1997

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Abstract: North Dakota is a major fall staging area for the Mid-continent Population (MCP) of sandhill cranes (*Grus canadensis*), which is composed of 3 subspecies: the greater (*G. c. tabida*), Canadian (*G. c. rowani*), and lesser (*G. c. canadensis*). The number of cranes killed by hunters in North Dakota averaged 6,793 during the 1990-94 seasons, ranking second highest among crane-hunting states. The distribution of harvest among subspecies is important, due to concerns about the poorly known status of these subspecies, especially the greater. We estimated subspecies composition of the harvest in North Dakota by using morphometric data collected from field samples of birds harvested since 1968. Subspecies composition varied both spatially (across counties from east to west) and temporally (among 3 periods of distinct harvest regulations and within season). Lessers predominated in the west and Canadians and greaters in the east. For the 1990-94 period we estimated that mortality from hunting in North Dakota averaged at least 1,085 (18%) greaters, 2,138 (36%) Canadians, and 2,716 (46%) lessers.

PROC. NORTH AM. CRANE WORKSHOP 7:201-208

Key Words: *Grus canadensis*, hunting, Mid-continent Population, North Dakota, sandhill crane, subspecies.

The Mid-continent Population (MCP) of sandhill cranes is the largest in North America, numbering about 500,000 (Sharp and Vogel 1992, Sharp 1995). Although currently managed as a single population, 3 subspecies have been recognized (Walkinshaw 1973): greater, Canadian, and lesser. Lessers are the most abundant, and greaters the least abundant, but there are no programs in place to monitor subspecific status or trends. The MCP is subject to legal sport hunting along much of its migration path, resulting in an average estimated yearly kill of 28,098 for the 1990/91-1994/95 period in Canada, the United States, and Mexico (Sharp 1996). The distribution of harvest among the 3 subspecies is not known. Because the greater represents the smallest portion of the MCP, and was once listed as a rare subspecies (Committee on Rare and Endangered Wildlife Species 1968), there is a desire among wildlife managers that harvest pressure be applied primarily to the most plentiful lesser (59 Federal Register 67:16765, 1994; Central Management Unit Technical Committee 1995).

Within the MCP, subspecies are geographically separated mostly during their breeding season. In fall and spring staging areas and wintering areas, greaters and Canadians are generally distributed farther east than lessers (Johnson and Stewart 1973; Guthery and Lewis 1979; Lewis 1979; Melvin and Temple 1980, 1983; Gaines and Warren 1984; Tacha et al. 1984), but they intermix to varying degrees, making subspecific harvest management impractical at this time.

Tacha et al. (1984, 1994) proposed managing the MCP as 2 geographic subpopulations, (1) Western-wintering mostly in western Texas and consisting largely of lessers and very few greaters, and (2) Gulf Coast-wintering mostly along the Gulf Coast of Texas and consisting mostly of Canadians and greaters.

North Dakota is a major fall staging area for all 3 subspecies of the MCP. The state initiated sandhill crane hunting in 1968 (Sharp and Cornely 1997), and harvest (plus crippling loss) averaged 6,793 for the 1990-94 period, ranking the state second highest (after Texas) in the United States. Because of the concern for the greater subspecies, the state of North Dakota has coordinated the measurement of harvested sandhill cranes since 1968. In this paper we estimate the subspecies composition of the harvest in North Dakota by using data from the measured cranes. We also test for differences in subspecies composition among counties, across periods of years related to major changes in harvest regulations (Sharp and Cornely 1997), and within seasons.

We thank C. Schroeder (deceased) and M. A. Johnson of the North Dakota Game and Fish Department, and all the cooperators who measured cranes. We also thank R. C. Drewien, R. E. Shea, and G. W. Smith for helpful comments on previous drafts of the manuscript.

METHODS

State and federal biologists in North Dakota collected morphometric, sex, and age data from harvested cranes in the field. Because samples were collected opportunistically, sampling intensity varied widely among counties. Each crane was sexed internally and aged (immature or adult). Three

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Table 1. Subspecies composition (%) of hunter-killed sandhill cranes collected in North Dakota during 1968–94. Percentage data for each county are pooled within time period and presented with corresponding total cranes (*n*) collected.

	1968–76				1977–82				1983–94			
County	*n*	Greater	Canadian	Lesser	*n*	Greater	Canadian	Lesser	*n*	Greater	Canadian	Lesser
Benson					19	37	63	0	15	27	67	6
Bottineau									11	45	55	0
Burleigh					1	100	0	0	393	7	26	67
Divide									3	0	0	100
Emmons									12	0	0	100
Kidder	78	15	82	3	242	24	71	5	280	18	39	43
McHenry					11	55	36	9	85	24	53	24
McLean	53	0	15	85	182	4	16	80	128	5	14	81
Mountrail									3	0	33	67
Phillips	4	0	0	100								
Pierce	12	8	92	0	233	34	62	4	372	22	72	6
Sheridan					2	0	0	100	52	29	27	44
Stutsman					11	18	82	0	87	44	48	8
Ward									21	0	10	90
Wells									16	38	56	6

length measurements were taken: wing chord, tarsus, and culmen (from posterior nares). Assignment of birds to subspecies was based on results of discriminant function analysis involving those measurements. The discriminant functions ultimately were based on a series of measurements of cranes collected on breeding areas, so that their subspecies were known (Johnson and Stewart 1973). Sample sizes were limited, especially for greaters (7 females and 11 males) and Canadians (3 females and 10 males); lessers were better represented with 17 females and 36 males.

Johnson and Stewart (1973) found that the 3 subspecies differed significantly in morphological measurements. From their data, discriminant functions involving tarsus length, culmen length (from posterior nares), and wing chord length were developed. Separate functions were developed for adult males and females; juveniles were not used. The discriminant function analysis assigned to each specimen a "probability" that it belonged to each of the 3 subspecies. We classified each specimen into the subspecies with highest associated probability.

We compared subspecies composition spatially among counties, and temporally both between and within seasons. For comparisons across years, we pooled data for each county into 3 time periods a priori, defined by major differences in harvest regulations: (1) 1968–76, season lengths of 30 days beginning in early November; (2) 1977–82, with 5- to 16-day seasons in early to mid-September; and (3) 1983–94, with 21- to 58-day seasons in much of the state (excluding the portion east of U.S. Hwy. 281, which was closed to hunting). There were minor regulatory changes within these periods, such as small changes in season length, creation and dissolution of zones, and addition of counties, which could be used to refine these time periods (Sharp and Cornely 1997) but would reduce samples in each period. We used likelihood ratio tests (LRT) between generalized logit models (Agresti 1990:307) to test for a period effect on subspecies composition and for an interaction between period and county effects. We used Pearson Chi-square tests for comparisons among counties within each period.

For within-year temporal comparisons we considered only the most recent period, 1983–94. For each county with sufficient sample size, we compared 4 periods: (1) 1–15 September, (2) 16–30 September, (3) 1–15 October, and (4) 16–31 October, by using Pearson Chi-square tests.

RESULTS

Table 1 and Figures 1–3 illustrate the subspecies composition of sampled cranes across counties for the 3 time periods described above. Subspecies composition differed among counties within each of the 3 periods (1968–76: $\chi^2 = 105$, 4 df, $P < 0.001$; 1977–82: $\chi^2 = 443$, 10 df, $P < 0.001$; 1983–94: $\chi^2 = 541$, 22 df, $P < 0.001$). In each period there is an apparent cline in subspecies composition from west to east, with lessers predominant in the west, and Canadians and greaters predominant in the east.

Because of the small number of counties sampled in the early years, we first compared the 1968–76 and 1977–82 periods based only on Kidder and McLean Counties (sample of ≥10 cranes in both periods), and found no period effect

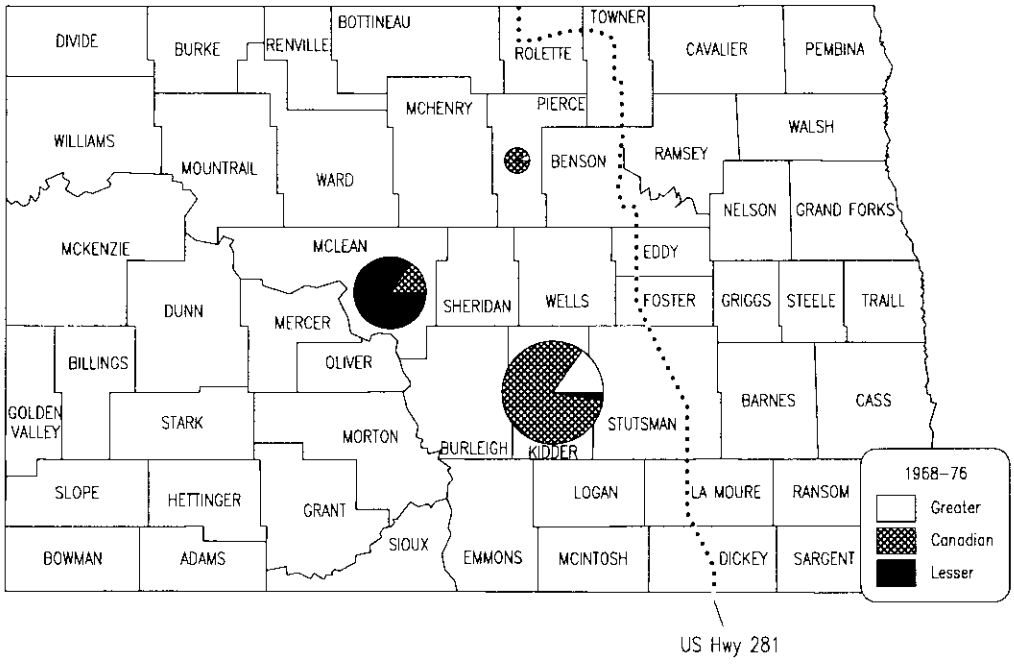

Fig. 1. Subspecies composition, by county, of harvested sandhill cranes collected in North Dakota, 1968–76.

(LRT $\chi^2 = 4.35$, 2 df, $P = 0.12$). We compared periods 1977–82 and 1983–94 based on data from Benson, Kidder, McHenry, McLean, Pierce, and Stutsman Counties, and found both a period effect and an interaction between period and counties (LRT $\chi^2 = 67$, 10 df, $P < 0.001$). Figures 2 and 3 indicate proportionally more lessers in eastern counties during 1983–94 than during 1977–82. This increase was not uniform from north to south, however, producing an interaction effect. For example, whereas a large proportional increase of lessers was indicated in Kidder County, there was

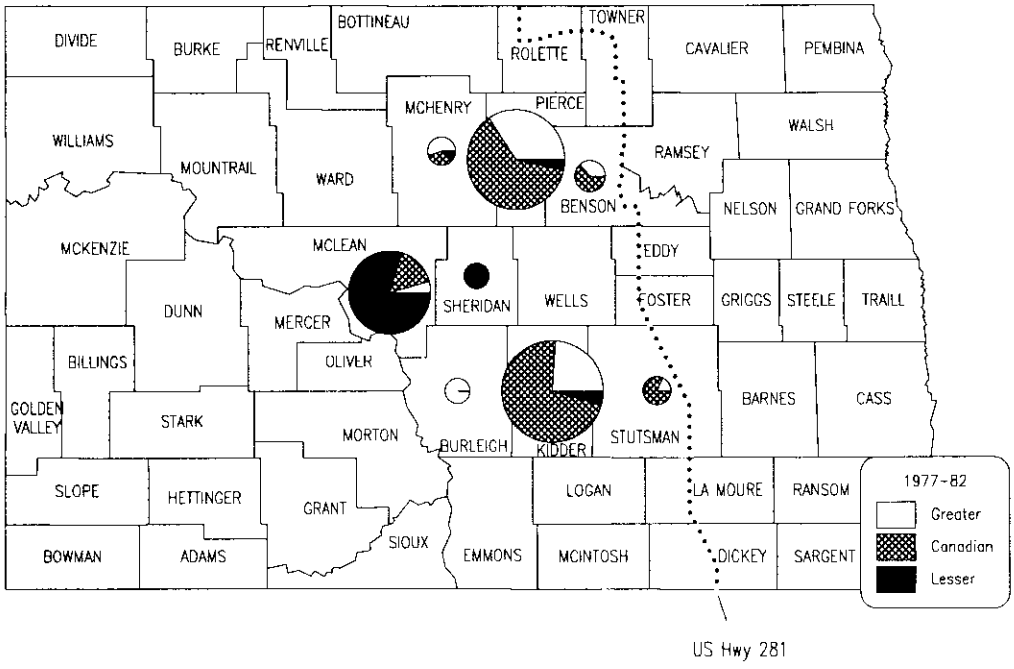

Fig. 2. Subspecies composition, by county, of harvested sandhill cranes collected in North Dakota, 1977–82.

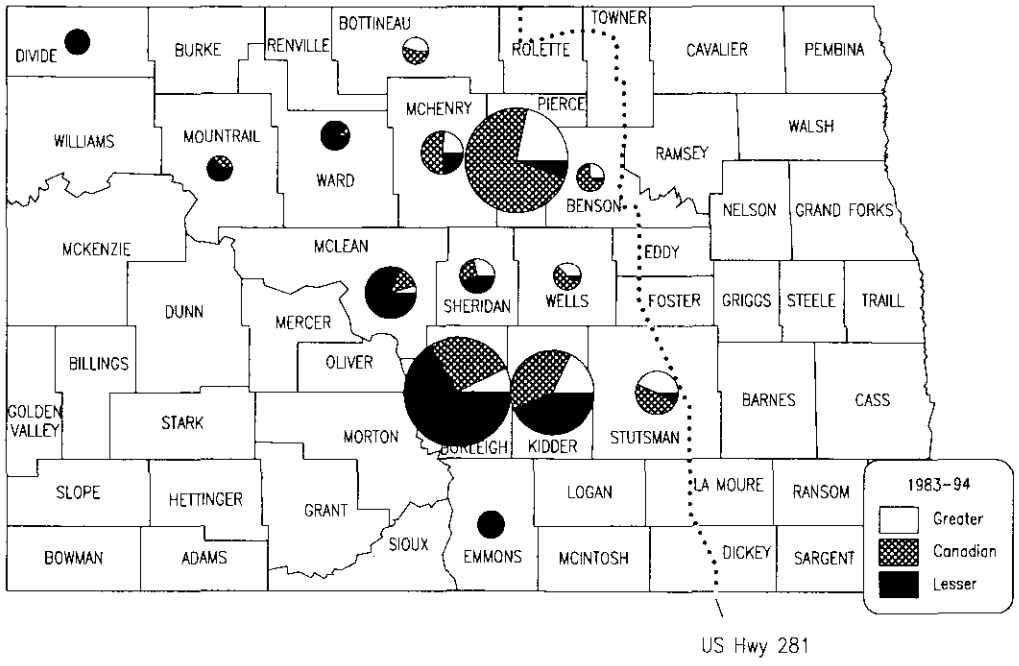

Fig. 3. Subspecies composition, by county, of harvested sandhill cranes collected in North Dakota, 1983–94.

a proportional increase in Canadians in Pierce County.

Table 2 contains county-specific subspecies composition by half-month intervals, pooled for the most recent multi-year period, 1983–94. For Burleigh, Kidder, and McHenry Counties the proportion of greaters and Canadians decreased from early September to mid-October, whereas the proportion of lessers increased for the same span of time. This pattern was statistically significant for Burleigh and Kidder Counties ($\chi^2 = 14$, 4 df, $P < 0.01$ and $\chi^2 = 12$, 4 df, $P = 0.02$, respectively), but not for McHenry County ($\chi^2 = 5.4$, 4 df, $P = 0.25$). The data for Sheridan County also displayed this pattern for 16 September–15 October ($\chi^2 = 13$, 2 df, $P < 0.01$). For McLean County, from 16 September to 15 October the proportion of greaters and Canadians increased, whereas the proportion of lessers decreased ($\chi^2 = 6.1$, 2 df, $P = 0.04$). Subspecies composition was stable during 1 September–15 October for Pierce ($\chi^2 = 2.6$, 4 df, $P = 0.63$) and Stutsman ($\chi^2 = 2.1$, 4 df, $P = 0.72$) Counties. Sample sizes were small for 16–31 October in all counties.

We estimated a lower bound on the average annual subspecies-specific mortality due to hunting in North Dakota for the most recent 5 years, 1990–94. Figures 4 and 5, respectively, illustrate the distribution of subspecies composition and average total hunter kill for this period. Total average kill due to hunting in North Dakota for this period was 6,793 cranes (Novara and Handy 1991; Martin 1992, 1993, 1994, 1995). Table 3 lists the estimated kill per county, calculated by applying the subspecies composition of field-sampled cranes to the average kill for the county. For Benson and Ward Counties, where subspecies composition for 1990–94 was based on <10 cranes, we used the subspecies composition for the 1983–94 period. We estimated an average kill of at least 1,085 greaters, 2,138 Canadians, and 2,716 lessers per year. Because some harvest occurred in unknown counties, and some cranes were taken in counties either not sampled for subspecies or insufficiently sampled, an annual average of 854 hunter-killed cranes was unaccounted for in this analysis.

DISCUSSION

We found differences in subspecies composition of harvest among counties within each of the 3 periods: 1968–76, 1977–82, and 1983–94. The cline in subspecies composition suggested in Figures 1–4, i.e., Canadians and greaters predominating in the east and lessers predominating in the west, is consistent with previous studies (Johnson and Stewart 1973, Melvin and Temple 1983). In addition, subspecies composition has changed over time within some counties, at least between the 1977–82 and 1983–94 periods. This is especially apparent in Kidder County, where the proportion of lessers in the sample of harvested cranes rose from 5% to 43%. When combined with increasing numbers of observations of cranes in areas east of U.S. Hwy. 281 (North Dakota Game and Fish Department, unpubl. data), where few were seen in the past and hunting is prohibited,

Table 2. Subspecies composition of hunter-killed sandhill cranes collected in North Dakota during 1983-94. For each county, data are pooled within 4 half-month periods. Only those counties for which ≥10 cranes were collected for ≥2 periods are represented.

County	Subspecies	1-15 Sep		16-30 Sep		1-15 Oct		16-31 Oct	
		n	(%)	*n*	(%)	*n*	(%)	*n*	(%)
Burleigh	Greater	10	(9)	18	(8)	1	(3)	0	(0)
	Canadian	40	(37)	60	(25)	3	(9)	0	(0)
	Lesser	58	(54)	158	(67)	29	(88)	12	(100)
	Total	108		236		33		12	
Kidder	Greater	14	(27)	25	(14)	5	(16)	5	(36)
	Canadian	25	(48)	63	(35)	12	(37)	8	(57)
	Lesser	13	(25)	93	(51)	15	(47)	1	(7)
	Total	52		181		32		14	
McHenry	Greater	5	(33)	12	(23)	3	(20)	0	(0)
	Canadian	9	(60)	29	(57)	6	(40)	1	(25)
	Lesser	1	(7)	10	(20)	6	(40)	3	(75)
	Total	15		51		15		4	
McLean	Greater	0	(0)	3	(4)	3	(8)	0	(0)
	Canadian	0	(0)	7	(9)	9	(24)	2	(18)
	Lesser	2	(100)	67	(87)	25	(68)	9	(80)
	Total	2		77		37		11	
Pierce	Greater	29	(21)	44	(22)	7	(26)	1	(50)
	Canadian	104	(74)	145	(71)	20	(74)	1	(50)
	Lesser	7	(5)	14	(7)	0	(0)	0	(0)
	Total	140		203		27		2	
Sheridan	Greater	2	(100)	5	(42)	8	(22)	0	(0)
	Canadian	0	(0)	7	(58)	7	(20)	0	(0)
	Lesser	0	(0)	0	(0)	21	(58)	2	(100)
	Total	2		12		36		2	
Stutsman	Greater	6	(50)	24	(41)	8	(53)	0	(0)
	Canadian	6	(50)	29	(49)	6	(40)	1	(100)
	Lesser	0	(0)	6	(10)	1	(7)	0	(0)
	Total	12		59		15		1	

this result indicates the possibility of a shift or expansion of the fall staging area to the east. This phenomenon, if it exists, could be caused by a variety of natural or man-made causes, including increased harvest pressure. Hunting seasons during 1983-94 were 58 days long in western counties and 21-58 days long in eastern counties, whereas season lengths during 1977-82 were 5-16 days. In addition, average crane kill by hunters during 1983-94 (6,344) was 91% higher than during 1977-82 (3,329) (Sharp and Cornely 1997).

For most counties sampled, we found that the proportion of lessers in the harvest increased from early September to mid-October, whereas the proportions of both greaters and Canadians decreased. This pattern is consistent with the belief that the larger subspecies migrate through earlier than the lessers (Johnson and Stewart 1973, Carlisle and Tacha 1983). Regardless of whether the larger subspecies leave the state earlier, large numbers of lessers arriving later could reduce the proportion of Canadians and greaters in the harvest. Conversely, for McLean County the proportion of Canadians and greaters in the harvest increased during 16 September-15 October. Movement between areas could cause either of these patterns. For Pierce and Stutsman counties, subspecies composition was relatively constant during 1 September-15 October, predominated by Canadians and greaters. This suggests that lessers simply have not made much use of those counties. Data from harvest after 15 October were too sparse to analyze.

For counties where subspecies composition varies within a season, the temporal distribution of samples should match that of the harvest, to minimize bias in estimates of subspecies composition. Because data were collected opportunistically, we do not know to what extent this was achieved.

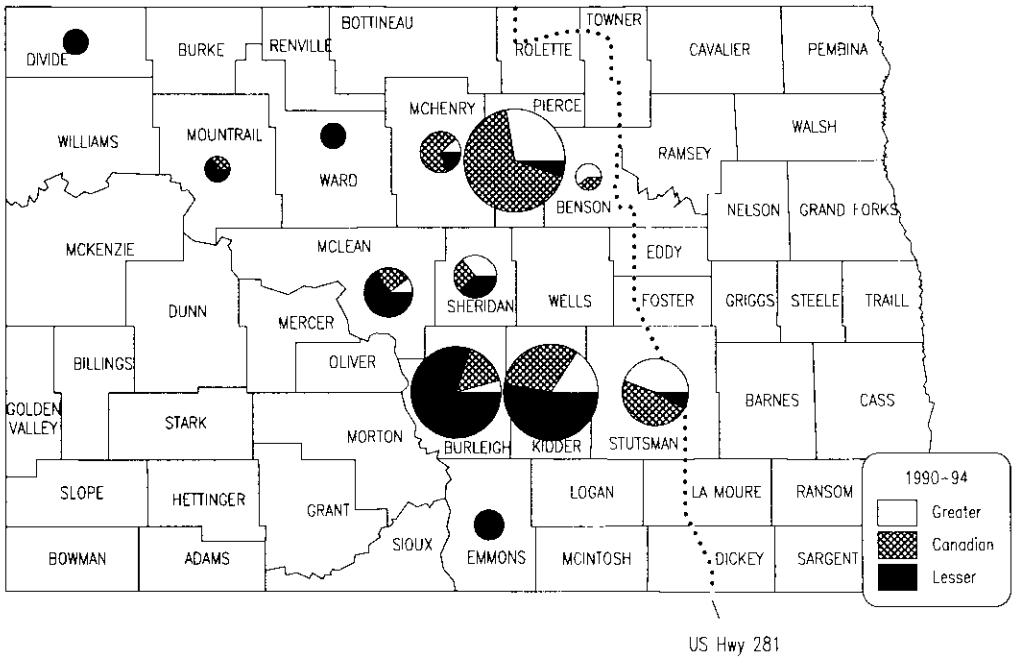

Fig. 4. Subspecies composition, by county, of harvested sandhill cranes collected in North Dakota, 1990–94.

The validity of the Canadian subspecies has been questioned (Stephen 1967), although the lesser and greater subspecies have long been recognized (Walkinshaw 1949, American Ornithologists' Union 1957). The Canadian subspecies was not formally described until 1965 (Walkinshaw 1965), although earlier references suggested its presence (e.g., Oberholser 1921, Walkinshaw 1949:64). Some authors (e.g., Tacha et al. 1985) have opined that subspecific designation, especially of Canadians, may be unwarranted, but that the various forms represent only a cline in body size, from large birds (greaters) breeding in more southern locations, to small birds (lessers) breeding farthest north, and with intermediate birds (Canadians) breeding in between.

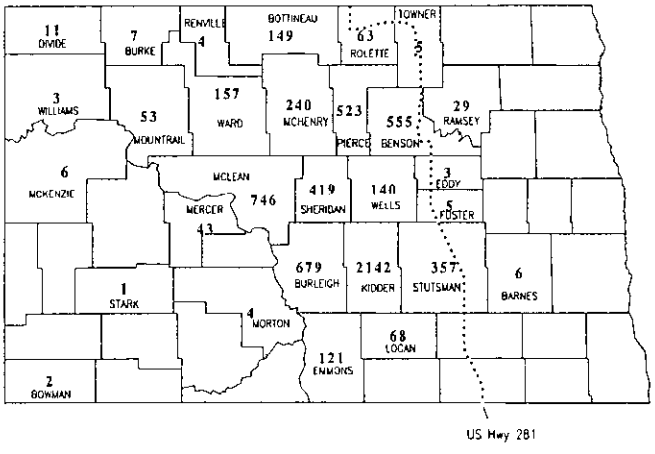

Fig. 5. Average mortality from hunting, by county, in North Dakota, 1990–94. An average of 248 cranes is unaccounted for here, due to unknown county of harvest.

Currently available evidence suggests that the 3 subspecies should be distinguished, however. Johnson and Stewart (1973) found that each of 13 breeding-ground specimens of Canadians clearly differed from both lesser and greater populations on the basis of several morphometric measurements. Baldwin (1976) found that greater nestlings required an average of 9 hours to attain homeothermy, whereas Canadian and lesser nestlings were homeothermic at hatch. Baldwin (1977) noted differences in development as well: wings, height, tarsi, culmen, and midtoes of young greaters developed in proportion to overall body size, Canadian chicks showed priority for height, tarsus, and culmen development, and young lessers showed priority for wing development over body development. Gaines and Warren (1984) discovered that the presence or absence of protein P1 in the pancreas consistently distinguished 13 Canadians collected in Saskatchewan from 5 lessers collected in Alaska. They did not examine greaters for genetic distinction.

Johnson and Stewart (1973) noted, however, that their morphometric analysis could not exclude the possibility of a cline. Breeding specimens were not collected uniformly throughout the breeding range of sandhill cranes, and intermediate groups could have been missed. In addition, sandhill cranes have increased in number and range during

Table 3. Subspecies composition of hunter-killed sandhill cranes (%) and total kill from hunting in North Dakota, 1990–94. A county was included if the sample size of collected cranes was ≥10 for 1983–94. Subspecies composition of total hunter kill based on subspecies composition of collected cranes.

County	Sampled cranes				Average kill	Estimated kill		
	n	Greater	Canadian	Lesser		Greater	Canadian	Lesser
Benson	5	60	40	0	555	150[a]	372[a]	33[a]
Burleigh	138	6	15	79	679	41	102	536
Emmons	12	0	0	100	121	0	0	121
Kidder	145	16	31	53	2,142	343	664	1,135
McHenry	35	11	69	20	240	26	166	48
McLean	51	10	24	66	746	75	179	492
Pierce	158	28	67	5	523	146	351	26
Sheridan	40	35	28	37	419	147	117	155
Stutsman	86	44	48	8	357	157	171	29
Ward	2	0	0	100	157	0[a]	16[a]	141[a]

[a] Due to sample size of <10 cranes for 1990–94, estimated composition of harvest was based on 1983–94 collection (see Table 1).

the past 50 years, and it is possible that populations that once had distinct and non-overlapping breeding ranges now have expanded and possibly melded. Research to better assess the validity of the 3 subspecies and to develop improved classification schemes is now under way (D. H. Johnson and J. E. Austin, Northern Prairie Science Center, pers. commun.).

Because of the variation in subspecies composition of the harvest presented here, especially the extensive overlap of greaters and Canadians, we believe that subspecific harvest management in North Dakota would not be practical at this time. Tacha et al. (1994) suggested subpopulation-specific harvest management based on wintering populations. The U.S. Fish and Wildlife Service has stated its intent to manage the MCP based on 2 subpopulations (59 Federal Register 67:16765, 1994), and the Central Management Unit Technical Committee will consider revising its Mid-continent Population Management Plan to accommodate subpopulations in 1998 (Central Management Unit Technical Committee 1995).

Ideally, division of North Dakota into distinct geographic areas for each subpopulation would be based on banding or telemetry data relating fall staging areas to wintering areas. However, with the exception of limited studies by Melvin and Temple (1980) and Tacha et al. (1984), no such studies have been conducted and none are in progress. In the absence of such banding data, delineation of subpopulations in North Dakota based on the data presented here would be even more difficult, especially given that there is some movement between counties within a season. Nevertheless, the apparent cline in subspecies composition from east to west is consistent with the cline in the wintering grounds discussed by Tacha et al. (1994), and could lend itself to some kind of division.

The Central Flyway will be collecting measurements on harvested sandhill cranes for at least 2 more years before it considers changes to the crane management plan to account for subpopulations. We believe, however, that the results presented here could be useful in separating subpopulations. Managers should also consider that, although the entire MCP is apparently stable in size, the status and demographics of each subpopulation (especially the Gulf Coast subpopulation), and of the subspecies comprising those subpopulations (especially the greater), are poorly known or unknown. Modeling exercises such as that conducted for the Gulf Coast subpopulation by Johnson and Kendall (1997) could be helpful in setting reasonable bounds on harvest for each subpopulation, and for identifying additional demographic information needed to better manage these subpopulations.

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