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Special Scientific Report—Wildlife No. 221

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Preface

The impact that hunting may have on populations of sandhill cranes (*Grus canadensis*) has been a subject of some controversy in recent years (Sherwood 1971; Miller et al. 1972; Miller 1974; Miller and Botkin 1974). Much of the debate stems from a lack of information about the population dynamics of sandhill cranes and the numbers taken by hunters. This prompted the U.S. Fish and Wildlife Service to initiate new studies aimed at a better understanding of sandhill cranes and their management needs, particularly in the Central Flyway where most of the crane hunting occurs in the United States.

The results of one of these studies, conducted from 1974-77 (R. J. Buller, in cooperation with biologists from the Canadian Wildlife Service and several States and Canadian Provinces) constitute *Special Scientific Report—Wildlife 221. Special Scientific Report—Wildlife 222* contains an analysis of data emanating from Buller's study, and other recent work on sandhill cranes, in the form of a series of mathematical models of sandhill crane populations.

These studies and analyses provide new and useful information about sandhill cranes in the Central Flyway and should be of interest to those concerned about the welfare of these birds. It is apparent, however, that additional efforts are needed to develop reliable information on population size. Until this is done and until satisfactory measurements of other key population characteristics are obtained, mathematical models for sandhill crane populations must be regarded as preliminary and incomplete.

For this reason, the Fish and Wildlife Service intends to continue with its studies and investigations of sandhill cranes. In addition to more intensive population surveys, a number of other studies are currently planned or under way. These are focused on breeding biology and behavior, breeding age, population age structure, social organization, distribution and movement patterns, sex ratios, feeding behavior, and habitat requirements.

John P. Rogers
Chief, Office of Migratory Bird Management

LESSER AND CANADIAN SANDHILL CRANE POPULATIONS, AGE STRUCTURE, AND HARVEST

Lesser and Canadian Sandhill Crane Populations, Age Structure, and Harvest[1]

by

Raymond J. Buller

Central Flyway Representative
U.S. Fish and Wildlife Service
P. O. Box 1306
Albuquerque, New Mexico 87103

Abstract

Lesser (*Grus canadensis canadensis*) and Canadian (*G. c. rowani*) sandhill cranes were studied from 1974 through 1977 in portions of the Central Flyway and Saskatchewan, Canada. The primary purposes of the study were to obtain estimates of (1) the lesser and Canadian sandhill crane populations during the fall and spring, (2) percent of juveniles in the population, and (3) hunting pressure, harvest, and crippling loss. Visual estimates of the numbers of cranes occurring within the main fall staging areas and on the principal wintering grounds were made during periods of peak migration each October, and on the Platte River in Nebraska each spring. Feeding, roosting, and flying sandhill cranes were aged throughout the study area during fall and winter with the aid of binoculars and spotting scopes. Hunters were contacted in the field in 1974 to obtain information on harvest. After the three subsequent hunting seasons, 1975-76, 1976-77, and 1977-78, questionnaires were mailed to holders of crane hunting permits in an effort to determine hunting pressure, harvest, and crippling loss. Results of fall, flyway-wide surveys varied from about 94,900 to 219,700 cranes and continuation of the surveys is not recommended because it is practically impossible to consistently select a time period that will coincide with the peak of migration and to avoid logistical problems. The spring inventories indicated 153,800 to 227,500 cranes in the various years and this spring inventory holds the greatest potential for assessing the total size of the lesser and Canadian sandhill crane population. The proportion of juveniles averaged 11.6%, and 20% of the successful breeders were accompanied by "twin" young. The total kill of sandhill cranes in the conterminous United States reached 14,170 in the 1977-78 hunting season.

This is a report on the results of a special study, conducted during the autumn of 1974 through the spring of 1977, of lesser (*Grus canadensis canadensis*) and Canadian (*G. c. rowani*) sandhill cranes in relation to hunting in the Central Flyway. The primary purposes of the study were to obtain estimates of (1) the lesser and Canadian sandhill crane populations during the fall and spring, (2) percent of juveniles in the population, and (3) hunting pressure, harvest, and crippling loss. Incidental information was also obtained concerning the application of the family group technique, already used for winter appraisals of productivity among arctic-nesting geese (Lynch and Singleton 1964), to evaluate annual production among cranes. Results of a remote sensing (thermal imagery, near infrared, and white light photography) project to obtain population estimates of cranes along the Platte River in Nebraska during spring are also included.

Sandhill cranes have been hunted in one or more designated areas of the Central Flyway in the United States since 1 January 1961, when a 30-day season was permitted in eastern New Mexico and western Texas. Before that time hunting had not been permitted in the United States since 1916. In 1967 hunting was permitted in the Central Flyway portion of Colorado, exclusive of the San Luis Valley and, in the following year, in western Oklahoma, the eastern portion of the Texas panhandle, and prescribed areas of North and South Dakota. In 1972 hunting was permitted in prescribed areas of Montana and Wyoming. The birds have been legally hunted in Mexico at least since 1940, and in portions of Canada since 1959.

[1]Final report in compliance with Contract 14-16-0008-885.

Information about the 1961 seasons in New Mexico and Texas was reported by Boeker et al. (1961, 1962). Information developed during a 4-year cooperative study, 1962-65, which preceded hunting seasons in other parts of the Central Flyway was reported by Buller (1967). Information from the present study supplements that provided by these earlier investigations.

Study Area

The present study was conducted in those portions of Saskatchewan and the States of the Central Flyway that represent important fall and spring staging areas, and wintering areas for sandhill cranes. Specifically, these included the Last Mountain-Kutawagan-Quill Lakes complex of south-central Saskatchewan and the Outlook-Kyle, Kindersley district of west-central Saskatchewan; McLean, Pierce, Kidder, and Stutsman counties, North Dakota; the Pollock area, South Dakota; the Platte River Valley, Nebraska; southwestern Oklahoma; Bitter Lake and Grulla National Wildlife refuges, New Mexico; and the South and West Plains regions of Texas, including Muleshoe National Wildlife Refuge (Fig. 1).

The primary study areas were harvested grain fields, pastures, unharvested sorghum and cotton fields, and roost sites (lakes, sloughs, impoundments, and playas) from Saskatchewan to Texas.

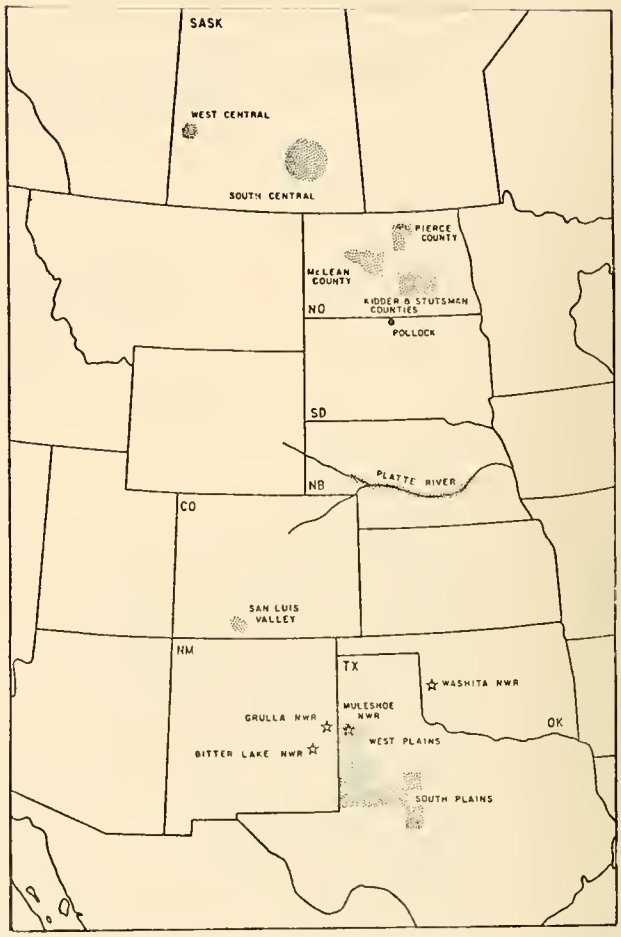

Fig. 1. Congregation sites, used by sandhill cranes during the fall, winter, and spring, that were portions of the study area.

Methods

Population Size

Visual estimates of the numbers of cranes occurring within the main fall staging areas and on the principal wintering grounds were made during periods of peak migration each October, and on the Platte River in Nebraska each spring. Most of the estimates were derived from counts by observers on the ground; however, aerial surveys were made in Nebraska, North Dakota, Saskatchewan, and South Dakota.

The Platte River in Nebraska is a traditional spring staging area for sandhill cranes enroute to their nesting ground. Moreover, all the lesser and Canadian sandhill cranes that winter in Texas, Oklahoma, New Mexico, and the Republic of Mexico appear to stop along the Platte River (Wheeler and Lewis 1973). The spring inventory, started in 1959, was originally designed to monitor population trends rather than provide a total population count. Modifications in the census techniques in 1974 were aimed at making the census a total population count; the survey was expanded to include major crane use areas in other cooperating States of the Central Flyway.

The spring survey is frequently delayed or interrupted by logistical problems, and must be accomplished within a very short time span. Also, the population in the Platte River Valley is concentrated in the smallest area when the cranes are roosting in the River at night. Consequently, the U.S. Fish and Wildlife Service entered into a contract with the U.S. Army to evaluate remote sensing equipment as a nighttime census technique. A prototype mission was flown at Bitter Lake National Wildlife Refuge, New Mexico, in January 1975. Three types of sensors were utilized: a classified thermal infrared (IR) line scanner, near IR photography, and white light flash photography. The same equipment was used in conjunction with the 1975 spring survey along the Platte River.

Age Determination

Juvenile sandhill cranes are distinguishable from adults by size, voice, head and body plumage, eye

color, and the color of the bill (Miller and Hatfield 1974; Lewis 1979*a*), but head plumage was the most commonly used characteristic for field determination of young birds during this study. Postjuvenile cranes have papillose skin on the crown, forehead, and loral regions which is sparsely covered with short, black, hair-like bristles and is usually red to red-orange. The forehead and crown of juvenile cranes are fully feathered and are light gray to brown (Fig. 2).

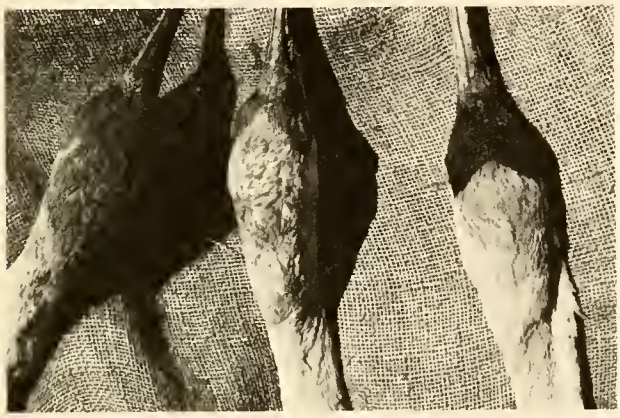

Fig. 2. The head of a postjuvenile sandhill crane is reddish papillose skin sparsely covered with short, black bristles (right); the juvenile's head is fully feathered and light gray or brown (left). The postjuvenile molt is under way on the specimen in the center. (Photo by Tom Smiley, U.S. Fish and Wildlife Service)

The head of a juvenile presents a rounded profile, whereas that of the adult appears flattened. A juvenile crane's head profile resembles the head profile of a redhead duck (*Aythya americana*); a postjuvenile's head profile resembles the head profile of a canvasback duck (*A. valisineria*). Moreover, the red area of the crown and forehead of the postjuvenile is distinguishable under most light conditions. Observers generally positioned themselves between the sun and flocks of cranes that were to be inspected for adult/juvenile ratios, and most counts were limited to morning hours before afternoon heat waves began to distort images. Neither heat waves nor position with respect to the sun were important on cloudy, overcast days.

Feeding, roosting, and flying sandhill cranes were aged during fall and winter with the aid of binoculars (7 x 34, 8 x 40) and 20x to 60x spotting scopes. Cranes feeding in fields or on their roost were aged from a vehicle or other form of concealment. Feeding and roosting cranes can usually be approached within 400 m or less in a vehicle, but will flush from an observer in the open at this or a greater distance. As a feeding flock is approached by a vehicle most of the birds will cease feeding, but after the vehicle is stopped they will usually move away, feeding as they go.

Cranes at rest on roost sites were also aged when possible, but were sometimes too densely congregated. The ideal roost situation for making age composition counts was encountered at midday and early afternoon when cranes were spaced along the shoreline.

Cranes in flight were aged as they moved between their roost and primary feeding area. Others were aged as they came to watering areas following the morning feeding period or alighted at a feeding area as singles, pairs, family groups, or small flocks.

In Saskatchewan, age composition data were irregularly recorded in 1974; however, in 1975 these data were recorded weekly at Last Mountain Lake and Quill Lakes. In 1976, age data were also recorded weekly at Last Mountain Lake and Kutawagan Lake. Elsewhere in Saskatchewan, age counts were irregularly recorded from mid-August through early November.

In the United States, age structure was irregularly recorded from early September through the 3rd week of January. Since Lewis (1974, 1979*a*) noted that adult/juvenile ratios collected in December and January probably underestimate the true percentage of juveniles in the population, only those birds aged through November were used to determine adult/juvenile ratios. Furthermore, R. Drewien (personal communication) advises that some color-marked greater sandhill cranes have acquired the unfeathered heads of postjuveniles as early as November. Therefore, adult/juvenile numbers tallied in December and January were eliminated from the estimates of annual recruitment. Limiting age counts to the August-November period reduced the total number (207,902) of sandhill cranes aged by 11,668 birds.

The family group technique, used for winter appraisals of productivity in arctic-nesting lesser snow geese (*Anser c. caerulescens*) and white-fronted geese (*A. albifrons frontalis*), was evaluated during the collection of age data in eastern New Mexico and west Texas in October 1974. Family group counts were obtained in those situations where birds were alighting near water or moving to feeding sites.

Hunting Pressure, Success, and Crippling Loss

Hunters were contacted in the field during 1974 to obtain information on their numbers, success, and numbers of birds knocked down but not retrieved. This method proved to be unsatisfactory and a special sandhill crane hunting permit system was initiated during the 1975-76 hunting season.

The permits were supplied to the States by the U.S. Fish and Wildlife Service and were issued free of charge to hunters upon request. Each permit holder

was mailed a questionnaire at the close of the hunting season. The questionnaire included inquiries about the number of days hunted, numbers of cranes harvested, numbers crippled, and counties hunted. One followup questionnaire was mailed to nonrespondents about 3 weeks after the first mailing. Nonrespondents to the followup were assumed to have the same average hunting activity and harvests as respondents, and reported harvests were expanded accordingly.

Estimates of the number of successful crane hunters, the mean seasonal bag per successful hunter, and the total crane bag were also derived from responses to the annual Federal Waterfowl Hunter Questionnaire Survey (Sorensen and Reeves 1976; Sorensen 1977, 1978).

Table 1. *Results of coordinated fall population surveys of sandhill cranes in the Central Flyway, 1974-76.*

Province or State	Numbers of cranes		
	1974	1975	1976
Alberta	—	800	—
Saskatchewan	32,600	58,000	45,952
Montana	—	3,000	—
North Dakota	11,120	10,000	33,075
South Dakota	7,515	12,000	20,000
Colorado	—	5,435	3,008
Kansas	—	—	5
Oklahoma	4,767	587	4,850
New Mexico	12,700	2,175	51,863
Texas	132,398	2,889	60,954
Total	201,100	94,886	219,707

Results and Discussion

Fall Populations

Population surveys were conducted at all important congregation sites 30 October-1 November 1974, 20-24 October 1975, and 27-29 October 1976. These dates generally coincided with the peak of the fall migration but each survey was hampered by weather or logistical problems. Inclement weather caused a delay in the 1974 survey in Saskatchewan and North Dakota until 5-7 November, and logistical problems caused a delay in the 1975 survey in these areas until 6 November. Each year, large numbers of sandhills were noted in migration in Saskatchewan, Montana, Wyoming, Colorado, and Nebraska, and it is not known if these birds were tallied in New Mexico and Texas before the survey was concluded.

During the 1974, 1975, and 1976 fall population surveys, observers tallied 201,100, 94,886, and 219,707 sandhill cranes, respectively (Table 1). These represent minimum estimates of the fall population because (1) it is doubtful that those birds in migration during the survey period were recorded (as previously noted counts were made during periods of peak migration); (2) generally only the main congregation areas were surveyed, e.g., the Platte River (Nebraska) was not included in the fall surveys, and smaller groups could have been overlooked; (3) many counts were made during the feeding period and feeding flocks are frequently overlooked; and (4) an unknown number arrived on wintering grounds in the Republic of Mexico before the surveys were conducted.

Attempts to enumerate the fall population of sandhill cranes in the Central Flyway were only partially successful. Moreover, it is likely that efforts to survey sandhill cranes for total population purposes during the fall never will prove satisfactory. It is difficult to preselect a survey period that will coincide with ideal weather conditions and a time when most of the cranes are available to be counted. Furthermore, it is difficult to assemble the same survey effort from year to year.

Two of the three coordinated fall population surveys resulted in population estimates of about 201,000 and 220,000. The 1975 survey was 7 to 10 days earlier than the 1974 and 1976 surveys, and more than twice as many cranes were counted in the latter 2 years. Several factors may have caused the low count in 1975. The survey period may have been too early, weather conditions may not have prompted the major migration, or the bulk of the population may have been in migration, and as a consequence, not included in the tally.

The low numbers of sandhill cranes tallied in New Mexico and Texas during the 1975 fall survey are further evidence that the census was too early. Prehunting-season population surveys have been conducted in these two States since 1960 (exclusive of 1973) and these surveys have yielded population estimates ranging from about 135,000 to 339,000 birds (Table 2). Thus, the 1975 fall population estimate was less than any of the previous preseason populations in New Mexico and Texas.

The magnitude of that segment of the sandhill crane population which winters in the Republic of Mexico is also unknown. A field officer of the New Mexico Department of Game and Fish reported that while on patrol in the Guadalupe Mountains southwest of Roswell in the latter part of October 1975, he daily observed large flocks of sandhills moving in a southerly direction. These birds were not recorded at Bitter Lake National Wildlife Refuge, nor were they tallied in the Dell City area, Trans Pecos region, Texas. Thus, it is likely these flocks were enroute to wintering grounds in Mexico.

The sighting of these migrating flocks over the Guadalupe Mountains might indicate that the 1975 fall population survey was too late; however, the low

Table 2. *Results of preseason population surveys of lesser and Canadian sandhill cranes in eastern New Mexico and west Texas, 1960-72 and 1974-76.*

Date	No. of cranes	Date	No. of cranes
14-15 December 1960	134,673	30 October 1968	339,185
3 November 1961	147,416	31 October 1969	258,500
2 November 1962	180,901	30 October 1970	210,200[a]
25 November 1963	207,405	29 October 1971	147,416[a]
3-6 November 1964	213,896	27 October 1972	184,901[a]
29 October 1965	198,027	25 October 1974	136,340
28 October 1966	139,199	22-23 October 1975	4,710
3 November 1967	210,074	27-29 October 1976	110,964

[a]Incomplete survey.

Table 3. *Results of spring sandhill crane population surveys in Nebraska, 1959-73, and expanded spring surveys in 1974-78.*

Date	No. of cranes	Date	No. of cranes
20 March 1959	147,496	2 April 1969	154,978
4 April 1960	125,870	26 March 1970	193,600
21 March 1961	136,276	28-29 March 1971	207,500
21 March 1962	142,830	27-28 March 1972	183,600
21 March 1963	101,925	26-29 March 1973	195,350
30 March 1964	156,028	25-31 March 1974	177,015[a]
30 March 1965	80,315	25-30 March 1975	227,527
25 March 1966	123,087	25-26 March 1976	153,784
23 March 1967	123,043	17-19 March 1977	219,154
22 March 1968	169,194	22-24 March 1978	159,898

[a]In addition to the Platte River Valley, surveys were made simultaneously at major crane use areas in other States beginning in 1974. These cooperating States were: 1974, the Dakotas, Kansas, Oklahoma, and Texas; 1975, as 1974 plus Colorado, Montana, New Mexico, and Wyoming; 1976, Kansas, Oklahoma, and Texas; 1977, Oklahoma, Texas, South Dakota, and partial surveys in Kansas, Nebraska, and New Mexico; 1978, Kansas, New Mexico, South Dakota, Texas, and incomplete participation data received from Colorado, Nebraska, and Oklahoma.

count (4,710) recorded in eastern New Mexico and west Texas probably resulted from a count that was made too early rather than too late.

Spring Inventory

The spring population surveys of sandhill cranes associated with the Platte River in Nebraska, which have been conducted since 1959, were expanded to include other States in 1974. The expanded surveys were continued during the current study; however, the coverage has been highly variable (Table 3). Since the spring survey was expanded in 1974, 79-99% of the cranes tallied (171,570; 225,945; 150,119; 174,575; and 152,021 in 1974, 1975, 1976, 1977, and 1978, respectively) have been in the Platte River Valley.

The 1975 survey was scheduled for 23 March; however, spring snowstorms delayed the count along the Platte River until 29 and 30 March. The 1976 survey was conducted on 22-26 March, the 1977 survey was made on 17-19 March, and the 1978 survey on 22-24 March.

During this study, observers recorded 227,527, 153,784, and 219,954 sandhill cranes during the spring survey. On the Platte River the 225,945 birds recorded in 1975 were the highest population tallied since the spring surveys were initiated. Observers recorded 159,898 sandhill cranes during the 22-24 March 1978 survey.

During the prototype mission in New Mexico to test nighttime census techniques, cranes were separable as individuals under both test pen and natural conditions by all three sensor techniques. However, the semioperational mission was delayed by equipment malfunctions, a series of blizzards accompanied by low temperatures, and slush ice in the River (Munro and Lewis 1976), and only two flights were possible in the study period 23 March to 3 April 1975.

The first was flown on the evening of 31 March under marginal flying conditions and examination of the processed films revealed three problems. The film magazine of the thermal IR scanner had frozen, the entire width of the river channel was not being photographed in a single pass because the plane was too low, and cranes were flushing as the aircraft flew over. The flushing behavior of roosting cranes was unanticipated. During the test mission at Bitter Lake National Wildlife Refuge, one roost was overflown 10 times in 2 hours without any significant movement by the cranes. On the Platte River, cranes flushed from the roost as the plane passed over, even when the white light photography, with its associated light flash, was not used.

The scanner magazine was replaced on the 2 April flight and the altitude was increased to permit coverage of the entire width of the river channel. The increased altitude proved to be critical. Certain features of the scanner were influenced by the increased coverage of snow and ice, causing a loss in contrast. The efficiency of both the near IR and white light photography was affected by less intense light flash at the target surface which caused a loss of contrast. All images acquired on the 2 April flight were uniformly unsuitable.

All sensors provided acceptable results under test conditions but the semioperational mission was not successful. Munro and Lewis (1976) concluded that prospects for nighttime remote sensing of sandhill cranes on the Platte River are not good for the follow-

ing reasons: (1) restricted availability of equipment, (2) associated high costs, (3) limited width of coverage, (4) likelihood of bad weather during the survey period, and (5) the aircraft frightening the cranes from a surveyed strip to a parallel unsurveyed strip with the consequence that some birds might be counted twice.

Failure of the nighttime remote sensing technique to yield an estimate of the total spring sandhill crane population on the Platte River in 1975 prompted Lewis (1979*b*) and two assistants to make ground counts of those cranes that departed from specific roosts during the 1976 survey before the aircraft passed over. These ground counts were then used to correct the results of the aerial count and provide an estimate of the total population of sandhill cranes on the Platte River.

Based on ground counts, which indicated that 3.1 to 99.0% of the cranes had left various sections of the River before the aerial crew arrived, Lewis (1979*b*) considered the minimum population on the Platte to have been 300,000 and said the total population may be close to 400,000.

Attempts to replicate this procedure in 1977 were unsuccessful. The ground counts were made but a series of storms, a dead aircraft battery, and finally a mass exodus of the cranes prevented the late March combined aerial-ground inventory (Lewis 1979*b*).

Although the annual spring inventory was found to be inadequate, e.g., failure to (1) count when the population peaks in Nebraska, (2) count all cranes in the Platte River Valley, and (3) count all cranes north and south of Nebraska (Lewis 1979*b*), it holds greater potential for enumerating the total population of lesser and Canadian sandhill cranes than does the fall population survey.

Age Composition

The proportion of juvenile sandhill cranes recorded during the study (Table 4) represents the combined counts of cranes at feeding fields, on their roosts, or flying between roosts and fields.

The first migrants to reach south-central Saskatchewan in August generally are accompanied by fewer young than those arriving in September and October. For example, August arrivals included 2.9% young in 1975 whereas juveniles made up 11.5% of the migrants in September and 13.2% in October.

During the 3-year study, juveniles constituted 13.9, 10.3, and 12.1%, respectively, of the cranes in south-central Saskatchewan. In west-central Saskatchewan, young made up 10.7 to 11.4% of the population. Collectively, juveniles averaged 11.4% in Saskatchewan. In the Last Mountain-Kutawagan-Quill Lakes region, juveniles were almost 3 times as common (11.7 versus 4.3%) as recorded by Miller and Hatfield (1974) in 1966, 1967, 1972, and 1973.

There is an inherent unknown degree of error associated with estimating annual recruitment from age structure. The frequency with which the same flocks are sampled is unknown because the rate at which birds are replaced by new arrivals is unknown. Moreover, each flock may not be adequately sampled as it utilizes staging or wintering areas, nor is it possible to weight the age structure data because estimates of the numbers of cranes were not made when adult/juvenile counts were made.

The age data indicate that collectively lesser and Canadian sandhill cranes experienced better production during 1974-76 than that recorded by Miller and Hatfield (1974) in 1966, 1967, 1972, and 1973. Why was the average annual recruitment rate during the present study nearly 3 times that reported by Miller and Hatfield? One possibility is that production was exceptionally good during 1974-76 whereas 1966, 1967, 1972, and 1973 were poor years. Sandhill cranes nest over a broad area including Siberia, Alaska, arctic Canada, and Baffin Island, as well as the subarctic where weather is a less important limiting factor. Broods are small, breeding is delayed until age 3 or older, and the subadult population component is large. Therefore, it seems unlikely that the age ratio in the population changes much from year to year.

Miller and Hatfield (1974) noted their data were based on samples from about 10% of the cranes that migrate through the Central Flyway. They suggested that early migrants are mostly nonbreeders and that early age ratios are therefore unreliable. For example, the weekly proportion of juveniles ranged from 0.1 to 3.2% from 13 August to 16 September 1972, and 4.2 to 6.5% from 26 August to 8 September 1973. Analysis of age data of the present study by weeks (1975 and 1976) also indicates that the proportion of young increases as the fall migration progresses (Fig. 3). The 1974 age composition data were irregularly recorded by 10-day periods; thus, these data cannot be analyzed by weekly periods.

Miller and Hatfield (1974) limited their observations to the east-central portion of Saskatchewan, whereas observations during the present study were much more extensive. Furthermore, they counted only flying flocks in 1972 and 1973 because they considered these gave the least biased estimate of age structure. In 1975, weekly age tallies recorded during the present study at Last Mountain Lake ranged from 0.8 to 14.2% young between 17 August and 27 September, and averaged 9.2%. In 1976, weekly age compositions collected in the Last Mountain-Kutawagan-Quill Lakes region ranged from 6.8 to 13.1% young between 22 August and 25 September, and averaged 12.1%.

Possibly the low percentages of young recorded by Miller and Hatfield (1974) are related, in part, to their decision to use age data collected only from flying

Table 4. *Percentage of young sandhill cranes in the Central Flyway, 1974-76.* (Sample size in parentheses.)

Area	August			September			October			November			Total			3-year average
	1974	1975	1976	1974	1975	1976	1974	1975	1976	1974	1975	1976	1974	1975	1976	
Saskatchewan																
Eastern	9.2	2.9	12.0	14.1	11.5	11.9	14.6	13.2	12.2				13.9	10.3	12.1	11.7
	(54)	(3,017)	(1,665)	(895)	(5,759)	(26,177)	(157)	(5,474)	(25,838)				(1,106)	(14,250)	(53,680)	
Western	5.9	20.3	9.9	11.5	7.4	10.5	10.7	13.3	12.2		11.2	10.7	10.7	10.7	11.4	11.1
	(356)	(350)	(956)	(2,792)	(4,244)	(11,846)	(9,506)	(3,954)	(17,938)		(1,288)	(3,774)	(12,654)	(9,836)	(34,514)	
Total	6.3	4.7	11.2	12.1	9.8	11.5	10.7	13.2	12.2		11.2	10.7	11.0	10.5	11.8	11.4
	(410)	(3,367)	(2,621)	(3,687)	(10,003)	(38,023)	(9,663)	(9,428)	(43,776)		(1,288)	(3,774)	(13,760)	(24,086)	(88,194)	
North Dakota																
McLean Co.				7.0	10.9	12.1		15.5	10.4				7.0	11.8	11.8	10.9
				(2,892)	(3,229)	(5,580)		(850)	(1,343)				(2,892)	(4,079)	(6,923)	
Pierce Co.				13.6	13.5	13.9							13.6	13.5	13.9	13.8
				(103)	(325)	(677)							(103)	(325)	(677)	
Kidder Co.				17.7	12.9	17.7	15.5			18.8			17.2	12.9	17.7	15.9
				(203)	(1,331)	(2,695)	(573)			(570)			(1,346)	(1,331)	(2,695)	
Total				7.9	11.6	13.5	15.5	15.5	10.4	18.8			10.4	12.2	13.5	12.5
				(3,198)	(4,885)	(8,952)	(573)	(850)	(1,343)	(570)			(4,341)	(5,735)	(10,295)	
South Dakota																
Pollock					15.7		14.3	18.8	23.0	14.2	16.8		14.3	17.9	23.0	17.8
					(989)		(927)	(2,859)	(1,313)	(1,190)	(113)		(2,117)	(3,961)	(1,313)	
Montana																
Bowdoin NWR								7.4						7.4		
								(3,000)						(3,000)		
Colorado																
Two Buttes							22.6						22.6			
Reservoir							(208)						(208)			
Oklahoma																
Washita NWR							17.4	28.8		26.7	18.8	10.6	22.5	24.2	10.6	16.4
							(258)	(205)		(319)	(175)	(1,112)	(577)	(380)	(1,112)	
New Mexico																
Bitter Lake							7.2	7.5	10.0	6.6	13.6	11.8	7.2	7.7	10.9	8.8
NWR							(3,476)	(3,391)	(2,226)	(76)	(110)	(2,365)	(3,552)	(3,501)	(4,591)	
Grulla NWR							10.0	13.9					10.0	13.9		11.4
							(3,417)	(1,892)					(3,417)	(1,892)		
Columbus											12.4			12.4		
											(608)			(608)		
Total							8.6	9.8	10.0	6.6	12.7	11.8	8.6	10.7	10.9	9.9
							(6,893)	(5,283)	(2,226)	(76)	(718)	(2,365)	(6,969)	(6,001)	(4,591)	
Texas																
West Plains							8.0		12.8	4.9	10.7		7.2	10.7	12.8	9.3
							(3,408)		(2,431)	(1,404)	(1,270)		(4,812)	(1,270)	(2,431)	
South Plains							8.6		10.5		11.3		8.6	11.3	10.6	10.6
							(1,553)		(3,059)		(4,205)		(1,553)	(4,205)	(3,059)	
Lower Coast							18.3	15.1		24.3	12.6	12.6	22.3	14.2	12.6	19.6
							(525)	(284)		(1,028)	(182)	(245)	(1,553)	(466)	(245)	
Total							9.2	15.1	11.5	13.1	11.2	12.6	10.4	11.4	11.6	11.1
							(5,486)	(284)	(5,490)	(2,432)	(5,657)	(245)	(7,918)	(5,941)	(5,735)	
United States																
Total				7.9	12.3	13.9	9.9	12.1	12.0	14.9	12.0	11.5	10.6	12.0	12.9	11.9
				(3,198)	(5,874)	(8,952)	(14,345)	(12,481)	(10,372)	(4,587)	(6,663)	(3,722)	(22,130)	(25,018)	(23,046)	
Grand Total	6.3	4.7	11.2	10.1	10.7	11.9	10.2	12.6	12.3	14.9	11.6	11.1	10.7	11.3	12.0	11.6
	(410)	(3,367)	(2,621)	(6,885)	(15,877)	(46,975)	(24,008)	(21,909)	(54,148)	(4,587)	(7,951)	(7,496)	(35,890)	(49,104)	(111,240)	

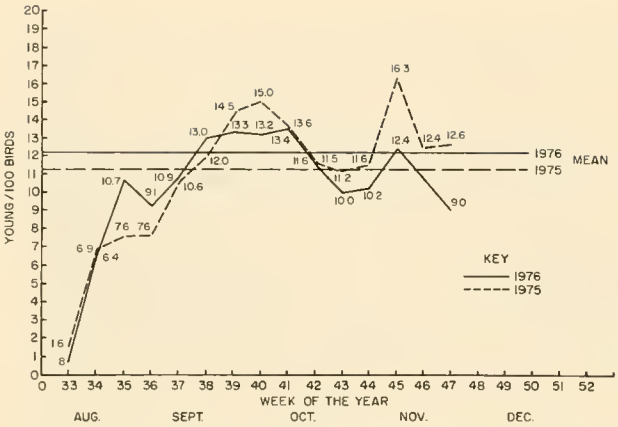

Fig. 3. Average weekly sandhill crane age ratios in the Central Flyway, 1975 and 1976.

flocks in 1972 and 1973. During the present study, I aged flying birds at every opportunity. It was essential that I position myself at right angles to the flight path, but not directly under it. Juvenile birds are sometimes difficult to distinguish when viewed from directly below, especially in flocks of 15-20 birds, and when the flocks are passing the observation point in rapid succession.

There also is some evidence that the sandhill cranes which stage in the Last Mountain-Kutawagan-Quill Lakes region may be from a different section of the breeding range than those that stage in west-central Saskatchewan (Gollop 1976). Furthermore, Miller and Hatfield (1974) sampled during August and September only, whereas I sampled from the time the first migrants arrived, through the fall, and into the winter months.

During the present study the proportion of juveniles averaged 11.6% (Table 4). Age composition varied greatly within the same population segment during the present study. For example, the proportion of young among the cranes that remained during the day on Bitter Lake and Muleshoe National Wildlife refuges was always less than the incidence of young among the birds that departed the refuges to feed. Thus, combining all counts rather than utilizing only those counts of feeding flocks, flying flocks, or cranes on roost sites provides a more realistic estimate of the annual recruitment among lesser and Canadian sandhill cranes in the Central Flyway. Moreover, the proportion of young was consistently greater at some staging areas; e.g., Kidder County, North Dakota; Pollock area, South Dakota; Washita National Wildlife Refuge, Oklahoma; Aransas and Laguna Atascosa National Wildlife refuges, Texas; and Grulla National Wildlife Refuge versus Bitter Lake National Wildlife Refuge, New Mexico.

Age counts can also be used to derive separate estimates of production in the Canadian and lesser subspecies. Cranes collected in Kidder and Pierce counties, North Dakota, during the 1962-65 study (Buller 1967) and by Johnson and Stewart (1973) in 1970 and 1971 primarily represent the Canadian race. The Canadian race is also prevalent among sandhill cranes wintering along the Texas Coast (Guthery 1972; Lewis 1974; Guthery and Lewis 1979). Sandhill cranes collected in McLean County, North Dakota, and the Pollock, South Dakota, area were predominately lessers (Buller 1967; Johnson and Stewart 1973). If the same pattern of distribution persisted during the present study, then annual recruitment averaged 16.4% in the Canadian race and 14.3% in the lesser race.

A detailed examination of nearly 2,000 cranes in 756 small groups (1 to 4 birds), using the family group technique, indicated 222 families averaging 1.16 young per family (Andrews 1975). Although family group counts can be obtained simultaneously with sandhill crane age composition data, the technique has somewhat less utility than when applied to goose populations because most families contain only one young, and subadults cannot be distinguished from adults.

Although Miller (1973) indicated that successful breeders rarely raise more than one young, noting in 623 family groups only one instance of a family with two young, the present study indicated that 16.9% of the successful breeders were accompanied by "twin" young in 1974. In 1975, twin families were recorded at the rate of 23.5% at Lake Williams, McLean County, North Dakota. At Last Mountain Lake, Saskatchewan, 25% of the successful breeders had two young. In 1976, 17% of 703 successful pairs were tallied with twin young at Last Mountain Lake through 30 September; in the United States, 24.8% of the successful pairs were accompanied by twin young. Thus, an average of 20.0% of the successful pairs were accompanied by twin young during the present study.

Hunting Pressure, Success, and Crippling Loss

Sandhill crane hunters were contacted during the 1974 hunting season to obtain an estimate of their numbers and success. This proved to be an unsatisfactory method of obtaining hunter numbers because the survey effort could not be proportional to the hunting effort throughout the season, sample sizes were small, and the only information collected in Texas came from a "day-shoot" facility adjacent to Muleshoe National Wildlife Refuge. Although this method of deriving hunter numbers was unsuccessful, some data on success, vulnerability of juveniles, and crippling loss were obtained (Table 5).

Table 5. *Incomplete sandhill crane hunting statistics, Central Flyway, 1974.*

State	No. hunters contacted	No. birds bagged		No. birds unretrieved	
		Adult	Juvenile	Knocked down	Hit
Colorado	12	3	2	1	1
Montana	18	37[a]			
New Mexico	95	27	8	0	10
North Dakota	12	6	6	5	6
South Dakota	21	5	1	0	2
Texas	293	347	163		
Wyoming	5	5	1	0	0
Totals	456	393	37[a] 181	6	19

[a]Age composition unavailable.

The limited sandhill crane hunting statistics obtained during the 1974 season indicate that hunters averaged 1.3 birds each, bagged 2.2 more adults than juveniles, and reported a crippling loss of about 1%.

The mail survey of the holders of sandhill crane hunting permits indicated that the total bag ranged from approximately 7,400 to 12,150 during the study (Table 6). Adding to the bag the estimated crippling loss indicated the total kill ranged from about 8,800 to 14,200 cranes. The estimated average crippling loss during the three hunting seasons was 15% of the total kill (18% of the bag). Fifty nine, 45, and 58% of the permit holders indicated that they hunted at least once in 1975-76, 1976-77, and 1977-78, respectively. Only 40, 34, and 43% of those who hunted bagged one or more cranes. Total days of hunting varied from about 18,800 to 25,400 in the three hunting seasons (Table 6).

The 1975-76 waterfowl hunter survey provided a 25% larger estimate of the harvest than did the survey of sandhill crane hunters. The 1976-77 and 1977-78 waterfowl hunter surveys gave estimates of the harvest that were 13% and 38% larger. The waterfowl hunter surveys also overestimated the number of successful hunters; e.g., 8.6, 62.9, and 78.3% more than surveys of sandhill crane hunters following the 1975, 1976, and 1977 hunting seasons, respectively.

Estimates based on the special sandhill crane hunting permit system during the 1975, 1976, and 1977 seasons in the Central Flyway, the Saskatchewan Department of Tourism and Renewable Resources mail surveys in 1964-75, and responses to the waterfowl hunter survey in Alaska, indicate a minimum average annual sandhill crane harvest of about 13,000 birds. Adding the harvest in Mexico, and by Indians and Eskimos in Canada and Alaska, the annual harvest, including crippling losses, may now be close to 18,000 cranes annually (see Johnson 1979).

Table 6. *Sandhill crane hunting statistics, Central Flyway, 1975-76, 1976-77, and 1977-78. (Sorensen, personal communication; Sorensen and Reeves 1976; Sorensen 1977).*

Hunting statistics	Year		
	1975-76	1976-77	1977-78
Number of permits issued	11,863	11,352	13,800
Number of mail questionnaire respondents	9,320	8,909	10,267
Response rate	78.56	78.4	74.3
Number of active hunters[a]			
Respondents	5,476	3,978	6,018
Expanded	6,949	5,092	8,048
Active hunter means			
Days hunted	3.4	3.7	3.2
Crane bag	1.4	1.45	1.5
Crane loss	0.27	0.27	0.25
Expanded estimates			
Hunter days	23,646	18,780	25,412
Crane bag	9,497	7,393	12,151
Crane loss	1,885	1,384	2,013
Crane kill	11,382	8,778	14,167

[a]Hunted at least once.

Management Recommendations

The flyway-wide fall population survey should be discontinued because it is practically impossible to consistently select a time period that will coincide with the peak of migration and avoid logistical problems. However, the U.S. Fish and Wildlife Service and the conservation agencies of New Mexico and Texas should consider continuing the preseason population survey which was initiated in 1960.

The expanded spring sandhill crane population survey should be continued annually by the Office of Migratory Bird Management, U.S. Fish and Wildlife Service. Efforts such as those initiated in the springs of 1976 and 1977 by Lewis (1979*b*) to obtain data to correct aerial estimates of sandhill cranes on the Platte River in Nebraska should be continued. The spring population survey holds the greatest potential for assessing the size of the total lesser and Canadian sandhill crane population as it stages on the Platte River enroute to the breeding grounds.

There is little justification to collect adult/juvenile ratios annually because an adequate sample was collected during the present study. However, age data should be collected every 3-5 years for comparative purposes and to evaluate the premise that the average annual recruitment rate in the lesser and Canadian sandhill crane population is about 13%.

The special sandhill crane hunting permit system was adopted for 3 years (1975-77), and the U.S. Fish and Wildlife Service and the Central Flyway Water-

fowl Council have agreed to continue the permit system for the 1978-79 season. These hunting permits should be required until biologists are confident that the annual waterfowl hunter survey is adequate to develop estimates of the number of successful crane hunters, the mean seasonal bag per succesful hunter, and the number of cranes bagged.

Acknowledgments

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MODELING SANDHILL CRANE POPULATION DYNAMICS

Modeling Sandhill Crane Population Dynamics

by

Douglas H. Johnson

U.S. Fish and Wildlife Service
Northern Prairie Wildlife Research Center
Jamestown, North Dakota 58401

Abstract

The impact of sport hunting on the Central Flyway population of sandhill cranes (*Grus canadensis*) has been a subject of controversy for several years. A recent study (Buller 1979) presented new and important information on sandhill crane population dynamics. The present report is intended to incorporate that and other information into a mathematical model for the purpose of assessing the long-range impact of hunting on the population of sandhill cranes.

The model is a simple deterministic system that embodies density-dependent rates of survival and recruitment. The model employs four kinds of data: (1) spring population size of sandhill cranes, estimated from aerial surveys to be between 250,000 and 400,000 birds; (2) age composition in fall, estimated for 1974-76 to be 11.3% young; (3) annual harvest of cranes, estimated from a variety of sources to be about 5 to 7% of the spring population; and (4) age composition of harvested cranes, which was difficult to estimate but suggests that immatures were 2 to 4 times as vulnerable to hunting as adults.

Because the true nature of sandhill crane population dynamics remains so poorly understood, it was necessary to try numerous (768 in all) combinations of survival and recruitment functions, and focus on the relatively few (37) that yielded population sizes and age structures comparable to those extant in the real population. Hunting was then applied to those simulated populations. In all combinations, hunting resulted in a lower asymptotic crane population, the decline ranging from 5 to 54%. The median decline was 22%, which suggests that a hunted sandhill crane population might be about three-fourths as large as it would be if left unhunted. Results apply to the aggregate of the three subspecies in the Central Flyway; individual subspecies or populations could be affected to a greater or lesser degree.

This report contains an analysis of data from Buller's (1979) study of sandhill cranes (*Grus canadensis*) in the Central Flyway and from other recent work on the species. The report describes a mathematical model of sandhill crane populations, summarizes recent data that serve as input to the model, and presents the results of computer simulations of the model. The discussion section treats shortcomings of the model and data, and briefly recommends further research, operational data-gathering, and management strategies.

The utility of a mathematical model as a predictive tool depends on the validity of the assumptions incorporated in the model and the accuracy of the data that the model uses. Little is known about many key features of sandhill crane population dynamics. As a result, the model described herein, and any other that could be created now, will be unable to predict crane populations with any but fortuitous accuracy. With that thought in mind, I present a model that can be simulated with many different sets of parameter values, reflecting a variety of plausible assumptions about the real crane population. The resulting scenarios can be viewed as potential behaviors to be expected of the crane population under a variety of circumstances. No single result is offered as the "best" representation of the true population.

The Model

The model reported is a simple one, incorporating age-dependent and density-dependent rates of survival and recruitment. I assumed the existence of 25 age classes, with N(1), N(2), . . ., N(25) representing the number of cranes in each class (e.g., there are N(1) cranes less than 1 year old). Cranes are assumed to initiate breeding as 4-year-olds (age class 5) and to die after their 25th year. The simulated population is otherwise homogeneous; no differences in survival or recruitment are associated with subspecies, area of breeding, or other features. Figure 1 displays the logical flow of the model.

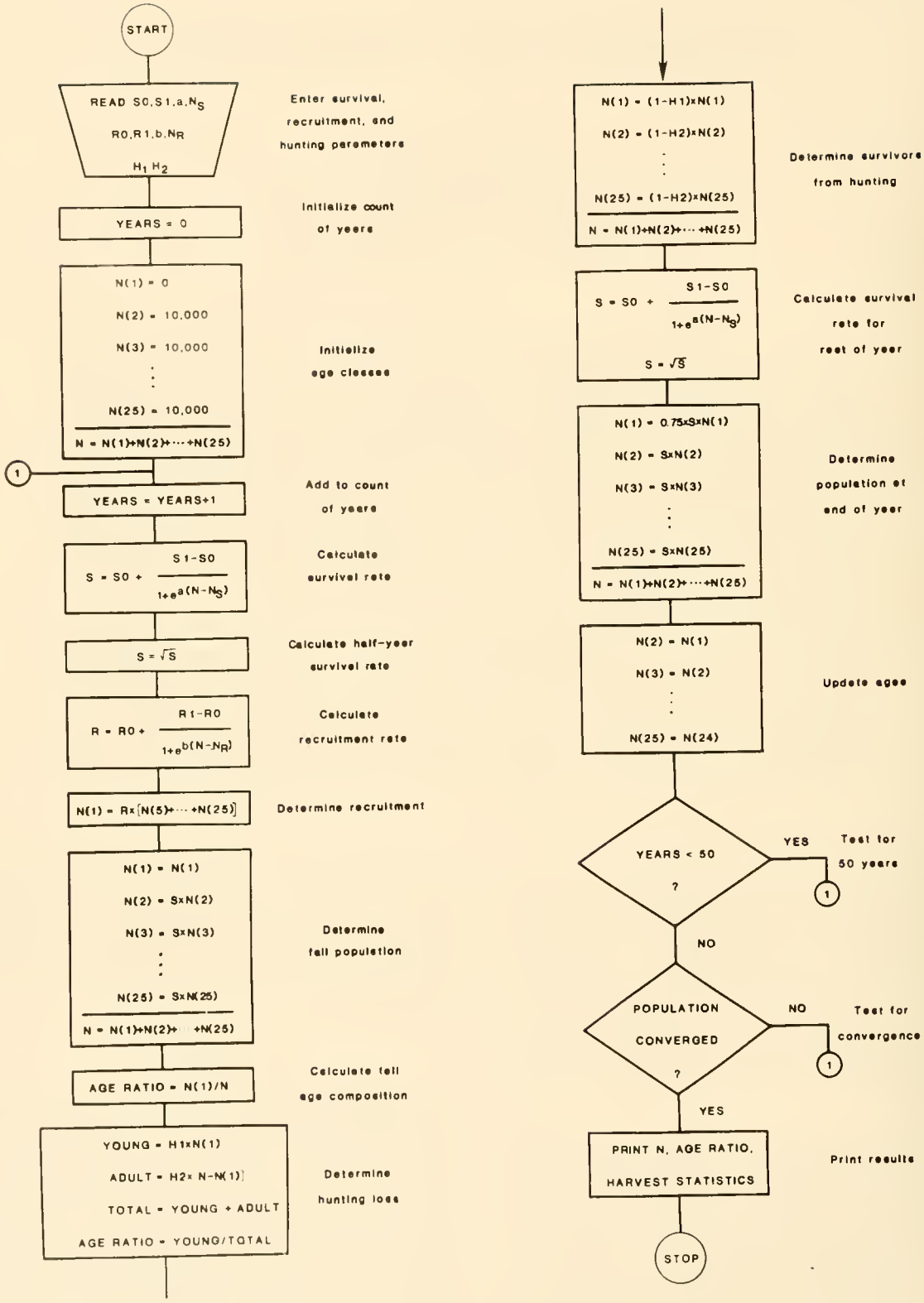

Fig. 1. Flow chart of sandhill crane population dynamics model.

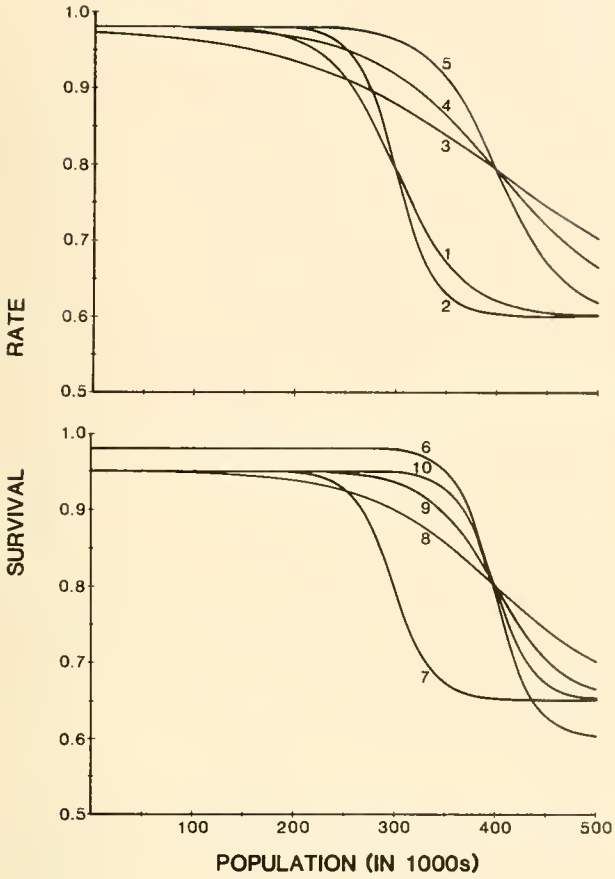

Fig. 2. Survival curves (1-10) corresponding to various combinations of parameters in Equation 1 of the text.

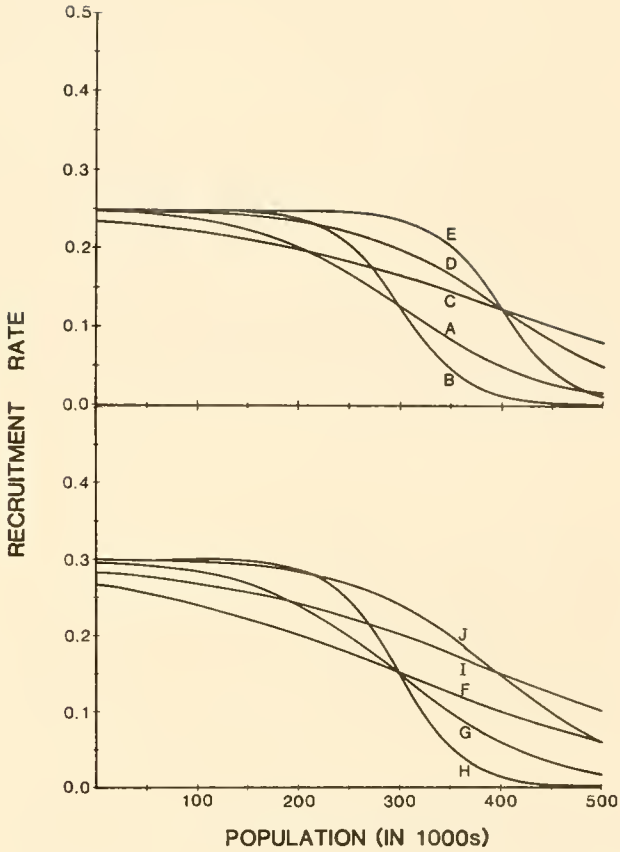

Fig. 3. Recruitment curves (A-J) corresponding to various combinations of parameters in Equation 2 of the text.

Survival rates of adults (birds more than 1 year old) are assumed to be density-dependent, following a reverse logistic function (Fig. 2)

$$S = S0 + \frac{S1 - S0}{1 + e^{a(N - N_S)}} \qquad (1)$$

N is the total number of cranes in the population. S0, S1, N_S, and a are parameters of the logistic function. At very low density ($N \rightarrow 0$) the survival rate approaches the upper asymptote

$$S = S0 + \frac{S1 - S0}{1 + e^{-aN_S}}$$

$$= S1, \text{ approximately.}$$

As the population becomes large ($N \rightarrow \infty$) the survival rate declines, most rapidly at $N = N_S$, and ultimately approaches a lower limit of S0. The exponential parameter a governs the rate of decline. Survival rates are calculated separately for the half-year beginning with the spring breeding season and ending in fall, and the half-year from fall (after hunting) to the beginning of the next breeding season. Each half-year survival rate is the square root of the value obtained from Equation 1. Survival rates for spring and summer are calculated at the beginning of the breeding season, and depend on the spring population size. Survival rates for the fall and winter period are calculated after the hunting season, and depend on the number of cranes that survive to that point. The survival rate of young birds is taken to be 75% of the adult rate for the half-year from fall to spring.

Recruitment rates are also density-dependent, highest at low population densities and declining (to zero) as the population becomes extremely large (Fig. 3). Recruitment functions follow the equation

$$R = R0 + \frac{R1 - R0}{1 + e^{b(N - N_R)}}, \qquad (2)$$

where R0 (= 0) and R1 are the extremes, N_R the inflection point, and b the rate parameter. The calculated recruitment rate is applied to all birds in the spring population 4 years of age or older, and it results in birds added to the fall population.

To start each simulation, every age class at least 1 year old in the simulated population was initially set at 10,000 birds. The annual cycle was repeated 50 times, or more if the population had not converged by then.

The model is deterministic, as opposed to stochastic. It will thus exhibit far less variation than does a natural population. In a sense, it will yield conservative results; for example, a simulated population with random components might become extinct while its deterministic counterpart exhibits steady, or even increasing, numbers.

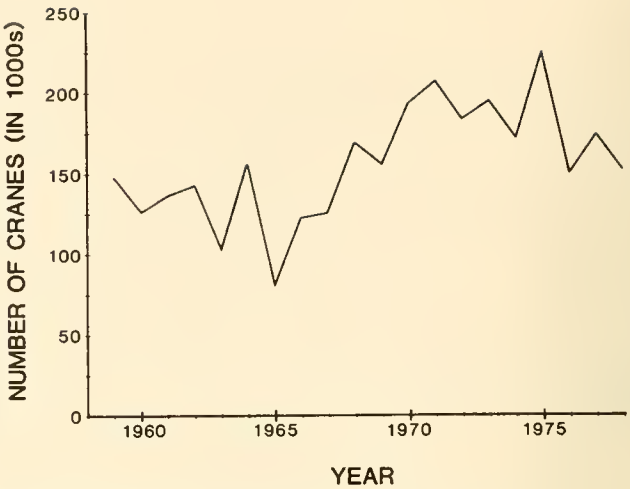

Fig. 4. Results of spring sandhill crane population surveys in Nebraska, 1959-78.

The Data

Four quantities pertinent to the population dynamics of sandhill cranes were used in the model: (1) the size of the spring population, (2) the age composition of the population during the hunting season, (3) the number of cranes killed during the hunting season, and (4) the age composition of cranes in the harvest.

Spring Population Size

Sandhill cranes have been counted each spring since 1959 in an aerial survey conducted along the Platte River in Nebraska (Buller 1979). The survey was originally devised to monitor population trends. Counts have ranged from 80,315 to 225,945 birds, those in recent years averaging larger than in the earlier years of the survey (Fig. 4). It is not known whether the apparent increase is real or a reflection of improved survey skills. Aerial surveys include only cranes remaining on the river roosts at the time the aircraft flies over. Because most cranes leave their roost within 30 min after sunrise (Lewis 1976), these counts are biased low. Lewis (1979) determined the proportion of cranes that had left the roost before passage of the aircraft by ground checks. Using this information Lewis (1979) considered 300,000 cranes to be a minimum population estimate and believed that the number in the Central Flyway was close to 400,000 in 1976.

It would seem that the current population of Central Flyway sandhill cranes contains between 250,000 and possibly 400,000 birds. This population is a mixture of three subspecies (Johnson and Stewart 1973): the greater sandhill crane (*Grus canadensis tabida*), the Canadian sandhill crane (*G. c. rowani*), and the lesser sandhill crane (*G. c. canadensis*). The composition of the population according to subspecies is unknown, although most are lessers. Braun (1975) provided estimates of 230,000-260,000 lessers in the Central Flyway and 15,000-20,000 Canadians. Aldrich (1979) indicated that the population size of Canadians is poorly known, but could number more than 60,000 birds. Greaters probably make up a smaller proportion of the total than does either of the other two subspecies.

Fall Age Composition

The age composition of sandhill crane populations was assessed annually during 1974-76 by Buller (1979), who conducted ground counts of flocks throughout the Central Flyway. Buller found the following percentages of immatures in the fall populations: 10.7 of 36,000 cranes aged in 1974, 11.3 of 49,000 birds in 1975, and 12.0 of 111,000 in 1976. The unweighted average for the 3 years was 11.3%.

Losses to Hunting

Harvest data were not systematically collected in the United States until the 1975-76 hunting season, when crane hunters in the Central Flyway were required to obtain (at no cost) a permit, and questionnaires were sent to applicants after the season terminated. Projections from the questionnaire response indicated that, in 1975-76, 9,497 cranes were harvested, and an additional 1,885 downed but lost, for a total kill of 11,382 (Sorensen and Reeves 1976). The corresponding figures for the 1976-77 season were 7,393 cranes harvested, 1,384 crippled, and a total kill of 8,777 (Sorensen 1977). In 1977-78 the estimated harvest was 12,151 cranes, the crippling loss 2,013, and the total kill 14,164 cranes (Sorensen 1978). The 3-year average total kill was 11,441 cranes. These values are estimates for the Central Flyway only.

Additional birds are taken in Alaska, Canada, Mexico, and possibly Siberia (Lewis 1977). Lewis (1977:27) provided estimates of harvest by hunters in Alaska as 502 cranes in 1971 and 765 in 1972. The kill in Alaska during the 1975 season, estimated by Sorensen and Reeves (1976) from the Waterfowl Hunter Questionnaire Survey, was 288 cranes. In addition to reported harvest by hunters, cranes are taken by Alaskan natives in the spring. D. R. Klein (in Lewis 1977:26) stated that the spring harvest by natives probably does not exceed 2,000 birds, although 1,000 were taken in 1 year on the Yukon-Kuskokwim Delta. Because of increased human populations in native communities and use of modern hunting methods, current harvest could be much greater (C. P. Dau, personal communication).

Surveys in Canada suggest that the kill there averaged 2,959 cranes per year in 1972-76 (Table 1). The Canadian data do not include birds crippled but lost (Gollop 1976), nor birds taken by natives (a number not believed to be large—Lewis 1977:25).

Table 1. *Estimated harvest of sandhill cranes by license-holders in Canada, 1972-76.*[a]

Year	Saskatchewan	Manitoba	Total
1972	2,030	113	2,143
1973	3,592	683	4,275
1974	3,142	58	3,200
1975	3,048	164	3,212
1976	1,757	210	1,967
Average			2,959

[a]Sources: Cooch and Raible (1975) for all 1972 and 1973 data and 1974 Manitoba data; Cooch, Newell, and Wendt (1978) for 1975 and 1976 Manitoba data; Smith and Cooch (1978) for 1974-76 Saskatchewan data.

The kill in Mexico is unknown but, of 28 recoveries of cranes banded along the Platte River in Nebraska, 5 came from Mexico. This rate would suggest that the Mexican harvest is 22% of that in Canada and the United States. K. Baer (in Lewis 1977:28) estimated that the annual harvest in Mexico is 500-1,000 cranes. Interest in hunting cranes is reported to be increasing in Mexico.

The total annual hunting kill of sandhill cranes in recent years can be estimated by adding together estimates from the various sources:

Alaskan native	2,000 +
Alaskan hunter	288-765
Canadian native	small
Canadian hunter	2,959 + crippling loss
Central Flyway	11,441
Mexico	500-1,000

It appears that the harvest totals about 18,000 cranes per year and could be larger. If the population estimates presented earlier are realistic, this harvest would represent about 5 to 7% or more of the spring population.

Harvest Age Composition

The age composition of harvested sandhill cranes has been reported by Buller (1979), who found from bag checks that 31.5% of 574 cranes taken in 1974 were immatures. This rate compares to a percentage of 10.7 immatures in the population that year, and suggests that immatures are about 3.8 times as vulnerable to hunting as are adults, the relative risk being $0.315 \times (1-0.107)/[(1-0.315) \times 0.107]$. (The relative risk to hunting is the ratio of young to adult in harvest divided by the ratio of young to adult in the exposed population.)

An earlier estimate of the relative risk was given by Miller et al. (1972:23), who reported that, in Saskatchewan, immatures made up 4% (in 1966) and 6% (in 1967) of the total population, yet they made up 19% and 20%, respectively, of the harvest. The relative risk, as estimated from their pooled data, would be 4.6. The latter figure may be biased high because the authors included ground counts made before as well as during the hunting season. It is now recognized (Buller 1979) that early-migrating flocks contain a lower percentage of immatures than do later-migrating flocks. If we assume the total population in 1966-67 contained 11.3% young (the 1974-76 average), then the relative risk of juveniles would be 1.9.

Another estimate of the age ratio among harvested cranes was given by Boeker et al. (1961), who found 30 immatures and 107 adults in hunter bags checked in January 1961 in New Mexico. These authors indicated that the composition of 21.9% young closely paralleled age ratios of cranes trapped for banding before the hunting season. The authors did not draw any conclusions about differential susceptibility of young cranes to hunting, possibly because trapping itself may be age-selective. If, however, we assume that the percentage of young available to hunters was 11.3% (the average age ratio in 1974-76), then the relative vulnerability of juveniles to hunting is 2.2 times that of adults.

The Approach

Although much has been learned in recent years about sandhill crane population dynamics, the lack of certain critical information precludes the construction of a single model that could somehow be deemed "valid." At best, one can incorporate assumptions thought to be reasonable, and determine the implica-

tions of those assumptions as reflected by the behavior of the model.

The series of models proffered by Miller and his colleagues (Miller et al. 1972; Miller 1974; Miller and Botkin 1974) represents certain sets of assumptions about crane population dynamics. In my view, the crucial relationship is the density-dependence of natural mortality; less likely to be consequential is the density-dependence of recruitment. The dependence of natural mortality on density would be manifested in the impact that hunting has on the population level. If natural mortality rates are largely independent of the number of cranes, then reducing the population by hunting will not reduce other mortality rates, and a population otherwise at equilibrium will decline as a result of hunting. If natural mortality rates are substantially density-dependent, then it is possible that they will be lower in a population reduced by hunting, which will thereby "make up" at least some of the loss from hunting. Miller's models apparently were sufficiently density-independent to cause the simulated population to plummet with the advent of hunting.

The approach I followed was to try various survival functions (Fig. 2) and recruitment functions (Fig. 3) in combination and select those combinations that yielded realistic values of known population parameters under the situation of no hunting. Hunting was then applied to the simulated population to determine its impact. Unhappily there is little knowledge of the population dynamics of sandhill cranes that are not hunted. Virtually all data described in the previous section were collected while cranes were legally hunted. For this reason I cannot portray what the population would do without hunting. I can only assume that current levels of hunting have not yet seriously affected survival and recruitment rates.

Moreover, no one knows which combination of parameters is "correct." It is only known that the selected ones yield results that are consistent with what is known about the sandhill crane population.

Specifically, one seeks combinations of parameters that yield (1) an equilibrium spring population between 250,000 and 400,000 cranes, and (2) an age composition in the fall of 10.3-12.3% young (within 1% of the 1974-76 mean). When hunting is applied to the population, it will remove about 5% of the entire population annually.

Results

A total of 768 combinations of 32 survival functions and 24 recruitment functions were executed without hunting to determine if they yielded population sizes and age ratios comparable to the data described above. Thirty-seven combinations (Table 2) gave asymptotic populations between 250,000 and 400,000 cranes and fall age compositions between 10.3 and 12.3% young.

Each combination of survival and recruitment functions described in Table 2 yielded an asymptotic population and age composition, under the situation of no hunting, consistent with what is known of the actual crane population. Thus, without additional information, one cannot discriminate among them. One cannot select from these, or from the multitude of other plausible combinations, the one that most closely parallels the true situation.

Hunting was then applied to the simulated population under each of the 37 combinations. Two sets of hunting rates were used: 10.7% on young birds (H_1 = 0.107) and 4.3% on adults (H_2 = 0.043); and 14.9% on young (H_1 = 0.149) and 3.7% on adults (H_2 = 0.037). Under the first set of rates, young birds are about 2.5 times as vulnerable as adults; under the second, about 4.0 times. Because this differential vulnerability ratio is so poorly known, it is fortunate that very similar results were obtained from both sets of hunting rates (Table 2). For the sake of brevity, I will discuss only the results under the second set of hunting rates. The first set produced similar, but slightly lower, asymptotic populations.

Under all 37 combinations the population declined with the advent of hunting. The extent of the decline varied markedly, however, ranging from 5.1 to 54.4%. The median decline was 22.3%. Figure 5 shows the results of a typical simulation, this one combining survival curve 8 and recruitment curve B. Without hunting, the population ultimately increased from the initial 240,000 to 272,000 cranes. When hunting was applied, the population eventually decreased to 201,000 cranes, and yielded an annual harvest of about 12,000 birds.

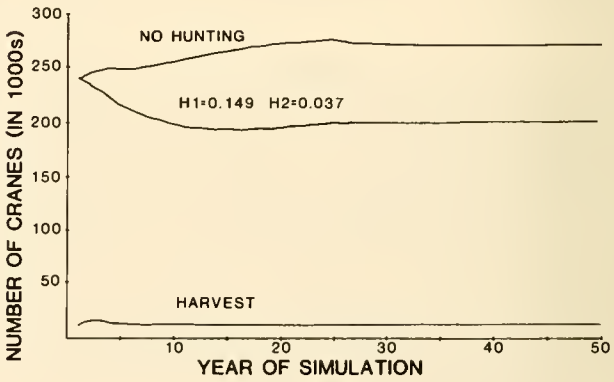

Fig. 5. Results of model under combination of survival curve 8 and recruitment curve B. Shown are simulated results under situation of no hunting and under hunting rates H1 = 0.149 and H2 = 0.037. Also shown is the annual harvest.

Table 2. *Combinations of survival and recruitment curves that yielded realistic asymptotic populations and age ratios under situation of no hunting. Also shown are harvest (in 1,000's), asymptotic population (in 1,000's) and percent decrease for two hunting situations. Harvest values are numbers taken after population stabilizes.*

Survival curve	Recruitment curve	Unhunted population	$H_1 = 0.107, H_2 = 0.043$			$H_1 = 0.149, H_2 = 0.037$		
			Harvest	Population	Decrease (%)	Harvest	Population	Decrease (%)
1	F	250.8	12.2	212.3	15.4	12.3	213.6	14.8
2	A	267.3	13.4	238.1	10.9	13.5	239.3	10.5
2	B	272.9	14.6	253.5	7.1	14.8	253.9	7.0
2	C	273.8	14.0	246.0	10.2	14.1	247.0	9.8
2	F	270.8	13.7	241.6	10.8	13.7	242.8	10.3
2	G	273.9	14.5	252.4	7.8	14.7	253.0	7.6
3	C	250.0	9.1	156.9	37.2	9.4	159.7	36.1
4	A	278.5	12.6	220.1	21.0	12.7	222.2	20.2
4	B	285.9	14.4	247.4	13.5	14.6	248.6	13.0
4	C	298.4	13.0	226.9	24.0	13.2	229.6	23.1
4	F	289.2	12.7	222.4	23.1	12.9	224.7	22.3
4	G	291.8	14.2	244.9	16.1	14.4	246.2	15.6
4	H	294.7	15.5	264.3	10.3	15.9	265.0	10.1
5	C	341.9	16.2	287.2	16.0	16.2	290.0	15.2
5	D	349.9	17.9	313.5	10.4	18.1	314.6	10.1
5	I	352.8	18.0	314.3	10.9	18.2	315.5	10.6
6	D	368.9	19.1	339.4	8.0	19.1	340.7	7.6
6	E	374.6	20.4	355.0	5.2	20.6	355.4	5.1
6	I	372.8	19.4	343.1	8.0	19.5	344.3	7.6
6	J	375.8	20.3	354.0	5.8	20.5	354.5	5.7
7	A	256.5	10.1	172.5	32.7	10.5	177.4	30.8
7	C	264.4	8.7	148.3	43.9	9.4	159.7	39.6
7	F	260.5	9.9	169.9	34.8	10.4	175.6	32.6
8	A	255.1	8.6	146.0	42.8	9.1	151.2	40.7
8	B	271.7	11.8	197.5	27.3	12.3	200.7	26.1
8	C	273.4	6.8	115.8	57.6	7.4	124.7	54.4
8	F	263.6	8.6	145.5	44.8	9.0	150.2	43.0
8	G	273.8	12.0	200.9	26.6	12.4	203.1	25.8
9	C	322.2	8.7	148.2	54.0	9.5	160.0	50.3
9	D	336.7	14.9	252.7	24.9	15.4	257.5	23.5
9	F	308.1	10.0	170.4	44.7	10.4	176.5	42.7
9	G	306.0	13.5	230.3	24.7	13.9	233.2	23.8
9	I	339.3	14.8	251.7	25.8	15.3	256.1	24.5
10	C	348.6	8.7	149.6	57.1	9.6	161.9	53.6
10	D	357.7	15.7	268.4	25.0	16.3	274.3	23.3
10	E	367.2	19.2	325.8	11.3	19.7	328.0	10.7
10	I	362.1	15.6	265.7	26.6	16.1	271.7	25.0

Discussion

In their original report, Miller et al. (1972) voiced a concern that the information needed to manage sandhill crane populations properly was lacking or inadequate. Research in recent years has provided better data on certain characteristics, but has also demonstrated how little is known about other aspects of sandhill crane population dynamics. In this section I discuss some of the limitations of the model developed here and the data used in it. I also make recommendations for further research, for data-gathering on an operational basis, and for strategies to manage sandhill crane populations.

Limitations of the Model and Data

In the model presented here, several assumptions were made about the population dynamics of sandhill cranes. It was assumed that cranes first breed as 4-year-olds. Although age at first breeding is an important species characteristic, its value is of little direct consequence to the population as modeled here. Because estimates are available of the percentage of young in the fall population (e.g., 11%), it is not necessary to know which age segment of the population produced them (e.g., 11 young produced by 50 birds age 4 or greater, or 11 young produced by 60 birds age 3 or greater). The age of initial breeding is an implicit

parameter in the present model.

Another assumption concerns the longevity of sandhill cranes in the wild. The model assumes a 25-year life-span, after which cranes die. This limit is artificial, of course, but serves as a computational convenience. An indeterminate life-span would yield similar results. Analogously, instead of constant survival and recruitment rates for all adults in the population, senescence could be invoked with lowered survival and reproduction among old cranes. Again, this modification would make but small changes in the results.

The degree to which recruitment and survival are density-dependent is of prime importance to the modeling. A small change in the form of the recruitment curve or survival curve can inspire major changes in the resulting asymptotic population and its response to hunting. It is very doubtful, however, that the near future will see either recruitment or survival measured with sufficient accuracy to detect and delineate density dependence. Thus the information most needed to improve the model will probably be long in coming.

The model is deterministic, in contrast to the stochastic nature of the real world. Too little is known to develop a realistic model of randomness in the parameters. The averages of most parameters are at best poorly known; their variations and inter-correlations could scarcely be guessed. A deterministic model should suffice, however, if it is viewed conservatively. The real world will be more variable than its deterministic counterpart in a model; decisions based on the model should be made with that caveat in mind. As stated earlier, it is possible for a simulated population incorporating randomness to become extinct while its deterministic analog held steady, or even increased in number.

An oversimplification in the model that is most troublesome to me is the aggregation of three subspecies. Birds in the Central Flyway are referred to as *the* sandhill crane population, but the birds involved include greaters, Canadians, and lessers, and originate in nesting areas extending from Siberia, through vast areas of Alaska and western Canada, and possibly into northern Minnesota. The Central Flyway population of lessers is large, the number of Canadians is modest, and the number of greaters is small. During fall migration, different subspecies migrate along somewhat different routes, and at somewhat different times (Johnson and Stewart 1973). Hunting cannot be expected to affect each of them equally, and more attention must be given to evaluating the effects of hunting on the different subspecies.

It was further assumed that parameters measured recently, while cranes were subjected to legal hunting, are not too different from the values appropriate if cranes were not hunted. The impact of this assumption is less than one might imagine. The crucial result is that the level of a stable population lies in a balance maintained by mortality rates and recruitment rates. Any increase in mortality rates, by hunting for example, will result in a lower level of the population, *unless* (1) the total mortality rate stays constant, through a decrease in natural mortality, or (2) recruitment is increased, presumably because of lowered densities. The model offered here includes the possibility of compensatory effects in both natural mortality and recruitment. In the multitude of combinations examined, however, their combined effect was insufficient to compensate completely for the increased mortality due to hunting. This result is not surprising in view of the nature of sandhill cranes.

Recommendations

Further Research

The key concern in analyzing the impact of hunting on sandhill crane numbers is the extent to which that form of mortality is compensated for by other forms of (natural) mortality. If only a certain number of cranes are destined to survive the winter, for example, it matters little that the "doomed excess" is taken by hunters. At the other extreme, if hunting mortality is completely additive to natural mortality, then the loss of a single crane to a hunter will be reflected proportionately in the next year's spring population.

Most likely, hunting mortality is neither completely compensatory nor completely additive. It seems probable that each crane shot by a hunter in the fall will be reflected in a fractional decrease the next spring. The size of the fraction is in doubt.

There seems little hope of ascertaining the value of that fraction by the usual methods based on banding. Even with the intensively studied mallard (*Anas platyrhynchos*), with more than two-thirds of a million preseason bandings available for analysis, the question of compensation in hunting mortality has only recently been addressed (Anderson and Burnham 1976). I doubt that information based on sandhill crane banding will ever be adequate to determine the degree to which hunting mortality is compensatory. Other methods are called for.

A method that may prove fruitful involves the following line of inquiry: To what degree is one mortality agent compensatory to another within a K-selected species? The question need not be restricted to only hunting mortality or to only sandhill cranes. Research on other mortality factors and on other species of birds may provide parallels for hunting and sandhill cranes.

Among birds, sandhill cranes are a relatively K-selected species (e.g., Pianka 1974; Southwood 1976). They are large, long-lived, and have low fecundity (de-

ferred breeding, small clutch size). Young cranes are invested with considerable parental care and develop rather slowly. Other attributes associated with K-selection may bear directly on the question of the compensatory nature of mortality. Populations of K-selected species tend to be stable when at equilibrium, mortality is normally noncatastrophic and density-dependent, and birth rate tends to be density-dependent, but populations are relatively easily extinguished.

The nature of a K-selected species is such that it cannot recover rapidly from a severe population reduction (Miller 1978). Although birth rate and survival may increase as the population becomes sparse, neither rate can rise very much, and extinction looms as a real possibility. Analogies with other K-selected species, both endangered and common, may prove instructive for making decisions about sandhill cranes.

Operational Data Gathering

There is little question that improvements in methods of collecting sandhill crane data should be sought. Most sandhill cranes in the Central Flyway stage their spring migration along the Platte River in Nebraska. This concentration of birds should be relatively easy to count, at least compared with most populations of wild birds. Yet, counts in past years have been erratic, suggesting high variability from censusing procedures. Other evidence (e.g., Lewis 1979) points to biases as well as variability in the spring survey data. Modifications of the survey have been made and evaluated (Ferguson et al. 1979), and further work along this line is under way.

Improved surveys may more accurately indicate the size of the sandhill crane population. It is doubtful that they will permit us to detect changes in sandhill crane numbers caused by hunting, however, except possibly over extended periods of time. The annual decline due to hunting (e.g., about 4,000 cranes per year in the example displayed in Fig. 5) is rather small in comparison to the variability in the counts, and would additionally be masked by natural variation in numbers of cranes.

The age composition of fall-migrating sandhill cranes has been well documented for 3 consecutive years (Buller 1979). Little annual variation was detected. Nonetheless, it is possible for the age composition to undergo an important change, which could seriously alter the results of the model presented here. It would seem prudent to develop a periodic survey for estimating the fall age composition for a number of years.

The size of the sandhill crane harvest, together with the population size, are the most critical parameters now being estimated. The requirement that hunters in the Central Flyway obtain permits to hunt cranes has imparted much more precision to harvest estimates in that area, but harvest in other important areas (e.g., Alaska and Mexico) is poorly known. The permit system should probably be continued for a time, particularly as changes are made in regulations. For example, in North Dakota the switch from a November season to one in September resulted in an increase in harvest from an average of about 380 cranes per year in 1968-76 (Johnson 1977) to 4,078 in 1977 (Sorensen 1978), and about 2,800 in 1978 (M. F. Sorensen, personal communication). Better information on harvest outside the Central Flyway and Canada is sorely needed.

Only once has the age composition of harvested cranes been estimated concurrently with the age composition in the hunted population. Fortunately, the simulation model provided very similar results when two rather different values of differential vulnerability to hunting (2.5 and 4.0) were used. Thus, this parameter appears to be less consequential to the population dynamics than the others discussed.

It is also important to delineate the various populations of sandhill cranes that are subjected to hunting, and to evaluate their status. Ideally, measures of productivity as well as mortality from both natural causes and hunting should be obtained for each population. At a minimum, various marking programs could be undertaken to ascertain the derivation of harvest of cranes, and measurements should be taken on hunter-shot cranes to determine their racial composition.

Management Goals

In addition to implementing some operational data-gathering procedures, prudent management seems to require some difficult decisions. Primary among them are population goals for each identifiable component of the sandhill crane population. How many cranes do we want in each breeding, migrating, and wintering area? Conservationists may desire more, some grain farmers, fewer. Once population goals are identified, the question becomes how to attain these goals. What magnitude of harvest is consistent with the goal? And then, how shall the harvest be allocated? Indians and other natives take cranes in subsistence hunting; Canadian, American, and Mexican hunters take them for sport. Deciding who gets how many will be a challenging task, particularly as demands grow and if crane populations dwindle.

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