a group by recording fewer measurements but using larger samples of birds.

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Appendix. Intercepts and coefficients of linear discriminant functions developed to distinguish female and male sandhill cranes into subspecies.

	Females			Males		
Variable	*canadensis*	*rowani*	*tabida*	*canadensis*	*rowani*	*tabida*
Intercept	-325.05	-398.25	-481.18	-391.98	-479.07	-569.78
Culmen	0.57	0.77	0.87	0.95	1.19	1.31
Tarsus	0.81	1.07	1.20	0.81	1.01	1.11
Wing	1.06	1.07	1.16	1.20	1.26	1.36