Demographics of the Gulf Coast Subpopulation of Mid-continent Sandhill Cranes

Bart. M. Ballard, *Caesar Kleberg Wildlife Research Institute, Campus Box 218, Texas A&M University-Kingsville, Kingsville, TX 78363*

Jonathan E. Thompson, *Caesar Kleberg Wildlife Research Institute, Campus Box 218, Texas A&M University-Kingsville, Kingsville, TX 78363*

M. Todd Merendino, *Texas Parks and Wildlife Department, County Courthouse, Room 101, Bay City, TX 77414*

James D. Ray,[1] *Texas Parks and Wildlife Department, P. O. Box 659, Canyon, TX 79015*

Jay A. Roberson, *Texas Parks and Wlldlife Department, 4200 Smith School Road, Austin, TX 78744*

Thomas C. Tacha,[2] *Caesar Kleberg Wildlife Research Institute, Campus Box 218, Texas A&M University-Kingsville, Kingsville, TX 78363*

Abstract: Current recommendations for subpopulation management for mid-continent sandhill cranes *(Grus canadensis)* are based on tentative evidence that suggests geographic separation of crane concentrations during migration and winter and possible variation in demographic characteristics between these groups. We determined distribution, abundance, subspecific composition, and annual recruitment of the Gulf Coast subpopulation of mid-continent sandhill cranes because little information was available on most demographic characteristics of this subpopulation. Based on aerial line transect surveys conducted along the Texas Coast during winter, subpopulation abundance was 120,072 cranes (SD=31,845) during 1996–1997 and 121,057 cranes (SD=31,521) during 1997–1998. Winter age ratios (percent hatch-year cranes) along the Texas Gulf Coast ranged from 9.5% (SE=0.52, *N*=3,239 cranes) to 10.8% (SE=0.61, *N*=2,570 cranes), indicating that annual recruitment was lower than previously reported. Subspecific composition of cranes wintering along the Texas Coast included 28%–32% greater sandhill cranes *(G. c. tabida)*, 62%–68% Canadian sandhill cranes *(G. c. rowani)*, and 4%–8% lesser sandhill cranes *(G. c. canadensis)* during the winters of 1995–1997. Few greater sandhill cranes were present in either the Rolling Plains or South Texas Plains

1. Present address: Mason and Hanger Corporation, P. O. Box 30020, Amarillo, TX 79120.
2. Deceased.

during the hunting season. A subpopulation boundary through these regions would include the majority of greater sandhill cranes in the Gulf Coast subpopulation.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 53: 449–463

The Mid-continent population of sandhill cranes is currently managed as a single population (Central and Pacific Flyway Counc. 1993). However, geographic separation of crane concentrations during fall and winter (Johnson and Stewart 1973; Tacha et al. 1984, 1986), as well as differences in demographic characteristics of wintering aggregations (Tacha 1981, Tacha and Vohs 1984), provided evidence for recognition of 2 subpopulations (henceforth referred to as the Gulf Coast and western subpopulations) and indicated the need to manage them separately (Mid-continent Sandhill Cranes Ad Hoc Subcomm. of the Central Flyway Counc., unpubl. rep.). Furthermore, differences in internal parasites between Western and Gulf Coast subpopulation (GCS) sandhill cranes suggested separation during the breeding season and further supported the concept of 2 distinct subpopulations (Iverson et al. 1983).

Although extensive work has been conducted to estimate demographic parameters of the Western subpopulation of mid-continent sandhill cranes (Iverson et al. 1982, 1985*a, b,* 1987; Carlisle and Tacha 1983; Tacha and Vohs 1984; Tacha et al. 1985*a, b*), little information is available on most demographic variables for the GCS. Previous estimates of abundance for the GCS vary widely (Guthery and Lewis 1979:22,000 [no variance]; Tacha et al. 1986: 30,000 [no variance]; Muehl 1994: 166,000 [95% CI=±160,000]) and are imprecise or have no associated measures of variability. Annual recruitment has been estimated by age ratio surveys during migration when nonbreeding cranes and family units may be segregated (Miller and Hatfield 1974, Buller 1979, Carlisle and Tacha 1983, Tacha and Vohs 1984), or from limited areas on wintering grounds (Buller 1976, Tacha et al. 1986). Furthermore, concern over the small number of greater sandhill cranes within the GCS is based on limited data.

The GCS includes greater, lesser, and Canadian sandhill cranes (Guthery and Lewis 1979, Tacha et al. 1994). Greater sandhill cranes are considered most limited in abundance and distribution within the range of the mid-continent population. Consequently, this subspecies has attracted special concern among agencies responsible for mid-continent sandhill crane management. Ideally, management of subpopulations would involve identifying a subpopulation that includes most of the mid-continent greater sandhill cranes, which would facilitate protection of this subspecies. Based on previous subspecific composition studies, it is thought that most greater sandhill cranes are part of the GCS (Johnson and Stewart 1973, Tacha 1981). However, without a reliable estimate of the GCS size and subspecific composition, the number of greater sandhill cranes in the mid-continent population remains speculative. Because sandhill cranes exhibit delayed sexual maturation and low annual recruitment rates, accurate delineation of abundance and harvest of subspecies is essential. Currently, the mid-continent population is hunted in 9 Central Flyway states, Alaska, Arizona, Canada, and Mexico (Tacha et al. 1992, 1994) Additionally, sandhill crane harvest in the Central Flyway has steadily increased over the past 20 years (Sharp et al. 1997).

The purpose of this study was to investigate demographic characteristics of the GCS of mid-continent sandhill cranes including distribution, abundance, subspecific composition, and annual recruitment to help facilitate management at the subpopulation level.

We thank F. S. Guthery for technical advice throughout this study. We are also grateful to the King Ranch, Inc., Kennedy Ranch, and other private landowners who allowed access to their properties. We appreciate assistance and information provided by D. S. Benning, R. L. Bingham, and D. H. Johnson. We thank J. Steiner for analyzing aerial photographs. We acknowledge assistance in data collection by J. Hurst, D. Lobpries, M. Nelson, T. Pilcik, R. Sims, R. Taylor, G. Waggerman, and many other Texas Parks and Wildlife Department (TPWD) employees. M. A. Bishop, F. Chavez-Ramirez, A. M. Fedynich, F. S. Guthery, D. G. Hewitt, D. H. Johnson, and K. J. Reinecke commented on the manuscript. Cooperative funding was provided by the 1995 Webless Migratory Bird Research Program (U.S. Fish and Wildl. Serv. and U.S. Geol. Survey-Biol. Resour. Div.), TPWD, and Caesar Kleberg Wildlife Research Institute at Texas A&M University-Kingsville. This is publication number 97–123 of the Caesar Kleberg Wildlife Research Institute.

Methods

Subpopulation Abundance

Sandhill crane abundance along the Texas coast was determined using aerial line transect surveys (see Buckland et al. 1993). Twenty-seven counties (Fig. 1) were divided into 5 strata based on traditional crane distribution (TPWD unpubl. data). We allocated 75 aerial transects such that the variance and extrapolated estimate of regional population size was minimized. Buckland et al. (1993:311) showed that optimum allocation is approximately

$$P_v = \frac{A_v D_v}{\Sigma A_v D_v}$$

where P_v is the proportion of total transect length allocated to stratum v, A_v is the area of stratum v, and D_v is the density of cranes in stratum v. Each transect totaled 32 km and consisted of 2 parallel 16-km segments that were 3.2 km apart and oriented north-south. Starting points for each transect were determined by randomly selecting latitude-longitude coordinates within each county. We allocated transects to counties within strata in approximate proportion to county size, which provided better spatial distribution of transects. Because strata were not contiguous, allocation to counties ensured that a transect would not cross a county boundary and enter another stratum.

Observers counted cranes from fixed-wing aircraft and recorded flock size and right-angle distance (m) from the center of the flock to the transect line. Aerial surveys were conducted during the third week of December each year to correspond with peak crane abundance (Tacha et al. 1986). Preliminary surveys were conducted in December 1995; however, they were incomplete because of logistical constraints and therefore are not reported. In subsequent years, 2 crews completed surveys during the third week of December. Flight speed (160 km/hour) and altitude (150 m) were consistent between survey crews and years.

Population abundance in each stratum was estimated using the equation

$$\hat{G}=\left[\sum \frac{g_v A_v}{2L_v}\right] f(0)$$

where $\hat{G}$ is the number of flocks in v strata, g_v is the number of flocks observed in stratum v, A_v is the area of stratum v, $f(0)$ is the probability of detecting a flock on the transect line, and L_v is the total transect length in stratum v (Buckland et al. 1993). The associated variance is calculated using the equation

$$var(\hat{G})=G^2\left[\frac{f(0)}{2}\right]\left[\frac{b_2}{\Sigma L_v D_v}+b_l \sum \frac{(G_v/G)^2}{}\right]$$

where $var(\hat{G})$ is the variance of flocks, D_v is the density of flocks in stratum v; b_1 is calculated as

$$b_1=\frac{var(n)}{E(n)}$$

where $var(n)$ is 2 times the number of flocks, and $E(n)$ is $2LD/f(0)$; and b_2 is calculated as follows (Buckland et al. 1993).

$$b_2=\frac{E(n)\,var\,(f(0))}{[f(0)]^2}$$

The number of cranes (N) is calculated as $N=(\hat{G})\,E(s)$, where $E(s)$ is the expected flock size and the variance associated with the number of cranes is calculated by

$$var(N)=var(\hat{G})\,E(s)^2+var(E(s))\,\hat{G}^2-var\,(\hat{G})var\,(E(s))$$

where $var(N)$ is the variance of the subpopulation estimate, $E(s)$ is the expected flock size, and $var(E(s))$ is the estimated variance of the expected flock size. Estimates of crane abundance in Kleberg and Nueces counties were calculated similarly to compare to roost counts. To calculate flock density and regional estimates of the probability of detection of flocks on the transect line we used program DISTANCE (Buckland et al. 1993). Based on histograms of distance data, we analyzed data using several robust models (Buckland et al. 1993). We chose a half-normal detection function with a cosine adjustment because it had the smallest Akaike Information Criterion value and the goodness of fit tests ($P>0.251$) gave no indications that the model was inappropriate or that any assumptions were seriously violated (see Buckland et al. 1993).

Each year on mornings concurrent with aerial surveys, we conducted ground counts of cranes at all known roosts in Kleberg and Nueces counties to evaluate the accuracy of aerial survey estimates. Several large roosts were located in proximity to county boundaries, and cranes leaving these roosts and exiting either county were not counted. Roost counts were assumed to be complete counts of cranes using these 2 counties and were compared to 95% confidence intervals derived from aerial survey data. In addition, photographs were taken of random crane flocks during aerial surveys in 1996 to measure error in group size estimation for each observer. Photographs (25.4-cm × 30.5-cm prints from 35-mm color oblique) were magnified to determine number of cranes within flocks, similar to methods used during the spring Mid-continent Population survey conducted by the U.S. Fish and Wildlife Service (Walter 1996).

Age Ratios

Age ratios of sandhill cranes were determined by observing flocks in 19 counties along the Texas coast (Fig. 1) during 15–31 December 1995–1997. Roads were systematically driven north to south in each county to reduce the chance of counting a flock more than once. A flock was defined as ≥2 cranes separated from other flocks of ≥2 cranes by >50 m. We only sampled flocks that were on the ground and within distances that distinguishing characteristics were observable. Crown feathering and nape feather coloration were used to determine age (Lewis 1979). Both Tacha and Vohs (1984) and Drewien et al. (1995) found >98% of hatch-year (HY) cranes were distinguishable from after-hatch-year (AHY) cranes as late as January and February using crown and nape feather characteristics. Age ratios were expressed as (HY cranes/total cranes) × 100. We used χ^2-tests to investigate differences in age structure among years and among counties within years.

Distribution and Subspecific Composition

Sandhill cranes were collected from 14 counties along the Gulf Coast of Texas during mid-December through late January 1995–1996 and 1996–1997 (Fig. 1). We determined sex by gonadal examination and measured length (mm) of culmen postnares, wing chord, and tarsus for each AHY crane collected (Table 1). Sandhill cranes also were collected from 3 counties in the South Texas Plains and 6 counties in the Rolling Plains (Fig. 1) to determine the westward extent of greater sandhill crane distribution. Crane collections were conducted during November in 1995 and from mid-November through mid-December 1996 and 1997 to determine the proportion of greater sandhill cranes present during the hunting season in this region. Optimally, we hoped to establish subpopulation boundaries that would include the majority of mid-continent greater sandhill cranes. We collected cranes by shooting as they flew to roosts in the evening or to feeding areas in the morning. We attempted

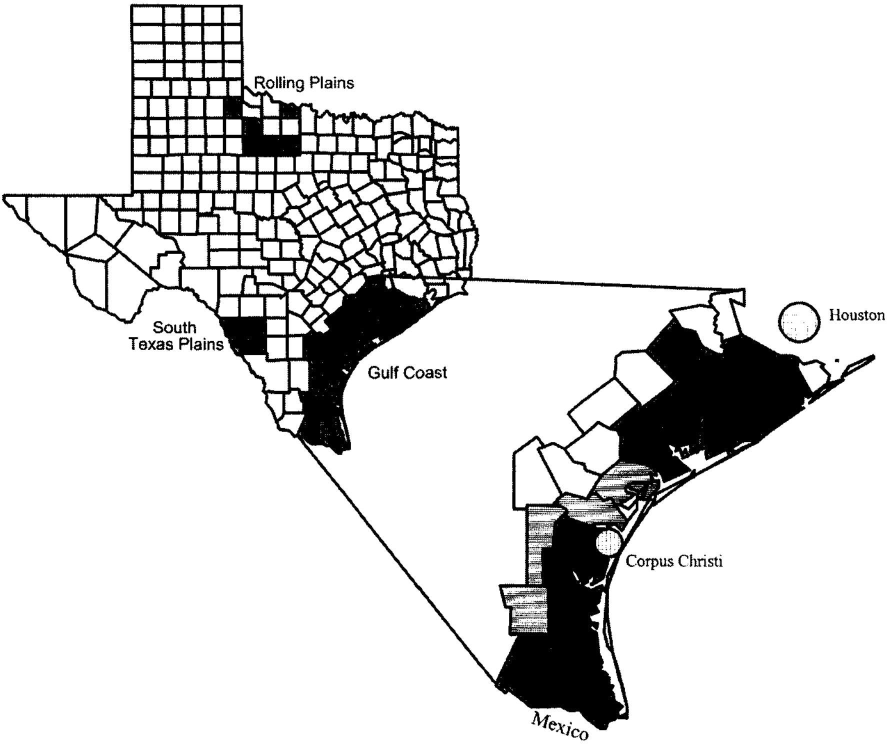

Figure 1. Shaded areas indicate counties within 3 regions of Texas where this study took place. Cranes were collected in the Rolling Plains and South Texas Plains regions. Within the Gulf Coast region (enlarged area), aerial surveys were conducted in all counties, cranes were collected in counties that are shaded, and age ratio surveys were conducted in counties that are shaded or hatched.

to randomly collect 1 crane per flock. Because of age-, sex- (Tacha andVohs 1984) and potential subspecific differences in vulnerability to harvest we did not use decoys except for 6 hunter-shot birds in the Rolling Plains. Discriminant models (D. H. Johnson, U.S. Geol. Survey, unpubl. data) derived from measurements of AHY sandhill cranes of known sex and breeding origin were used to partition our sample of cranes into the 3 respective subspecies. Subspecific composition is reported as the percentage of each subspecies within each region . We used χ^2 analysis to test for differences in subspecific composition between years for each region and between regions within years. We used a *Z*-test to test for differences in the proportion of greater sandhill cranes between the lower and mid-coasts. We also evaluated our sampling effort to determine if it was proportional to sandhill crane distribution along the Gulf Coast. This was accomplished by weighting our estimates of subspecific composition within each stratum by the estimated stratum population size based on our current aerial survey data. We then compared the weighted subspecific populations with the samples of cranes collected along the Gulf Coast using χ^2 analysis.

Table 1. Measurements (mm) of culmen post-nares (culmen), tarsus, and unflattended wing chord from sandhill cranes collected in 3 regions of Texas during winters 1995–96 and 1996–97.

	Females			Males		
Subspecies	Culmen	Tarsus	Wing chord	Culmen	Tarsus	Wing chord
Lessers						
N	37	37	37	43	43	43
$\bar{x}$	73.5	185.9	455.1	77.1	199.3	475.1
SE	0.7	2.3	3.4	0.8	2.4	3.1
min.	64.2	142	415	68.5	158	435
max.	82.6	207	503	89.2	222	514
Canadians						
N	96	96	96	147	147	147
$\bar{x}$	84.3	211.7	479.2	88.7	228.5	499.1
SE	0.4	1.0	1.9	0.4	1.0	1.6
min.	74.2	187	437	73.8	196	432
max.	92.6	235	522	101	255	555
Greaters						
N	45	45	45	55	55	55
$\bar{x}$	93.6	229.0	494.8	98.6	237.4	528.9
SE	0.6	1.6	2.4	0.6	1.9	1.7
min.	87.3	211	465	90.0	197	505
max.	102.8	263	549	110.6	263	552

Results

Subpopulation Abundance

We counted cranes along 72 aerial line transects in December 1996 and 68 transects in 1997 (Table 2). During both years, survey crews completed surveys during the third week of December. Estimated subpopulation abundance was 120,072 cranes (SD=31,845) in 1996 and 121,057 cranes (SD=31,521) in 1997.

Table 2. Aerial survey data from sandhill crane surveys conducted along the Gulf Coast of Texas during December 1996 and 1997.

Year Stratum	*N* transects	*N* flocks	*N* cranes	Estimate[a]
1996	72	124	3,792	120,072
1	11	21	554	6,759
2	32	55	1,063	39,249
3	14	19	626	26,565
4	11	28	1,525	41,300
5	4	1	24	6,199
1997	68	224	4,426	121,057
1	11	49	654	8,530
2	31	135	2,763	53,791
3	14	16	512	12,101
4	8	15	280	16,456
5	4	9	217	30,179

a. Estimates were derived using methods of Buckland et al. (1993:310).

Tests that evaluated the accuracy of our surveys suggested that our estimates from aerial surveys in Nueces and Kleberg counties in 1996 (5,127 cranes >3,339 ± 461). Extensive flooding prevented access to much of the 2-county area during 1997, and roost counts were <95% confidence intervals (1,745<20,428 ± 1,681). Analysis of aerial photographs taken during surveys indicated that observers underestimated flock sizes by an average of 14% (range=2%–21%, N=33 photos) in 1996 and 12% (range=7%–10%, N=36 photos) in 1997.

Age and Sex Ratios

Age ratios of cranes wintering along the Texas Gulf Coast were obtained from 223 flocks containing 4,752 cranes in December 1995, 307 flocks containing 3,239 cranes in December 1996, and 107 flocks containg 2,570 cranes in December 1997. Percent HY cranes in the GCS was 10.6% (SE=0.45) in 1995, 9.5% (SE=0.52) in 1996, and 10.8% (SE=0.61) in 1997. Proportions of HY cranes were similar among years (P=0.243) and among counties in December 1996 (P=0.193) and 1997 (P=0.301) but differed among counties in 1995 (χ^2_{18}=32.8, P<0.001).

Cranes collected from all 3 geographic regions consisted of nearly 60% males in each region each year. For example, AHY cranes collected along the Gulf Coast consisted of 63.7% males (72/113) in 1995 and 58.6% males (112/191) in 1996 and did not vary among counties either year (P>0.40).

Distribution and Subspecific Composition

Wintering AHY sandhill cranes were collected along the Texas coast during 1995–96 (N=113) and 1996–1997 (N=191). During winter 1996–97, when both

Table 3. Subspecific composition of sandhill cranes collected in coastal counties (listed in north-south order) of Texas during winters 1995–96 and 1996–97.

	G. c. Canadensis		*G. c. rowani*		*G. c. tabida*	
County	*N*	%	*N*	%	*N*	%
Fort Bend	0	0	14	42.4	19	57.6
Brazoria	1	3.3	15	50.0	14	46.7
Wharton	1	2.3	26	60.5	16	37.2
Colorado	2	6.9	20	69.0	7	24.1
Matagorda	0	0	21	60.5	8	27.6
Jackson	0	0	21	61.8	13	38.2
Calhoun	3	16.7	12	66.6	3	16.7
Victoria	3	8.8	21	61.8	10	29.4
Nueces	4	50.0	4	50.0	0	0
Kleberg	1	6.3	15	87.4	1	6.3
Kenedy	1	11.1	8	77.8	1	11.1
Willacy	0	0	4	100	0	0
Hildalgo	3	25.0	8	66.7	1	8.3
Cameron	0	0	3	100	0	0

Table 4. Numbers and percentages of 3 subspecies[a] of sandhill cranes (*Grus canadensis*) collected in 3 regions of Texas during November–January 1995–96 and 1996–97.

Year		*G. c. canadensis*		*G. c. rowani*		*G. c. tabida*	
Region	*N*	*N*	%(SE)	*N*	%(SE)	*N*	%(SE)
1995–96							
Gulf Coast	113	4	3.5 (1.73)	77	68.2 (4.38)	32	28.3 (5.00)
South Texas Plains	32	22	68.8 (8.19)	9	28.1 (7.95)	1	3.1 (3.06)
Rolling Plains	27	7	25.9 (8.43)	15	55.6 (9.56)	5	18.5 (7.47)
1996–97							
Gulf Coast	191	15	7.9 (1.95)	115	60.2 (3.54)	61	31.9 (3.37)
South Texas Plains	26	20	76.9 (8.27)	6	23.1 (8.27)	0	
Rolling Plains	34	12	35.3 (8.20)	21	61.8 (8.33)	1	2.9 (2.88)
1997–98[b]							
Rolling Plains	21	3	14.3 (7.64)	18	85.7 (7.64)	0	

a. Based on discriminant function models derived from morphological measurements on adult sandhill cranes of known sex and breeding origin (D. H. Johnson, U.S. Geol. Surv., unpubl. data).

b *Sandhill crane collections were only conducted in the Rolling Plains in Nov–Dec 1997.*

aerial surveys and sandhill crane collections were conducted concurrently, analysis showed that our sampling effort along the Gulf Coast was proportional to sandhill crane strata population (χ^2_4=7.13, P=0.129). Subspecific composition differed (P<0.001) within our sampling area along the Gulf Coast between the lower and upper half both years. Morphological variation in our sample indicated gradation from smaller to larger cranes moving northeastward along the Gulf Coast (Table 3). The majority of birds along the Gulf Coast were Canadian sandhill cranes during both years (1995: 68.2%, SE=4.38; 1996: 60.2%, SE=3.54) (Table 4). Greater sandhill cranes comprised 28.3% (SE=4.24) to 31.9% (SE=3.37) of cranes collected along the coast, whereas lesser sandhill cranes represented 3.5 (SE=1.73) to 7.9% (SE=1.95) of our samples.

Approximately 30 sandhill cranes were collected from the Rolling Plains and South Texas Plains each year (Table 4). Lesser sandhill cranes were the dominant subspecies in the South Texas Plains, where only 1 greater sandhill crane was collected during 2 years (58 cranes). Proportions of greater sandhill cranes from the Rolling Plains showed high variability among years, representing from 0 to 18.5% of collected cranes during 1995–1997 (Table 4). However, during the 2 years when collections were concurrent with the sandhill crane hunting season, only 1 greater sandhill crane was detected.

Subspecific composition was similar (P=0.120) between years within each region, but differed (1995–96: χ^2_2=52.79, P<0.001; 1996–97: χ^2_2=68.03, P <0.001) between coastal and western regions. Proportions of greater sandhill and Canadian sandhill cranes were higher in the coastal region, whereas lesser sandhill cranes were more prevalent in the 2 western regions (Table 4).

Discussion

Subpopulation Abundance

Previous estimates of crane abundance in the GCS ranged from 22,000 (Guthery and Lewis 1979) to 166,000 cranes (Muehl 1994) and often lacked associated measures of variability. Guthery and Lewis (1979) incorporated aerial surveys, roadside counts, and roost counts to estimate crane abundance along the Texas coast during December–January 1971. They tallied approximately 22,000 cranes wintering along the Texas coast; however, they suggested that their count was conservative because they did not survey several locations were cranes were present. They also suggested that cranes may have changed distribution during their survey period. Tacha et al. (1986) attempted to estimate crane abundance along the Texas coast and encountered similar problems to Guthery and Lewis (1979). Weekly counts to determine migration chronology of sandhill cranes using national wildlife refuges along the Texas Gulf Coast found that crane abundance peaked in mid-December (Tacha et al. 1986). However, their surveys to estimate crane abundance were conducted in early February when numbers of cranes in this region were approximately 13% of peak according to the migration chronology data. This survey led to an estimated population of approximately 30,000 cranes from counties associated with the GCS's winter range (east of Hwy. 16; see Tacha et al. 1986). Muehl (1994) incorporated a systematic sampling technique to survey 1,009 random quarter sections along the Texas coast, which were allocated among 5 strata (based on dominant land use) in approximate proportion to stratum size. His estimate of 165,824 cranes in November 1992 was accompanied by a relatively high standard error (SE=81,499) which reduced confidence in the estimate. A subsequent survey in January 1993 estimated 63,542 cranes along the Texas coast; however, it also had a relatively large standard error (SE=34,617; Muehl 1994).

We attempted to overcome many of the problems faced by these early studies by conducting systematic crane surveys during peak crane abundance as well as by stratifying sampling effort to minimize the variance associated with our extrapolated estimates of population size. Additionally, we used roost counts and aerial photos of random flocks during the aerial surveys to evaluate accuracy of aerial survey estimates. Results from booth roost count comparisons and analysis of aerial photos suggested that survey estimates were conservative.

Age Ratios

Understanding population dynamics is essential for effective management of hunted species or populations that exhibit low recruitment rates (Johnson 1979, Tacha et al. 1989). Age structure and age-related productivity are key factors that influence recruitment in long-lived species of migratory birds (Raveling 1981). Delayed breeding and low annual recruitment rates make sandhill crane populations sensitive to overharvest, and estimates of recruitment rates are essential to ensure that recreational harvest and crop depredation control are compatible with long-term population viability.

We found that percentages of HY cranes in the GCS were approximately half of previous estimates. Previous estimates of annual recruitment ranged from 18.2%–20.0% for the GCS and were considerably higher than estimates from the western subpopulation and other sandhill crane populations (see Drewien et al. 1995). Tacha et al. (1989) speculated that high recruitment rates of cranes in the GCS may result from an earlier age of fist successful breeding compared to cranes in the western subpopulation. Age ratios (percent HY cranes) for the GCS of sandhill cranes at several migration stopover areas ranged from 17.1% to 24% HY cranes (Buller 1976, Tacha and Vohs 1984). However, reliability of these estimates is questionable due to differences in migration chronology between family and nonbreeding groups (Miller and Hatfield 1974, Buller 1979, Carlisle and Tacha 1983, Tacha and Vohs 1984) and the resulting uncertainty that both social classes are present in representative proportions in migrational stopover areas. Tacha et al. (1986) provided the only age ratios for the GCS of sandhill cranes during winter; their estimate of 18.2% HY cranes was based on weekly counts of flocks observed around 2 lakes along the Gulf Coast of Texas during mid-December through February. Interestingly, the percentage of HY cranes in their sample of 162 harvested cranes (11.7%) was 36% lower than that estimated through flock observations. This disparity is particularly interesting because HY cranes are approximately 3.7 times more vulnerable to harvest than AHY birds (Tacha and Vohs 1984); therefore, HY birds should represent a larger rather than smaller component in harvested samples. Estimates of the proportion of HY cranes within the subpopulation should be most representative during the period of peak abundance. The reliability of previous estimates of annual recruitment for the GCS is unknown due to restricted sampling areas and sampling well outside the period of peak crane abundance (Tacha et al. 1986). The extensive geographic coverage and appropriate sampling period employed in our study suggest that estimates of recruitment may be more representative of the subpopulation, with the possible bias that our estimates were obtained after some hunting mortality in northern states and Canadian provinces. Furthermore, estimates of the proportion of HY cranes were similar ($P>0.243$) among years, and fell within the range of other sandhill crane populations (see Drewien et al. 1995).

Sex composition of the 304 AHY sandhill cranes collected during this study was similar to previous reports of 54%–62% males in harvested samples from North Dakota and Texas (Johnson and Stewart 1973, Tacha and Vohs 1984, Tacha et al. 1986), but differed from nonhunted samples (43%–47% males; Tacha and Vohs 1984). Disparate adult sex ratios in monogamous species, such as sandhill cranes, can have negative effects on recruitment rates (Tacha and Vohs 1984).

Subspecific Composition

We observed a north-south gradient in winter distribution of subspecies along the Gulf Coast of Texas with larger cranes wintering farther north. Guthery and Lewis (1979) were the first to document greater sandhill cranes wintering along the Gulf Coast of Texas; they also found this subspecies was more abundant in more northern portions of the Gulf Coast. Variation in winter distribution from smaller to larger cranes along a south to north gradient has also been reported in other wintering populations of sandhill cranes (Drewien and Bizeau 1974, Drewien et al. 1996).

Our estimates of subspecific composition of sandhill cranes in the GCS were similar between years. We estimated higher proportions (28% to 32%) of greater sandhill cranes than previous studies (9%; Guthery and Lewis 1979, Tacha et al. 1986), suggesting that this subspecies is more numerous than previously reported or has increased in abundance. Furthermore, our sampling was proportional to sandhill crane distribution in coastal Texas based on our aerial line transect survey data. Additionally, sampling effort by Guthery and Lewis (1979) proved to be markedly different from sandhill crane distributions during this study ($X^2=73.77$, df=4, $P<0.001$) and historic distributional data (TPWD, unpubl. data) ($X^2=32.66$, df=4, $P<0.001$), suggesting that differences in subspecific composition between previous research and our study may have been caused by sampling effort not being proportionate to crane distribution in earlier studies.

Tacha et al. (1986) used morphological and electrophoretic characteristics to distinguish subspecies and subpopulation affiliation of cranes in southern Texas. They reported that subspecific composition of cranes wintering in the South Texas Plains was similar to birds in the western subpopulation based on comparative morphology. In addition, electrophoretic profiles for cranes in the South Texas Plains were different from cranes along the Gulf Coast, but were similar to western subpopulation cranes (Gaines and Warren 1984). Our results, based on morphological characteristics, provided additional support that cranes wintering in the South Texas Plains more closely resemble birds from the western subpopulation (see Tacha et al. 1984, 1986) than to cranes wintering along the Gulf Coast.

Disparity in the proportion of greater sandhill cranes collected from the Rolling Plains between 1995 and subsequent years apparently stemmed from a change in our sampling schedule. During 1995, we sampled in mid- to late-November, prior to the opening of crane hunting season. Subsequently, we collected cranes during early to mid-December to better understand subspecific composition during the sandhill crane hunting season in this region. It appeared that fewer greater sandhill cranes were in the Rolling Plains during the hunting season (typically 1 Dec–10 Feb). Because this is both a wintering area and migrational corridor for sandhill cranes, temporal or spatial variability in migration chronology within or between years may have affected our results. Given the low proportions of greater sandhill cranes in samples from both the Rolling Plains and South Texas Plains during the crane hunting season, a subpopulation boundary through these regions would include the majority of greater sandhill cranes in the GCS.

Management Implications

To further improve our survey methodology to determine subpopulation abundance, better delineation of the winter distribution of the GCS will provide a more representative area to sample. Reports of large numbers of cranes supposedly from the GCS that traditionally remain in eastern Oklahoma and Kansas later in fall and early winter (see Tacha et al. 1984) and during the time of our surveys may warrant inclusion in the survey.

Harvest management restrictions within the GCS's winter range in Texas that were initiated due to concern about limited numbers of greater sandhill cranes, may warrant reappraisal. Our estimates of subspecific composition indicated that there was a higher proportion of greater sandhill cranes in the GCS than previously reported. Additionally, higher estimates of subpopulation abundance provided further evidence that greater sandhill cranes were considerably more abundant than previously reported.

Establishing a boundary between the Gulf Coast and western subpopulations that would include the majority of wintering greater sandhill cranes in the GCS is possible based on our findings. However, because the Rolling Plains serve as both a migration and wintering area, more data collected over a broader temporal and spatial distribution are needed to understand subspecific differences in migration chronology through this region. Results from this and previous studies (Gaines and Warren 1984, Tacha et al. 1986) suggested that the boundary between the Gulf Coast and western subpopulations in South Texas should be the eastern border of the South Texas Plains.

The basic premise behind management of the mid-continent population of sandhill cranes at the subpopulation level was because of marked differences in demographics between crane concentrations, namely differences in recruitment rates and the presence of a subspecies of limited abundance in one crane concentration. However, our findings refute previous reports of significantly higher recruitment rates in the GCS than the western subpopulation (see Drewein et al. 1995). Furthermore, even though the GCS would encompass most of the greater sandhill cranes wintering in the mid-continent region, this subspecies may be >10 times more abundant than currently acknowledged by managers based on our findings. Given this information, the justification for subpopulation management may need to be reevaluated.

Literature Cited

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundances of biological populations. Chapman and Hall, New York. 446pp.

Buller, R. J. 1976. Recent studies of age ratios of sandhill cranes in the Central Flyway. Proc. Internatl. Crane Workshop 1:78–85.

———. 1979. Lesser and Canadian sandhill crane populations, age structure, and harvest. U.S. Fish and Wildl. Serv. Special Sci. Rep., Wildl. Publ. 221. 10pp.

Carlisle, M. J. and T. C. Tacha. 1983. Fall migration of sandhill cranes in west central North Dakota. J. Wildl. Manage. 47:818–821.

Central and Pacific Flyway Councils. 1993. Management plan for the mid-continent population of sandhill cranes. U.S. Fish and Wildl. Serv. Migratory Bird Manage. Off., Golden, Colo.

Drewien, R. C. and E. G. Bizeau. 1974. Status and distribution of greater sandhill cranes in the Rocky Mountians. J. Wildl. Manage. 38:720–742.

———, W. M. Brown, and D. S. Benning. 1996. Distribution and abundance of sandhill cranes in Mexico. J. Wildl. Manage. 60:270–285.

———, ———, and W. L. Kendall. 1995. Recruitment in Rocky Mountain greater sandhill cranes and comparison with other crane populations. J. Wildl. Manage. 59:339–356.

Gaines, G. D. and R. J. Warren. 1984. Genetics and morphology of sandhill crane populations in Texas. J. Wildl. Manage. 48:1387–1393.

Guthery, F. S. and J. C. Lewis. 1979. Sandhill cranes in coastal counties of southern Texas: taxonomy, distribution, and populations. Proc. 1978 Internatl. Crane Workshop 2:121–128.

Iverson, G. C., T. C. Tacha, and P. A. Vohs. 1982. Food contents of sandhill cranes during winter and spring. Proc. Internatl. Crane Workshop 3:95–98.

———, P. A. Vohs, A. A. Kocan, and K. A. Waldrup. 1983. Some helminth parasites of sandhill cranes from mid-continental North America. J. Wildl. Diss. 19:56–59.

———, ———, and T. C. Tacha. 1985*a*. Distribution and abundance of sandhill cranes wintering in western Texas. J. Wildl. Manage. 49:250–255.

———, ———, and ———. 1985*b*. Habitat use by sandhill cranes wintering in western Texas. J. Wildl. Manage. 49:1074–1083.

———, ———, and ———. 1987. Habitat use by mid-continent sandhill cranes during spring migration. J. Wildl. Manage. 51:448–458.

Johnson, D. H. 1979. Modeling sandhill crane population dynamics. U. S. Fish and Wildl. Serv. Special Sci. Rep., Wildl. Publ. 222. 10pp.

——— and R. E. Stewart. 1973. Racial composition of migrant populations of sandhill cranes in the northern plains states. Wilson Bull. 85:148–162.

Lewis, J. C. 1979. Field identification of juvenile sandhill cranes. J. Wildl. Manage. 43:211–214.

Miller, R. S. and J. P. Hatfield. 1974. Age ratios of sandhill cranes. J. Wildl. Manage. 38:234–242.

Muehl, G. T. 1994. Distribution and abundance of water birds and wetlands in coastal Texas. M. S. Thesis, Texas A&M Univ.–Kingsville, Kingsville. 129pp.

Raveling, D. G. 1981. Survival, experience and age relation to breeding success in Canada geese. J. Wildl. Manage. 45:817–829.

Sharp, D. E., R. E. Trost, E. M. Martin, D. S. Benning, J. W. Solberg, and R. C. Drewien. 1997. Status and harvests of sandhill cranes. Unpubl. Rep., U. S. Fish and Wildl. Serv., Off. Migratory Bird Manage., Golden, Colo. 26pp.

Tacha, T. C. 1981. Behavior and taxonomy of sandhill cranes from mid-continent North America. Ph. D. Diss., Okla. State Univ., Stillwater. 112pp.

———, D. E. Haley, and R. R. George. 1986. Population and harvest characteristics of sandhill cranes in southern Texas. J. Wildl. Manage. 50:80–83.

———, ———, and P. A. Vohs. 1989. Age of sexual maturity of sandhill cranes from mid-continental North America. J. Wildl. Manage. 53:43–46.

———, C. Jorgenson, and P. S. Taylor. 1985*a*. Harvest, migration, and condition of sandhill cranes in Saskatchewan. J. Wildl. Manage. 49:476–480.

———, S. A. Nesbitt, and P. A. Vohs. 1992. Sandhill crane. No. 31 *in* A. Poole, P. Stettenheim, and F. Gill, eds. The birds of North America. Acad. Nat. Sci., Philadelphia and Am. Ornithol. Union, Washington, D.C.

———, ———, and ———. 1994. Sandhill crane. Pages 77–94 *in* T. C. Tacha and C. E. Braun, eds. Migratory shore and upland game bird management in North America. Internatl. Assoc. Fish and Wildl. Agencies, Washington, D.C. 24pp.

——— and P. A. Vohs. 1984. Some population parameters of sandhill crane from mid-continental North America. J. Wildl. Manage. 48:89–98.

———, ———, and G. C. Iverson. 1984. Migration routes of sandhill cranes from mid-continent North America. J. Wildl. Manage. 48:1028–1033.

———, ———, and W. D. Warde. 1985*b*. Morphometric variation of sandhill cranes from mid-continental North America. J. Wildl. Manage. 49:246–250.

Walter, J. S. 1996. Coordinated spring mid-continent sandhill crane survey.Unpubl. Rep., U.S. Fish and Wildl. Serv., Off. Migratory Bird Manage., Laurel, Md. 12pp.