BEHAVIOR AND TAXONOMY OF SANDHILL CRANES

FROM MID-CONTINENTAL

NORTH AMERICA

By

THOMAS CRAIG TACHA
\\
Bachelor of Science
Kansas State University
Manhattan, Kansas
1973

Master of Science
South Dakota State University
Brookings, South Dakota
1976

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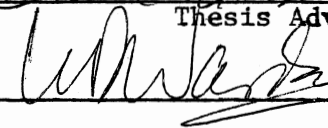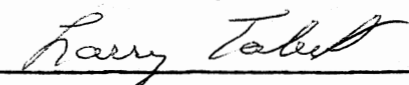DOCTOR OF PHILOSOPHY
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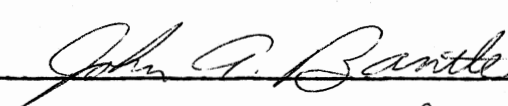
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Thesis Adviser

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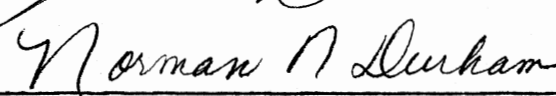
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Dean of the Graduate College

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CHAPTER I

INTRODUCTION

This thesis is composed of 4 manuscripts written in formats suitable for submission to selected scientific journals. Each manuscript is complete without supporting materials. The order of arrangement for each manuscript is text, literature cited, tables, and figures. Chapter II, "Subspeciation of Sandhill Cranes from Mid-Continental North America", and Chapter V, "Alert Behaviors of Sandhill Cranes", are written in the format of the ornithological journal AUK. Chapter III, "Maintenance Behaviors of Sandhill Cranes", and Chapter IV, "Preflight Behaviors of Sandhill Cranes", are written in the format of the WILSON BULLETIN.

CHAPTER II

SUBSPECIATION OF SANDHILL CRANES FROM

MID-CONTINENTAL NORTH AMERICA

Thomas C. Tacha[1], Paul A. Vohs[1,3], and William D. Warde[2]

[1]Cooperative Wildlife Research Unit, 404 Life Sciences West,

Oklahoma State University, Stillwater, Oklahoma 74078

[2]Department of Statistics, 301 Mathematical Sciences, Oklahoma

State University, Stillwater, Oklahoma 74078

Abstract.-Measurements of culmen post-nares, tarsus, and wing

chord were used to derive subspecies designations for 1,097 adult

Sandhill Cranes (Grus canadensis) sampled from 6 states and Saskatchewan.

Linear and quadratic discriminate functions derived from measurements

of 60 adult specimens used to define currently described subspecies

provided the standard of comparison. Juvenile Sandhill Cranes did not

reach full growth until 10-12 months of age and were not included in

the analysis. Female cranes were significantly ($P < 0.05$) smaller than

males within subspecies and were analyzed separately. Univariate plots

of the 3 measurements from 531 adult male and 566 adult female cranes

in the study suggested that more than 1 morphometric population might

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[3]Present address: Office of Cooperative Research Units, USDI-Fish and

Wildlife Service, Washington, D.C. 20240.

be represented. Bivariate nearest-neighbor analyses and trivariate cluster analyses suggested that sample cranes represented a uniform, contiguous size gradient forming 1 group and not 3 groups as suggested by the theoretical presence of G. c. canadensis, G. c. rowani, and G. c. tabida. Mid-continental Sandhill Cranes could not be discriminated into subspecies on the basis of morphology alone. Behavioral observations of marked birds suggest that 12-72% of mid-continent Sandhill Cranes cross subspecies designations to pair. We hypothesize that management of mid-continental Sandhill Cranes by subspecies is not realistic, and that if 3 subspecies were ever present among mid-continental Sandhill Cranes, the subspecies are rapidly being degraded by inter-subspecific pairing.

Our purpose was to determine if Sandhill Cranes that migrate through mid-continental North America could be discriminated into 3 subspecies on the basis of 3 morphological characteristics. Mayr (1970:210) defined a subspecies as "an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species". Mayr further defined taxonomic differences as differences in diagnostic morphological characters.

The American Ornithologists' Union (1959) recognizes 3 subspecies of Sandhill Cranes; G. c. canadensis, G. c. tabida, and G. c. pratensis. However, more recent literature recognizes 6 subspecies (e.g. Lewis 1977). Three of the 6 subspecies (G. c. pratensis, G. c. pulla, and G. c. nesoites) are non-migratory (Lewis 1977) and are not the subject of this paper. Four populations of G. c. tabida (Eastern, Rocky

Mountain, Colorado River Valley, and Central Valley) have nesting and wintering areas in eastern and western North America (Lewis 1977) and were not included in this study. About 500,000 Sandhill Cranes migrate through the great plains of North America, winter primarily in Oklahoma, Texas, New Mexico, and Mexico (unpublished data, Oklahoma Cooperative Wildlife Research Unit) and are referred to as mid-continent Sandhill Cranes. Mid-continent Sandhill Cranes have been subdivided to represent 3 subspecies; G. c. canadensis, G. c. rowani, and G. c. tabida (Johnson and Stewart 1973, Lewis 1977, Aldrich 1979). Subspeciation of mid-continent Sandhill Cranes was the focus of this study.

Sandhill Cranes are currently hunted in 9 states and Canada, and most of the harvest occurs at southern migration stops and wintering areas of mid-continent cranes (Lewis 1977). The presence and distribution of subspecies in the mid-continent area is important to management of these birds (see Johnson and Stewart 1973, Lewis 1977, and Aldrich 1979). Lewis (1977) recommended that the number of valid subspecies of Sandhill Cranes be determined to facilitate the evaluation of the impact of potential differential rates of harvest on subspecies.

Materials and Methods

Morphological characteristics.-Analysis by each age and sex class has been recognized as important in identifying subspecies of Sandhill Cranes (Johnson and Stewart 1973, Aldrich 1979). Culmen post-nares, tarsus, and wing chord are the best diagnostic characteristics for discriminating subspecies of mid-continent Sandhill Cranes (pers. comm.,

J.W. Aldrich). Juvenile (young-of-the-year) Sandhill Cranes had a feathered crown and/or brown feathers on the nape of the neck (Lewis 1974) that were lacking in adults. Sex was determined by gonadal examination.

Statistical procedures.-Discrimination of subspecies was accomplished by comparison of measurements from cranes in our sample with measurements of specimens obtained from nesting grounds where subspecies status was identified by J.W. Aldrich on the basis of location, measurements, and comparison with type specimens. Appropriate measurements from a total of 60 "known-subspecies" adult Sandhill Cranes were obtained (Table 1) from birds described by Aldrich (1979). Data from 1,563 mid-continental Sandhill Cranes were collected for this study from birds killed by hunters, hail, or impact with highlines, or that died during trapping related to banding operations (Table 2).

Subspecies designations for each of the sample cranes were derived by using the multivariate discriminate analysis program from the Statistical Analysis System (SAS) (Barr et. al 1979). Data from known-subspecies specimens (Table 1) were entered as a calibration data set from which both linear (pooled variance-covariance matrices) and quadratic (unpooled variance-covariance matrices) discriminate functions were generated. Two measures of whether or not the calibration data set was statistically adequate in discriminating subspecies were used. The first was to subject the calibration data set to the discriminate functions (linear and quadratic) generated from it and to determine the number of subspecies misclassifications. Using a linear discriminate function only 1 female was misclassified (Table 3). The second measure of statistical adequacy of the calibration data set was to determine

by sex if, within the calibration data set, each of the variables (culmen post-nares, tarsus, and wing chord) was different between subspecies. All univariate and trivariate analyses of variance found significant ($P = 0.001$) differences between subspecies within the calibration data set (Table 4). Thus, the calibration data set was found to be capable of statistical discrimination of subspecies using either linear or quadratic discriminate function analysis.

The 1,563 Sandhill Cranes sampled for this study were considered a stratified (by state and age) random sample of cranes from the mid-continent population (population used in the statistical sense) (Table 2). Measurements from cranes were analyzed using t-tests to determine if differences in lengths of culmen post-nares, tarsus, and wing chord occurred between ages, within months of the year. Measurements from cranes were analyzed to determine if 3 groups (representing the 3 subspecies) were present. Univariate analyses were conducted by plotting data in 20 class levels (e.g. tarsus lengths of sample data were divided into 20 equal classes; 59-62 mm, 63-66 mm, etc.). The Kolmogorov-Smirnov D-statistic and resulting probability levels for tests of normality were generated by SAS. Values for skewness and kurtosis were generated by SAS and transformed into probability statements using tests from Snedecor and Cochran (1967:86). Bivariate plots of data were analyzed for clumping or uniformity using the Clark-Evans nearest-neighbor model (Clark and Evans 1954) as applied by Miller and Stephen (1966). Trivariate sample data from North Dakota, Oklahoma, and Texas were subjected to an unweighted-average agglomerative cluster analysis (from McCammon and Wenninger 1970).

Results

Differences related to age and sex.-Measurements of culmen
post-nares, tarsus, and wing chord were compared between adults and
juveniles of the study sample (Table 5). Tarsus length between
adults and juveniles was not different ($\underline{P}$ > 0.05) during the period
October to May (except among males in October when juveniles had
unexplainably longer tarsi). However, culmen post-nares and wing
chord measurements for juveniles were shorter than adults from
October through March. There were no differences ($\underline{P}$ > 0.13) in
culmen post-nares and wing chord measurements between adults
and juveniles of either sex in April and May. Adult females
were consistantly smaller than adult males during October to
May.

Subspecies designations of sample data.-The distribution of
subspecies varied by state using either linear (χ^2 = 457.87, df = 12,
$\underline{P}$ = 0.001) or quadratic (χ^2 = 176.85, df = 12, $\underline{P}$ = 0.001) discriminate
functions to designate subspecies (Table 6). Within North Dakota,
cranes obtained from eastern counties had a significantly higher
proportion of larger subspecies designations ($\underline{G}$. $\underline{c}$. rowani and $\underline{G}$. $\underline{c}$.
tabida) using either linear (χ^2 = 141.06, df = 2, $\underline{P}$ = 0.001) or
quadratic (χ^2 = 55.32, df = 2, $\underline{P}$ = 0.001) discriminate functions. When
data obtained from birds in Texas, New Mexico, western Nebraska, and
western North Dakota were pooled and compared to data obtained from
Oklahoma and eastern North Dakota, there was a significant difference
in the distribution of subspecies designations (larger subspecies east)
using either linear (χ^2 = 349.79, df = 2, $\underline{P}$ = 0.001) or quadratic

(χ^2 = 124.06, df = 2, $\underline{P}$ 0.001) methods. When data from all states were

pooled, there was a significant difference (χ^2 = 450.33, df = 4,

$\underline{P}$ = 0.001) in the distribution of subspecies as designated by linear

and quadratic discriminate functions. When culmen post-nares, tarsus,

and wing chord measurements of designated subspecies from the sample

of adults were compared after pooling across states, all univariate and

trivariate analyses of variance indicated significant ($\underline{P}$ = 0.001)

differences; these differences were found using subspecies designated

by either linear or quadratic methods.

Adult discrimination.-None of the univariate plots of culmen

post-nares, tarsus, and wing chord from adult male and adult female

Sandhill Cranes had normal distributions (Fig. 1). Adult male and

adult female culmen post-nares and wing chord distributions were

significantly ($\underline{P}$ < 0.05) and positively skewed. Distributions of

adult female tarsus and adult male culmen post-nares and tarsus

measurements were significantly ($\underline{P}$ < 0.05) negatively kurtosed.

Bivariate distributions of culmen post-nares by tarsus, culmen

post-nares by wing chord, and tarsus by wing chord for each adult sex

were subjected to nearest-neighbor analysis (Table 7). Values of R

near 0 indicated clumped, near 1 indicated random, and near 2 indicated

uniform bivariate distributions. The $\underline{Z}$ value evaluated departure from

a random distribution. All adult male and adult female bivariate

distributions indicated highly significant ($\underline{P}$ = 0.001) departures of

data from random toward uniform distributions.

Adult male and female Sandhill Cranes from North Dakota (Fig. 2),

Oklahoma (Fig. 3), and Texas (Fig. 4) were subjected to trivariate

cluster analysis. The resulting dendrograms revealed a single grouping

of cranes with 6 outlying birds. For each sex from each state, the initial 6 outlying birds were removed and the remaining data reclustered: the same pattern of 1 group with 6 outlying cranes resulted. The second set of 6 outlying birds was removed and data again reclustered. The pattern of 1 group and 6 extraneous birds was again observed. The net effect of this repeated clustering was similar to peeling 3 layers off the surface of a sphere. Outlying cranes were of all sizes and not related to either linear or quadratic subspecies designations (distributions of linear and quadratic subspecies designations of the 18 outlying cranes from 3 dendrograms for each sex in each state were not different, $P > 0.10$, from subspecies distributions of n cranes subjected to initial cluster analyses).

About 2,000 Sandhill Cranes were captured, measured, and marked with individually identifiable neck collars in Texas and Nebraska in 1979 and 1980. Of these marked cranes, 20 pairs of mated adults were marked at the same time and later observed. The status of a pair and the sex of each crane were determined by observation of behaviors including the unison call (described by Archibald 1975). Measurements of the 40 paired cranes were subjected to linear and quadratic discriminate function analyses and the most probable subspecies was designated for each crane. Pairs were matched, and the number of within and cross-subspecies pairs was tabulated (Table 8). Expected values for 20 pairs of cranes randomly pairing across subspecies were calculated from 432 cranes captured in Texas and Nebraska. Observed pairing was not different ($P = 0.66$) from random using linear subspecies designations. Observed pairing using quadratic subspecies designations was nearly different from random ($P = 0.08$), with a

higher than expected number of cross-subspecies pairs. The projected proportion of mid-continent Sandhill Cranes that paired only with birds of the same subspecies was 0.65 + 0.23 (95% CI) using linear designations, and 0.50 + 0.22 using quadratic designations. All but 2 cross-pairings were between G. c. canadensis and G. c. rowani due to the relative abundance of these 2 subspecies. However, 2 cross-pairings were between G. c. tabida (the largest subspecies) and G. c. canadensis (the smallest subspecies).

Discussion

Differences related to age and sex.-Juvenile Sandhill Cranes do not reach full growth until they are 10-12 months old. At 10 months of age, juvenile Sandhill Cranes begin to molt brown neck feathers and crown feathers (unpublished data, Oklahoma Cooperative Wildlife Unit) and the probability of mis-identification increases as the molt progresses. Thus, juvenile Sandhill Cranes were not used in subspecies analyses. The consistant and significant differences in size between adult sexes within subspecies necessitated treating the sexes separately in analysis of subspecies.

Subspecies designations of sample data.-Discriminate function designations representing the 3 subspecies were present for all the major wintering and southern migration staging areas that were sampled. Subspecies designations reflected body size differences (G. c. tabida larger than G. c. rowani larger than G. c. canadensis) and the proportions of larger and smaller Sandhill Cranes varied with sampling locations. A larger proportion of G. c. rowani and G. c. tabida (84% using linear designations) were found in southeastern migration areas

(Oklahoma) than in southwestern areas (24% in Texas). In North Dakota, 96% G. c. rowani and G. c. tabida (using linear designations) were collected from the eastern half of the state, but only 34% G. c. rowani and G. c. tabida were collected in the western half. When all sampling locations in the mid-continent area were divided into eastern and western flyways, a much larger proportion of eastern cranes were large in size (77% G. c. rowani and G. c. tabida east using linear designations, 20% west). Johnson and Stewart (1973) found this same trend in the northern Great Plains.

Adult discrimination.-Analysis of univariate distributions of culmen post-nares, tarsus, and wing chord measurements from adult Sandhill Cranes in our sample indicated the possibility of more than 1 morphometric population (if normal curves are expected) of cranes existing within the mid-continent group (based on negative kurtosis of distributions). Wing chord distributions exhibited positive kurtosis, and the positive kurtosis reduced the value of wing chord as a diagnostic characteristic.

Bivariate and trivariate analyses strongly indicated that a uniform continuum of body sizes exists within the grouping of birds designated as mid-continent Sandhill Cranes. Since only a single group could be identified in both bivariate and trivariate analyses, the mid-continent group was not considered to contain 3 identifiable morphometric groups. We believe the observed discrete size classes found among the small samples obtained from nesting areas were the product of selective sampling. Division of our large sample of cranes into 3 distinct groups, using the measurements obtained and discriminate function analyses, was an arbitrary procedure.

Mid-continent Sandhill Cranes are highly polymorphic. This polymorphism appears to be expressed as a uniform continuum in size and may be related to general breeding distribution where smaller cranes breed north and west. However, the birds in our sample could not be forced into 3 or even 2 groups of morphologically distinct taxa. The pairing between birds clearly of different sizes observed in this study adds additional support to the low likelihood of 3 discrete subspecies being present among mid-continent Sandhill Cranes.

The application of the subspecies concept may impede understanding of geographic variation (Selander 1971). When studies of geographic variation are limited to delineation of subspecies, taxonomic concerns interfere with systematic analysis (Selander 1971:75). We believe that delineation of identifiable breeding populations (and their migration routes and wintering areas) of mid-continent Sandhill Cranes is more important than determining subspecies status of individual cranes or groups of cranes. According to Mayr's (1970:210) definition, identification of the association between geographic distribution of breeding populations and morphological variation is a prerequisite to application of subspecies nomenclature.

Conclusions and Hypotheses

Mid-continent Sandhill Cranes could not be assigned with distinction to the 3 subspecies (G. c. canadensis, G. c. rowani, and G. c. tabida) on the basis of the morphological characteristics we measured. Aldrich (1979:140) stated "I believe that we have now enough evidence, based on comparisons by different people using different methods, to consider (that) the population of Sandhill Cranes breeding

in the forested areas of western Canada, named the Canadian sandhill crane (Grus canadensis rowani) by Walkinshaw (1965), is sufficiently discrete and recognizable by morphological characters to be a practical unit in crane management". Our findings, based on a large sample and application of statistical methods, and the general absence of information concerning the breeding range of G. c. rowani, do not support the contention that G. c. rowani be recognized as a subspecies.

Mid-continent Sandhill Cranes form pairs during northward migration, primarily when all 3 subspecies are present in the Platte River Valley of Nebraska in March and April (unpublished data, Oklahoma Cooperative Wildlife Research Unit). About 80-90% of mid-continent Sandhill Cranes stop along the Platte River each spring (Lewis 1977). Evidence suggests that 12-72% of mid-continent Sandhill Cranes cross subspecies designations to pair. We hypothesize that availability of high energy foods resulting from growing corn has allowed concentration of cranes along the Platte River during critical periods of pair formation, accelerating rates of cross-subspecies pairing, and rapidly moving mid-continent Sandhill Cranes toward monomorphism.

G. c. tabida was officially designated as rare by the U.S. Bureau of Sport Fisheries and Wildlife until late 1971 (Anon. in Johnson and Stewart 1973). Subspecies designations constitute legal entities under current endangered species laws. Recognition of subspecies among mid-continent Sandhill Cranes could result in the need to justify hunting of specific subspecies such as G. c. tabida. We believe that recognition of subspecies among mid-continent Sandhill Cranes should be held in abeyance pending further study.

There is a distinct association between presence of cranes with

larger body size and eastern migration routes within the mid-continent area. Because identification of subspecies based on morphometry is innaccurate or impossible, alternatives to harvest management that requires identification of individual birds by subspecies should be considered. We hypothesize that management of Sandhill Crane harvest on the basis of an eastern and western flyway is a viable alternative. While possible flyway definitions were described in this paper, further research is needed to refine flyway boundaries.

Insufficient data are currently available to allow identification of breeding populations among Sandhill Cranes inhabiting the mid-continent area. Analysis of the morphometry of pairs of mid-continent Sandhill Cranes systematically sampled from across their breeding range is needed in conjunction with identification of specific breeding populations (if there are any) in order to more fully address the question of subspeciation.

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Table 1. Morphological description of adult Sandhill Cranes from
nesting grounds where the subspecies were identified by size and
geographic location by J.W. Aldrich (data from Aldrich 1979).

Morphological characteristic	Sex	n	$\bar{x}$ (mm)	SE	df	Mean square	F	P
G. c. canadensis								
Culmen p-n[a]	M	20	71.50	1.03	1	22.23	1.03	0.317
	F	14	69.86	1.25				
Tarsus	M	20	189.80	3.05	1	405.18	2.32	0.067
	F	14	182.79	3.38				
Wing chord	M	20	465.65	4.66	1	3,320.05	9.97	0.004
	F	14	445.57	3.65				

MANOVA, Wilks' Λ = 0.76, P = 0.039[b]

G. c. rowani								
Culmen p-n[a]	M	5	90.40	2.06	1	113.61	3.46	0.105
	F	4	83.25	3.47				
Tarsus	M	5	224.00	5.97	1	200.56	1.67	0.237
	F	4	214.50	3.23				
Wing chord	M	5	502.60	6.27	1	1,947.02	10.69	0.014
	F	4	473.00	6.39				

MANOVA, Wilks' Λ = 0.36, P = 0.138[b]

Table 1. Continued.

Morphological characteristic	Sex	n	x̄ (mm)	SE	df	Mean square	F	P
G. c. tabida								
Culmen p-n[a]	M	9	107.11	2.29	1	206.71	7.60	0.015
	F	8	100.13	0.74				
Tarsus	M	9	247.11	4.29	1	1,932.55	16.25	0.001
	F	8	225.75	2.87				
Wing chord	M	9	543.56	8.89	1	6,093.43	12.08	0.003
	F	8	505.63	5.79				

MANOVA, Wilks' Λ = 0.37, P = 0.004[b]

[a] Culmen post-nares.

[b] Culmen post-nares, tarsus, and wing chord are the variables in the MANOVA between sexes within subspecies.

Table 2. Numbers and age and sex distribution of Sandhill Cranes sampled for this study.

State	Months[a]	Adult males	Adult females	Adult total	Juv. males	Juv. females	Juv. total	Total
Alaska	5	12	6	18	8	4	12	30
Nebraska	3,4	44	50	94	6	9	15	109
North Dakota	9	157	140	297	69	75	144	441
New Mexico	11,12,1	16	19	35	0	2	2	37
Oklahoma	10	120	182	302	80	85	165	467
Saskatchewan	4	8	5	13	2	0	2	15
Texas	11,12,1,2	174	164	338	67	59	126	464
Total	9-12,1-5	531	566	1,097	232	234	466	1,563

[a] Months when data on measurements, age, and sex were collected.

Table 3. Comparison of subspecies (as identified by size and breeding location) with linear and quadratic discriminate function subspecies designations using calibration data from Table 1.

Variance-covariance matrix	Correct subspecies	No. correct	Misclassified No.	Misclassified %
Males				
	G. c. canadensis	20	0	0
Pooled	G. c. rowani	5	0	0
(linear DF)	G. c. tabida	9	0	0
	Total	34	0	0
	G. c. canadensis	20	0	0
Unpooled	G. c. rowani	5	0	0
(quadratic DF)	G. c. tabida	9	0	0
	Total	34	0	0
Females				
	G. c. canadensis	13	1	7.7
Pooled	G. c. rowani	4	0	0
(linear DF)	G. c. tabida	8	0	0
	Total	26	1	3.8
	G. c. canadensis	14	0	0
Unpooled	G. c. rowani	4	0	0
(quadratic DF)	G. c. tabida	8	0	0
	Total	26	0	0

Table 4. Results of univariate and trivariate analysis of variance
testing differences in morphological characteristics between
subspecies within sexes (see Table 1 for n, $\bar{x}$, and SE of each group,
data from Aldrich 1979).

Sex	Morphological character	df	Mean square	F-value	P
	culmen p-n[a]	2	2,341.64	116.74	0.001
Female	tarsus	2	5,136.90	44.34	0.001
	wing chord	2	9,232.91	44.38	0.001
	MANOVA, Wilks' Λ = 0.06, P = 0.001[b]				
	culmen p-n[a]	2	4,066.98	145.74	0.001
Male	tarsus	2	10,767.96	59.99	0.001
	wing chord	2	11,983.54	40.41	0.001
	MANOVA, Wilks' Λ = 0.09, P = 0.001[b]				

[a]Culmen post-nares.

[b]Culmen post-nares, tarsus, and wing chord are 3 variables of MANOVA
for differences between subspecies within sexes.

Table 5.   Comparison of 3 morphological characteristics between adult and juvenile Sandhill Cranes.
Comparisons are by month with sexes separated for analysis.   All measurements are in mm.

Morphological character		Oct		Nov		Dec		Jan		Feb		Mar		Apr		May	
		male	female	male	female	male	female	male	female	male	female	male	female	male	female
Culmen post-nares — Adults	$\bar{x}$	86.07	81.14	74.06	72.58	76.00	74.78	79.89	74.57	79.56	75.70	76.32	71.45	77.17	71.19	75.70	72.67
	SE	0.57	0.47	0.88	0.67	1.32	2.49	0.57	0.61	0.71	0.81	0.66	0.79	1.40	0.88	1.14	1.31
	n	128	195	16	24	13	9	87	84	64	53	31	28	23	27	10	6
	OSL[a]	0.001	0.001	0.010	0.001	0.210	0.008[b]	0.001[b]	0.001	0.060	0.045	0.002	0.650	0.174	0.530	0.167	0.350
Culmen post-nares — Juveniles	$\bar{x}$	81.78	77.55	71.83	66.57	73.94	66.00	71.24	69.71	75.00	71.56	70.00	70.60	72.10	69.60	73.00	70.33
	SE	0.65	0.67	0.94	0.99	0.98	0.86	0.75	1.29	1.44	1.02	2.35	1.89	2.77	3.47	1.46	2.03
	n	80	85	23	23	17	12	21	17	9	5	5	5	5	5	6	3
Tarsus — Adults	$\bar{x}$	220.68	209.41	199.39	187.58	192.08	179.11	194.92	185.81	198.05	181.08	197.77	184.50	200.00	187.04	188.10	185.83
	SE	1.47	0.99	3.31	1.92	4.00	3.12	1.68	1.39	1.84	1.69	1.87	1.52	3.84	2.97	2.92	3.34
	n	128	195	18	24	13	9	87	84	64	53	31	28	23	27	10	6
	OSL[a]	0.014[b]	0.099	0.750	0.443[b]	0.554	0.120	0.303	0.816	0.274	0.082	0.529	0.991[b]	0.383	0.298	0.386	0.825
Tarsus — Juveniles	$\bar{x}$	225.83	212.31	200.91	190.65	195.53	169.00	191.00	185.00	191.00	189.11	194.60	194.60	208.20	194.80	193.50	184.00
	SE	1.20	1.35	3.32	3.45	4.00	1.82	3.30	3.53	7.35	4.79	4.53	7.97	9.15	5.39	6.17	9.61
	n	80	85	23	23	17	12	21	17	9	5	5	5	5	5	6	3
Wing chord — Adults	$\bar{x}$	483.38	459.29	478.06	449.92	482.77	463.00	471.38	451.77	468.23	445.92	483.00	456.32	484.61	461.81	474.10	461.33
	SE	2.00	1.45	3.32	2.57	6.14	6.61	2.02	2.20	2.77	2.66	2.69	3.04	4.26	4.94	4.26	5.16
	n	128	195	18	24	13	9	87	84	64	53	31	28	23	27	10	10
	OSL[a]	0.001	0.021	0.025	0.423	0.044	0.003	0.004[b]	0.054	0.241	0.405	0.003	0.052	0.141	0.420	0.130	0.564
Wing chord — Juveniles	$\bar{x}$	470.99	453.42	467.39	446.17	466.00	432.75	449.57	441.12	457.00	439.56	458.20	439.40	469.10	452.20	461.67	456.67
	SE	2.24	1.90	3.09	3.89	5.11	5.71	6.50	5.40	9.48	9.97	9.45	10.70	7.93	4.52	7.07	2.33
	n	80	85	23	23	17	12	21	17	9	5	5	5	5	5	6	3

[a] OSL - observed significance level for 2-group t-test between adults and juveniles.

[b] Unequal variances, $P < 0.05$.

Table 6. Distribution of subspecies of adult Sandhill Cranes sampled for this study as designated by linear and quadratic discriminate functions based on calibration data from Aldrich (1979).

State or province	n / %	G. c. canadensis			G. c. rowani			G. c. tabida			Total
		male	female	total	male	female	total	male	female	total	
Linear											
Alaska	n	12	6	18	0	0	0	0	0	0	18
	%	66.7	33.3	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
Nebraska	n	40	44	84	4	6	10	0	0	0	94
	%	42.6	46.8	89.4	4.2	6.4	10.6	0.0	0.0	0.0	100.0
North Dakota	n	37	35	72	111	75	186	6	29	35	293
	%	12.6	12.0	25.6	37.9	25.6	63.5	2.1	9.8	11.9	100.0
New Mexico	n	15	17	32	1	2	3	0	0	0	35
	%	42.8	48.6	91.4	2.9	5.7	8.6	0.0	0.0	0.0	100.0
Oklahoma	n	18	31	49	102	143	245	0	8	8	302
	%	6.0	10.2	16.2	33.8	47.4	81.1	0.0	2.7	2.7	100.0

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Table 6. Continued.

State or province	n %	G. c. canadensis			G. c. rowani			G. c. tabida			Total
		male	female	total	male	female	total	male	female	total	
Saskatchewan	n	4	3	7	4	2	6	0	0	0	13
	%	30.8	23.0	53.8	30.8	15.4	46.2	0.0	0.0	0.0	100.0
Texas	n	122	135	257	57	28	80	0	1	1	338
	%	36.1	39.9	76.0	15.4	8.3	23.7	0.0	0.3	0.3	100.0
Quadratic DF											
Alaska	n	12	6	18	0	0	0	0	0	0	18
	%	66.7	33.3	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
Nebraska	n	37	50	87	7	0	7	0	0	0	94
	%	39.4	53.2	92.5	7.5	0.0	7.5	0.0	0.0	0.0	100.0
North Dakota	n	35	89	124	97	29	126	22	21	43	293
	%	21.0	30.4	42.4	33.1	9.9	43.0	7.5	7.2	14.7	100.0
New Mexico	n	13	19	32	3	0	3	0	0	0	35
	%	37.1	54.3	91.4	8.6	0.0	8.6	0.0	0.0	0.0	100.0

Table 6. Continued.

State or province	n / %	G. c. canadensis			G. c. rowani			G. c. tabida			Total
		male	female	total	male	female	total	male	female	total	
Oklahoma	n	37	147	184	65	26	91	18	9	27	302
	%	12.2	48.7	60.9	21.5	8.6	30.1	6.0	3.0	9.0	100.0
Saskatchewan	n	4	5	9	4	0	4	0	0	0	13
	%	30.8	38.4	69.2	30.8	0.0	30.8	0.0	0.0	0.0	100.0
Texas	n	115	158	273	57	6	63	2	0	2	338
	%	34.0	46.8	80.8	16.9	1.7	18.6	0.6	0.0	0.6	100.0

Table 7. Results of nearest-neighbor measurements on bivariate

distributions of morphometric characters from adult Sandhill Cranes

sampled for this study.

Bivariate distribution	Sex	n	rho	$\bar{r}_a$	$\bar{r}_e$	R	σ_{r_e}	$\underline{Z}^a$
Culmen p-n[b]X	M	531	0.718	1.059	0.590	1.790	0.013	35.01
Tarsus	F	566	0.834	0.974	0.548	1.779	0.012	35.46
Culmen p-n[b]X	M	531	0.554	1.240	0.672	1.845	0.015	37.27
Wing chord	F	566	0.595	1.202	0.648	1.854	0.014	38.90
Tarsus X	M	531	0.244	2.108	1.012	2.082	0.023	47.72
Wing chord	F	566	0.290	1.927	0.928	2.076	0.020	48.97

[a] All $\underline{Z}$-tests indicate a highly significant ($\underline{P} = 0.001$) departure from random.

[b] Culmen post-nares.

Table 8. Distribution of within and cross-subspecies pairing of 20 pairs of marked Sandhill Cranes using both linear and quadratic subspecies designations for observed pairs. χ^2 test is for H_o: random pairing among subspecies.

Discriminate function	G. c. canadensis	G. c. rowani	G. c. tabida	Crosses
Linear				
Observed	11	2	0	7
Expected[a]	12.46	0.87	0.00	6.67
Cell χ^2	0.17	1.47	0.00	0.02
	Overall χ^2 = 1.66, df = 3, $\underline{P}$ = 0.66			
Quadratic				
Observed	10	0	0	10
Expected[b]	13.88	0.52	0.00	5.60
Cell χ^2	1.08	0.52	0.00	5.21
	Overall χ^2 = 6.81, df = 3, $\underline{P}$ = 0.08			

[a] Expected values for random pairing of subspecies based on linear DF designation of 432 adult sandhill cranes from Texas and Nebraska where observed pairs were marked (e.g. 78.94% of 432 cranes were designated G. c. canadensis using linear DF, expected value for pairs where both cranes were canadensis = $(0.7894)^2$ 20 = 12.46).

[b] Same as a above except results of quadratic DF were used.
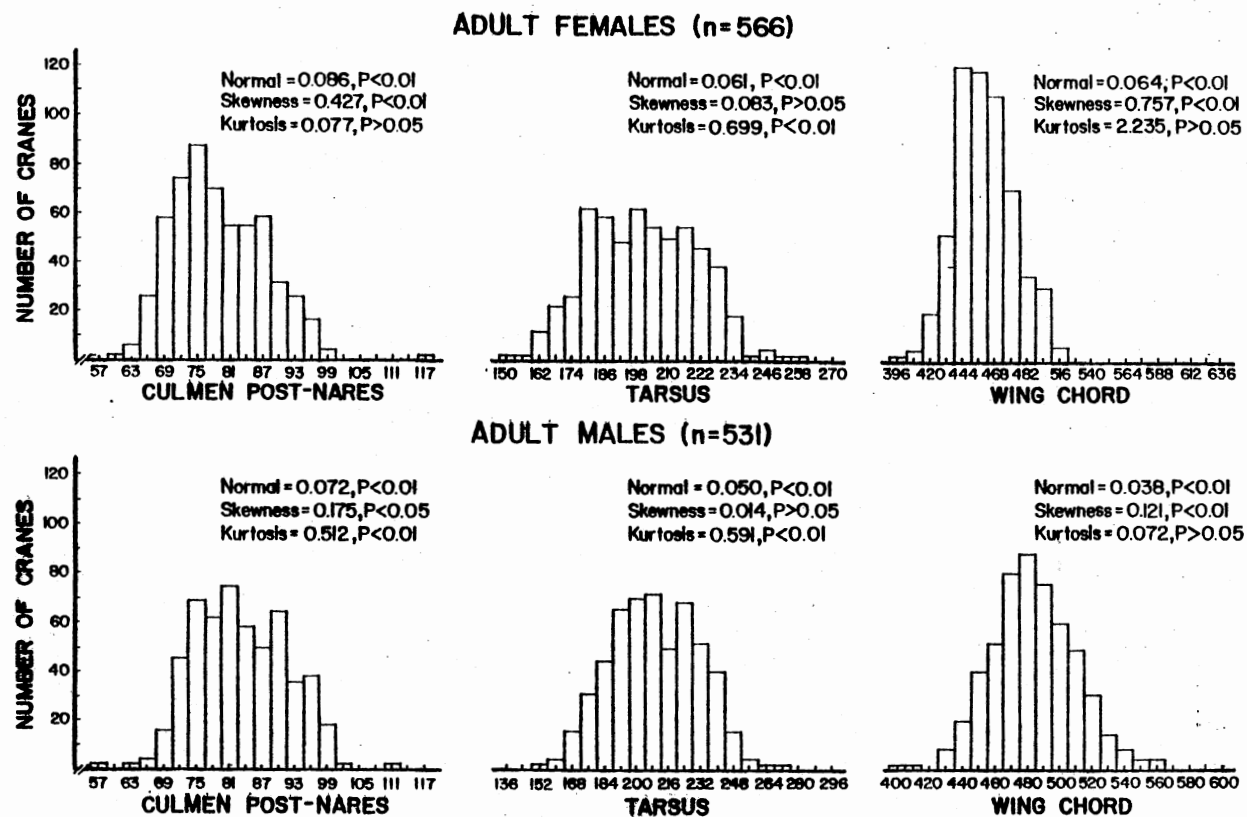
Figure 1. Univariate distributions of culmen post-nares, tarsus, and wing chord for adult female and adult male Sandhill Cranes.

ADULT MALES

	Linear	Quadratic
G. c. canadensis (C)	37	35
G. c. rowani (R)	111	97
G. c. tabida (T)	6	22
Total	154	154

ADULT FEMALES

	Linear	Quadratic
G. c. canadensis (C)	35	89
G. c. rowani (R)	75	29
G. c. tabida (T)	29	21
Total	139	139

A.
0.1

148 R R R R R C
   T R R T T R

A.
0.1

133 R T T R C R
    C R C C C C

B.
0.1

142 R R R R R R
    T R T R R R

B.
0.1

127 T R R R T R
    T C C C R C

C.
0.1

136 C T C R R R
    C T C R R R

C.
0.1

121 R T R R R R
    C C C C C R
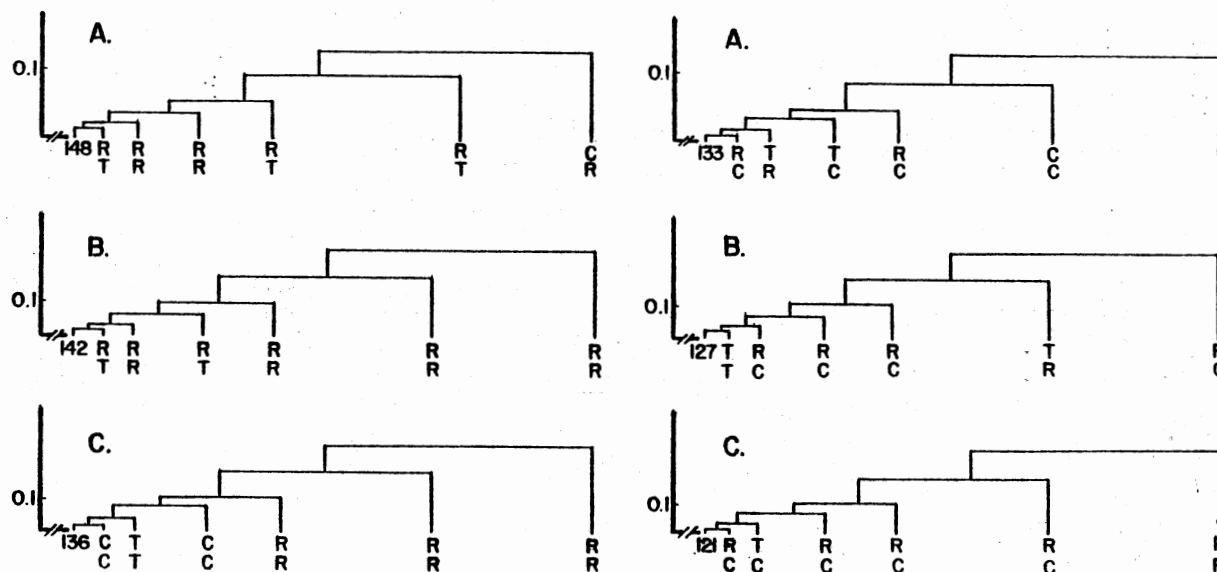
Figure 2.   Trivariate cluster analyses of Sandhill Cranes from North Dakota.   Dendrogram A for each sex represents initial clustering of 154 male or 139 female cranes.   Dendrogram B is the result of cluster analysis after removing the 6 outlying cranes from dendrogram A.   Dendrogram C is the result of cluster analysis after removing the 12 outlying cranes from dendrogram A and 6 from dendrogram B.   The left-hand point of each dendrogram represents n cranes clustered at 1 point; other points in each dendrogram represent 1 outlying crane for which linear (upper letter) and quadratic (lower letter) subspecies designations are shown.   Distributions of linear and quadratic subspecies designations of the initial sample for each sex are shown above the dendrograms.

ADULT MALES

G.c. canadensis (C)	Linear	Quadratic
G.c. canadensis (C)	18	37
G.c. rowani (R)	102	65
G.c. tabida (T)	0	18
Total	120	120

ADULT FEMALES

G.c. canadensis (C)	Linear	Quadratic
G.c. canadensis (C)	31	147
G.c. rowani (R)	143	26
G.c. tabida (T)	8	9
Total	182	182

A.

0.1

114 C R R C R R
C C T C R T

B.

0.1

108 R R R R R R
C R C C R T

C.

0.1

102 R C R R R R
C C C R R R

A.

0.1

176 R R T R R R
C C T C C

B.

0.1

170 R R R C R R
C C C C C C

C.

0.1

164 R R R C R R
C C C C C C
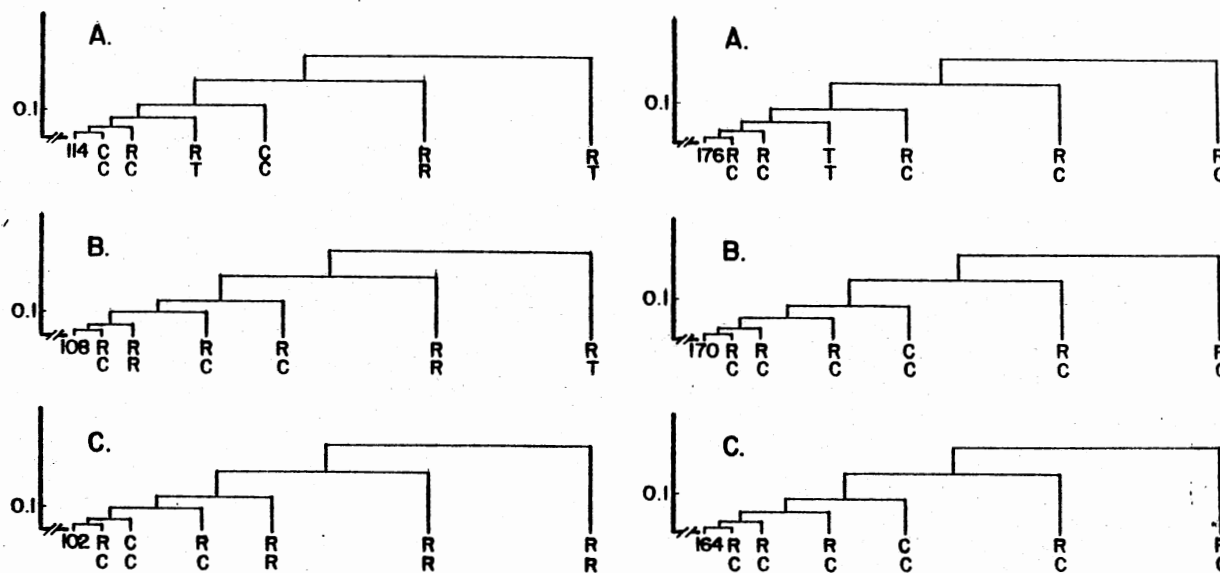
Figure 3. Trivariate cluster analyses of Sandhill Cranes from Oklahoma. Dendrogram A for each sex represents initial clustering of 120 male or 182 female cranes. Dendrogram B is the result of cluster analysis after removing the 6 outlying cranes from dendrogram A. Dendrogram C is the result of cluster analysis after removing the 12 outlying cranes from dendrogram A and 6 from dendrogram B. The left-hand point of each dendrogram represents n cranes clustered at 1 point; other points in each dendrogram represent 1 outlying crane for which linear (upper letter) and quadratic (lower letter) subspecies designations are shown. Distributions of linear and quadratic subspecies designations of the initial sample for each sex are shown above the dendrograms.

ADULT MALES

	Linear	Quadratic
G. c. canadensis (C)	122	115
G. c. rowani (R)	52	57
G. c. tabida (T)	0	2
Total	174	174

ADULT FEMALES

	Linear	Quadratic
G. c. canadensis (C)	135	158
G. c. rowani (R)	28	6
G. c. tabida (T)	1	0
Total	164	164
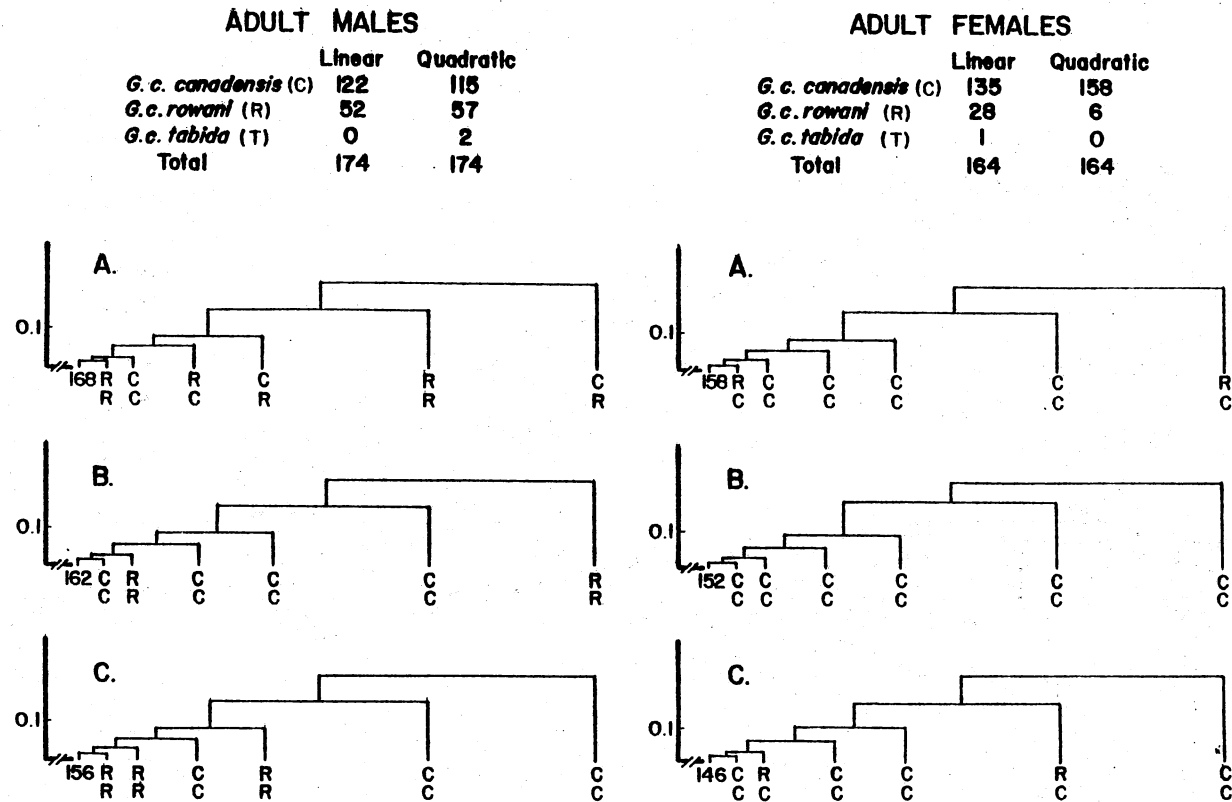
Figure 4. Trivariate cluster analyses of Sandhill Cranes from Texas. Dendrogram A for each sex represents initial clustering of 174 male or 164 female cranes. Dendrogram B is the result of cluster analysis after removing the 6 outlying cranes from dendrogram A. Dendrogram C is the result of cluster analysis after removing the 12 outlying cranes from dendrogram A and 6 from dendrogram B. The left-hand point of each dendrogram represents $\underline{n}$ cranes clustered at 1 point; other points in each dendrogram represent 1 outlying crane for which linear (upper letter) and quadratic (lower letter) subspecies designations are shown. Distribution of linear and quadratic subspecies designations of the initial sample for each sex are shown above the dendrograms.

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CHAPTER III

MAINTENANCE BEHAVIORS OF SANDHILL CRANES

Thomas C. Tacha

Maintenance behaviors are general or specific activities (including comfort movements) that serve to maintain an animal physiologically (Marler 1956). The purpose of this paper is to provide a quantitative description of the maintenance behaviors of sandhill cranes (Grus canadensis). These descriptions will aid in interpreting the evolution of social signals in sandhill cranes (presented elsewhere) and for comparative studies of other Gruids. Quantification of maintenance behaviors will aid in interpreting refuging patterns (Hamilton and Watt 1970) and social organization of migrating and wintering cranes.

METHODS

Sandhill cranes were studied from early January through February 1978 to 1980 near Rich Lake, Terry County, Texas, and during March and early April 1978 to 1980 along the Platte River between Southerland and North Platte, Nebraska. Additional observations were made during the last 2 weeks of April 1980 near the north end of Last Mountain Lake, Saskatchewan; during May 1980 near Delta Junction, Alaska; and immediately prior to nesting in May 1980 near Old Chevak, Clarence Rhodes National Wildlife Refuge, Alaska.

Observations were aided with a 15 X 60 telescope. Postures and movements were recorded on 35 mm slides and 16 mm motion pictures. Descriptions and social interactions were verbally recorded on tape during 1,109 20-minute time budgets in 1979 and 1980. Behaviors recorded were the maintenance catagories defined in this paper and the social signals defined elsewhere.

Juvenile (young-of-the-year) sandhill cranes were distinguished from adults by having brown feathering on the nape of the neck (Lewis 1974). Sex of some cranes was determined in the field by observation of the unison call (described by Archibald 1975). Sex was designated during 54 time budgets for members of a pair on the basis of females following males, and later verified by observation of the unison call. None of the designations made on the basis of the female following the male was found to be incorrect during the subsequently observed calls. On that basis, the observation of one crane of a pair following another for extended periods was used to assume sex in some time budgets where the unison call was not observed. Pairs (2 adults) and family units (2 adults and 1 or 2 juveniles) were identified by their close proximity (compared to other cranes in larger flocks), the tendency for adult females of pairs to follow the male, and the propensity of juveniles of family units to follow their parents. The sex of juveniles could not be determined in the field, and no juveniles were observed as members of a mated pair. The sex of adults not in pairs or family units could not be determined.

When time budgets were transcribed from tapes to coding sheets for subsequent computer analyses, behaviors were recorded to the nearest full second. Cranes were selected for observation and time budgets

using stratified random sampling with these strata: time budgets were taken in all major habitats used by cranes at all hours of the day, sampling was stratified by age groups to insure adequate sampling of juveniles, and a stratified sampling design for cranes marked (neck collar and leg band) longer than 7 days was employed. Statistical tests were performed using the Statistical Analysis System (Barr et al. 1979). Three methods of quantifying behaviors used were: frequency of occurrence of behaviors using each time budget as an experimental unit and recording presence or absence of each behavior; duration of each behavior using each observation of the behavior in a time budget as the experimental unit; and % of total time spent in each behavior using time budgets as the experimental units. Observed Significance Levels (OSL) less than 0.05 were considered sufficient to reject statistical hypotheses.

RESULTS

FORAGING

Searching, gleaning, probing, and drinking were grouped as foraging activities. Frequency of occurrence of foraging activities did not vary between age or sex classes (Table 1), but adult males of pairs were observed foraging 10% more often than adult males of families (Table 2). Juveniles spent 1.25 times the percentage of time spent foraging by adults, and adult females spent a higher percentage of time (64%) foraging than adult males (53.9%, Table 4). Adults in pairs and family units spent 1.14 times the percentage of time that adults without mates or young spent foraging (Table 5).

Searching. - Sandhill cranes exhibited a stereotyped food-searching

posture (Fig. 1a). The body was held on a horizontal plane, the neck curved downward and the bill held near a 45 degree angle. This food-searching posture was observed at all locations in all habitats where cranes attempted to feed.

No difference in frequency of occurrence (Table 1) or duration (Table 3) of searching behaviors was observed between adult and juvenile sandhill cranes. However, adults of both sexes spent a higher percentage of time (4.72%) searching for food than did juveniles (3.82%, Table 4). Adult males searched for periods 80% as long as adult females (Table 3), but frequency of occurrence (Table 1) and percentage of time searching (Table 4) did not differ between sexes. Adult cranes in pairs and family units searched more frequently than adults without mates or young (Table 2); but the percentage of time spent searching did not vary between social classes (Table 5).

Gleaning. - The retrieval and/or ingestion of food items from the surface of the medium upon which a crane is feeding is called gleaning (Fig. 1b). Gleaning was the major method of feeding in harvested small grain fields or other areas where surface food items were abundant. Posture of the body while gleaning was similar to that of searching but cranes moved their heads from side to side while walking forward, ingesting food items as they walked.

Juvenile sandhill cranes were observed gleaning with the same frequency as adults (Table 1); but juveniles gleaned for 10% longer periods (Table 3). Juveniles spent nearly twice as high of a percentage of time gleaning (Table 4) as adults. No differences in frequency of occurrence (Table 1), duration (Table 3) or percentage of time (Table 4) spent gleaning was observed between sexes of adult cranes.

Adults without mates or young gleaned 1.25 times as frequently (Table 2) and spent 1.3 times the percentage of time gleaning (Table 5) as did adults in pairs or family units. Juveniles in family units gleaned nearly twice as frequently (Table 2) and spent twice the percentage of time gleaning (Table 5) as did juveniles without parents.

Probing. - Probing was used by sandhill cranes to locate and extract subsurface food items (Fig. 2). A typical performance included a vertical (10 cm) hammering motion of the head and bill (Fig. 2a) to dislodge soil or break up stems and roots. Loose particles from the probing site were removed with a lateral flip of the head in about a 30 degree arc (Fig. 2b). Lateral compression of the bill made side to side particle removal more efficient than forward or backward movements. Movements of the head and neck were variable. Films at 24 fps did not record all movements in probing when peak rates of head movements were achieved. As a crane began to probe, movements were usually deliberate and methodical. As probing continued, rates of vertical strokes exceeded my ability to see the individual motions.

Rarely have I seen cranes probe deeper into a substrate than the distance from the tip of the bill to the crown of the head (100-150 mm). However, cranes often probed in mud in shallow ponds as much as 0.3 m below the surface of the water. Juveniles in families often probed in the same hole as their female parent. Adult females were observed to feed invertebrates (resulting from probing) to young 48 times during time budgets.

No differences in frequency of occurrence of probing was observed between age and sex classes (Table 1). Juvenile cranes spent 1.2 times the percentage of time probing (Table 4) that adults did. Among adults,

females probed for 50% longer periods (Table 3) and spent 1.25 times the percentage of time probing (Table 4) as did males. Adults without mates spent 75% of the time probing (Table 5) as did adults in pairs. Adult males of pairs probed 1.26 times as frequently as adult males in family units, but frequency of occurrence of probing did not vary between adult females of pairs and family units. Juveniles without parents probed 1.21 times more frequently than juveniles with parents (Table 2), but juveniles with and without parents spent approximately the same percentage of time probing (Table 5).

Drinking. - Sandhill cranes exhibited a stereotyped pattern of ingesting water (Fig. 3). Cranes nearly always stood in water with the head and neck extended forward and down, and the lower mandible submerged (Fig. 3a) prior to drinking. The mandibles were closed, and the head was raised above a 60 degree angle from horizontal during ingestion. All birds spent approximately the same effort in drinking (Tables 1-5).

LOAFING

Loafing (up and down combined) was observed in 75% of the time budgets (Table 1). Adults loafed 1.1 times more frequently than juveniles (Table 1), and adults without mates or young were observed loafing 1.3 times more often than adults in pairs or families (Table 2). Adults spent 1.5 times more time loafing than juveniles (Table 4), and adults without mates or young spent nearly twice the time loafing as did adults in pairs and families (Table 5).

Loafing-down. - Sandhill cranes were observed to loaf-down (fig. 4a) primarily on warm afternoons. Cranes would lie down, tuck the tarsus forward under the body, and position the head and neck in the

same posture as loafing-up (Fig. 4b).

Loafing-down was observed in time budgets only 30 times (Table 3), but the duration of loafing-down varied from a mean of 229 seconds among adult males to mean of 674 seconds among adult females. Adults without social bonds spent 4 times the percentage of time loafing-down as did adults in pairs or families (Table 5).

Loafing-up. - Sandhill cranes had a stereotyped loafing posture when standing (Fig. 4b). Loafing-up involved a stance on 1 or both legs, but with no locomotion. The position of the head and neck were consistant during loafing, and only a slight variation resulted in alert or threat postures.

Observations of sandhill cranes loafing-up varied from a mean duration of 29.08 seconds among adult females to 43.73 seconds among adult males (Table 3). Adults spent a higher percentage of time (14%) loafing-up than juveniles (10%), and adult males spent more time (11%) loafing-up than did adult females (7%, Table 4). Adults without mates spent 3 times more time loafing-up than adults in pairs, and juveniles in families spent twice the time loafing-up as did juveniles without parents (Table 5).

SLEEPING

Sleeping (up and down combined) was observed in 9% of time budgets, with adults sleeping twice as frequently as juveniles and adult females sleeping twice as frequently as adult males (Table 1). Adult cranes in pairs were observed sleeping 4 times less often than adults of family units or adults without mates or young (Table 2). Adults spent nearly 3 times the percentage of time sleeping as did juveniles, and adult females slept 5 times as high a percentage of time as adult males

(Table 4).

Sleeping-up. - Sandhill cranes had a stereotyped sleeping posture (Fig. 5a). The head was turned back over a shoulder and the bill tucked under the scapular feathers, often while standing on 1 leg.

Cranes slept for extended periods (Table 3), often for all of a 20-minute time budget. Adults spent twice the percentage of time sleeping-up that juveniles did, and adult females slept-up 4 times more than males (Table 4). The percentage of time spent sleeping-up did not vary between social classes (Table 5).

Sleeping-down. - During the day, sandhill cranes were often observed to be sleeping-down (Fig. 5b). After a period of loafing-down, cranes would tuck their bill under scapular feathers, resulting in the sleeping-down posture.

Adult females slept-down for 6 times longer periods than adult males or juveniles (Table 3). No differences in percentage of time spent sleeping-down were observed between age, sex, or social classes (Tables 4 and 5).

BATHING

Sandhill cranes were observed bathing during 4 time budgets. Cranes waded into water 20-40 cm deep, submersed themselves in a quick diving motion (Fig. 6), and often rolled in water following the initial diving motion. Following immersion, cranes would wade from the water while alternately body shaking and wing flapping. A prolonged preening session followed the shaking and flapping. Bathing was only observed among adults in time budgets (Table 4), and sample sizes were to small for analysis by age, sex, or social classes.

PREENING

When all forms of preening were combined, adults preened 1.3 times more frequently than juveniles, and males preened 1.3 times more frequently than females (Table 1). Adults without mates or young preened 1.5 times more frequently (Table 2) and spent twice as much time preening (Table 5) as adults in pairs or families.

Preening the wings. - The wing preen followed spreading of the wings. Coverts and upper wing feathers were preened in a nibbling movement (Fig. 7). Contour feathers were grasped between the distal ends of the mandibles, and the individual feathers were stroked from calamus to tip while the wing was half extended.

Wing preening lasted an average of 35 seconds (Table 3). No differences in percentage of time spent preening wings were observed between age, sex, or social classes (Tables 4 and 5).

Preening the neck. - Sandhill cranes preen the lower half of their neck using a nibbling motion with the bill. Duration of neck preening did not vary between age and sex classes (Table 3). No differences in percentage of time spent preening the neck were observed between age, sex, or social classes (Tables 4 and 5).

Preening the chest. - Sandhill cranes preened the chest and belly feathers with a nibbling motion (Fig. 8a). Duration of chest preening bouts did not vary between age and sex classes (Table 3). No differences in percentage of time spent preening the chest were observed between age, sex, or social classes (Tables 4 and 5).

Preening the back. - Sandhill cranes preened the area of the back between the wings in short bouts (Table 3). Adult males preened the back for periods twice as long as adult females or juveniles. Adults

without mates or young spent over 10 times more time preening the back than adults in pairs or families (Table 5).

Head rub. - The head rub (Fig. 8b) served to preen the feathers of the back of the head and to distribute oil from the europigial gland on feathers. Cranes would rub the back of the head on the europigial gland and then on feathers of the wings and back. I did not observe cranes oiling neck or chest feathers with the bill.

Head rubbing was exhibited for short periods (Table 3). Adults without mates or young head rubbed 10 times the percentage of time observed for adults in pairs or families (Table 5).

Head scratch. - Scratching of the upper neck, head and bill was accomplished using the claw on the middle toe of either foot (Fig. 9). The head and neck were stretched forward and downward 20-30 degrees during scratching. The head was often rotated as much as 120 degrees to make all parts of the head and upper half of the neck available to be scratched.

Head scratching bouts lasted 5-10 seconds, with adult males scratching 50% longer periods than adult females and adult females scratching 50% longer periods than juveniles (Table 3). While the percentage of time spent scratching did not vary between ages or sexes (Table 4); juveniles in family units spent nearly 3 times as much time scratching as did juveniles without parents (Table 5).

Body shake. - The body shake was a movement apparently intended to rearrange the feathers of the body and wings of sandhill cranes. Body shaking was nearly always performed after flights, more exerting social signals, or bathing. The feathers of the body were erected while the crane violently shook. Cranes often began to preen their wings

following a body shake.

Body shaking occurred for only 1-5 seconds (Table 3). Adults
spent 1.5 times more time exhibiting the body shake than juveniles
(Table 4), but percentage of time spent exhibiting the body shake did
not vary between sexes. Adults without mates or young spent 10 times
more time body shaking than adults in pairs or family units (Table 5).

STRETCHING

Frequency of occurrence of all 3 forms of stretching did not differ
between age and sex classes (Table 1). However, adults without mates or
young stretched twice as frequently as adults in pairs or families
(Table 2). No differences in percentage of time spent stretching were
observed between age, sex, or social classes (Tables 4 and 5).

Wing-and-leg stretch. - During the wing-and-leg stretch, the wing
on one side was fully extended while the leg on the same side was
stretched backward (Fig. 10a). This position was held for several
seconds, then the wing was folded and the leg returned to the ground.

The wing-and-leg stretch lasted 4-8 seconds, with juveniles
stretching for 30% shorter periods than adults (Table 3). No difference
in the percentage of time spent in wing-and-leg stretching was observed
between age, sex, or social classes (Tables 4 and 5).

Wing-flapping. - Wing-flapping consisted of vigorously flapping
fully extended wings while standing with the body in a 60 degree
upright position. Wing-flapping apparently functioned to stretch flight
muscles and to shed excess water after bathing. Often wing-flapping
was used as a displacement activity or preceeding flight.

Wing-flapping bouts lasted from 2 to 10 seconds (Table 3). Adult
males wing-flapped for periods twice as long as adult females or

juveniles. No differences were observed in percentage of time spent wing-flapping between age, sex, or social classes (Tables 4 and 5).

Double wing stretch. - In the double wing stretch the head was stretched forward and downward in line with the body axis at about a 20-30 degree angle below horizontal, while both wings were raised (but not extended) upward and backward (Fig. 10b).

The double wing stretch lasted from 3-7 seconds (Table 3) and occurred rarely in time budgets other than when cranes awakened in the morning on the roost. No differences in percentage of time spent in the double wing stretch were observed between age, sex, or social classes (Tables 4 and 5).

LOCOMOTION

Locomotion behaviors were observed in 72% of time budgets, with adults using locomotor behaviors 15% more frequently than juveniles, and adult males using locomotor activities 20% more frequently than adult females (Table 1). Frequency of occurrence of locomotor activities did not differ between social classes (Table 2). Males spent a 50% higher percentage of time in locomotor activities than females, but percentage of time exhibiting locomotor behaviors did not vary between ages or social classes (Tables 4 and 5).

Flying. - Sandhill cranes normally became airborne by running 3-6 steps. However, cranes sprang directly into the air when frightened. Sandhill cranes landed by extending their legs (from their trailing position during flight) and reducing air speed to nearly 0 by rapid wing strokes. Legs were bent slightly upon contact with the ground, absorbing the shock of landing. Cranes took off and landed into the wind except when escaping danger.

No differences in frequency of occurrence of flight were observed between age, sex or social classes (Table 1). Flight averaged 110 seconds in time budgets (Table 3), but this estimate was low because flight was often the terminal behavior in a time budget. No differences in percentage of time spent in flight were observed between age, sex, or social classes (Tables 4 and 5).

Soaring. - Sandhill cranes soared with wings outstretched and no wing beats. The head and neck and legs were outstretched as when flying.

Sandhill cranes soared for prolonged periods, but duration of soaring did not differ between age and sex classes (Table 3). No differences were detected in percentage of time spent soaring between age, sex, or social classes (Tables 4 and 5).

Walking. - Sandhill cranes walked in a deliberate manner with wings folded, each foot lifted and placed in front of and to the proper side of the other. The head moved slightly forward and back with each step. Pace length varied by size of the bird but averaged 12-15 cm. The birds did not hop.

Walking occurred in 71% of time budgets, with adult males walking 1.16 times more frequently than adult females (Table 1). No differences in durations or percentages of time spent walking were observed between age, sex, or social classes (Tables 3-5).

Running. - Movement of sandhill cranes while running resembled walking except that the pace was faster and the head was lowered slightly for balance. Running (outside a social signal context) was rarely observed among sandhill cranes (Table 3). Juveniles spent 8 times more time running than adults (Table 4), but percentage of time spent running did not differ between sexes or social classes

(Tables 4 and 5).

Swimming. - Sandhill cranes were observed to swim in water over leg length depth and floated erect and balanced (much like Fig. 4a), with about 25% of the body submerged. Cranes swam with alternating strokes of the feet much as anatids do. Forward progress was slow due to lack of webbing in the feet. Sandhill cranes could attain flight from a floating position. Cranes were never observed swimming during time budgets, and swimming was rare except on roosting areas.

MAINTENANCE BEHAVIORS

Adult and juvenile cranes spent 86.7% and 89.4% of their time respectively, using maintenance behaviors (Table 4). Females spent 10% more time in maintenance activities than males. Adults without mates or young spent a higher percentage of time (89.5%) in maintenance activities than adults in pairs (84.3%) or family units (79.8%) (Table 5).

DISCUSSION

One of the attributes of K-selected species is lengthy parental investment (Brown 1975). Juvenile sandhill cranes remain with their parents for nearly a year (Drewien 1973). Iverson (1981) found that juvenile sandhill cranes were in better physiological condition (higher lipid level) than adults throughout winter and during early spring migration; the period when juveniles were still subject to parental investment. Results of my study illustrated some of the ways that juveniles benefited from parental investment.

Juveniles in family units were able to glean for longer periods without interruption than adults, probably as a result of parental

protection from other cranes. I hypothesize that juveniles of family units spent less time searching than juveniles without parents because parents located areas of comparatively high food density for them. Direct feeding of invertebrates to juveniles by parents, and the tenacity of juveniles in following parents closely when foraging, suggest that juveniles were allowed priority access to food by parents. The higher percentage of time spent foraging by juveniles may have been related to higher nutritional needs associated with growth as juveniles did not reach full growth until 10-12 months of age (Tacha 1981).

Tacha (1981) hypothesized that adult male sandhill cranes from pairs and family units served a protective role directed primarily towards their mates. Adult males spent more time exhibiting social signals than females which is consistant with the theory that adult males serve a protective role directed primarily at their mates. Adult females with mates appeared to benefit from this protection by being able to sleep and forage a much higher percentage of time than males. Adult males were more mobile than adult females, spending a higher percentage of time in locomotor activities. Adult males searched, gleaned, and probed for shorter periods and slept less frequently and for shorter periods than adult females. Males were interrupted by agonistic or alert responses to other (probably male) cranes. Loafing and sleeping-down provided the advantage of removing cranes from social interactions. Only once was a crane loafing-down or sleeping-down observed to be involved in a social interaction. Adult males spent a higher percentage of time loafing-up and a lower percentage of time loafing-down than females. Loafing-up provided a non-signaling method of observing surroundings, and the higher

percentage of time spent loafing-up by males was consistant with the male protective role.

Maintenance of social bonds is expensive in terms of time and energy (Brown 1975). Adult sandhill cranes without mates or young were able to spend more time in foraging activities that resulted in ingestion of high energy foods (gleaning) than cranes with social bonds. Adult cranes with mates and young spent more time exhibiting social signals than cranes without social bonds; implying that adult cranes with social bonds were protecting those bonds via social signals. Sandhill cranes appear to have evolved a social system and resource exploitation strategies that maximize survival of young via high parental investment, and allow relatively inexperienced cranes (subadults without mates or young) to survive without social bonds that are costly in time and energy.

SUMMARY

Most maintenance behaviors of sandhill cranes are stereotyped in their performance. Acquisition of essential nutrients, comfort movements, and locomotor activities accounted for over 85% of time expenditures of sandhill cranes. Juvenile sandhill cranes benefited directly from parental investment through reduced time spent searching and increased time spent gleaning. Mated adults spent a lower percentage of time gleaning and a higher percentage of time exhibiting social signals than adults without mates. Adult males spent a higher percentage of time exhibiting social signals; searched, gleaned, and probed for shorter periods; slept less frequently and for shorter periods; and were more mobile than adult females.

ACKNOWLEDGMENTS

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COOPERATIVE WILDLIFE RESEARCH UNIT, 404 LIFE SCIENCES WEST, OKLAHOMA
STATE UNIVERSITY, STILLWATER, OKLAHOMA 74078.

Table 1

Comparison Between Age and Sex Classes of the Percentage Occurrence of Maintenance Behaviors in Time Budgets

of Sandhill Cranes

Behaviors	Age				Sex			
	Adult (n=711)	Juvenile (n=339)	Z	OSL	Male (n=150)	Female (n=141)	Z	OSL
Searching	85.51	85.84	0.14	0.888	92.67	89.36	0.99	0.323
Gleaning	30.24	34.22	1.30	0.194	21.33	20.57	0.16	0.873
Probing	70.32	67.55	0.91	0.362	82.00	87.94	1.41	0.158
Drinking	5.77	3.54	1.54	0.123	8.00	4.26	1.33	0.185
Foraging[a]	90.72	93.51	1.53	0.127	95.33	95.04	0.12	0.906
Loafing[b]	77.78	70.80	2.46	0.014	69.33	64.54	0.87	0.385
Sleeping[c]	11.39	5.60	2.99	0.003	5.33	12.06	2.05	0.041
Preening[d]	54.85	41.89	3.93	0.001	54.00	41.13	2.20	0.028
Stretching[e]	14.21	13.86	0.15	0.882	8.67	13.48	1.31	0.190
Flying	18.14	16.52	0.65	0.518	17.33	20.57	0.70	0.481

Table 1. Continued.

Behaviors	Age				Sex			
	Adult (n=711)	Juvenile (n=339)	Z	OSL	Male (n=150)	Female (n=141)	Z	OSL
Walking	71.87	61.95	3.24	0.001	77.33	63.83	2.53	0.011
Locomotor[f]	75.67	66.37	3.16	0.002	80.67	68.79	2.33	0.020

[a] Foraging includes searching, gleaning, probing, and drinking.

[b] Includes loafing-up and loafing-down.

[c] Includes sleeping-up and sleeping-down.

[d] Includes preening wings, neck, chest, back, head rub, head scratch, and body shake.

[e] Includes wing and leg stretch, wing flap, and double wing stretch.

[f] Includes flying, soaring, walking, and running.

Table 2

Comparison Between Social Classes of the Percentage Occurrence of Maintenance Behaviors in Time Budgets of

Sandhill Cranes

Behavior	Adults					Juveniles				Males				Females			
	Alone (n=128)	Pair (n=57)	Family (n=180)	χ^2	OSL	Alone (n=62)	Family (n=210)	χ^2	OSL	Pair (n=71)	Family (n=19)	χ^2	OSL	Pair (n=86)	Family (n=32)	χ^2	OSL
Searching	80.47	92.98	87.78	6.04	0.049	90.32	86.67	0.76	0.444	95.77	89.47	1.06	0.287	83.72	96.88	1.91	0.057
Gleaning	32.81	26.32	17.22	10.12	0.006	19.35	34.29	2.24	0.025	11.27	21.05	1.11	0.265	17.44	25.00	0.92	0.357
Probing	74.22	75.44	86.11	7.68	0.022	80.65	66.67	2.11	0.035	92.96	73.68	2.37	0.018	87.21	81.25	0.82	0.413
Drinking	10.94	0.00	7.78	6.67	0.036	6.45	2.86	1.32	0.186	11.27	0.00	1.53	0.125	6.98	0.00	1.53	0.125
Foraging[a]	91.41	92.98	93.33	0.42	0.811	93.55	96.19	0.89	0.373	98.59	89.47	1.97	0.049	93.02	96.88	0.79	0.431
Loafing[a]	82.03	61.40	62.22	15.58	0.001	56.45	69.52	1.92	0.055	57.75	57.89	0.00	0.991	60.47	59.38	0.11	0.914
Sleeping[a]	13.28	1.75	8.89	6.28	0.043	9.68	5.71	1.10	0.270	1.14	0.00	0.52	0.603	10.47	3.13	1.27	0.203
Preening[a]	63.28	42.11	43.89	13.12	0.001	40.32	36.19	0.59	0.554	46.48	42.11	0.34	0.734	39.53	34.38	0.51	0.608
Stretching[a]	18.75	8.77	8.89	7.52	0.023	14.52	14.29	0.04	0.964	4.23	5.26	0.19	0.845	11.63	6.25	0.86	0.390
Flying	14.06	19.30	20.00	1.90	0.386	14.52	13.33	0.24	0.811	19.72	10.53	0.93	0.352	20.93	25.00	0.47	0.635
Walking	71.88	71.93	62.78	3.45	0.178	53.23	60.95	1.09	0.277	70.42	78.95	0.74	0.461	54.65	65.63	1.07	0.284
Locomotor[a]	75.78	73.68	67.78	2.51	0.285	56.45	64.76	1.19	0.234	74.65	78.95	0.39	0.699	61.63	68.75	0.71	0.475

[a]See footnotes for Table 1.

Table 3

Comparison Between Age and Sex Classes of Duration of Sandhill Crane Maintenance Behaviors (Measured in

Seconds)

Behavior	Adult males				Adult females				Juveniles			ANOVA		
	n	$\bar{x}$	SE		n	$\bar{x}$	SE		n	$\bar{x}$	SE	EMS	F	OSL
Searching	1031	8.52	0.56	*	673	10.77	0.72		1731	9.41	0.41	312.61	3.32	0.036
Gleaning	208	67.03	6.02		103	95.94	15.01	*	839	105.01	5.53	22,167.49	5.43	0.005
Probing	941	80.69	3.07	*	678	135.14	6.88		1276	133.70	5.41	26,889.74	33.83	0.001
Drinking	15	28.67	6.50		6	29.00	14.05		20	28.20	5.66	709.54	0.00	0.997
Loafing														
Up	546	43.73	4.40	*	467	29.08	2.49		1493	33.31	2.18	7,091.14	4.38	0.013
Down	5	229.20	112.15	*	3	673.67	296.22	*	22	172.55	53.18	77,213.96	4.29	0.024
Sleeping														
Up	11	224.64	58.28		25	298.60	81.16		23	402.43	79.89	134,915.57	1.03	0.365
Down	3	39.00	17.04		2	1200.00	0.00	*	8	231.13	114.83	74,016.29	12.47	0.002

Table 3. Continued.

Behavior	Adult males			Adult females			Juveniles			ANOVA		
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	EMS	F	OSL
Preening												
Wings	156	37.68	3.39	168	34.56	2.96	456	34.68	2.03	1,772.09	0.32	0.723
Neck	7	24.86	9.30	11	16.82	4.08	76	13.76	2.09	333.37	1.25	0.292
Chest	26	9.92	1.80	26	11.31	1.77	72	16.10	2.47	291.55	1.60	0.206
Back	26	19.58	3.52 *	4	9.50	2.22	61	11.51	1.40	173.21	3.64	0.030
Head rub	40	7.58	1.18	28	6.11	0.73	140	5.99	0.48	34.81	1.15	0.320
Head scratch	24	10.54	2.43 *	22	7.32	1.22 *	75	5.75	0.42	41.79	5.04	0.008
Body scratch	30	2.93	0.43	27	2.18	0.36	88	3.00	0.40	10.48	0.67	0.512
Stretching												
Wing and leg	14	7.50	0.90	18	7.00	0.66 *	48	5.40	0.33	6.92	4.75	0.011
Wing flap	4	7.00	1.68 *	1	2.00	0.00	12	3.67	0.53	5.05	3.88	0.046
Double wing	2	5.50	1.50	9	3.33	0.37	22	3.91	0.41	3.01	1.32	0.283

Table 3. Continued.

Behavior	Adult males			Adult females			Juveniles			ANOVA		
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	EMS	F	OSL
Locomotion												
Flying	28	110.93	29.93	31	78.84	10.36	60	116.33	16.73	15,242.74	0.98	0.378
Soaring	2	833.00	367.00	1	340.00	0.00	2	446.50	145.50	155,859.25	0.71	0.585
Walking	463	24.09	1.62	312	24.22	2.40	870	24.64	1.46	1,656.65	0.03	0.969
Running	1	1.00	0.00	1	5.00	0.00	17	8.71	1.93	63.47	0.52	0.603

* Differences between adjacent means, $\underline{P}$ < 0.05, from Duncans Multiple Range Test.

Table 4

Comparison Between Sandhill Crane Age and Sex Classes of Percentage of Time Spent Exhibiting Maintenance

Behaviors

Behavior	Adults (n=711)			Juveniles (n=339)		Males (n=150)			Females (n=141)	
	$\bar{x}$	SE	OSL	$\bar{x}$	SE	$\bar{x}$	SE	OSL	$\bar{x}$	SE
Searching	4.724	0.301	0.038[a]	3.819	0.315	4.844	0.778	0.562[a]	4.258	0.645
Gleaning	12.083	0.947	0.001[a]	20.116	1.859	7.779	1.675	0.405	5.840	1.605
Probing	34.409	1.314	0.016[a]	40.423	2.109	41.038	2.592	0.001	54.103	3.076
Drinking	0.216	0.049	0.293[a]	0.139	0.054	0.239	0.085	0.197[a]	0.103	0.062
Total foraging	51.433	1.305	0.001	64.497	1.857	53.901	2.453	0.006	64.305	2.849
Loafing										
Up	14.635	0.791	0.002[a]	10.087	0.948	11.106	1.482	0.030[a]	6.991	1.175
Down	1.101	0.326	0.603[a]	0.852	0.351	0.166	0.128	0.257[a]	1.091	0.803
Total	15.736	0.841	0.003[a]	10.938	1.005	11.272	1.501	0.121	8.082	1.384
Sleeping										
Up	5.121	0.692	0.001[a]	2.065	0.628	1.373	0.602	0.016[a]	5.836	1.730

Table 4. Continued.

Behavior	Adults (n=711)			Juveniles (n=330)		Males (n=150)			Females (n=141)	
	$\bar{x}$	SE	OSL	$\bar{x}$	SE	$\bar{x}$	SE	OSL	$\bar{x}$	SE
Down	1.023	0.324	0.199[a]	0.455	0.302	0.006	0.006	0.150[a]	1.418	0.999
Total	6.144	0.756	0.004[a]	2.159	0.693	1.378	0.602	0.005[a]	7.255	1.968
Bathing	0.008	0.006	0.168[a]	0.000	0.000	–	–	–	–	–
Preening										
Wings	4.420	0.413	0.153[a]	3.466	0.524	3.175	0.661	0.874	3.024	0.069
Neck	0.297	0.070	0.698[a]	0.257	0.077	0.097	0.061	0.992	0.098	0.059
Chest	0.215	0.029	0.373[a]	0.284	0.072	0.128	0.045	0.770[a]	0.150	0.062
Back	0.159	0.036	0.993	0.159	0.050	0.272	0.132	0.056[a]	0.015	0.010
Head rub	0.258	0.057	0.491[a]	0.199	0.062	0.169	0.074	0.099[a]	0.043	0.019
Head scratch	0.144	0.019	0.129[a]	0.105	0.017	0.141	0.053	0.185[a]	0.065	0.019
Body Shake	0.082	0.009	0.041[a]	0.053	0.011	0.047	0.012	0.418[a]	0.035	0.009
Total	6.234	0.500	0.285	5.308	0.689	4.896	0.872	0.357	3.781	0.832
Stretching										
Wing and leg	0.059	0.009	0.788[a]	0.055	0.011	0.058	0.020	0.626[a]	0.074	0.026

Table 4. Continued.

Behavior	Adults (n=711)			Juveniles (n=330)		Males (n=150)			Females (n=141)	
	$\bar{x}$	SE	OSL	$\bar{x}$	SE	$\bar{x}$	SE	OSL	$\bar{x}$	SE
Wing flap	0.017	0.006	0.143[a]	0.007	0.003	0.016	0.009	0.125[a]	0.001	0.001
Double wing	0.014	0.003	0.482	0.018	0.005	0.006	0.006	0.193	0.018	0.006
Total	0.089	0.011	0.581[a]	0.079	0.013	0.080	0.025	0.721	0.093	0.028
Locomotion										
Flying	1.938	0.261	0.536[a]	1.683	0.316	1.926	0.602	0.676[a]	1.444	0.299
Soaring	0.355	0.173	0.568[a]	0.220	0.163	0.926	0.714	0.330[a]	0.201	0.201
Walking	4.714	0.290	0.214	4.083	0.411	6.123	0.657	0.052	4.251	0.698
Running	0.004	0.001	0.029[a]	0.034	0.014	0.001	0.001	0.426[a]	0.003	0.003
Total	7.047	0.420	0.139[a]	6.018	0.552	8.774	1.093	0.035[a]	5.899	0.803
Out of sight	6.714	0.535	0.366	5.905	0.708	5.571	1.138	0.450	6.811	1.182
Total										
Maintenance	86.690	0.646	0.011[a]	89.359	0.646	80.301	1.544	0.001	89.415	1.425

[a] Unequal variances, $\underline{P} < 0.05$.

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Table 5

Comparison of Percentages of Time Spent Exhibiting Maintenance Behaviors Among Social Classes of Adult and

Juvenile Sandhill Cranes

Behavior	Adults					Juveniles				
	Alone (n=128)	Pair (n=180)	Family (n=57)	ANOVA EMS	OSL	Alone (n=62) $\bar{x}$	SE	OSL	Family (210) $\bar{x}$	SE
Searching	4.403	3.213	2.656	0.003	0.074	5.441	1.105	0.012[b]	2.517	0.215
Gleaning	11.752 *	4.997	8.975	0.040	0.014	10.210	3.240	0.003[b]	22.537	2.502
Probing	32.143 *	52.186	44.186	0.119	0.001	47.090	4.680	0.647	44.443	2.817
Drinking	0.524	0.253	0.000	0.257[a]	0.010	0.140	0.076	0.815[b]	0.117	0.057
Total foraging	48.822 *	60.519	55.817	0.114	0.012	62.880	4.488	0.160	69.614	2.232
Loafing										
Up	18.315 *	6.601	13.341	0.035	0.001	5.859	1.532	0.027[b]	10.185	1.186
Down	3.701 *	0.911	0.000	0.013	0.044	1.254	1.150	0.841[b]	1.004	0.445
Total	22.015 *	7.512	13.341	0.044	0.001	7.113	1.857	0.072[b]	11.190	1.269
Sleeping										
Up	5.383	5.184	1.754	0.036	0.435	5.219	2.568	0.183[b]	1.654	0.652

Table 5. Continued.

Behavior	Adults Alone (n=128)	Pair (n=180)	Family (n=57)	ANOVA EMS	OSL	Juveniles Alone (n=62) $\bar{x}$	SE	OSL	Family (210) $\bar{x}$	SE
Down	0.697	1.390	0.000	0.008	0.537	1.493	1.493	0.429[b]	0.293	0.208
Total	6.079	6.574	1.754	0.042	0.293	6.712	2.927	0.117[b]	1.947	0.681
Bathing	0.027	0.000	0.000	0.003[a]	0.397	-	-	-	-	-
Preening										
Wings	5.671	3.220	2.950	0.009	0.051	6.651	1.892	0.041[b]	2.560	0.528
Neck	0.752	0.180	0.085	0.001	0.078	0.144	0.078	0.190[b]	0.332	0.120
Chest	0.294	0.123	0.151	0.050[a]	0.105	0.483	0.279	0.279[b]	0.171	0.058
Back	0.158 *	0.009	0.070	0.006[a]	0.008	0.000	0.000	0.009[b]	0.117	0.044
Head rub	0.307 *	0.029	0.032	0.098[a]	0.039	0.022	0.013	0.062[b]	0.083	0.030
Head scratch	0.170	0.131	0.010	0.022[a]	0.104	0.038	0.018	0.012[b]	0.113	0.024
Body shake	0.121 *	0.025	0.034	0.005[a]	0.001	0.022	0.008	0.165[b]	0.040	0.011
Total	7.521 *	3.723	3.439	0.012	0.006	7.360	2.066	0.073[b]	3.438	0.614

Table 5. Continued.

Behavior	Adults					Juveniles				
	Alone (n=128)	Pair (n=180)	Family (n=57)	ANOVA EMS	OSL	Alone (n=62) $\bar{x}$	SE	OSL	Family (210) $\bar{x}$	SE
Stretching										
Wing and leg	0.058	0.050	0.038	0.004[a]	0.796	0.036	0.022	0.329	0.062	0.013
Wing flap	0.046	0.000	0.000	0.004[a]	0.128	0.011	0.008	0.336[b]	0.002	0.002
Double wing	0.027	0.010	0.021	0.001[a]	0.360	0.022	0.011	0.852	0.019	0.006
Total	0.132	0.059	0.059	0.009[a]	0.097	0.069	0.027	0.654	0.084	0.017
Locomotion										
Flying	1.429	1.369	1.398	1.951[a]	0.993	0.884	0.311	0.303[b]	1.414	0.409
Soaring	0.135	0.216	0.000	0.497[a]	0.811	1.200	0.887	0.181[b]	0.000	0.000
Walking	3.328	4.354	4.016	0.004	0.352	3.831	0.844	0.326[b]	2.925	0.358
Running	0.010	0.002	0.007	0.001[a]	0.380	0.071	0.055	0.475[b]	0.031	0.015
Total	4.903	5.940	5.421	0.006	0.531	5.987	1.299	0.255[b]	4.368	0.551

Table 5. Continued.

Behavior	Adults					Juveniles				
	Alone (n=128)	Pair (n=180)	Family (n=57)	ANOVA EMS	OSL	Alone (n=62) $\bar{x}$	SE	OSL	Family (210) $\bar{x}$	SE
Out of sight	7.018	6.724	9.583	0.021	0.421	3.410	1.315	0.201	5.667	0.873
Total maintenance	89.499 *	84.327	79.830	0.034	0.003	90.121	1.499	0.788[b]	90.640	1.070

[a] Multiply EMS by 10^{-3}.

[b] Unequal variances, $P < 0.05$.

* Differences between adjacent means, $P < 0.05$, Duncans Multiple Range Test.
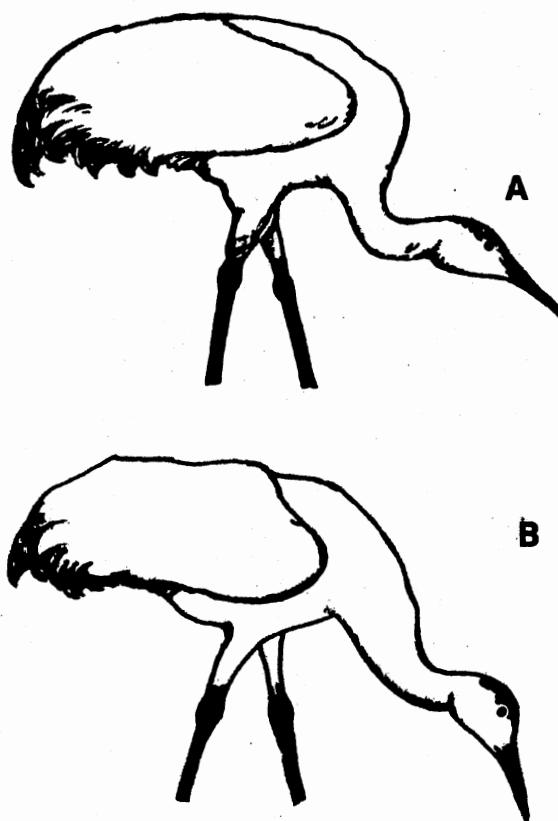
Fig. 1. Posture of sandhill cranes while
searching (A) for food items,
and gleaning (B) food items
from the surface (from 35 mm
slides).
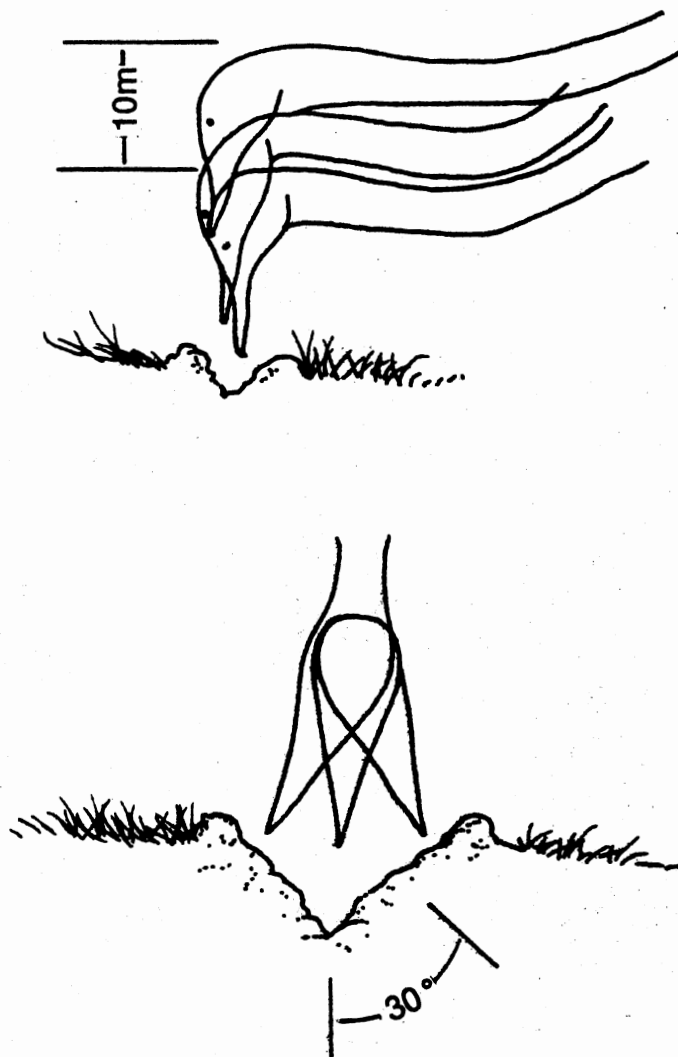
Fig. 2. Vertical and lateral movements of the
head and neck when sandhill cranes
probe for subsurface food items
(from 35 mm slides).
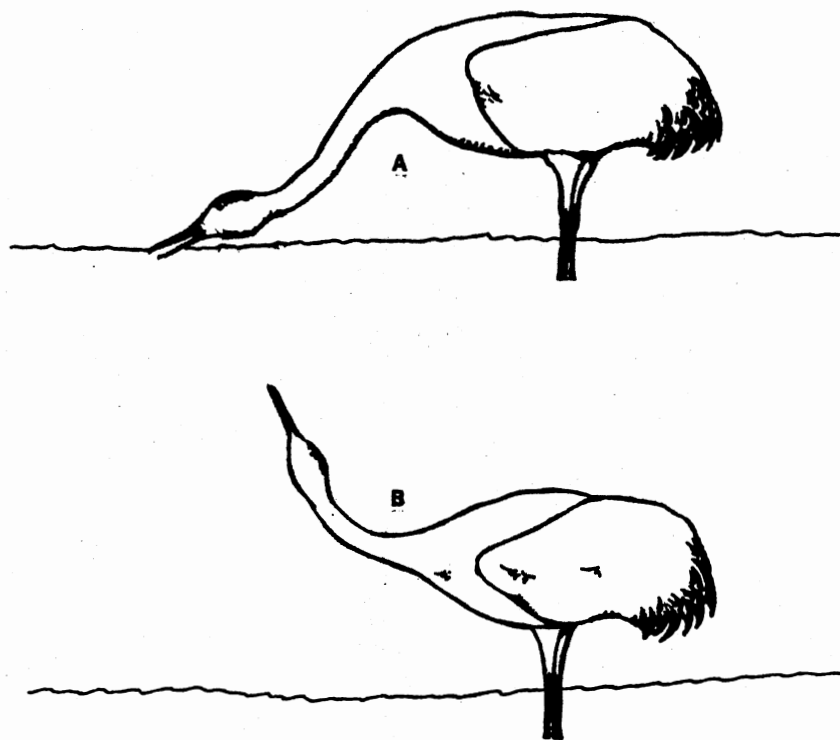
Fig. 3. Drinking movements of sandhill cranes (from
16 mm films).
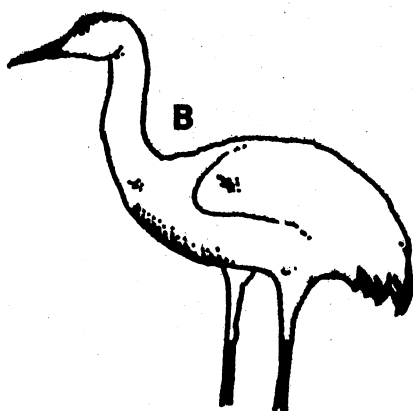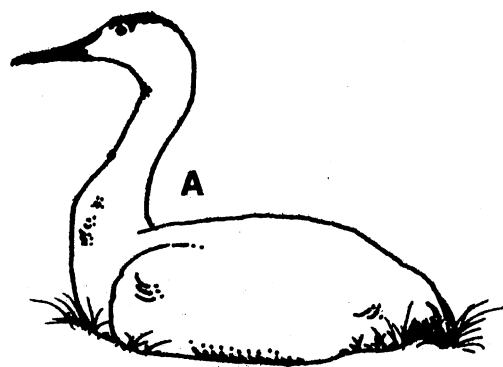
Fig. 4. Postures of sandhill cranes
while loafing-down (A)
and loafing-up (B)
(from 35 mm slides).
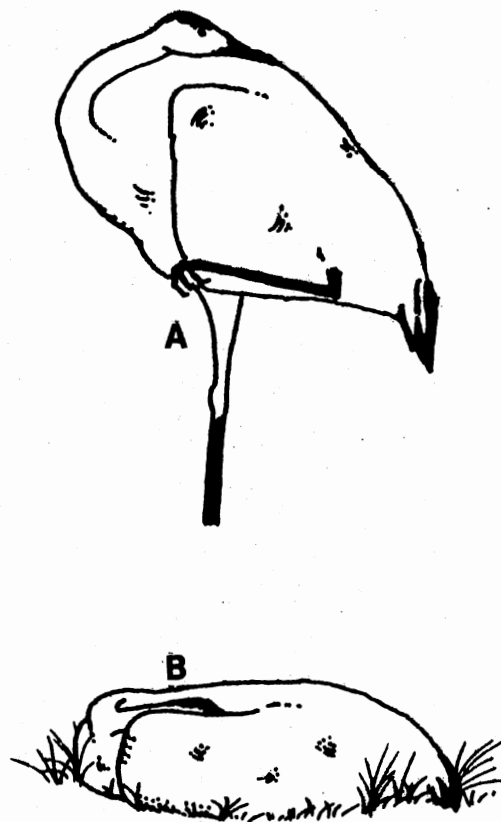
Fig. 5.   Postures of sandhill cranes
          while sleeping-up (A) and
          sleeping-down (B) (from
          35 mm slides).
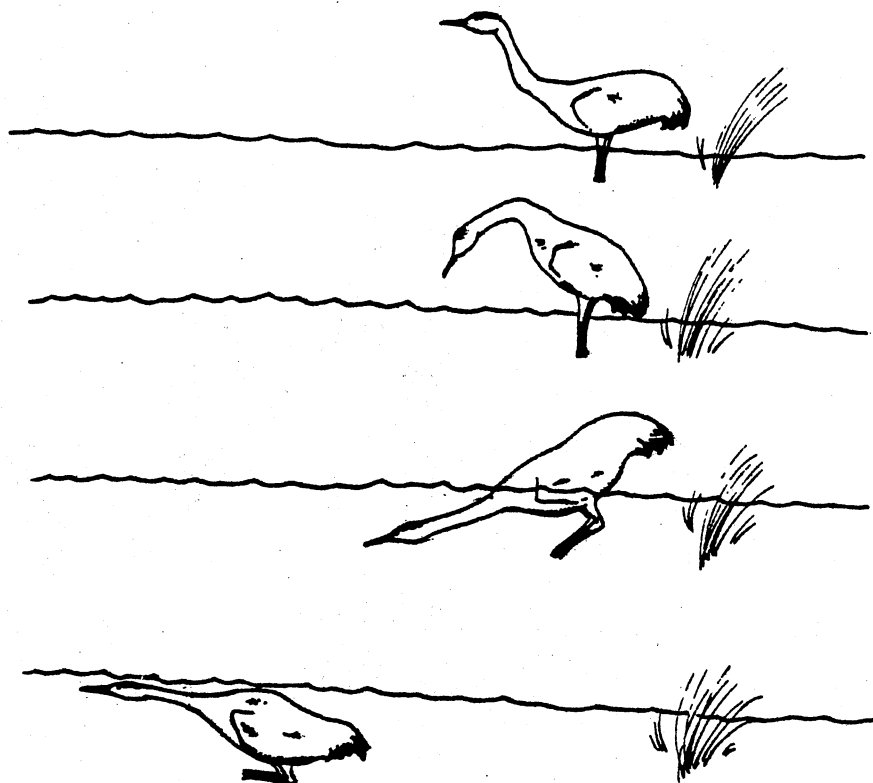
Fig. 6. Movement pattern of a sandhill crane while bathing (freehand drawing).

Fig. 7. Wing preening by a sandhill
          crane (from 35 mm slides).
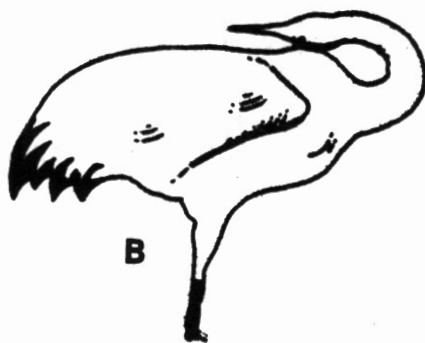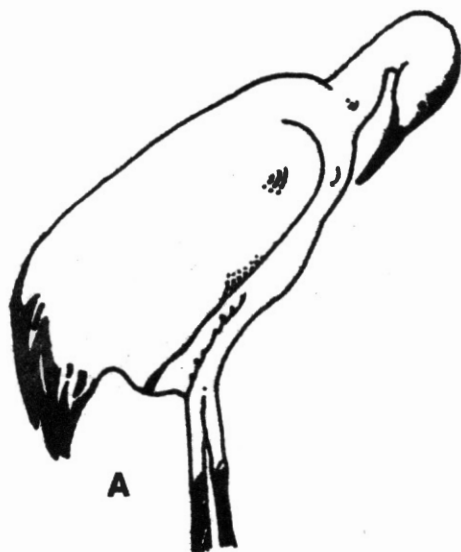
Fig. 8. Chest preening (A) and head
          rub (B) movements of
          sandhill cranes (from
          16 mm films).
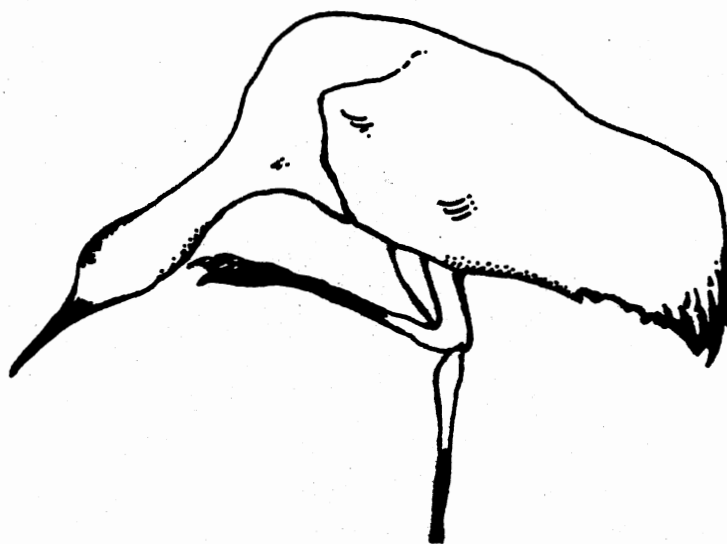
Fig. 9.   Scratching movement of a sandhill crane
(from 35 mm slides).
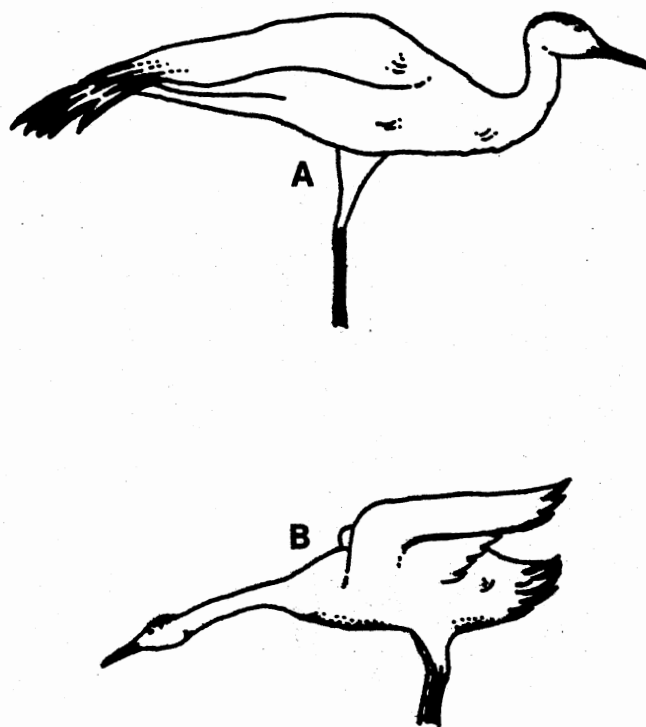
Fig. 10. Single wing and leg (A) and double
wing (B) stretches of sandhill
cranes (from 16 mm films).

CHAPTER IV

PREFLIGHT BEHAVIOR OF SANDHILL CRANES

Thomas C. Tacha

The purpose of this paper is to describe and quantify preflight

behavior of sandhill cranes, including the exit of cranes from overnight

roost sites. Preflight behaviors are included in the broader category

of social signals that serve to convey information from one individual

or group to another (Heymer 1977). The description, quantification,

and interpretation of preflight signals (including the sequence of

events leading to departure from the roost) of sandhill cranes assist

in interpreting refuging patterns (Hamilton and Watt 1970) and social

organization. Preflight behavior is integral with other behavioral

activities, habitat uses, and physiological data in the evaluation of

the importance of habitats used, population energetics, and the

interpretation of reproductive and survival strategies.

METHODS

Sandhill cranes were studied from early January through February

1978 to 1980 near Rich Lake, Terry County, Texas; and during March and

early April 1978 to 1980 along the Platte River between Southerland and

North Platte, Nebraska. Cranes were also studied during the last 2

weeks of April 1980 near the north end of Last Mountain Lake,

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Saskatchewan; during May 1980 near Delta Junction, Alaska; and immediately prior to nesting in May 1980 near Old Chevak, Clarence Rhodes National Wildlife Refuge, Alaska.

Observations were aided with a 15 X 60 telescope. Postures and movements were recorded on 35 mm slides and 16 mm motion pictures; descriptions and social interactions were verbally recorded on tape during 1,109 time budgets. Behaviors were recorded continuously for 20 minutes during time budgets using behavioral catagories defined in this paper (preflight behaviors) and elsewhere (maintenance behaviors and other social signals).

Juvenile (young-of-the-year) sandhill cranes were distinguished from adults by having brown feathering on the nape of the neck (Lewis 1974). Sex of some cranes was determined in the field by observation of the unison call (described by Archibald 1975). Sex was designated during 54 time budgets for members of a pair on the basis of females following males, and later verified by observation of the unison call. None of the designations of sex made on the basis of females following males was found to be incorrect during the subsequently observed unison calls. On that basis, the observation of one crane of a pair following another was used to assume sex in some time budgets where the unison call was not observed. Pairs (2 adults) and family units (2 adults and 1 or 2 juveniles) were identified by their close proximity (compared to other cranes in larger flocks), the tendency for adult females of pairs to follow the male, and the propensity of juveniles of family units to follow their parents. The sex of juveniles could not be determined in the field, and no juveniles were ever observed to be members of a mated pair. The sex of adults not in pairs or family units could not be

determined.

When time budgets were transcribed from tapes to coding sheets for subsequent computer analyses, behaviors were recorded to the nearest full second. Cranes were selected for observation and time budgets using stratified random sampling with these strata: time budgets were taken in all major habitats used by cranes at all hours of the day, sampling was stratified by age groups to insure adequate sampling of juveniles, and a stratified sampling design for cranes marked (neck collar and leg band) longer than 7 days was employed. Statistical tests were performed using the Statistical Analysis System (Barr et al. 1979). Three methods of quantifying preflight behaviors used were: frequency of occurrence of behaviors using each time budget as an experimental unit; duration of each behavior using each observation of the behavior in a time budget as the experimental unit; and % of total time spent in each behavior using time budgets as the experimental units. Observed Significance Levels (OSL) less than 0.05 were considered sufficient to reject statistical hypotheses.

Stepwise, backward-elimination, multiple regression was used to evaluate the association between frequency of occurrence of preflight signals and environmental variables. The initial model used 7 classification variables (each variable had 2 or more class levels) including period of the year, hour of day, habitat, general flock activity, flock size (7 levels), and year. Non-significant variables were removed 1 at a time, in descending order of the OSL for their partial sums of squares.

RESULTS AND DISCUSSION

Preflight Intention Movements

Preflight intention movements were divided into 2 categories based on hypothesized message content (message content interpreted following principles of Smith 1969). The first catagory signaled "I may fly soon" and sometimes lead to the second catagory of "I am going to fly" if the stimulus persisted. The second catagory did not need to be a product of an external stimulus; motivation to change location appeared sufficient.

The two displays that signaled "I may fly soon" were wing flapping (Tacha 1981) and leaping into the air with wings outspread and flapping. Wing flapping often resulted in activities other than flight. Leaping with wings flapping had a higher stimulus threshold and led to flight if the stimulus (usually danger) approached or persisted. Wing flapping and leaping with wings flapping were observed only twice in time budgets in a preflight context, and were considered displacement activities resulting from conflicting motivations to depart or to stay.

Sandhill cranes exhibited a stereotyped preflight intension display that signaled "I am going to fly". This neck-stretch display had 3 distinct intensities (Figs. 1a, 1b, 2). The simple neck-stretch consisted of a crane standing on both legs and arching the neck forward. The body was held upright at about 20-30 degrees above horizontal with wings folded. Orientation of the bill indicated the direction of intended takeoff.

The function of the neck-stretch display may be to elicit other cranes of a pair or family to take flight with the displaying bird. If

the simple neck-stretch did not urge signal receivers to flight, the
next most intense display was employed. The simple neck-stretch was
augmented by fully or partially spreading the wings (Fig. 1b). The
displaying crane would turn its head, presumably to observe the response
of intended signal receivers. If no response occurred, the third level
display was employed by running for a short distance, with neck
stretched forward and wings outspread (Fig. 2).

Neck-stretch signals resulted in flight on 49 of 54 occasions
when observed in time budgets; the 5 exceptions occurred when juveniles
exhibited the simple neck-stretch. The neck-stretch-wings-spread
display preceeded flight only 5 times; and the neck-stretch-wings-
spread-run was exhibited only twice.

Frightened sandhill cranes went directly to the neck-stretch-wings-
spread-run while uttering an alarm call (call described by Archibald
1975), but the above reaction to danger was not observed in time
budgets. Archibald (1975:11) described a "flight intention call" for
sandhill cranes. I did not notice any call associated with preflight
intention movements of sandhill cranes other than the rare alarm call.

The preflight neck-stretch or one of its' variations occurred in
5.5% of time budgets (Table 1). No difference in frequency of
occurrence of preflight signals (hereafter referring to the neck-
stretch and its variations) was observed between age, sex or social
classes of sandhill cranes.

The neck-stretch display had a mean duration of 17.6 seconds among
adult females, 10.1 seconds among juveniles, and 8.2 seconds among
adult males in time budgets. These differences approached significance
(ANOVA EMS = 126.6; df = 2,51; F = 2.44; OSL = 0.097). Only one adult

male exhibited the neck-stretch-wings-spread display; while juveniles exhibited the neck-stretch-wings-spread-run twice. Preflight signals from adult males resulted in flight with signal receivers more quickly and more often (100%, n = 23) than preflight signals from either adult females (75%, n = 16) or juveniles (53%, n = 17). The reduced duration and high response rate to preflight signals from adult males suggests that adult males may play a leadership role in determining when to fly.

Sandhill cranes spent an average of 0.074% of time in time budgets performing preflight intention movements (Table 2). No differences in percentage of time spent exhibiting preflight displays were observed between age, sex, or social classes.

The association between frequency of occurrence of preflight signals and environmental variables was evaluated using stepwise, backward elimination, multiple regression. The best model I could produce (Table 3) included habitat, location, and year variables with an R^2 of only 0.06. Differences within variables (Table 4) suggested that higher frequencies of preflight signals were associated with the Delta Junction area of Alaska and plowed fields in Texas. Cranes flew into and out of plowed fields in Texas and the Delta Junction Alaska area more often than other habitats or locations (based on marked cranes, unpublished data, Oklahoma Cooperative Wildlife Research Unit). The low R^2 from regression analysis suggested that most of the variation in use of preflight signals was not associated with variables I could monitor in this study. Preflight signals were probably associated with motivation to change locations.

Departure From Roosting Areas

Individual cranes were observed from waking until flight from

roost sites in Texas and Nebraska on 39 occassions (Table 5). Seven

categories of behavior (described by Tacha 1981) were observed during

sequences of behaviors between waking and flight from roost sites.

Behaviors occurred only once in each sequence; except for loafing which

occurred an average of 1.26 times per sequence. The double wing-stretch

was observed in 82% of sequences; nearly always the first or second

behavior after waking. Wing flapping was observed in 90% of sequences

and occurred throughout the order of behaviors. Body shakes were

observed in 85% of sequences and tended to occur in the center of a

sequence. Preening was observed in 85% of roost exit sequences and

throughout the order of behaviors. Walking was observed in 56% of

sequences and occurred toward the center of the order of behaviors.

Preflight signals occurred in 77% of sequences and were always the

terminal behavior of the sequence. A typical sequence was as follows:

> Awaken–Loafing up–Double Wing Stretch–Body Shake–
> Walking–Preen–Wing Flapping–
> Preflight–Flight.

Cranes in mated pairs and families appeared to leave roost sites

together with a coordinated takeoff that resulted from preflight

intention movements. Cranes without mates or young appeared to take off

alone or in small (5-15 birds) groups. Once airborne, pairs and family

units and unmated adults would form larger flocks as distance from the

take off point increased. Cranes flying less than 2-3 km would remain

in an unstructured group at low altitudes. Cranes flying to a

destination farther than 3 km would form long lines perpendicular to

the direction of flight and fly at altitudes in excess of 300 m.

Sandhill cranes often formed communal roosts of as many as 100,000

(unpublished data, Oklahoma Cooperative Wildlife Research Unit) birds

in western Texas and Nebraska. On 12 occasions these large numbers of cranes were observed to flush all at once from roost sites. On each occasion, many cranes appeared to be separated from members of social units, resulting in expenditures of time and energy to locate parents or mates. The use of preflight signals and a somewhat standardized sequence of behaviors after waking apparently allowed a coordinated takeoff of pairs and family units, limited confusion resulting from separation of social units, and reduced potential for in-flight collision during departure of cranes from roost sites.

SUMMARY

Sandhill cranes exhibited a preflight intension display that signaled "I am going to fly". This neck-stretch display appeared to be directed at cranes within a family or pair. Preflight signals from adult males resulted in flight with mates or young more quickly and more often than preflight signals from adult female or juvenile sandhill cranes. Only 6% of the variation in frequency of occurrence of preflight displays could be associated with environmental variables. Sandhill cranes exhibited a consistency within sequences of behavior after waking and before departure from roost sites. Over 77% of these sequences ended with preflight signals. A somewhat standardized sequence of behaviors, terminating in preflight signals, appeared to aid in coordinating takeoff of social units and reduce confusion during departure of cranes from roost sites.

ACKNOWLEDGMENTS

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COOPERATIVE WILDLIFE RESEARCH UNIT, 404 LIFE SCIENCES WEST, OKLAHOMA
STATE UNIVERSITY, STILLWATER, OKLAHOMA 74078

TABLE 1

Percentage Occurrence of Preflight Signals in Time Budgets of

Sandhill Cranes

Status	n	%	$\underline{Z}$	OSL
Adult		6.19		
	1050		0.76	0.45
Juvenile		5.01		
Male		8.00		
	291		0.78	0.43
Female		5.67		
Adults[a]				
Alone		7.81		
Pair	365	6.67	0.41[b]	0.81
Family		5.26		
Juveniles[a]				
Alone		6.45		
	272		1.09	0.27
Family		3.33		
Males[a]				
Pair		7.04		
	90		0.28	0.78
Family		5.26		
Females[a]				
Pair		6.98		
	118		0.79	0.43
Family		3.13		

[a] Data for time budgets on cranes of known social status.

[b] χ^2 value.

TABLE 2

Percentage of Time Spent Exhibiting Preflight Signals by Sandhill Cranes

Status	n	$\bar{x}$	SE	$\underline{t}$	OSL
Adults	711	0.074	0.021	0.01	0.99
Juveniles	339	0.074	0.027		
Males	150	0.066	0.031	0.57[a]	0.57
Females	141	0.116	0.083		
Adults					
Alone	128	0.131			
Pair	180	0.102	0.545[b]	0.11[c]	0.90
Family	57	0.080			
Juveniles					
Alone	62	0.117	0.074	1.39[a]	0.17
Family	210	0.013	0.006		
Males					
Pair	71	0.038	0.019	0.27	0.79
Family	19	0.053	0.053		
Females					
Pair	86	0.170	0.135	1.11[a]	0.27
Family	32	0.018	0.018		

[a] Unequal variances, $\underline{P} < 0.05$.

[b] ANOVA error mean square X 10^{-4}.

[c] ANOVA F-value.

TABLE 3

Regression Analysis of Variables Explaining Significant Variance of

Frequency of Use of Preflight Signals

Predictor variable	df	Partial SS	F-value	OSL
Habitat	11	12.74	4.35	0.001
Location	4	11.95	11.23	0.001
Year	1	1.11	4.19	0.040

Full model error df = 16,1030; EMS = 0.266; F = 4.12; OSL = 0.001;

R^2 = 0.06.

TABLE 4

Frequency of Occurrence of Preflight Signals in Time Budgets Using

Significant Variables From Regression Analysis

Habitat	n	$\bar{x}$	DMRT[a]	Location	n	$\bar{x}$	DMRT[a]
Plowed	39	0.333	A	AK-DJ	64	0.313	A
Cotton	114	0.167	A B	TX	350	0.120	B
Native Hay	91	0.165	A B	NE	457	0.077	B
Marsh	69	0.159	A B	SK	120	0.075	B
Alfalfa	122	0.107	B	AK-OC	56	0.054	B
Milo	227	0.079	B				
Corn	203	0.074	B	Year	n	$\bar{x}$	DMRT[a]
Tundra	35	0.057	B				
Wheat	69	0.043	B	1979	193	0.165	A
Barley-planted	18	0.000	B	1980	854	0.090	B
Barley-stubble	12	0.000	B				
Mixed alfalfa-hay	48	0.000	B				

[a] Duncans Multiple Range Test.

TABLE 5

Sequences of Behaviors of Sandhill Cranes on Roosting Areas

After Waking but Before Taking Flight

Behavior	Order of behaviors after waking and before flight								
catagory	1	2	3	4	5	6	7	8	Total
Double wing stretch	15	15	1	1	0	0	0	0	32
Wing flap	3	6	7	6	8	5	2	0	35
Body shake	0	7	13	5	6	2	0	0	33
Loafing	18	5	4	6	6	5	3	0	49
Preening	2	4	9	9	3	3	3	0	33
Walking	1	2	5	4	4	2	4	0	22
Preflight	0	0	0	2	5	6	8	9	30
Total	39	39	39	33	32	23	13	9	
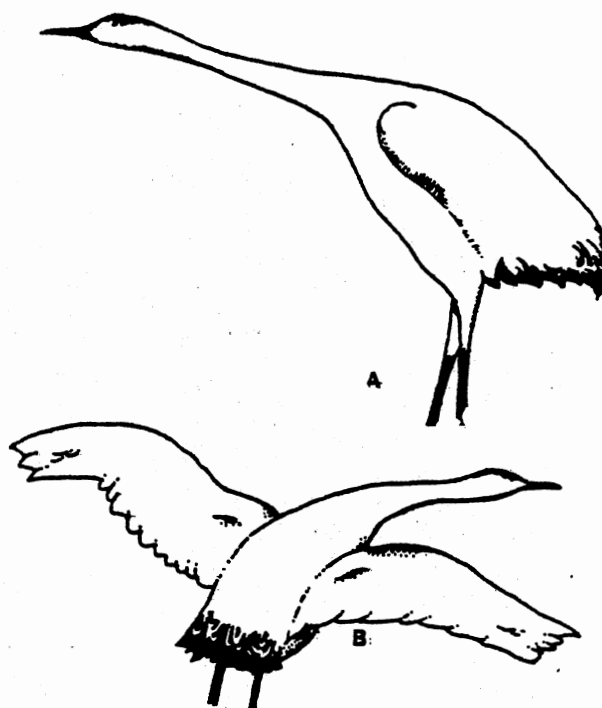
Fig. 1. Neck stretch (A) and neck stretch-wings-
spread preflight signals of sandhill
cranes (A from 35 mm slides, B from
16 mm films.
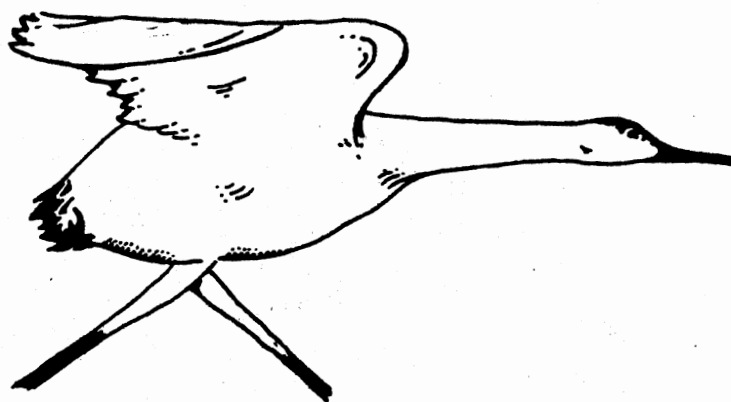
Fig. 2. The neck stretch-wings-spread-run preflight
signal of sandhill cranes (from 35 mm
slides).

CHAPTER V

ALERT BEHAVIORS OF SANDHILL CRANES

Thomas C. Tacha

Cooperative Wildlife Research Unit, 404 Life Sciences West, Oklahoma

State University, Stillwater, Oklahoma 74078

Abstract. - Sandhill Cranes (Grus canadensis) exhibited 2 stereotyped

alert signals; the alert investigative and the contagious tall alert.

Frequency of occurrence of alert signals varied ($p < 0.05$) between age,

sex, and social classes; and years, periods of year, locations, general

flock activities, habitats, flock sizes, and observers. Of alert

responses for which a stimulus could be identified, 69% were stimulated

by cranes in flight or on the ground. Use of the tall alert posture was

highly associated with the month of January and human-related stimuli.

Alert signals were associated with protection of mates and young, and

the protective role of adult males became more intense as the breeding

season approached. Groups of 1 social unit (alone, paired, or family

units) used alert signals more frequently than larger flocks.

Communication between Sandhill Cranes, in the form of alert signals,

probably served to increase the probability of survival of individual

birds.

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The purpose of this paper was to quantitatively describe the alert behaviors of Sandhill Cranes. Maintenance and preflight behaviors of Sandhill Cranes have been described (Tacha 1981). Social signals were defined as any behavior that conveyed information from one individual or group to another, regardless of whether it served another function as well (Heymer 1977). Message content of specific alert signals was hypothesized after interpretation and following principles outlined by Smith (1969).

The description, quantification, and interpretation of alert signals of Sandhill Cranes will aide in understanding refuging patterns (Hamilton and Watt 1970) and social organization. Information reported in this paper will be integrated with other behavior, habitat use, and physiological data to evaluate the importance of habitats used, model population energetics, and interpret reproductive and survival strategies of Sandhill Cranes.

Methods

Sandhill Cranes were studied from early January through February 1978 to 1980 near Rich Lake, Terry County, Texas, and during March and early April 1978 to 1980 along the Platte River between Southerland and North Platte, Nebraska. Cranes were also studied during the last 2 weeks of April 1980 near the north end of Last Mountain Lake, Saskatchewan; during May 1980 near Delta Junction, Alaska; and immediately prior to nesting in May 1980 near Old Chevak, Clarence Rhodes National Wildlife Refuge, Alaska.

Observations were aided with a 15 X 60 telescope. Postures and movements were recorded on 35 mm slides and 16 mm motion pictures;

while descriptions and social interactions were verbally recorded on tape during 1,109 time budgets in 1979 and 1980. Behaviors were recorded continuously for 20 minutes during time budgets using behavioral catagories defined in this paper (alert behaviors) and elsewhere (maintenance behaviors and other social signals).

Juvenile (young-of-the-year) Sandhill Cranes were distinguished from adults by having brown feathering on the nape of the neck (Lewis 1974). Sex of some cranes was determined in the field by observation of the unison call (described by Archibald 1975). Sex was designated during 54 time budgets for members of a pair on the basis of females following males, and later verified by observation of the unison call. None of the designations made on the basis of females following males were found to be incorrect during the subsequently observed unison calls. On that basis, the observation of one crane following another for extended periods was used to assume sex in some time budgets where the unison call was not observed. Pairs (2 adults) and family units (2 adults and 1 or 2 juveniles) were identified by their close proximity (compared to other cranes in larger flocks), the tendency for adult females of pairs to follow the male, and the propensity of juveniles of family units to follow their parents. The sex of juveniles could not be determined in the field, and no juveniles were ever observed to be members of a mated pair. The sex of adults not in pairs or families could not be determined.

When time budgets were transcribed from tapes to coding sheets for subsequent computer analyses, behaviors were recorded to the nearest full second. Cranes were selected for observation and time budgets using stratified random sampling with these strata: time budgets were

taken in all major habitats used by cranes at all hours of the day,
sampling was stratified by age groups to insure adequate sampling of
juveniles, and a stratified sampling design for cranes marked (neck
collar and leg band) longer than 7 days was employed. Statistical
tests were performed using the Statistical Analysis System (Barr et al.
1979). Three methods of quantifying alert behaviors used were:
frequency of occurrence of behaviors using each time budget as an
experimental unit; duration of each behavior using each observation of
the behavior in a time budget as the experimental unit; and % of total
time spent in each behavior using time budgets as the experimental
units. Observed Significance Levels (OSL) less than 0.05 were
considered sufficient to reject statistical hypotheses.

Stepwise, backward-elimination, multiple regression was used to
evaluate the association between frequency of occurrence of alert
signals and environmental variables. The initial model included 9
classification variables. Partial sums of squares for the hour of day
variable were not significant and hour of day was removed from analysis.
The same regression procedure was used for the ratio of tall alert/total
alert signals using individual time budgets as experimental units.
Non-significant variables regressed against this ratio were removed 1
at a time in descending order of the OSL for their partial sums of
squares.

<div align="center">Results</div>

Description of Alert Signals

Tall Alert. - When alarmed, Sandhill Cranes stood rigidly erect
in the tall alert posture (Fig. 1a). The body axis was held near

vertical, elevating the head with maximum extension of the neck. The bill was held horizontally, feathers were flattened against the body, and no motion or sound was evident. Mean duration of tall alert postures (from time budgets) for adult females was 50.9 seconds (n = 7), 23.7 seconds for adult males (n = 11), and 15.1 seconds for juveniles (n = 55). The difference in duration of tall alerts between adult females and juveniles was significant (ANOVA; df = 2,70; EMS = 973.7; F = 4.18; OSL = 0.019).

The primary function of the tall alert posture appeared to be to gather information for the individual. However, the tall alert posture was contagious and appeared to deliver the message to other cranes that danger was near, particularly when 1 or more cranes would snap to the tall alert posture from some other activity.

Alert investigative. - Sandhill Cranes using the alert investigative posture (Fig. 1b) were not alarmed, but appeared inquisitive about something in the environment. The body axis varied from that exhibited during loafing-up (near horizontal) to near tall alert (almost vertical). The neck was extended vertically, but the head was often rotated on a horizontal axis. Movement of the head and neck was commonly observed during alert investigative posturing. The alert investigative was not contagious. However, the alert investigative posture attracted attention (especially from mates or other family members) if held long enough. The mean duration for alert investigative behaviors in time budgets was 23.8 seconds for adult males (n = 840), 17.8 seconds for juveniles (n = 611); and 17.2 seconds for adult females (n = 256). The difference in duration of alert investigative postures between adult males and juveniles was

significant (ANOVA; df = 21,704; EMS = 1220.7; F = 6.84; OSL = 0.001).

Use of Alert Signals

Associations with age, sex, and social classes. - Adult male Sandhill Cranes exhibited alert signals nearly 3 times as often as adult females (Table 1). Adults without mates or young used alert signals less than half as often as adults in pairs or families. Juveniles without parents were on alert nearly twice as often as juveniles with parents. There was no difference in frequency of alert responses between adult males in families and adult males in pairs or between adult females in families and adult females in pairs.

Adults spent twice the percentage of time exhibiting alert postures as did juveniles (Table 2), and adult males spent 5 times the percentage of time in alert postures as did adult females. Adults in pairs and family units spent 4 times more time on alert than adults without mates or young, and juveniles without parents spent 4 times more time on alert than juveniles with parents. There was no difference in the amount of time spent in alert postures between adult males of pairs and adult males in families or between adult females of pairs and adult females in families.

Associations with environmental variables. - Regression analysis evaluated the association between frequency of occurrence of alert behaviors and environmental variables (Table 3). Year, period of year, location, age, general flock activity, habitat, flock size, and observer were associated with use of alert signals. Cranes used alert behaviors more in April and May than during the period from January to March (Table 4). Cranes on the nesting grounds in Alaska (AK-OC) used alert signals nearly twice as frequently as cranes at any other

sampling location, and alert behaviors were observed most commonly when cranes were on the tundra of the nesting grounds. Cranes in feeding flocks were on alert more than cranes in flocks where the predominate activity was loafing or sleeping, and cranes in small flocks of 1-3 birds were on alert much more frequently than individual cranes in larger flocks.

Associations with specific stimuli. - Specific stimuli were associated with alert responses from Sandhill Cranes 1,619 times in the time budgets (Table 5). Stimuli were identified by orientation of cranes during alert responses and from obvious departures of some stimuli from normal environmental conditions. Cranes in flight ($n = 688$) and on the ground ($n = 423$) were responsible for 69% of the alert responses for which a stimulus was identified. The percentage of alert responses due to cranes on the ground increased from 7% in January to 87% in May ($n = 1619$, $\underline{Z} = 95.7$; $\underline{P} = 0.001$), and from 7% in Texas to 90% in Alaska ($n = 1619$, $\underline{Z} = 111.3$, $\underline{P} = 0.001$).

Juvenile Sandhill Cranes reacted to cranes in flight with alert postures a higher proportion of the time than expected (Table 5). However, adults reacted to cranes on the ground with alert postures a higher proportion of the time than expected. Adult females responded to cranes on the ground with alert postures less than expected compared with adult males (Table 6).

Adult male cranes of pairs used alert postures in response to cranes on the ground more frequently than expected when compared to adult males in family units (Table 7), and adult females of pairs reacted to cranes on the ground more than adult females of family units. Juvenile Sandhill Cranes without parents used alert postures

more frequently in response to cranes on the ground than did juveniles with parents.

Relative Use of Tall Alerts

The proportion of alert postures that were tall alerts did not vary (P > 0.33) between age, sex, or social classes of Sandhill Cranes.

Association with environmental variables. - Regression analysis indicated that period of the year, flock activity, and year were associated with the proportion of alert postures that were tall alerts (Table 8). The ratio of tall alert behaviors to all alert behaviors was 3 times higher in January than at any other time during the study period (Table 9). Cranes in flocks where the predominate activity was feeding used tall alert postures more commonly than did cranes in flocks of loafing or sleeping cranes.

Associations with specific stimuli. - Sandhill Cranes used tall alerts more in response to aircraft, cars, trucks and tractors, and hunters than expected when compared to use of the alert investigative behaviors (Table 10). Aircraft, car, truck and tractor, and hunter stimuli were combined and called human-related stimuli. Use of tall alert postures by Sandhill Cranes were highly associated with the human-related stimuli.

Discussion

Alert Signals in a Social Context

Alert signals were associated with the protection of social bonds. Use of alert signals increased as northward migration progressed and as the nesting season approached. Sandhill Cranes on nesting areas were defending territories and use of alert signals was at its peak there.

Alert responses to cranes on the ground became much more common as
period of year progressed and on the nesting grounds in Alaska. Adult
males of pairs reacted to cranes on the ground much more frequently than
other social classes of cranes. Pairs and family units of cranes began
to segregate themselves from larger flocks, and juveniles were driven
from family units with higher frequency, as northward migration
progressed (unpublished data, Oklahoma Cooperative Wildlife Research
Unit). The lack of difference in frequency of use of alert signals
between adult males of family units and adult males of pairs suggests
that males serve a protective function associated with their mates,
not their young. Thus, adult males served a protective role, directed
at their mates, that became progressively more intense and more
commonly stimulated by other cranes (probably other males), as the
nesting season approached. Juveniles in family units benefited from
adult male protection; as juveniles without parents used alert postures
much more frequently than juveniles with parents. Actual defense
(from other cranes) of social bonds was implemented through agonistic
encounters discussed elsewhere (based on unpublished data, Oklahoma
Cooperative Wildlife Research Unit). However, protection of pair or
family bonds was facilitated by alert responses to other cranes.

Alert Signals in a Survival Context

Alert signals were associated with stimuli that threatened the
survival of individual Sandhill Cranes. One of the adaptive advantages
of flocking by Sandhill Cranes was a clear reduction in use of alert
signals when flocks of more than 1 social unit (alone, paired, or
families of 3 cranes) aggregated together. One of the reasons why
adult cranes without mates or young used alert signals infrequently was

that these adults were rarely observed in flocks of less than 10 birds.
I believe that alert signals, and the contagious tall alert in
particular, served to reduce mortality from dangerous stimuli such as
hunters and predators. If mortality is reduced by alert signaling,
then it follows that one adaptive advantage of flocking among Sandhill
Cranes is a reduction in mortality.

The proportion of alert signals that were tall alerts did not vary
by age, sex, or social class, but rather was clearly associated with
specific (human-related) stimuli. Over 65% of observed tall alert
signals were during January in Texas. The hunting season for Sandhill
Cranes was open during January in Texas during both years of this study.
I believe that disturbances caused by hunters (particularly on
weekends) caused this high rate of use of tall alert signals. Hunters
presented a direct threat to survival of individual Sandhill Cranes,
and cranes reacted to this direct threat (and stimuli such as cars and
trucks associated with it) with a contagious alert signal. Thus,
communication between Sandhill Cranes, in the form of alert signals,
probably served to increase the probability of survival of individual
birds.

Acknowledgments

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Table 1. Frequency of occurrence of alert signals within time budgets of Sandhill Cranes.

Status	n	$\bar{x}$	SE	$\underline{t}$	OSL
Male	157	4.834	0.290	9.21^a	0.001
Female	146	1.699	0.179		
Adult					
Alone	151	1.225			
Pair	183	* 3.060	8.532^b	16.93^c	0.001
Family	58	2.690			
Juvenile					
Alone	71	2.817	0.307	4.90^a	0.001
Family	214	1.589	0.142		
Male					
Pair	71	4.849	0.408	0.85	0.401
Family	19	4.799	0.624		
Female					
Pair	88	1.148	0.155	0.46	0.644
Family	32	1.313	0.319		

[a] Unequal variances, $\underline{P} < 0.05$.

[b] ANOVA error mean square.

[c] ANOVA F-value.

* Different means, $\underline{P} < 0.05$, Duncan's Multiple Range Test.

Table 2. Percentage of time spent by Sandhill Cranes exhibiting alert signals.

Status	n	$\bar{x}$	SE	$\underline{t}$	OSL
Adult	711	4.731	0.294	5.23^a	0.001
Juvenile	339	2.723	0.246		
Male	150	11.199	0.966	8.30^a	0.001
Female	141	2.515	0.403		
Adult					
Alone	128	1.581			
Pair	180	6.139*	0.007^b	15.33^c	0.001
Family	57	8.148			
Juvenile					
Alone	62	5.995	0.810	5.35^a	0.001
Family	210	1.523	0.209		
Male					
Pair	71	13.357	1.381	0.87^a	0.396
Family	19	17.061	4.048		
Female					
Pair	86	1.568	1.135	1.49^a	0.144
Family	32	3.331	0.326		

[a] Unequal variances, $\underline{P} < 0.05$.

[b] ANOVA error mean square.

[c] ANOVA F-value.

* Different means, $\underline{P} < 0.05$, Duncan's Multiple Range Test.

Table 3. Regression analysis for variables explaining significant
variance in the frequency of occurrence of alert signals used by
Sandhill Cranes.

Variable	df	Partial SS	F-value	OSL
Year	1	598.32	93.74	0.001
Period of year	2	158.42	12.41	0.001
Location	1	62.31	9.76	0.001
Age	1	60.99	9.56	0.001
General flock activity	2	89.68	7.02	0.001
Habitat	13	179.32	2.16	0.010
Flock size	6	90.58	2.37	0.028
Observer	1	33.87	5.31	0.021

Full model: df = 30,1066; EMS = 6.38; F = 11.85; OSL = 0.001; R^2 = 0.25.

Table 4. Variation in the frequency of occurrence of alert signals
within significant class variables from regression.

Variable level	n	$\bar{x}$	DMRT[a]	Variable level	n	$\bar{x}$	DMRT[a]
Year				**Habitat**			
1979	210	3.976	A	Tundra	35	5.114	A
1980	887	1.809	B	Corn	208	3.038	B
Period of year				Milo	240	2.679	B
Apr (early)	125	2.944	A	Native hay	98	2.480	B
May	120	2.324	A B	Wheat	70	2.300	BC
Apr (late)	120	2.283	A B	Alfalfa	129	1.736	DC
Jan	179	2.263	B	Alfalfa-hay	49	1.571	DCE
Mar	352	2.094	B	Marsh	69	1.522	DCE
Feb	201	1.876	B	Plowed	39	1.000	D E
Location				Roost	15	1.000	D E
AK-OC	56	4.625	A	Cotton	114	0.930	E
NE	477	2.317	B	Barley-planted	18	0.722	E
SK	120	2.283	B	Barley-stubble	12	0.250	E
TX	380	2.058	B	Mesquite	1	0.000	E
AK-DJ	64	0.313	C	**Flock size**			
Age				1-3	74	3.824	A
Adult	731	2.468	A	501-1000	182	2.764	B
Juvenile	366	1.738	B	26-100	192	2.365	BC
Flock activity				100-500	412	1.978	DC
Feeding	770	2.508	A	1000 +	164	1.787	D

Table 4. Continued.

Variable level	n	$\bar{x}$	DMRT[a]	Variable level	n	$\bar{x}$	DMRT[a]
Loafing	332	1.581	B	4-10	17	1.294	D
Sleeping	5	0.000	B	11-25	56	1.250	D
				Observer			
				1	859	2.636	A
				2	238	0.739	B

[a] Duncan's Multiple Range Test, $\underline{P} < 0.05$, error from regression error mean square.

Table 5. Association of stimuli and alert signals among ages of Sandhill Cranes.

Stimulus	Adults			Juveniles			Total
	Observed	Expected	Cellχ^2	Observed	Expected	Cellχ^2	χ^2
Avian predator	2	2.9	0.3	2	1.1	0.8	1.1
Ground predator	4	3.7	0.0	1	1.3	0.1	0.1
Cranes in flight	476	504.6	1.6	212	183.4	4.4	6.0
Cranes on ground	383	310.2	17.1	40	112.8	47.0	64.1
Domestic stock	7	8.8	0.4	5	3.2	1.0	1.4
Aircraft	45	43.3	0.1	14	15.7	0.2	0.3
Cars	99	129.1	7.0	77	46.9	19.3	26.3
Trucks/tractors	166	169.4	0.1	65	61.6	0.2	0.3
Hunters	7	15.4	4.6	14	5.6	12.6	17.2
Total	1189			430			116.6[a]

[a] Significant $\underline{P}$ = 0.001, df = 8.

Table 6. Association of stimuli and alert signals among sexes of
adult Sandhill Cranes.

| Stimulus | Females | | | Males | | | Total |
	Observed	Expected	Cell χ^2	Observed	Expected	Cell χ^2	χ^2
Avian predator	0	0.2	0.2	1	0.8	0.1	0.3
Cranes in flight	56	48.3	1.2	152	159.7	0.4	1.6
Cranes on ground	61	77.7	3.6	174	257.3	1.1	4.7
Domestic stock	3	1.2	2.9	2	3.8	0.9	3.8
Aircraft	4	5.6	0.4	20	18.4	0.1	0.5
Cars	16	11.1	2.1	32	36.9	0.6	2.7
Trucks/tractors	23	20.2	0.4	64	66.8	0.1	0.5
Hunters	2	0.7	2.4	1	2.3	0.7	3.1
Total	165			546			17.4[a]

[a] Significant $\underline{P}$ = 0.015, df = 7.

Table 7. Association of stimuli from cranes and alert signals among social classes of Sandhill Cranes.

Status	Cranes on ground			Cranes in flight			Total χ^2	OSL
	Observed	Expected	Cell χ^2	Observed	Expected	Cell χ^2		
Adult males								
Pair	252	224.91	3.3	76	103.09	7.1	70.2	0.001
Family	12	39.08	18.8	45	17.91	41.0		
Adult females								
Pair	55	49.13	0.7	17	22.87	1.5	14.1	0.001
Family	3	8.87	3.9	10	4.13	8.3		
Juveniles								
Alone	22	15.57	2.7	78	84.43	0.5	6.0	0.015
Family	11	17.43	2.4	101	74.57	0.4		

Table 8. Regression for variables explaining significant variance in the proportion of alert signals that were tall alerts.

Variable	df	Partial SS	F-value	OSL
Period	5	1.31	22.19	0.001
Flock activity	2	0.13	5.43	0.005
Year	1	0.08	6.65	0.010

Full model: df = 8,1096; EMS = 0.01; F = 14.76; OSL = 0.001; R^2 = 0.10.

Table 9. Variation in the proportion of alert signals that were tall
alerts within significant class variables from regression.

Variable level	n	$\bar{x}$	DMRT[a]	Variable level	n	$\bar{x}$	DMRT[a]
Period				Flock activity			
Jan	180	0.093	A	Feeding	775	0.027	A
Feb	203	0.032	B	Loafing	325	0.012	B
Mar	355	0.005	C	Sleeping	5	0.000	B
April (early)	127	0.000	C	Year			
April (late)	120	0.000	C	1979	215	0.030	A
				1980	890	0.021	A
May	120	0.000	C				

[a] Duncan's Multiple Range Test, $P < 0.05$, error from regression error mean square.

Table 10. Association of alert stimuli and use of tall alert signals by Sandhill Cranes.

| Stimulus | Alert investigative | | | Tall alert | | | Total |
	Observed	Expected	Cell χ^2	Observed	Expected	Cell χ^2	χ^2
Avian predator	4	3.8	0.0	0	0.2	0.2	0.2
Ground predator	5	4.8	0.0	0	0.2	0.2	0.2
Cranes in flight	686	662.4	0.8	10	33.6	16.5	17.3
Cranes on ground	422	404.5	0.8	3	20.5	14.9	15.7
Domestic stock	12	11.4	0.0	0	0.6	0.6	0.6
Aircraft	49	56.2	0.9	10	2.8	18.0	18.9
Cars	156	159.4	1.1	22	8.6	21.0	22.1
Trucks/tractors	209	221.8	0.7	24	11.2	14.5	15.2
Hunters	11	20.0	4.0	10	1.0	79.7	83.7
Total	1554			79			174.1[a]
Human related	425	467.4	3.8	66	23.6	75.9	79.7
Other	1129	1094.6	1.6	13	55.4	32.4	34.0
Total	1554			79			113.8[b]

[a] Significant $\underline{P}$ = 0.001, df = 8.

[b] Significant $\underline{P}$ = 0.001, df = 1.
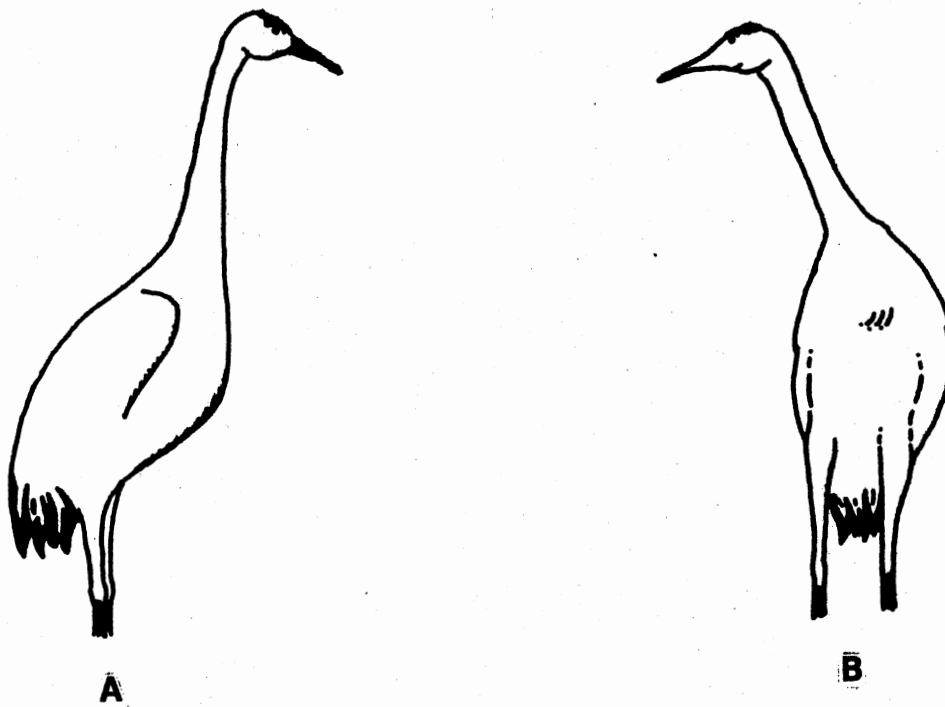
Figure 1.   The tall alert (A) and alert investigative (B)
            postures of sandhill cranes (from 35 mm slides).

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VITA

Thomas Craig Tacha

Candidate for the Degree of

Doctor of Philosophy

Thesis: BEHAVIOR AND TAXONOMY OF SANDHILL CRANES FROM MID-CONTINENTAL
NORTH AMERICA

Major Field: Wildlife Ecology

Biographical:

Personal Data: Born in Kansas City, Kansas, on December 19, 1951.

Education: Graduated from Salina High School, Salina, Kansas, May
1969; received Bachelor of Science degree in Wildlife Biology
from Kansas State University, December 1973; received Master
of Science degree in Wildlife and Fisheries Sciences from
South Dakota State University, May 1976; completed
requirements for Doctor of Philosophy degree in Wildlife
Ecology, May, 1981.

Professional Experience: Waterfowl Research Assistant for
Michigan Department of Natural Resources, 1973; Graduate
Research Assistant for South Dakota Cooperative Wildlife
Research Unit, 1974-76; Research Assistant for Texas A & M
University, 1976; Research Biologist for Delta Waterfowl
Research Station, 1976; Graduate Research Assistant for
Oklahoma Cooperative Wildlife Research Unit, 1977-81.

Professional Organizations: The Wildlife Society.