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A Simulation Model For The Management Of Sandhill Cranes

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A SIMULATION MODEL FOR THE MANAGEMENT OF SANDHILL CRANES

BY

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FOREWORD

FORESTRY at the Yale School of Forestry and Environmental Studies is concerned with the manipulation of ecosystems within the restriction and demands imposed by socio-economic systems with due regard for the long-term responsibilities and results. Of course there are interactions between the multiple-use objectives with feedback to both th ecosystem and the socio-economic system. The management objectives to be obtained from our forests and wildlands are on the one hand tree-drived products, and on the other hand indirect benefits, e.g. water, grazing, recreation, wildlife, amenity values and soil protection. This bulletin describes one of these "other benefits," namely, an analysis of wildlife management. Part of this research was supported with funds from the Oastler bequest and in part by funds from the Ford Foundation for a program in ecosystem management. The senior author, Professor Richard S. Miller, holds one of the Chairs established under the Oastler bequest, while Professor Daniel B. Botkin is sponsored under the Ford Foundation grant.

The Oastler bequest made it possible for the Forestry School to establish a teaching and research program in wildlife studies, an aspect of resource management that had previously received little attention at our School. Dr. Frank R. Oastler, an 1891 graduate of Yale College and a distinguished gynecologist, died in 1936. He was an avid naturalist and conservationist and an expert nature photographer. His fine collection of photographic slides and films housed in our School attests to his competence. In his will he stipulated that after his wife's death, all his personal property was to go to the Forestry School at Yale "for conservation of wildlife, both birds and mammals." Since the initiation of the program in 1965 significant contributions in this area have been made under this bequest by our faculty and students.

This contribution adds new knowledge to the biology and management of sandhill cranes, but its more important aspect is the attempt to develop systems models as a tool to manage game species. Regarding the life history of this species, it is of particular interest that the authors are using as illustrations two of the photographs that were taken by Dr. Oastler some 40 years ago (figures 1 and 2). These photographs thus bridge the time gap from the use of simple photographic equipment to the techniques of high speed computers in helping to develop a logic for the survival of a wildlife species.

The authors make only modest claims in the sophistication of their model; the approach and technique, however, do represent the direction that wildlife management needs to follow in the future.

François Mergen
Dean

INTRODUCTION

THE trumpet call of sandhill cranes, soaring and wheeling in flocks high overhead against the clouds, as they begin to arrive from their wintering grounds in the southwest, is one of the most distinctive sounds of the prairies. It heralds the start of a new season, when the prairie crocus will burst into flower and the marshes will begin to renew their annual cycle of life. After the arrival of the sandhill crane, the flow of spring migrants will quicken as more and more species reach their prairie breeding grounds and the marshes begin to assume their summer richness, but most of the cranes will continue north to breed along the arctic coast, after only a short stay on the prairies. They no longer remain, as they once did, to add their unique presence to the prairie scene. These large, graceful birds, like their relative the whooping crane, cannot live in the close proximity of man and cannot breed in the restricted confines of the marshes that have been left by the agricultural development of the west.

The distinctive qualities of the sandhill crane, measured against its gradual disappearance from its former breeding grounds, was described in a "Marshland Elegy" by Aldo Leopold in *A Sand County Almanac:* "On motionless wing they emerge from the lifting mists, sweep a final arc of sky, and settle in clangorous spirals to their feeding grounds. A new day has begun on the crane marsh.... When we hear this call we hear no mere bird. We hear the trumpet of evolution. He is the symbol of our untamable past, of that incredible sweep of millenia which underlies and conditions the daily affairs of birds and men." "And so they live and have their being - these cranes - not in the constricted present, but in the wider reaches of evolutionary time. Their annual return is the ticking of the geologic clock. Upon the place of their return they confer a peculiar distinction. Amid the endless mediocrity of the commonplace, a crane marsh holds a paleontological patent of nobility, won in the march of eons, and revocable only by the shotgun. The sadness discernible in some marshes arises, perhaps, from their once having harbored cranes. Now they stand humbled, adrift in history."

When sandhill cranes \vere abundant on the prairies they were hunted for food and recreation, but their numbers were continually reduced until they were placed under protection of the Migratory Birds Convention Act in 1918. They remained in protected status for over 50 years, until open hunting seasons were established in Texas and New Mexico in 1961 by order of the Secretary of" the Interior. Additional open seasons have subsequently been authorized in other states and provinces of Canada, and the sandhill crane is now a game species which is hunted for recreation.

In this paper we will examine the data which are available for the management of the species, and will develop a computer model which predicts the results of different management alternatives.

THE SANDHILL CRANES

PETERS (1934) recognized four subspecies of sandhill cranes, the Florida sandhill crane (*Grus canadensis pratensis*), the Cuban sandhill crane (*G. c. nesiotes*), the greater sandhill crane (*G. c. tabida*), and the lesser or little brown sandhill crane (*G. c. canadensis*). More recently, Walkinshaw (1965a) described a new subspecies, the Canadian sandhill crane (*G. c. rowani*) from specimens intermediate and size and locality between the greater and lesser sandhill cranes.

The Florida sandhill crane (Fig. 1-2) was formerly resident in southern Louisiana, Alabama, southern Mississippi, southern Georgia and south through Florida, but hunting and changes in habitat due to agriculture and other human activities have reduced the total population until it is now absent from Louisiana and Alabama and occurs only in scattered populations in the remainder of its range (Walkinshaw 1949). In 1949 the total population was estimated to be about 2650 birds but more recent estimates place their numbers at about 600 (IUCN 1966). The Florida sandhill crane is listed as "rare" in the Red Data Book of rare and endangered species (IUCN 1966) and on the U. S. Fish and Wildlife

Service list of Rare and Endangered Fish and Wildlife of the United States, and is now fully protected by law.

The Cuban sandhill crane is resident on the Isle of Pines in the Carribean and in very restricted areas of western Cuba. The Isle of Pines population is estimated to be about 100 individuals, and this subspecies is believed to be exceedingly rare and probably decreasing in the other parts of its range where it is still hunted for food and is unable to find the seclusion that sandhill cranes seem to need in order to sustain viable breeding colonies. The Cuban sandhill crane is also listed as "rare" in the Red Data Book (IUCN 1966).

The present breeding range of the greater sandhill crane extends from southern Michigan west through the northern United States in scattered colonies to Or-egon and northern California and north into British Columbia. Breeding populations of greater sandhill cranes and, perhaps all sandhill cranes, are usually small and isolated. Walkinshaw (1965bc) studied a population in southern Michigan \vhich has averaged about 45 pairs since 1952 and in the fall of 1964 estimated the total number of greater sandhill cranes in southern Michigan to be about 110 birds, breeding mostly in scattered colonies of only a few pairs. Sugden (1938) reviewed the status of the greater sandhill crane in Utah and southern Idaho and found that Fish Springs, Utah, at the southern end of the Great Salt Desert, is now the southern limit of the breeding range of this species in the intermountain region, but that cranes no longer occur in large colonies as they did in "the early days" and now are found only in scattered pairs or small groups in relatively inaccessible river valleys in Utah, southern Idaho and Wyoming. Wherever they have been subject to continued interference, they have been reduced to low numbers or have disappeared entirely. One of the largest local populations of greater sandhill cranes breeds on the Malheur National Wildlife Refuge in Oregon. This population contained 989 individuals in the fall of 1942, but some of these might have been migrants (Walkinshaw 1949) and Littlefield and Ryder (1966) estimate this population to consist of about 400 birds, of which about 320 are breeding adults.

Walkinshaw (1949) compiled a list of breeding populations of greater sandhill cranes in the United States and estimated the total number of breeding and non-breeding birds to be between 1,300 and 1,800 with an equal number in Canada. Littlefield and Ryder (1966) estimated the total population of this subspecies to be about 10,000, of which about 900 occur in the eastern part of the breeding range, 5500 in the central and 3600 in the western colonies. Buller (personal communication) also estimates a total population of about 10,000 on the basis of the number of birds that winter in New Mexico. The greater sandhill crane is also on the U. S. Fish and Wildlife Service list of Rare and Endangered Fish and Wild-

life of the United States, although Walkinshaw (1949) and Buller (personal communication) conclude that this subspecies is gradually increasing in numbers.

The lesser sandhill crane (Fig. 3) is, by far, the most abundant of the five subspecies, although very little is known of its breeding areas or population ecology. This subspecies apparently breeds in scattered groups from at least as far east as Bylot Island, across the high arctic of the Northwest Territories and Alaska and north into Siberia, and winters in the southwestern United States and Mexico. In spite of its numerical importance in the total species population, almost all of the observations of this subspecies have been on the wintering grounds or at concentration areas during migration, and there have been no studies of breeding populations.

The Canadian sandhill crane was described by Walkinshaw (1965a) from 10 specimens collected over a period of years from Alberta, central Saskatchewan, west-central Manitoba and the southern Mackenzie district. These specimens were previously referred to as "prairie intermediates" (Walkinshaw 1949) because they could not be assigned to either G. *c. canadensis* or G. *c. tabida* on the basis of size. Walkinshaw (1965a) concluded that there was "enough available material" to show that these specimens were, in fact, intermediate and could be used to describe a new subspecies, G. *c. rowani*. The summer range of the Canadian sandhill crane is described as covering "the Coniferous Forest Biotic Community in southern Mackenzie, Alberta, Saskatchewan and probably central western Manitoba. It may occur in northern Ontario where no cranes have been taken during the summer." Walkinshaw (1965a) does not explain how the wintering areas of this subspecies were determined but states that it winters in southern and eastern Texas and that one specimen has been reported from Cameron Parish in Louisiana.

If this is a valid subspecies it must be exceedingly rare and should also be designated as "rare" or "endangered". We know that sandhill cranes once bred quite extensively across the southern parts of the prairie provinces, but most of these breeding populations disappeared when the land was developed for agriculture. Small flocks occur at a few localities in Saskatchewan and Manitoba during the summer, but these seem to be mostly non-breeding birds of unknown taxonomic status and young are seldom observed in these groups (Stephen 1967).

THE MIGRATORY POPULATION

The Florida sandhill crane and the Cuban sandhill crane are resident subspecies which remain within their breeding areas throughout the year; the other three subspecies, the lesser sandhill crane, the greater sandhill crane and the Canadian sandhill crane, form the North American migratory population (Fig. 4). There is evidence of an eastern migration route for some greater sandhill cranes (Walkinshaw 1960) which presumably winter in the southeastern states with the Florida sandhill crane. Flocks observed during fall migration at the Jasper-Pulaski Game Preserve in Indiana have increased from 200 in 1939 to about 1500 in 1954 (Walkinshaw 1956). However, Buller (personal communication) estimates that 85 to 90 percent of the total migratory population of Nonh America, including birds which breed in the northcentral states, the Pacific northwest and the Provinces of Canada, as well as in the arctic, migrates through the Central Flyway and winters in the southwestern United States and Mexico. These are the cranes which are exposed to hunting.

Table 1. shows the results of pre-season surveys of the migratory population on their wintering grounds in New Mexico and Texas, and surveys on the Platte

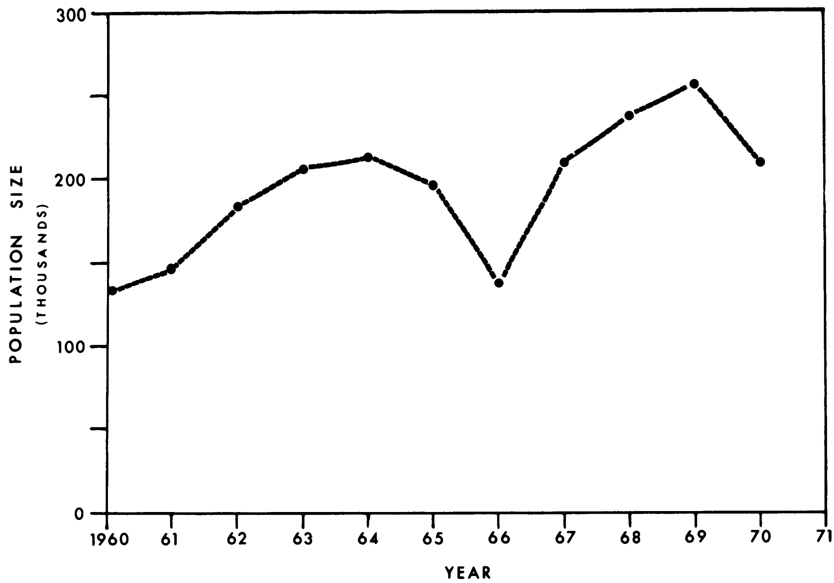
TABLE 1. PRESEASON SURVEYS OF SANDHILL CRANES IN NEW MEXICO AND TEXAS AND SPRING COUNTS AT CONCENTRATION AREAS IN NEBRASKA.

Year	Preseason Surveys in New Mexico and Texas	Spring Surveys in Nebraska
1959		147,496
1960	134,673	125,870
1961	147,416	136,276
1962	184.901	142,830
1963	207,405	101,925
1964	213,896	156,028
1965	198,027	80,315
1966	139,199	123,087
1967	210,074	126,043
1968	239,185	169,194
1969	258,500	154,978
1970	210,200*	193,600
1971		207,500

* Incomplete.

River during spring migration through Nebraska. The variation in the estimates in the New Mexico-Texas surveys is probably due more to the timing of fall migration in relation to the date of the surveys and to local conditions that affect the ability of observers to locate and count flocks, than to actual changes in population size. Sandhill cranes begin to arrive from the north and concentrate at staging areas in the prairie provinces of Canada in late August and remain through early October as a general rule (Stephen 1967). However, the date they leave these areas to continue their southward migration is partly influenced by weather. If conditions remain favorable they may delay their departure long enough for cranes to still be on their way to the wintering grounds when the pre-season surveys are made. If, on the other hand, weather conditions force an early departure, some cranes may have migrated through Texas and New Mexico and into Mexico before the survey is taken. It is, therefore, unlikely that the counts shown in Table 1 account for all of the birds in the migratory population.

The average count in Table 1 (including the incomplete count in 1970) is 194,861 cranes with a low of about 135,000 in 1960 and a high of about 260,000 in 1969. Figure 5 shows that there has been a general increase in the number of cranes counted each year, but because of the census problems mentioned earlier and the variation in these counts, this trend may merely represent increased efficiency of the surveys and cannot be regarded as sufficient evidence for a real increase in numbers. On the basis of these figures and the fact that it is unlikely that all of the cranes in the population are counted during the surveys, Buller (personal communication) estimates a total migratory population of lesser and



Canadian sandhill cranes of about 300,000, including the segment of the population that winters in Mexico.

The spring surveys (Table 1) show maximum concentrations observed along the Platte River near Hershey, Nebraska. While it is unlikely that the entire migratory population passes through this one locality every spring, these surveys are evidence of the large concentrations which can occur. The high count of 207,500 in 1971 represents more than 69 percent of the estimated total population of 300,000. The average of the spring counts is 143,472 which is 74 percent of the average wintering ground count. Thus, a very large proportion of the migratory population may occur at one place at one time along the flyway.

Subspecific Status

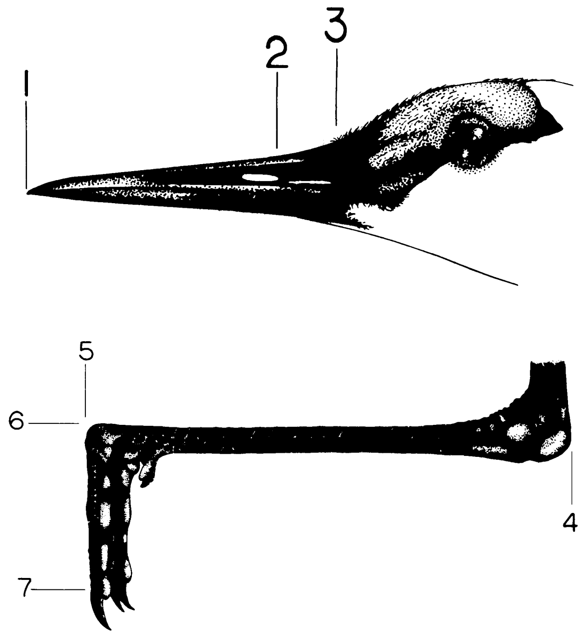
There is considerable uncertainty about the subspecific status of different segments of the migratory population and whether, in fact, individuals can be assigned to a subspecies on the basis of currently accepted taxonomic criteria. It is clearly desirable to protect small breeding colonies of sandhill cranes, regardless of subspecies, but it is not entirely certain that birds from such population can be adequately protected if they intermingle freely with the rest of the migratory population. For management purposes, the lesser sandhill crane and the Canadian sandhill crane are lumped together as "little brown cranes" (Sherwood 1971) to form the hunted population, while efforts are made to protect the rare, greater sandhill crane. However, as noted earlier, if we accept the Canadian sandhill crane as a valid subspecies, it would appear to be even less abundant than the greater sandhill crane.

The chief characters used by Walkinshaw (1949, 1965a) to distinguish between the three subspecies were body size, length of wing (wing chord), plumage color, color of the shafts of the primary feathers, and measurements of the tarsus, tibia anl culmen. Buller (1967) also states that greater and lesser sandhill cranes can be identified by the length of the midtoe (or footprints), but does not show how these two subspecies can be distinguished from the intermediate *G. c. rowani.* Table 2 shows the measurements used by Walkinshaw (1965a) to describe *G. c. rowani;* these are compared with measurements of the same characters for *G. c. canadensis* and *G. c. tabida.*

Stephen, Miller and Hatfield (1966) collected 303 specimens of sandhill cranes during the spring and fall migrations of 1961, 1962 and 1963 at Last Mountain Lake, Saskatchewan and compared the measurements of this sample with the subspecies descriptions given by Walkinshaw (1949, 1965a). The Last Mountain Lake Bird Sanctuary was the first sanctuary established by legislation in North America, and is traditionally used by sandhill cranes as a staging area during migration (Stephen 1967). Although a few cranes spend the breeding season at Last Mountain Lake each year, these are apparently non-breeding birds and the spring and

TABLE 2. MEASUREMENTS OF CHARACTERS OF SUBSPECIES OF SANDHILL CRANES (FROM WALKINSHAW 1965A)

Subspecies	(specimens)	Wing Length	Tarsus	Exposed Culmen	Bill from Tip to Posterior Nares	Bare Tibia
canadensis	males (33)	475.6 (439-503)	186.6 (156-210)	91.8 (69-102)	71.4 (65-76)	70.3 (52-85)
canadensis	females (17)	451.2 (420-490)	182.0 (162-198)	93.2 (84-103)	67.4 (63-74)	69.1 (50-83)
rowani	males (7)	507.3 (480-524)	222 (216-239)	118.3 (109-127)	85 (82-88)	86.6 (70-96)
rowani	females (3)	472.6 (456-495)	210.6 (205-216)	103.0 (93-114)	80 (73-87)	75.5 (63-88)
tabida	males (8)	561.5 (526-598)	244.5 (226-264)	137.1 (122-144)	107.2 (101-116)	111.2 (88-125)
tabida	females (9)	546.0 (510-575)	230.5 (222-239)	125.0 (113-134)	97 (1)	112.7 (108-117)



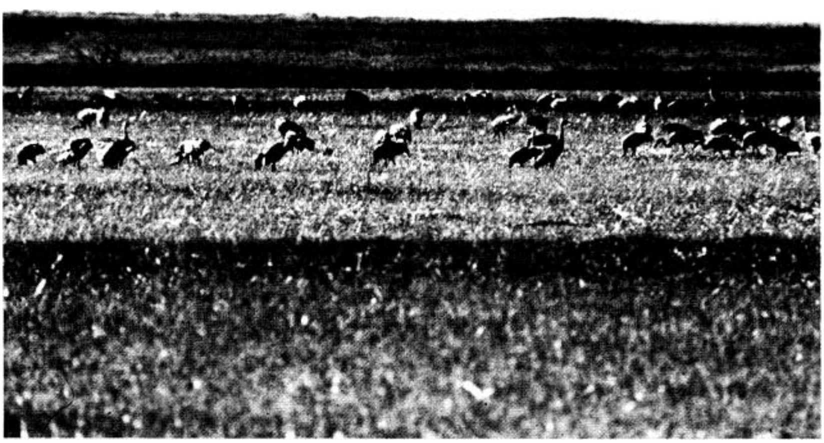
fall concentrations are of cranes which breed in the north, presumably in the arctic, and winter in the southwestern United States. Figure 6 shows the measurements that were made of the head, foot and tarsus. The bill was measured from the tip (1) to the posterior edge of the nares (2) and the point where the lores meet the upper mandible. This measurement (1 to 3) appears to correspond to what Walkinshaw (1949) referred to as the "exposed culmen", which is not a standard ornithological measurement. The tarsus length was measured from the posterior edge of the tibio-tarsus joint (4) to the anterior edge of the tarsal-metatarsal joint (5) and the midtoe was measured from the anterior edge of the tarsal-metatarsal joint (6) to the last scute on the toe (7). Total length was measured from the tip of the culmen to the longest retrix and color of the primary shafts was also recorded.

The analysis of the Last Mountain Lake specimens showed that some of the characters used by Walkinshaw are unreliable as taxonomic criteria, and others showed too much overlap between the Last Mountain Lake specimens and the values in Table 2 to allow specimens to be assigned to a particular subspecies. For example, dark grey primary shafts are supposed to be characteristic of the subspecies *canadensis* and white or yellowish shafts characteristic of *tabida* (Walkinshaw 1949); the primary shafts of *rowani* are supposedly lighter grey than those of *canadensis* (Walkinshaw 1965a). Of the 127 specimens that were examined for this character, 7 percent had dark grey shafts on all primary feathers, 51 percent had all whitish or yellowish shafts, and 42 percent had shafts of both colors. Also, 70 percent of the feathers with shafts which were whitish or yellowish showed signs of wear while only 33 percent of those with dark grey shafts were worn. It was concluded· from the lack of consistency of shaft color for individual birds, and the apparent relationship between shaft color and wear of the feathers, that this is not a reliable taxonomic character and similar conclusions were reached with regard to other plumage characters (Stephen 1967).

Frequency polygons were examined to determine the probable proportions of each subspecies present in the Last Mountain Lake sample. The range of measurements given for G. *c. canadensis* males (Table 2) overlapped the distribution of measurements of the Last Mountain Lake specimens by 38.2 percent in.1ength of exposed culmen, 15.4 percent in length of bill from tip to posterior nares, and 10.6 percent in length of tarsus. The range of measurements given for G. *c. rowani* males overlapped the distribution of measurements of Last Mountain Lake specimens by 29.5 percent in length of exposed culmen and occupied only 33.3 percent and 46.8 percent of the distribution of measurements of bill from tip to posterior nares and of tarsus length. There was less overlap with the measurements given for G. *c. tahida* males, with only 2.0 percent in exposed culmen and 0.2 percent in length of culmen from tip to posterior nares, but there was a 64.4 percent overlap in tarsus length. At least 75 percent of the Last Mountain Lake sample could not be assigned to one subspecies, and the measurements of all characters conformed to a normal distribution, indicating a single population. It was concluded from this study (Stephen 1967) that the preservation of local nesting populations should be attempted where this is desirable, but it is probably impractical to restrict management to particular subspecies within the migratory population.

MANAGEMENT HISTORY

Protection of sandhill cranes under the Migratory Birds Convention Act of 1916 was based on the view that the species might not be able to maintain its numbers if it was hunted and that rare subspecies, such as the greater sandhill crane, and the endangered whooping crane *(Grus americana)*, might be inadvertently exposed to hunting mortality and suffer further reductions in their populations. However, a history of repeated depredations by sandhill cranes on cereal crops in North Dakota and Saskatchewan (Fig. 7) prompted the Central Flyway Waterfowl Council to request open seasons (Boeker, Aldrich and Huey 1961), and especially heavy damage in areas where cranes congregate in Saskatchewan during fall migration (Munro 1950) finally led provincial officials and the Canadian Wildlife Service to authorize Saskatchewan farmers to shoot sandhill cranes under crop depredation orders in the fall of 1959. In 1960 the recommendation of the Central Flyway Waterfowl Council received support from the National Flyway Council, the Saskatchewan Department of Natural Resources and the Canadian Wildlife Service, and the U. S. Secretary of the Interior authorized an experimental hunting season to be held in eastern New Mex-



ico from 1 January to 30 January 1961. Hunting was based on the assumption that crop depredations in Saskatchewan would be alleviated by reducing the total size of the sandhill crane population (Boeker, Aldrich and Huey 1961). The success of the experimental season in New Mexico led to 30-day open seasons in Alaska, New Mexico and Texas in the fall of 1961. In 1964 limited seasons were also authorized in Manitoba and Saskatchewan in areas where complaints of crop damage were especially persistent.

Buller (1967) analysed the results of sandhill crane hunting in the United States from 1961 to 1965 and concluded that ample precautions were being taken to protect the whooping crane and greater sandhill crane, and that the migratory population could withstand additional hunting. Whooping cranes occasionally appear with sandhill cranes during fall migration when the hunting season is in progress, but daily aerial surveys are flown to detect their presence and the hunting season is immediately ended when a whooping crane appears. The management strategy for the protection of greater sandhill cranes is to restrict hunting to areas where significant numbers of this subspecies do not occur. Table 3 shows the proportion of greater sandhill cranes determined from footprint measurements in 14 samples from 7 states in the Central Flyway (Buller 1967). According to the estimate made by Littlefield and Ryder (1966) of the total number of greater sandhill cranes and their breeding distributions, they would be expected to constitute considerably less than 3 percent of the migratory population that occurs in the Central Flyway, whereas the lowest proportion in the samples shown in Table 3 is 5 percent and the average is 10 percent. This discrepancy suggests, as noted earlier, that the taxonomic criteria used to identify this subspecies are unreliable and individual birds cannot be properly identified. Nevertheless, the management practice in this case has been to avoid hunting in areas where "large cranes" occur and

TABLE 3. PROPORTION OF GREATER SANDHILL CRANES[1] (AS DETERMINED BY FOOTPRINT MEASUREMENTS) AT FALL CONCENTRATION SITES IN THE CENTRAL FLYWAY (FROM BULLER 1967).

State	Sites	Total Sample	Percent Greater
Montana	2	294	27
North Dakota	2	1239	13
South Dakota	1	726	3
Wyoming	1	157	41
Colorado	3	719	5
Kansas	2	347	50
Oklahoma	3	479	34
Pooled Sample	14	7252	10%

[1] An unknown number of *G. c. rowani* is included in these samples (Buller 1967).

Buller (personal communication) estimates that greater sandhill cranes constitute less than 1 percent of the annual harvest in the United States, Canada and Mexico. As a result of Buller's (1967) analysis, additional open seasons were authorized in areas of eastern Colorado in 1967 and in North Dakota, South Dakota and Oklahoma in 1968.

It is unlikely that reducing the total size of the migratory population of sandhill cranes would be an effective means of alleviating crop depredations unless the species were nearly eliminated. A flock of a few hundred cranes can cause significant damage to an individual farmer and the problem of wildlife damage is its effect upon individuals rather than its total effect upon the economy. Yet fall concentrations of over 35,400 cranes have been recorded in the Last Mountain Lake-Quill Lake region of Saskatchewan (Buller 1967) and as many as 207,500 cranes, or more than 69 percent of the total migratory population, have been observed in one census of the Platte River staging area in Nebraska <Table 1). Obviously, an extremely drastic reduction in the total population would be required to eliminate or significantly reduce the impact of local concentrations of sandhill cranes.

Stephen (1967) has shown that crop depredations can be reduced by the combination of lure crops and acetylene exploders and concluded that hunting is not an effective management practice. He noted, however, that sandhill crane hunting has a significant recreational value and recommended that it be developed further. Buller (1967) found that open seasons have tended to reduce the number of crop damage complaints from farmers in the United States, even though there is no evidence that crop damage has been reduced by a factor which is related to the numbers of cranes harvested, but also noted that the hunting of sandhill cranes provides a considerable amount of recreation.

'Although there has been no stated change in policy, it would appear that the management of sandhill cranes has shifted from efforts to reduce agricultural damage to hunting for recreation. The importance of this development is that it exposes a relatively scarce resource, whose demographic characteristics are not well known, to a different set of pressures and management decisions. Recreational hunting has led to requests for more liberal seasons and bag limits, and for open seasons in additional states and provinces. Some of these requests have been granted and others are pending. As long as there appears to be adequate protection for the greater sandhill crane and the whooping crane, the question of more liberal hunting regulations rests upon the amount of hunting the total migratory population can withstand. This is a judgment which must be made on the basis of available data, which may be inadequate, and which is subject to political pressures from states and provinces that want their "fair share" in the utilization of this resource. Experience has shown that these pressures are difficult to resist, especially when the species seems to be locally abundant and there is no evidence to show that it would suffer from additional hunting.

The sandhill crane is a long-lived bird with deferred breeding and a relatively low replacement rate. Sexes and sex ratios cannot be determined by field observation and juveniles cannot be identified by plumage and body size after their first year. Moreover, there are no breeding data for populations that nest in the arctic where ecological factors are undoubtedly more variable and more extreme than at southern latitudes, and demographic parameters such as clutch size, hatching success, sources of juvenile mortality and fledgling success must be inferred from data on other species, or from the relatively few populations of sandhill cranes that have been studied at more southern latitudes. Nor can we assume that conventional management practices which are applicable to other waterfowl are equally applicable to sandhill cranes. There is the possibility, for example, that a species with the demographic characteristic of the sandhill crane could enter into a long-term decline in population size before the evidence of such a decline was detected, and that the species might become endangered before it was returned to protected status.

Systems analysis and simulation models seem particularly suited to this type of management problem. Complex historical processes in which relevant variable change over long periods of time can be treated with systems analysis and recurrence formulae to predict the results of different management decisions (Watt 1966). This is particularly useful when a management decision such as the maximum allowable harvest may have a long-term or delayed effect on the behavior of the system. In this paper we have used the best available data to develop a simulation model that predicts the long-term effects of different levels of hunting upon the migratory sandhill crane population.

DEMOGRAPHIC PARAMETERS

Longevity

Walkinshaw (1949) compiled records of the maximum longevity of several species of captive cranes, some of which lived for more than 40 years; however, the maximum for most species is between 20 and 30 years and the oldest recorded sandhill crane was 24 years. Walkinshaw (1949) therefore estimates the maximum longevity of sandhill cranes to be from 20 to 25 years, which is probably a generous estimate for natural populations.

Age at First Breeding

Deferred breeding is presumably related to the better ability of older birds to successfully rear young (Lack 1966, 1968) and frequently occurs in long-lived species. For example, white storks (*Ciconia ciconia*) have lived for almost 20 years in nature and those which breed in their third year raise significantly fewer young than those that breed in their fifth year (Lack 1966). Common cranes (*Grus grus*) have been known to lay eggs when they are three years old but the average for this species in zoos is closer to six years (Griswold 1962, in Walkinshaw 1965d). There are no comparable records for sandhill cranes but Walkinshaw (1965d) estimates that they usually reach sexual maturity in their fourth year.

Clutch Size

Table 4 shows the clutch sizes recorded for 375 nests from localities within the breeding ranges of the greater and the Florida sandhill crane. Clutches of one and three eggs are uncommon and most nests for which the number of eggs in each nest was recorded (93 per cent) contained two eggs. Although several species of birds lay larger clutches of eggs at northern than at southern latitudes (Van Tyne and Berger 1959), the small range of variation above and below the mean clutch size of 1.89 in Table 4 suggests that the average clutch size of arctic-breeding sandhill cranes is probably less than two eggs.

Fledging Success

The effects of weather on arctic-breeding populations of sandhill cranes is unknown, although Novakowski (1966) found that inclement weather in May and June may result in poor nesting and hatching success and heavy precipitation

TABLE 4. CLUTCH SIZE OF SANDHILL CRANES.

Locality	Number of Nests	Number of eggs in nest 1	2	3	Total Eggs	Mean Clutch Size	Authority
Oregon	36	0	35	1	73	2.03	(Walkinshaw 1949)
Oregon	108	9	99	0	207	1.92	(Littlefield and Ryder 1966)
Michigan	133	4	121	1	249	1.87	(Walkinshaw 1965b)
Florida	34	6	28	0	62	1.82	(Walkinshaw 1949)
Florida	64	—	—	—	118	1.84	(Thompson 1970)
	375	19	283	2	709	1.89	

in July may lead to high juvenile mortality in whooping cranes. However, intrinsic factors may also play an important role in fledging success.

In a study of the population dynamics of whooping cranes on their nesting grounds in Wood Buffalo Park, Novakowski (1966) observed that each nest invariably contained two eggs, but that shortly after the first young hatched the other egg or its chick disappeared. He concluded that either both eggs hatch and one young soon dies, or that the second egg is destroyed after the first young is hatched. Of a total of 74 eggs laid in 12 years (1954-1965) by whooping cranes at Sass River, N.W.T., 39 hatched and only 32 young survived to fall migration. This represents a combined hatching and fledging success of 43 percent.

Hyde (1957) observed that the first sandhill crane to hatch from a clutch will often attack and kill its younger sibling and J. J. Lynch (personal communication) has found, in attempts to propagate sandhill cranes in captivity, that the antagonism between two chicks in any one brood is "almost frightening." On the basis of his observations of captive cranes, Lynch suggests that a fall census of family groups of sandhill cranes might show that only one young survives per brood. Observations by W. J. D. Stephen and the senior author in Saskatchewan tend to confirm this suggestion.

It is believed (Lack 1966) that asynchronous hatching in raptors and other birds has evolved to guarantee the successful fledging of only as many young as the parents can adequately feed, and that it is a means of increasing the potential for survival of those offspring that are fledged. Excess young are either killed or are allowed to starve in years when food supplies are inadequate. Selective pressures on the ability of cranes to raise more than one young with a high probability of subsequent survival may have led to sibling antagonism as the mechanism which results in the survival of only one young in most broods. If this has become a fixed behavior pattern, it obviously places severe limitations on the reproductive potential of these species, in that it reduces or eliminates the possibility of larger broods during favorable years, and the "effective" clutch size is actually one rather than two (Miller *in prep.*).

Annual Recruitment

Walkinshaw (1965c) recorded the breeding success of a population of greater sandhill cranes in southern Michigan and found that 45 pairs produced an average of 0.8 young per pair from 1952 to 1958. These observations were of breeding pairs and there is no information as to whether a non-breeding surplus existed in the total population of this region.

For no apparent reason, the productivity of this population decreased in 1963 and 1964 to 0.5 and 0.3 young per pair respectively. Annual recruitment therefore decreased from an average of 40.0 percent of the breeding pairs from 1952 to 1958 to 15·.2 percent in 1964. Walkinshaw (1965c) suggested the possibility of pesticide residues as a cause for reduced breeding success, but no analyses were made of birds from this population. Recent studies by Lewis (1970ab) have shown that sandhill cranes collected in Florida and Nebraska have relatively low amounts of pesticide residues in their tissues, but cranes collected in Oklahoma averaged 1.4 ppm DDT, 0.75 ppm DOE and 19.0 ppm Heptachlor Epoxide, while individual cranes from Oklahoma had residues as high as 7.8 ppm total DDT and 35.3 ppm Heptachlor Epoxide. While there is presently no evidence of a general decline in breeding success or of egg shell thinning due to pesticides, it is a possibility that should be carefully monitored.

A population of greater sandhill cranes on the Malheur Refuge consisted of about 320 breeding adults that produced between 35 and 45 young, or about 0.4 young per breedIng pair (Littlefield and Ryder 1966). About 25 percent of the total population on the refuge did not breed and annual recruitment was estimated to be 12 percent. Between 1954 and 1965 an average population of 28 whooping cranes produced 61 young that successfully completed their first fall migration. This was an annual recruitment of 0.4 young per pair per year, or an average of 17.8 percent for the total population. During this period there was a 34.4 percent increase, or about 1 adult per year, in the total population (Novakowski 1966).

In the preceeding section it was noted that sandhill cranes and whooping cranes seldom, if ever, produce more than one young. This suggests that the proportion of breeding pairs in the population may have a much greater effect on annual recruitment than the number of young raised per breeding pair, although hatching failure or poor survival of young from hatching to fledging may also be significant. The number of suitable nest sites, the number of pairs nesting, hatching success and survival of young could be strongly affected by weather, for which there are no data for arctic-nesting sandhill cranes, although Novakowski (1966) suggests that heavy snowfalls in May appear to reduce nesting success of whooping cranes and heavy precipitation in July causes high mortality of young.

Estimates of annual recruitment based on age ratios in game bag checks are probably not reliable, as they are biased by differential risk of juveniles and adults to hunting mortality. However, Boeker, Aldrich and Huey (1961) reported 22 percent juveniles among 137 cranes checked during the experimental hunting season in New Mexico in 1961. During the 1964 and 1965 hunting seasons in Saskatchewan and Manitoba the percentage of juveniles varied from as low as 15 percent of 343 birds checked in Saskatchewan to 40 percent of 73 birds: in Manitoba (Stephen, Miller and Hatfield 1966). Statistical tests of these data showed that annual recruitment may be as low as 11 percent.

TABLE 5. AGE RATIOS OF SANDHILL CRANES IN SASKATCHEWAN (DATA FROM STEPHEN, MILLER AND HATFIELD 1966; AND HATFIELD 1966, 1967).

Year	Hunted Sample Total	Hunted Sample Percent Juveniles	Ground Census Total	Ground Census Percent Juveniles
1961	32	22		
1962	69	17		
1963	62	13		
1964	360	19		
1965	343	13		
1966	520	19	1037	4
1967	171	20	1668	6
Pooled	1557	17%	2705	5%

In the fall of 1966 and 1967 Hatfield (1966, 1967) conducted ground counts of juveniles and adults prior to and during the hunting seasons at Last Mountain Lake, Saskatchewan. Table 5 shows the percentage of juveniles in hunted samples from 1961 to 1967 and the results of the ground counts in 1966 and 1967. The proportion of juveniles in the hunted samples varied from 13 to 22 percent with a pooled average of 17 percent. During the years when ground counts showed 4 and 6 percent juveniles, the hunted sample contained 19 and 20 percent respectively. Band returns from Canada geese (*Branta canadensis*) indicate that first-year birds are almost twice (1.6 times) as vulnerable as adults to hunting mortality (Grieb 1970) and returns from white-fronted geese showed that juveniles are 2.3 times more vulnerable (Miller, Dzubin and Sweet 1968). Field observations confirm that juvenile sandhill cranes are less expert flyers and are less wary than adults. Lynch (1964) observed that young-of-the-year in fall-migrant populations of sandhill cranes may experience considerable difficulty in controlling their flight and landing in strong winds. Our observations are that young sandhill cranes will often continue on a course over an observer or hunter after the adults in a flock have flared, making them much more liable to be shot. If the data in Table 5 provide a reliable comparison between age ratios in the migrant population and the proportion of juveniles in a hunted sample, juvenile sandhill cranes are at a 4 times greater risk of hunting mortality than adults.

Natural Mortality

Sandhill cranes have not been banded in sufficient numbers to provide reliable data on sources or rates of mortality, but if the greater sandhill cranes studied by Littlefield and Ryder (1966) constituted a stable population and natality and mortality were equal, the average annual mortality rate was about 12 percent.

In one of the few long-term population studies of a large bird with deferred breeding, Zink (1966) found that the mortality rate of one and two-year old white storks was about 30 percent, and probably higher, and the average annual mortality rate of mature adults was about 21 percent. The adult mortality rate was apparently the same for breeding and non-breeding birds. Lack (1966) considers this a very high rate for a species in which breeding is deferred until an age of three to five years, the mean expectation of life is only about 4½ years, and a pair can raise an average of two young per year. For example, the Procellariiformes have a clutch size of one egg, deferred breeding and relatively low annual mortality rates. Manx shearwaters *(Procellaria pufJinus*) which first breed when they are six and have an annual mortality rate of 7 percent with an expectation of funher life of about 14 years (Lack 1966). During 12 years (1954-1%5) of records for the whooping crane, first-year mortality has averaged 25 percent and adult mortality 11 percent (Novakowski 1966). The population increased from 21 to 32 birds (34 percent) in this period.

It is usually assumed that birds have an approximately constant rate of annual mortality throughout adult life, after they have reached breeding age (cf., Deevey 1947, Lack 1966). This assumption has been based on complete life tables for only a few short-lived species with relatively high mortality rates. Botkin and Miller (in press) have shown, however, that an age-independent mortality cannot be assumed for long-lived birds with adult mortality rates of about 15 percent or less, as the potential natural mortality which would theoretically result from such low mortality rates is inconsistent with the known maximum longevity and age distribution of these species. This is certainly the case with sandhill cranes, and in a later section we will develop an age-dependent mortality which is consistent with the other parameters of a stable population.

Hunting Mortality

The available estimates of the annual hunting harvests in New Mexico, Texas, Saskatchewan and Manitoba are shown in Table 6. These estimates are based on random mail surveys of license holders. The combined average harvest for the states and provinces shown in Table 6 is 6552 cranes, or 2 percent of the migratory population. However, an increase in the area of hunting and more liberal regulations have resulted in larger annual harvests in recent years. Hunter success in New Mexico has remained near an overall average of 0.90 cranes per hunter since the first open season in 1961 (Merrill 1969, 1970), but increased from 0.36 to 0.94 in Saskatchewan between 1964 and 1967. The increase in Saskatchewan is at least partly due to enlarging the area of hunting from restricted portions of two game management zones to all of five zones and raising the bag limit from two to four. The harvest in Nonh Dakota increased from 50 in 1968, when the season was

TABLE 6. ESTIMATED ANNUAL HARVEST OF SANDHILL CRANES IN NEW MEXICO, TEXAS, SASKATCHEWAN AND MANITOBA.

Year	New Mexico	Texas[2]	Saskatchewan[a]	Manitoba[3]
1961	1014	1200		
1962	1224			
1963	1042			
1964	1246		3030	143
1965	631			
1966	514			
1967	697	1070	1046	262
1968	1076	1339	2300	322
1969	1212	991	3790	654
1970	1805	2000	5046	298
Mean	1046	1350	3748	408

1 D'ata from Merrill (1967, 1968, 1969, 1970, 1971).
2 Data from Buller (personal communication) .
3 Data from Benson (1968, 1969, 1970, 1971) and Stephen, Miller and Hatfield (1966) .

first opened (Schroeder 1970), to 300 in 1969 (Schroeder 1971) and 500 in 1970 (Buller personal communication). This increase was due to greater hunter interest and enlarging the area of hunting from two to four counties (Schroeder 1971).

The combined annual harvest for Colorado, North Dakota, South Dakota and Oklahoma in 1970 was 675 cranes (R. J. Buller personal communication). Therefore, the total annual harvest for the United States and Canada in 1970 was over 9800 cranes. There are no data for Mexico, where the annual harvest mayor may not be significant.

Most sandhill crane hunting is "pass shooting" between roosts and fields, often at refuge boundaries. The result is that hunters often take long shots at birds that are beyond effective gunshot range, and when hunters are "backshooting" cranes returning from fields to roosts inside refuges the wounded birds cannot be retrieved. Grieb's (1970) data on crippling loss of Canada geese for a 13-year period in nine counties in southeastern Colorado show that an estimated 42,603 geese \vere crippled and not retrieved in a total kill of 176,370 birds. Thus there was a crippling loss of 24.2 percent of the total harvest. Fluoroscopic examination of geese from this area also showed that 46 percent of 4291 birds examined carried body shot (Grieb 1970). Rutherford (1970) analysed the results of "firing line" hunting, \vhich is more nearly comparable to most sandhill crane hunting, and estimated that there was a 38 percent crippling loss of geese at Two Buttes, Colorado. In this paper we have assumed a 30 percent loss of sandhill cranes from crippling and illegal hunting. This value applied to the average annual harvest would amount to 1966 cranes, or a total hunting mortality of 8518, which is 2.8 percent of the migratory population. The same rate of loss applied to the estimated harvest for 1970 would amount to 2947 birds, or a total hunting mortality of 12771. This is 4.3 percent of the migratory population.

We have deliberately selected the most favorable values for the parameters in this population model, so that the results of our simulations will provide conservative projections.. We have accepted, for example, an estimate of approximately 300,000 for the total migratory population and a life-span of 20 years, both of which are probably generous. In a recent article which took a more critical view of the management of sandhill cranes, Sherwood (1971) arrived at a different set of assumptions. He used the data shown in Table 1 to estimate a total population of about 200,000. He also estimated the annual harvest to be about '12,000 with a crippling loss of 30 percent, or 9 percent of the total population, and concluded that the annual harvest is almost equal to annual recruitment.

In the simulations in the following sections, we will test the effects of annual harvests of from 4 percent of the total population, which is our approximate estimate of the current harvest, to 10 percent, which is slightly greater than Sherwood's estimate; but these simulated hunting pressures will only be applied to a population with the parameters shown in Table 7, and we have no direct evidence to show that the more favorable values we have selected are more valid than those estimated by Sherwood (1971).

THE POPULATION MODEL

Approach to Simulation

The meagre data which are currently available regarding the present population of sandhill cranes will only support the simplest of population models. The goal of our simulation is, therefore, to examine the limitations and implications of these data with respect to generally accepted theories of avian population dynamics, and to extend them with simple yet reasonable assumptions where accepted theory seems limited or incorrect. Beginning with a basic model; we have created a number of small, simple computer programs of two kinds: (1) we have developed an equilibrium population which is consistent with the estimated parameters of the natural population, and (2) have examined various hunting regimes for this population. We use these simulations not for the purpose of actual prediction, but to illustrate how little is known and what kinds of information are essential to reasonable management of the sandhill crane population.

All computer programs were designed for interactive use. They were written in Fortran IV and have been operated successfully on an IBM 360/67 computer under CMS (Cambridge Monitor System). Simplicity and brevity, along with interactive capabilities, allowed us to examine each stage of the model from a biological point of view, and to extend it quickly and easily by re-programming via the interactive terminal. The model was built step by step and new characteristics were added only as they were necessary, or were useful to illustrate a point. The result is a program that can serve as a management game, allowing examination, of the best available information and theory, yet easily adjustable to new data and concepts. While in some ways this approach may seem mathematically naive, it places the model-building emphasis on biological and ecological factors, and serves as an appropriate tool for the study of populations that are hunted by man and might be threatened with extinction.

The Characteristics of the Model

The model assumes that spatial differences in the harvested segment of the migratory sandhill crane population can be ignored, and one set of parameters will describe the entire population in anyone year. Except for hunting, the size of the population changes primarily as a result of intrinsic events and the intra-population relationships are described with the simplest assumptions which will account for all observed changes. The model discriminates between age classes but assumes an equal sex ratio. It makes no allowances for the effects of an unstable environment, even though stochastic events undoubtedly affect breeding success and natural mortality, and are important factors in the population dynamics of arctic-nesting sandhill cranes. If relations between environmental conditions and recruitment and survival had been available, such stochastic effects could have been easily added to the model. However, lacking better data, we have developed an equilibrium population by assuming the parameters for maximum life span, age at first breeding, annual recruitment and density-independent mortality sho\vn in Table 7, and varying the values for density-dependent mortality and age-dependent mortality to achieve a combination of rates which is realistic and which would allow an initial population of 100 cranes to grow to an equilibrium population of about 300,000.

TABLE 7. PARAMETERS USED TO MODEL POPULATION.

Parameter	Value
Equilibrium Population Size	290,310
Maximum Life Span (years)	20
Age at First Breeding	4
Annual Recruitment (Percent of Breeding Population)	0.30
Density-Independent Mortality	
0-1 years	0.30
2 - 20 years	0.06
Density-Dependent Mortality	
0-1 years	2.4×10^{-7}
2 - 20 years	6.0×10^{-8}
Age-Dependent Mortality	0.013

Annual Recruitment

Reproduction is dealt with as recruitment to the fall population and is characterized in this model as a single process which depends upon the size of the breeding population, but which is corrected to account for summer mortality. Thus, the number of individuals recruited to the population is the net number surviving to join the fall migration. This avoids the problem of attempting to model events such as hatching and fledging success, which are poorly known, especially for arctic populations (the reader should be aware that these events might include density-dependent factors that could be important, but for which we have no data). Therefore

$$N_1 = b \sum_{i=4}^{20} N_i \qquad (1)$$

where N_1 is the number of cranes in their first year added to the fall population, N_i is the number of cranes in the ith age class, and b is the recruitment rate. With the age structure that results from a maximum life span of 20 years and reproductive maturity at age 4, an annual recruitment rate of 30 percent of the breeding population amounts to approximately 18 percent of the total population, which may, for reasons described earlier, be an overly generous estimate of annual recruitment.

Natural Mortality

We have assumed that natural mortality for first year and adult birds might occur in three different ways: (1) density-independent mortality, μ, which is a normal and constant rate of deaths which occur from accidents, predation and old age; (2) density-dependent mortality, β, arising from crowding or other social stresses; and (3) an adult age-dependent mortality, α, consistent with the first two rates and the maximum natural longevity of the species (see Botkin and Miller *in prep.*).

We assume that μ and β are constant for age classes 2 to 20 but have different values, μ_1, and β_1, for age class 1. In each case the age-dependent survivorship rate, S, is calculated for each simulated year as

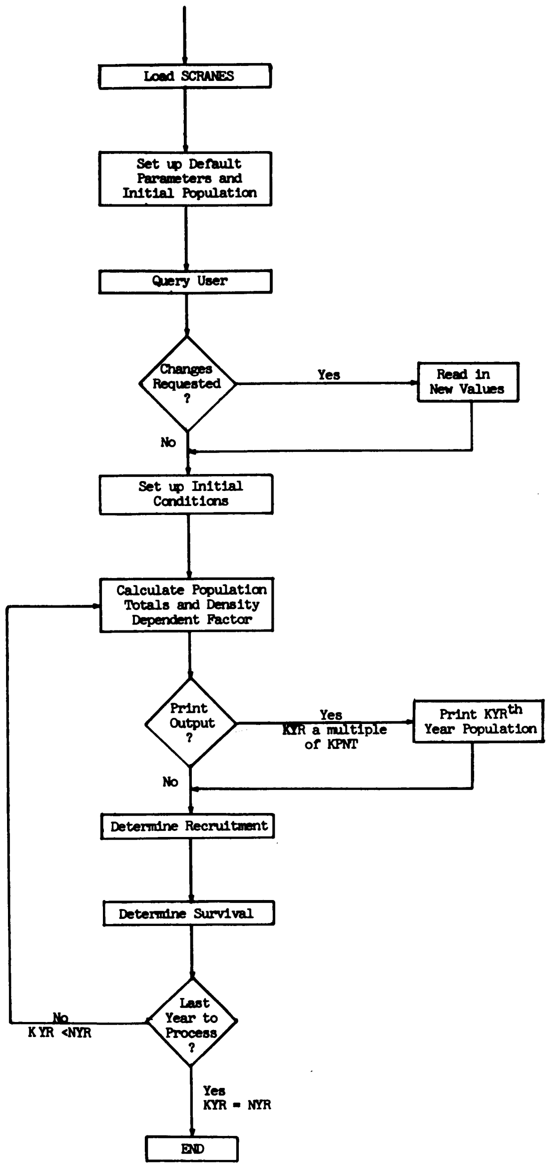
$$S = 1.0 - (\mu + (\beta N)) \qquad (2)$$

where N is the total population and μ and β are defined as above. Equation (2) is used to determine the fraction of the previous year's age class 2 that survives into the present year. Similarly, with μ_1 and β_1 substituted for μ and β, equation (2) determines the fraction of the previous year's age class 1 that survives into the present year. Each older age class i is subject to an age-dependent survivorship rate, Si, calculated as

$$S_i = S - \alpha \qquad (3)$$

where α is the age-dependent constant.

Flowsheet of SCRANES



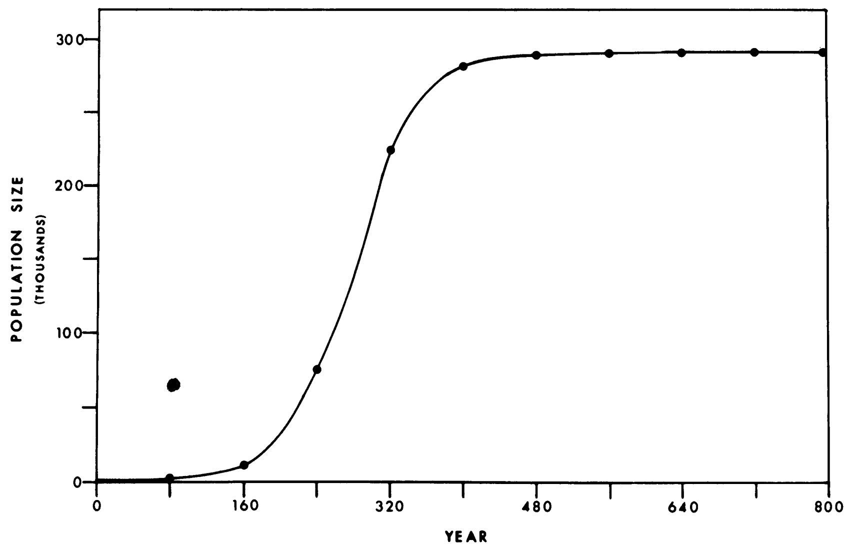
The density-independent and age-independent rates of 0.30 for juveniles and 0.06 for birds two years old and older (Table 7) are reasonably consistent with the available data for sandhill cranes and for birds of similar size with deferred breeding and a maximum longevity of about 20 years. Obviously this model is highly sensitive to density-dependent and age-dependent mortality rates and would stabilize at greatly different levels, depending upon these values. The combination of these two rates shown in Table 7 was arrived at through trial and error to obtain values which gave the best results for population growth and a stationary population of about 300,000. The reader should realize these are arbitrary adjustments for the purpose of illustration.

The Equilibrium Population

A flow chart of the equilibrium population model is shown in Figure 8. Table 8 illustrates the development of an equilibrium population with the parameters given in Table 7 from an initial 100 cranes of age class 4. As it is constrained to do, the growth of this population (Fig. 9) follows a logistic curve, growing slowly at first and requiring 160 years to reach 11,000 cranes, then growing rapidly to year 400, when it reaches 97% of its final value, and approaching this final value slowly over the next 400 years. Of course, one would expect that natural stochastic events such as fluctuations in climate would mask much of this final phase of the curve in a real population, and it is reasonable to conclude that a real population, which fit this model and the parameters in Table 7 would appear to have reached equilibrium in 400 years. As a simple test of the stability of the model, the population was perturbed to 500,000, after which it returned to within 5 percent of the equilibrium value in 80 years, and within 1 percent in 160 years.

TABLE 8. GROWTH AND DEVELOPMENT OF A STATIONARY POPULATION OF 290,310 FROM AN INITIAL POPULATION OF 100 CRANES.

Year	Annual Recruitment	Breeding population	Total population
80	203	696	1164
160	1839	6297	10526
240	13395	45597	76136
320	40443	135692	225991
400	50904	169817	282540
480	52212	174052	289549
560	52340	174468	290237
640	52352	174508	290303
720	52353	174511	290309
800	52353	174512	290310



The model we present is as detailed as present knowledge concerning the population dynamics of the sandhill crane allows. Although relationships no doubt exist in the real population which this model omits or only crudely approximates, even this limited model can help focus our thinking and point out the crucial gaps in our knowledge about the population dynamics of sandhill' cranes. The relative sensitivity of the model to changes in each parameters may help suggest the kind of information that is most crucial to reasonable management of this species.

Table 9 shows the effect on the equilibrium population of each parameter given in Table 7. It is mathematically obvious that the model does not have a unique solution. Trial 2 (Table 9) shows that using the upper limit of estimates of recruitment rate and adult mortality can produce an equilibrium population essentially identical in total number with that in trial 1. Similarly, a low estimate of recruitment rate and adult mortality (trial 3) will also produce an equilibrium value near 300,000. The age class distribution of the population is different in each case, however, and each case implies a different management program.

While we found no data that would allow us to test the realism of the time required for the population to reach 95 percent of its equilibrium value, this factor

TABLE 9. EFFECTS OF CHANGES IN PARAMETERS ON EQUILIBRIUM CONDITIONS OF MODEL.

Trial	b	$\mu 1$	μ	$\beta 1$	β	α	E	T′	Deviation
1	.30	.30	.06	2.4×10^{-7}	0.6×10^{-7}	0.013	290310	400	—
2	.40	.30	.10	2.4×10^{-7}	0.7×10^{-7}	0.013	291791	400	<.01
3	.25	.21	.05	2.4×10^{-7}	0.6×10^{-7}	0.013	317735	400	0.09
4	.35						481662	250	.66
5	.33						409254	300	.41
6	.31						331455	350	.14
7	.29						247532	450	.15
8	.27						155375	700	.47
9		.33					230120	500	.21
10		.31					270313	400	.07
11		.29					310239	400	.07
12		.27					349901	350	.21
13			.07				202654	550	.30
14			.066				238026	500	.18
15			.054				342211	350	.18
16			.05				376596	300	.30
17				2.64×10^{-7}			277023	400	.05
18				2.16×10^{-7}			304900	400	.05
19					0.66×10^{-7}		275921	400	.05
20					0.54×10^{-7}		306245	400	.06
21						0.0143	248387	450	.15
22						0.0117	333097	350	.15

Line 1 gives values used in simulated hunting (Table 7). On all other lines, parameters have these values unless otherwise noted. E = the equilibrium population, b = recruitment rate, μ = density independent mortality, β = density dependent factor and α the age dependent factor. The subscript 1 denotes values for age class 1. T′ is the number of years for the population to reach 95% of the equilibrium value when started with 100 individuals of age class 4. Deviation is the absolute value of the difference between the line 1 population and the i^{th} line divided by the line 1 population.

is relatively insensitive to small changes in the values of most parameters. Except for β and μ a 10 percent change in any of the parameters affects this time by 50 years, or one output interval in the simulations used to generate Table 9.

As one might expect, the effect of changing a parameter is generally symmetric; that is, the absolute value of a deviation of the population is similar for an equal increase or decrease in the parameter. Also the population is very sensitive to changes in these factors; a 10 percent change in β, the recruitment rate, changes the equilibrium population by more than 100,000, and a change in μ from .05 to .07 percent changes the equilibrium population from 377,000 to 203,000. Also, a 10 percent change in μ_1, μ and α changes the equilibrium population by approximately 60,000, 50,000 and 40,000 respectively.

The accurate determination of these factors is clearly important to an understanding of the natural population dynamics and to successful management of this species. The best management program would initiate experimentation with small populations of sandhill cranes to determine the effects of age and density on recruitment and survival. For example, one needs to determine if there is a fixed number of breeding sites, if clutch size or fledging survival increases at low population densities, if adult survival decreases linearly with density, and if so at what rate.

SIMULATED HUNTING

In the following simulations we have projected a management program of 100 years with the data shown in 10-year intervals. Unless otherwise specified, the parameters in the simulations are the same as those shown in Table 7. A flow chart of simulated hunting is shown in Fig. 10. These projections are made merely to illustrate a variety of possible hunting situations and to show the limitations and implications of the existing data; it should be clear that the projections should not be taken literally.

Obviously, when the combination of natural mortality and hunting mortality exceeds annual recruitment, the population will decline. The parameters in Table 7 provide a surplus of about 4 percent, and hunting at this rate or higher would of decline under a variety of hunting regimes.

Percent Annual Harvest

If we assume that hunter success and the number of hunters are directly related to the size of the crane population, the annual harvest might be a constant percentage of the population. Table 10 shows the results of annual harvests of 4, 6, 8 and 10 percent of the population in the year of harvest (e.g., standing crop). The number of years required for the population to reach extinction was determined for a maximum of 800 years.

With an annual harvest of 4 percent of the population, there is a fairly gradual decline in population size and the population still contained 64 cranes after 800 years. After 40 years of hunting at this rate the population was still above 100,000 cranes with an annual harvest of over 4,000. When the annual harvest is increased to 6 percent, only 20 years are required to reduce the population to about 120,000 birds and extinction was reached in 460 years. A 10 percent annual harvest would reduce the population to 62,000 in 20 years and it would be extinct in 200 years if hunting continued at this rate. As might be expected with a harvest rate which is a percentage of the total population, there is a fairly rapid decline in population size initially but total extinction requires many years.

Constant Annual Harvest

It was noted earlier (see Table 1) that sandhill cranes concentrate in large numbers at staging areas during migration and almost 70 percent of the migratory population has been observed at one time on the Platte River in Nebraska. Most hunting of sandhill cranes occurs along the Central Flyway where the cranes

Flowsheet *ot* HCRANES

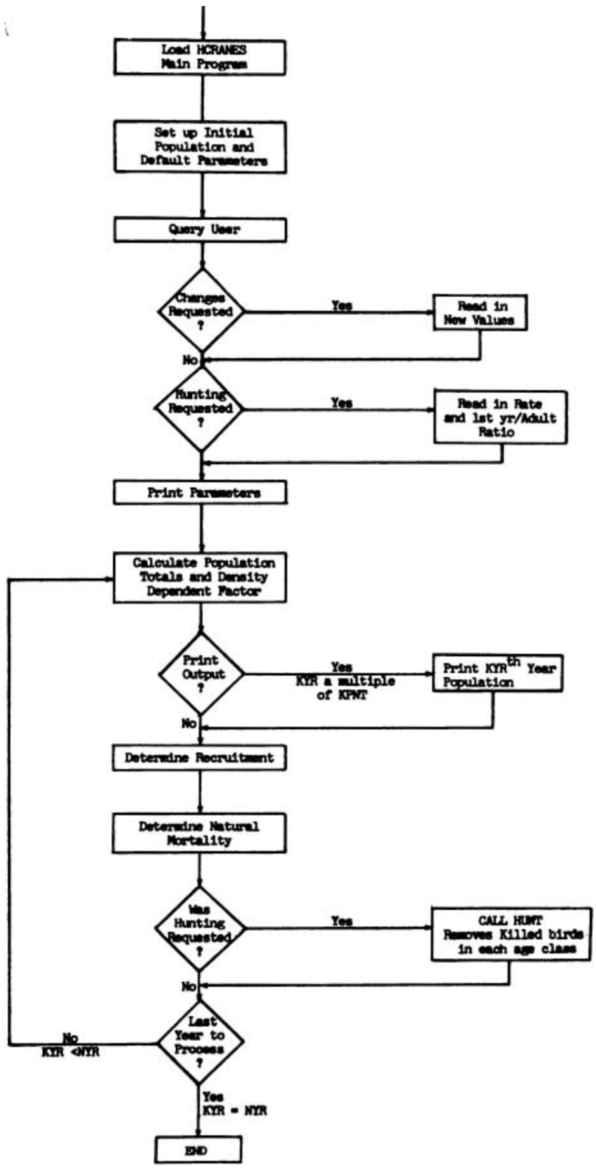


TABLE 10. PERCENT ANNUAL HARVEST.

Percent harvest:	4%		6%		8%		10%	
Year	Population size	Annual harvest	Population size	Annual harvest	Population size	Annual harvest	Population size	Annual harvest
1	290310	0	290310	0	290310	0	290310	0
10	214815	8857	183861	11556	156847	13364	133362	14450
20	163403	6703	120655	7497	87121	7370	62483	6721
30	129717	5302	82510	5132	51053	4302	30843	3306
40	105946	4320	58460	3627	30767	2587	15584	1667
50	88318	3595	42255	2617	18842	1582	7965	851
60	74760	3039	30959	1915	11649	978	4094	438
70	64041	2600	22901	1416	7244	608	2111	226
80	55381	2247	17056	1054	4521	379	1090	116
90	48263	1957	12767	788	2827	237	563	60
100	42327	1715	9591	592	1771	148	291	31
Year of extinction:	800+		458		276		197	

concentrate, and the bulk of the population is presumed to occur in Texas and New Mexico during the hunting season. Although local crane marshes may be "burned out" (Sherwood 1971), in that the cranes move to other areas when hunted excessively, they remain concentrated in large flocks and are more vulnerable than most species to heavy hunting mortality. We might assume, for lack of evidence to the contrary, that hunter success and the annual harvest are relatively independent of population size and would remain more or less constant until the population was reduced to very low numbers. This is probably a more realistic assumption for the nature of the harvest than an annual harvest which is a constant percentage of the total population.

TABLE 11. CONSTANT ANNUAL HARVEST OF 4, 6, 8 AND 10 PERCENT OF INITIAL POPULATION OF 290,310 CRANES (PARAMETERS AS IN TABLE 7).

Annual harvest	Year: 1	10	20	30	40	50	Extinction (year)
4% (=11612)	290310	203034	116130	25255			33
6% (=17419)	290310	158032	16490				22
8% (=23225)	290310	112136					17
10% (=29031)	290310	65355					14

Table 11 shows the results of constant annual harvests of 4, 6, 8 and 10 percent of the initial population of 290,310 cranes. Because of the rapid extinction of the populations under these conditions the simulations are only shown for 50 years. With an annual harvest of 4 percent of the initial population (=11,612 cranes), the population is reduced to about 25,000 in 30 years and becomes extinct in 33 years. At the high rate of 10 percent (=29,031 cranes), which is approximately the rate estimated by Sherwood (1971) for a smaller initial population, the total population is reduced to only about 65,000 birds in 10 years and becomes extinct in 14 years. However, if the recruitment rate were .35 rather than .30, and if mortality were lower than is assumed in Table 7, the population could be in equilibrium with a harvest of about 12,000 birds per year (Table 12).

TABLE 12. CONSTANT ANNUAL HARVEST OF 4 PERCENT OF INITIAL POPULATION WITH ALTERED PARAMETERS.

b	$\mu 1$	μ	$\beta 1$	β	α	Year 1	10	20
.35	.25	.05	2.4×10^{-6}	6×10^{-7}	0.013	290310	294600	301900
.35	.30	.03	2.4×10^{-6}	1×10^{-7}	0.013	290310	290000	289000

It is evident from these calculations that present information does not allow us to determine whether the population is or is not in equilibrium with present hunting practices, as population characteristics within a reasonable range of estimates allow both predictions. Obviously, a more accurate determination of these characteristics is needed for a reasonable management program.

Hunter Success

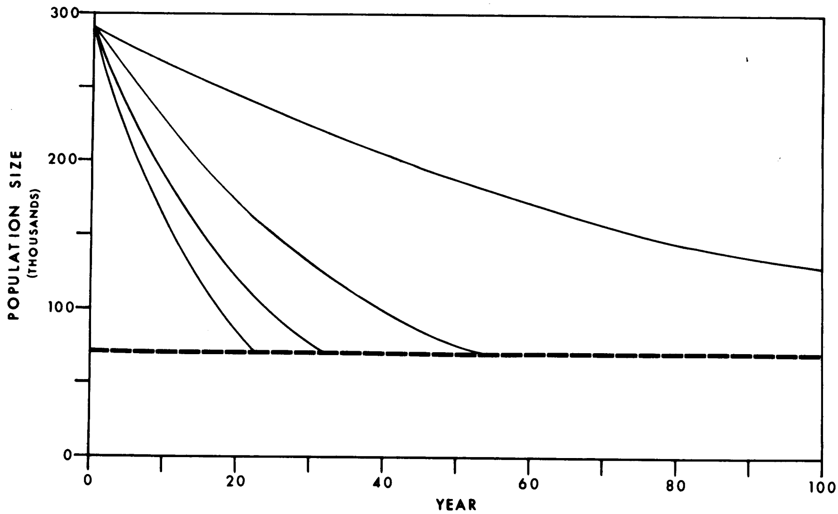
A constant annual harvest of the type shown in the previous section assumes that hunting will continue at the same level of efficiency, regardless of population size, even at low population levels. While this is basically a more realistic assumption than an annual harvest which is a constant percentage of the population, it is doubtful that hunter success and hunting efficiency would remain constant in a declining population.

Hunter success, expressed as the number of cranes shot per hunter, has averaged about 1.0 in New Mexico; in Saskatchewan hunters shot an average of 0.34 cranes per hunter when hunting first began in that province but the success rate has recently averaged about 1.0 also (Hatfield 1966, 1967). Several factors could affect the annual harvest of a declining population. If a population decrease resulted in reduced hunter success the same number of license holders might be content to shoot fewer birds and continue hunting; or the number of hunters might be reduced because of loss of interest, leaving a hard core of crane hunters who were more successful than the average. Hunter interest is also affected by the size of the bag limit, which seems to have contributed to the increase in hunter success in Saskatchewan (Hatfield 1967).

Let us assume (1) that hunter success is 1.0 at the equilibrium level of 290,310 cranes, (2) that hunter success decreases linearly with the size of the population, (3) that the annual harvest is directly related to hunter success, and (4) that hunting continues until the success rate is reduced to 0.25. This relationship is shown diagramatically in Fig. 11. The population behaves the same as it did in previous cases until it reaches the level of 25 percent of the equilibrium population, after which it fluctuates above and below the 25 percent level (Fig. 12).

Juvenile Vulnerability to Hunting

In all preceding simulations we have assumed that juveniles are 3 times as vulnerable as adults to hunting mortality (Table 7), although there is evidence from comparisons between ground counts and hunted samples that they might b.e 4 times as vulnerable. Table 13 shows the results of simulations of a constant annual harvest of 4 and 6 percent of the initial population for different ratios of juvenile to adult vulnerability to hunting.


300
200
100
0
POPULATION SIZE
(THOUSANDS)
0
20
40
60
80
100
YEAR

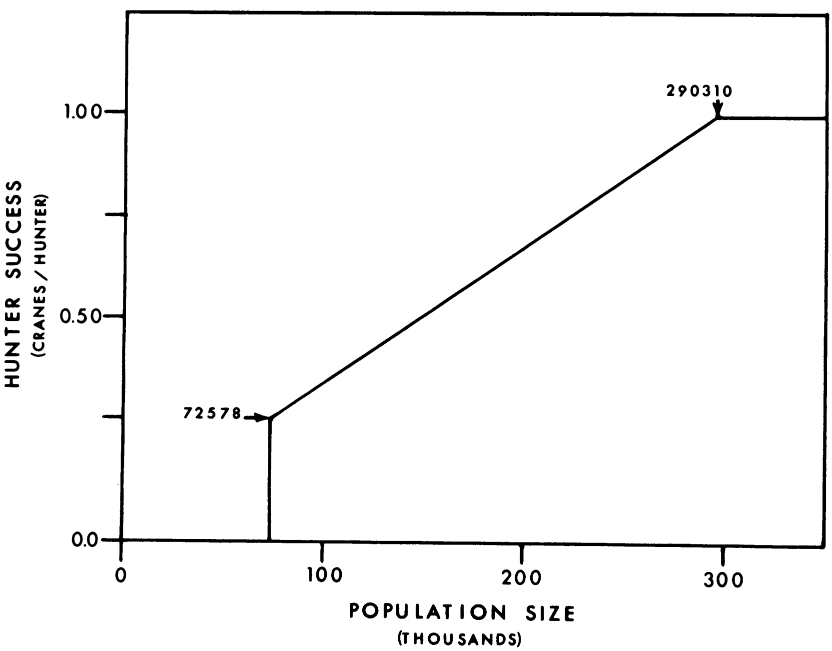

1.00
0.50
0.0
HUNTER SUCCESS
(CRANES / HUNTER)
290310
72578
0
100
200
300
POPULATION SIZE
(THOUSANDS)

TABLE 13. EFFECT OF JUVENILE VULNERABILITY TO HUNTING (RATIO OF FIRST YEAR/ADULT BIRDS IN ANNUAL HARVEST) ON RATE OF POPULATION DECLINE.

Ratio First Year/Adult in Annual Harvest Year:	1	10	20	30	40	50	Extinction (year)
Annual harvest =11612 (4%)							
1:1	290310	254124	203931	137491	49682		45
2:1	290310	259409	216677	160183	85701		50
3:1	290310	263341	226100	176898	112108	27142	54
4:1	290310	266370	233316	189664	132210	56844	57
Annual harvest =17419 (6%)							
1:1	290310	195605	60482				24
2:1	290310	203627	80326				26
3:1	290310	209610	94964				28
4:1	290310	214215	106100				29

As the proportion of juveniles in the annual harvest is increased and relatively fewer breeding adults are taken, the rate of population decline is decreased, but the gains from this factor are much greater for the lower harvest level of 4 percent than at 6 percent. With an annual harvest of 4 percent of the initial population, the difference between a 1:1 and 4:1 ratio between juvenile and adult vulnerability to hunting increases the number of years required for extinction by 12 years; with a harvest of 6 percent of the initial population the difference is only 5 years.

We have not tried to determine the upper limit of this affect (which would presumably disappear when annual recruitment fell below the level required to sustain an adequate breeding population), except to note from a series of simulations of increasing juvenile vulnerability that the benefits from this factor decrease progressively as the ratio is increased.

DISCUSSION

The principal aim of this study is to suggest the kinds of data required for proper management of the species. We have tried to point out that existing knowledge allows the construction of only relatively simple population models whose parameters are not accurately determined. It is evident that successful management of this species requires an understanding of the basic biological characteristics of sandhill crane populations, and that research is needed to determine how density and age affect recruitment and survival. We do not claim that this model, with these particular parameters, is predictive of actual events. Instead, we have tried to select the most reasonable values from the data that are available, and have n1ade only a few simple assumptions from a limited set of parameters. We feel that the model lacks the sophistication that would be possible with more and better data, especially from arctic-breeding populations which might have different demographic characteristics from those we have drawn from studies of more southern subspecies, but we have chosen not to speculate about factors which we cannot evaluate, even though they might be quite important in the Inanagement of sandhill cranes.

For example, one possible shortcoming in this model is that it contains no provision for the population to adjust to hunting mortality with compensating reductions in natural mortality. It is usually assumed that density-dependent regulation of vertebrate populations includes an intrinsic capacity of the species to adjust to excessive mortality in one time period with increased survival, usually of young, in a subsequent period. However, we have not estimated the effect of this potential in sandhill cranes, nor do we in fact know that it exists except by analogy with other species. Protection of the whooping crane has resulted in an average annual increase of only one bird per year while the breeding population has apparently remained constant (Novakowski 1966, Kuyt 1972). If the population characteristics of sandhill cranes are similar to those of whooping cranes, which they appear to be, the sandhill crane population might respond very slowly to reductions in numbers, as this model suggests. Protection from hunting would, in this event, be far less effective for the preservation of sandhill cranes than it would be for many species.

This model also assumes that annual recruitment is a constant 30 percent of the breeding population, or 18 percent of the total population. There are at least two reasons for regarding this as an overly generous estimate. If the ground counts conducted by Hatfield (1966, 1967) are a more accurate index of current age-ratios in the migratory population than the data obtained from hunted samples, annual recruitment might be as low as 5 percent of the total population. We also know from studies of arctic-nesting geese (cf. Barry 1962, Ryder 1967) that adverse weather and predation may eliminate nesting in some breeding areas in some years, and Novakowski (1966) has shown that weather may be an important factor in the nesting success and survival of young whooping cranes. Although we do not have breeding data for arctic-nesting sandhill cranes, it is reasonable to assume that their populations would be similarly affected. However, even for geese, we do not know whether these effects are local and occur in only a few breeding colonies in anyone year, or whether this is a more general phenomenon which affects a large proportion of the arctic-nesting population. Regularly conducted ground counts of age-ratios in the fall and winter population for several years might help to answer this question, but these data are not available at the present time. If widespread breeding failures occur in arctic-nesting colonies due to weather or excessive predation and this were included in the model as a stochastic variable, it might have a significant effect upon the simulated performance of the population.

The limited number of assumptions we have made about sandhill cranes suggests that an annual harvest of about 4 percent of the total population would produce a fairly gradual decline in population size, but that higher harvest rates might lead to serious reductions which could not be detected with current management data. For example, it was noted earlier (Table 1) that the annual counts of sandhill cranes on their wintering grounds have varied from 134,673 to 239,185 and a total population of 300,000 is estimated from an average count of 194,861 cranes. There is, therefore, a variation of approximately 44 percent in the annual census of a presumably stationary population and a difference of 35 percent between the average annual census and the estimated population size. These estimates are obviously too crude to detect a significant change in population size. Consider, for example, a constant annual harvest of 6 percent of an initial population of 290,310, or about 18,000 cranes. With no density-dependent mortality the population would not fall below the low value of 134,673 in the range of estimates in Table 1 until about year 12, but would have entered into a serious decline and would be extinct in 28 years. With a constant annual harvest of 8 percent of the initial population, there would still be about 156,000 cranes after 10 years but the population would become extinct in 19 years. If we were to accept Sherwood's (1971) estimate of an annual harvest of 9 percent of an initial population of only 200,000, we would have to conclude that the species is in imminent danger unless other factors not accounted for in this model act to moderate the population decline. We have not tried to model an equilibrium population of 200,000, but we cannot state with confidence that Sherwood's estimate, based on an average count of 194,861 cranes over a period of 11 years, is less accurate than the accepted estimate of 300,000.

In an earlier study of demographic factors affecting the management of sandhill cranes, Stephen, Miller and Hatfield (1966) cautioned that hunting would require that population trends be carefully monitored and the harvest closely regulated if the population were to be maintained. In view of public pressure for more liberal seasons and hunting in additional areas of the flyway, and considering the results of the simulations with this model, it is clear that there is a critical need for more and better data if the species is going to be adequately protected. The present study suggests that proper management of this species has the following requirements.

Management Requirements

Wintering Ground Surveys

The present level of accuracy of the total population census is clearly inadequate. Counts are conducted each fall before the hunting season, after most of the population is presumed to have reached the wintering grounds.. These counts are subject to error due to annual variations in the time of migration and arrival of cranes on the wintering grounds, and in locating and accurately counting individual flocks. Ho\vever, few species offer the opportunities for an accurate census that are provided by sandhill cranes - they are large, conspicuous birds; they restrict their activities to open areas where they are more easily seen than most species; and most of the population is congregated in a fairly restricted geographical area during the winter. The census could be considerably improved by more intensive ground counts and the use of aerial surveys (Stephen 1967), and possibly by infra-red or other photographic techniques. The counts should also be repeated often enough during the \vinter to obtain consistent estimates of the total population size and an accurate evaluation of the census error.

Juvenile sandhill cranes can be identified by plumage until their first molt. Accurate field identification of juveniles requires proper conditions of light and angle of viewing, but this technique has been shown to be practical (Hatfield 1966, 1967) and should be used by state, provincial, and' federal agencies at concentration areas throughout the Central Flyway during fall migration. This would provide the best possible estimate of anr.ual recruitment, and would allow comparisons between ground counts and hunted samples to determine juvenile vulnerability to hunting.

Hunter Surveys

Systematic bag checks were conducted in New Mexico during the experimental hunting season in 1961 (Boeker, Aldrich and Huey 1961) and during the first two seasons in Saskatchewan and Manitoba (Stephen 1967), but did not become standard management procedure. Bag checks provide data on the ratio of juveniles to adults in the hunted sample and standard measurements can also be taken easily in the field (Stephen, Miller and Hatfield 1966) to determine the subspecies composition of the annual harvest.

Estimates of the annual harvest are obtained from random mail surveys of license holders in some states and provinces, and by field estimates by state agency personnel where the mail survey is not used. The accuracy of the estimates from both sources is questionable, and a standard survey should be developed and tested and uniformly applied to all units where sandhill cranes are hunted.

Banding Studies

So few sandhill cranes have been banded that we do not know where particular segments of the nligratory population breed or where the bulk of the hunted population is produced. All we know is that sandhill cranes breed in scattered pairs from the eastern Canadian arctic to Siberia, and that most of the population migrates through the Central Flyway to the wintering ground in the southwestern United States and Mexico. Moreover, the few bandings that have been made have been mostly of birds of unknown age, so that we have no estimates of juvenile and adult mortality, expectation of life, or potential natural longevity from banding data, and must rely on the indirect sources of information that were used to construct this model. Cooperative programs should be established among Canadian and U.S. agencies, and possibly with the U.S.S.R., to trap and band sandhill cranes during fall migration when first year birds can be identified.

Breeding Ground Surveys

Extensive surveys of the breeding populations of arctic-nesting sandhill cranes would be difficult and expensive, but it would be desirable to obtain data on the geographical distribution of breeding populations, annual breeding success, and the effects of factors such as weather and predation on nesting and the survival of young. It would probably be unwise to attempt to band young cranes on their nests, but observations could be made of age-ratios in the colonies at the beginning of fall migration. These data would provide a better estimate of the potential for increase and natural mortality in crane populations than is now available.

SUMMARY AND CONCLUSIONS

Sherwood (1971) points out that open seasons on sandhill cranes and whistling swans were initiated mainly by government agencies, with very little demand from hunters. We have also noted that the emphasis in the management of sandhill cranes has apparently shifted from control of crop depredations to hunting for recreation, and that the original reason for authorizing an open season is no longer justifiable and seems to have been abandoned. The state and provincial agencies have responded by requesting more liberal seasons and regulations and expansion of the areas open to hunting. Unless the federal agencies can clearly demonstrate that additional hunting of sandhill cranes would be detrimental to the welfare of the species, these requests will be difficult to refuse. This raises a question that exists in the management of most game species, of whether decisions about hunting will be made on political grounds, or whether they will be based on biological data and the welfare of the species.

Currently available data do not allow the construction of models that might provide accurate predictions of population trends, but the simple models that can be created suggest that funher increases in hunting might seriously endanger the species, and that the population is not being monitored accurately enough to detect a major population decline if it did occur. We have recommended management procedures and research programs to improve the data base. On the basis of our analysis we would also recommend that hunting be restricted to its present level, or possibly be reduced, until the necessary data for proper management have been obtained.

Experience with the effects of hunlan pressures on natural environments and the increasing number of rare and endangered species indicates that it should become a cardinal principle of \vildlife management that a species. not be exploited as a resource until it can be clearly sho\vn, with adequate data, that its protection is insured. Our nl0del suggests that sandhill cranes do not now have this insurance, and that further research should be initiated to provide the necessary data for sound, responsible management of this species.

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