J. Field Ornithol., 61(2):224–231

PRODUCTIVITY OF FLORIDA SANDHILL CRANES IN THE OKEFENOKEE SWAMP, GEORGIA

ALAN J. BENNETT[1] AND LAUREL A. BENNETT[1]
Georgia Cooperative Fish and Wildlife Research Unit
School of Forest Resources
University of Georgia
Athens, Georgia 30602 USA

Abstract.—We studied nesting success and brood survival of Florida Sandhill Cranes (*Grus canadensis pratensis*) in the Okefenokee Swamp, Georgia during 1985–1988. Peak nesting occurred 15–30 March when 58% of the clutches were laid. Mean clutch size was 1.88 ± 0.12 eggs and 107 (57%) of 187 nests had at least one egg hatch. Predation, primarily by raccoons (*Procyon lotor*), was the cause of failure for 60 (75%) unsuccessful nests. In 1986–1988, 70% of the pairs that were unsuccessful on their first attempt renested. At least one chick in 34 of 74 broods (46%) fledged. Brood size at fledging averaged 1.12 chicks, range 1.00–1.20, and recruitment averaged 9.4%, range 7.7–11.6%.

PRODUCTIVIDAD DE *GRUS CANADENSIS PRATENSIS* EN LOS PANTANOS DE OKEFENOKEE, GEORGIA

Sinopsis.—Durante el 1985–1989 se estudió, en los pantanos de Okefenokee, Georgia, el éxito de anidamiento y la supervivencia de individuos de *Grus canadensis pratensis*. El pico del anidamiento ocurrió entre 15–30 de marzo, cuando el 58% de las camadas fueron puestas. El tamaño promedio de la camada resultó ser de 1.88 ± 0.12 huevos y el 57% (n = 187) de los nidos eclosionaron al menos un huevo. La depredación particularmente por mapaches (*Procyon lotor*) fue la causa del fracaso de 60 (75%) de los nidos malogrados. Durante 1986–1989 el 70% de las parejas que perdieron su primera camada, reanidaron. Al menos un polluelo de 34 de las 74 parvadas (46%) logró volar. El tamaño de los grupos de volantones fue de 1.12 polluelo (alcance 1.00–1.20) y el reclutamiento de la población promedió 9.4% (alcance 7.7–11.6%).

The Florida Sandhill Crane (*Grus canadensis pratensis*) is a nonmigratory subspecies that ranges from the Okefenokee Swamp in southeastern Georgia to the Everglades on the Florida peninsula (Walkinshaw 1973, Williams and Phillips 1972). The population is estimated at 5000–6000 cranes in Florida (Nesbitt 1982) and 400–450 in Georgia (Bennett 1989).

All productivity data on the Florida Sandhill Crane are from Florida (Bishop 1988; Layne 1983; Nesbitt 1988; Thompson 1970; Walkinshaw 1949, 1973). No studies of Florida Sandhill Cranes have been conducted in Georgia, which is the northern extreme of their range. In this study, we examined nesting success, brood survival, and recruitment of Florida Sandhill Cranes in the Okefenokee Swamp, Georgia.

STUDY AREA

The Okefenokee Swamp is a swamp-marsh complex of 1890 km^2 in southeastern Georgia and a mosaic of freshwater wetland types including

[1] *Current address: U.S. Fish and Wildlife Service, Agassiz National Wildlife Refuge, Middle River, Minnesota 56737 USA.*

marshes, shrub swamps, swamp forests, and lakes (Hamilton 1977). Water levels, fire, and underlying stratigraphy determine the spatial distribution of plant communities and pathways of succession (Cohen 1973, Rykiel 1977). Marshes occur as scattered forest openings and compose 220 km^2 (12%) of the Swamp (Bennett 1990). McCaffery and Hamilton (1984) identified three major marsh types: macrophyte marsh, which is dominated by water lily (*Nymphaea odorata*), neverwet (*Orontium aquaticum*), and pipewort (*Eriocaulon compressum*); herbaceous marsh, which is dominated by emergent graminoids, primarily maidencane grass (*Panicum hemitomon*), broomsedge (*Andropogon virginicus*), and sedge (*Carex* sp.); and mixed scrub-shrub marsh in which marsh forms a complex with patches of woody vegetation, primarily loblolly bay (*Gordonia lasianthus*), pond cypress (*Taxodium ascendens*), hurrah bush (*Lyonia lucida*), and titi (*Cyrilla racemiflora*).

The Okefenokee Swamp exhibits a long hydroperiod and the climate is humid subtropical. Water levels vary seasonally and are highest in February and lowest in June (Rykiel 1977). Annual precipitation ranges from 100 to 150 cm. A climograph based on 25-year average data (Rykiel 1977) revealed four seasons of unequal duration: long, hot summer (May–Sep.); warm, dry fall (Oct.–Nov.); cool, moist winter (Dec.–Feb.); and warm, moist spring (Mar.–Apr.).

METHODS

We located Sandhill Crane nests by airboat in 1985 and by helicopter and airboat in 1986–1988. We attempted to find the maximum number of nests and searches were systematic and designed to cover all habitats within a 50 km^2 survey unit. Some nests were located by tracking birds fitted with radio transmitters for another aspect of the study. Nest searches began in late February and were conducted at approximately 10 d intervals until no new nests were found (normally early June). A nesting attempt was defined as the construction of a nest and the laying of one egg.

We visited nests by boat at 5–7 d intervals to determine their status. Chicks at nests, or presence of angular egg shell fragments with detached membranes (Girard 1939) were used to confirm hatching. A successful nest was where at least one egg hatched. Nests destroyed by predators were examined and the responsible predators determined according to Reardon (1951). We determined nest initiation date (defined as the day on which the first egg was laid) by back-dating 32 d from the hatching date. Nestlings were aged by comparison with photos of known-age sandhill crane chicks. We studied renesting by monitoring a sample of color-marked and radio-tagged cranes. Renest rate is the percentage of pairs that laid a second or third clutch upon failure of a previous effort. We used a *t*-test (Nie et al. 1975:267) to compare nest success and clutch size among first and subsequent nesting attempts.

We determined chick survival and fledging success by monitoring a minimum sample of 25 pairs that nested successfully each year. A suc-

cessful brood was when at least one chick fledged. We located pairs a minimum of twice a week until their broods died or fledged. We calculated annual recruitment (juveniles/100 adult plumage cranes) using a ratio of the number of juveniles fledged to the total adult crane population in the nesting study area each April as established by Bennett (1989). We found age ratio counts in fall flocks (Lovvorn and Kirkpatrick 1981) were unreliable because this population is non-social (Bennett and Bennett 1990) and crane families remain on their territories throughout the year.

RESULTS AND DISCUSSION

Nesting chronology.—We established initiation dates for 123 nests. The earliest nest was started on 27 February and the latest on 9 June. Nest initiation peaked 15–30 March and when an average of 58% of the clutches were laid each year (Fig. 1). Among a tagged sample of 23 breeding pairs, 88 ± 6% made their first nesting attempt in March. A secondary peak in nest initiation occurred 14–29 April. This second peak was primarily renesting by pairs that were unsuccessful in their first attempt. Nests initiated after 10 May were usually renesting efforts by pairs that were unsuccessful on both their first and second attempts.

Nesting chronology varied among years and was strongly influenced by water levels. During 1985, a drought year, peak nest initiation occurred 10 d later than during 1986–1988 when water levels were at or above normal. A similar relationship existed between the central span of nest initiation (Table 1). In 1985, the central span was 16 d compared to 46 d in 1986 and 43 d in 1987.

Sandhill Cranes in the Okefenokee Swamp nest 3–4 weeks later than populations in central Florida. Walkinshaw (1981) reported that nest initiation at Kissimmee Prairie, Florida (330 km south of the Okefenokee Swamp) occurs from 7 January to 21 April and normally peaks 22–24 February. He also reported that air temperature and water levels influenced timing of nest construction. Nesbitt (1988) reported a mean laying date of 12 March at Paynes Prairie, Florida (160 km south of the Okefenokee Swamp). Nest initiation by Mississippi Sandhill Cranes (*G. c. pulla*) in southern Mississippi peaks near 7 April (Valentine 1982), about two weeks later than in our study area.

The renest rate for pairs that failed on their first attempt ranged from 6% in 1985 (n = 17), to 80% in 1987 (n = 25). Incidence of renesting was closely related to water levels. Excluding the drought season of 1985 when only one pair renested, the renest rate averaged 70%. The renest rate for pairs that failed on their second attempt was 29% in 1987 and 40% in 1988. Initiation of second and third nesting attempts occurred 16 ± 9 d after the previous effort failed. Incidence of renesting was not influenced by the incubation stage in which the previous attempt failed. In 34 second-nesting attempts, seven (20%) involved pairs that lost broods 15 d old or less and two pairs renested after incubation infertile clutches more than 45 d.

In Florida, Nesbitt (1988) reported renest rates of 77 and 76% for

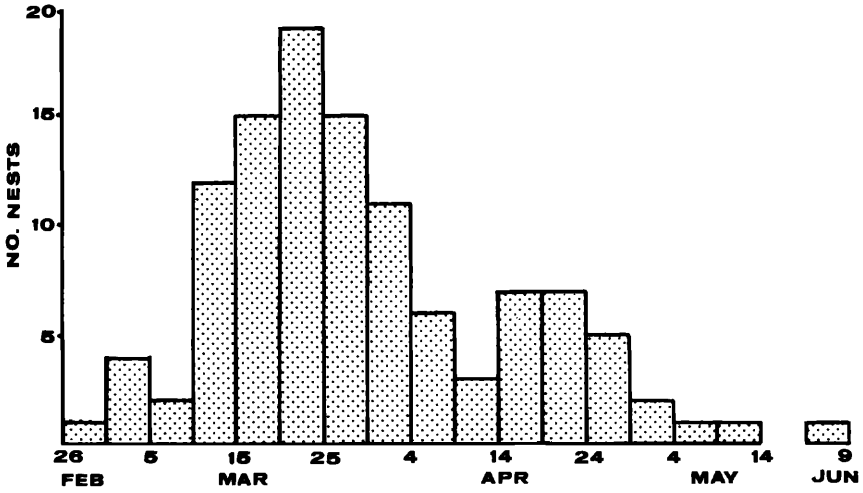

FIGURE 1. Chronology of nest initiation by sandhill cranes in the Okefenokee Swamp, Georgia, 1985–1988.

pairs that lost their first and second clutches respectively, and observed one pair laying a fourth clutch. Nesbitt (1988) reported a mean interval of 19.5 d between clutches.

Clutch size.—The mean size of 187 clutches was 1.88 ± 0.12 eggs. We found no three-egg clutches. Differences in clutch size among years and between first nests and renests in the same year were not significant ($P > 0.05$). The mean clutch size for Sandhill Cranes in the Okefenokee Swamp is similar to that found in Florida by Thompson (1970) and Walkinshaw (1982) 1.84 and 1.94 eggs respectively, but higher than 1.72 eggs reported by Nesbitt (1988).

Hatching success.—During 1985–1988, 107 (57%) of 187 Sandhill Crane nests hatched. Nest success was 47% in 1985 ($n = 32$), 61% in 1986 ($n = 46$), 56% in 1987 ($n = 57$), and 62% in 1988 ($n = 52$). Mean nest success rate for first nests (59%) and second nests (54%) did not differ significantly ($P > 0.05$).

TABLE 1. Median date, 10 and 90% quantities, and central span of nest initiation by Florida Sandhill Cranes in the Okefenokee Swamp, Georgia, 1985–1988.

		Initiation of incubation			Central span[a]
	n	Median	10%	90%	
1985	18	1 Apr.	28 Mar.	11 Apr.	16
1986	32	19 Mar.	8 Mar.	23 Apr.	46
1987	40	22 Mar.	13 Mar.	25 Apr.	43
1988	33	26 Mar.	18 Mar.	20 Apr.	33

[a] Number of days between 10 and 90% quantities.

Predation was identified as the cause of failure for 60 (75%) unsuccessful nests (Table 1). The complete clutch was destroyed at all depredated nests. Raccoons (*Procyon lotor*) destroyed 34 (57%) nests and were the major nest predator. Black bear (*Ursus americanus*) destroyed two nests and a river otter (*Lutra canadensis*) and an alligator (*Alligator mississippiensis*) each destroyed one. At 18 nests (32%) we were unable to positively identify the predator, but we suspect that raccoons destroyed many. Eight (11%) nests were abandoned and five nests (6%) contained eggs that were infertile. Nest abandonment was attributed to partial flooding of nests during heavy rains and disturbance from recreational motorboat traffic. Causes of failure for five nests was not determined.

Sandhill Crane nesting success in the Okefenokee Swamp is lower than that reported for most other populations in North America (Table 2). Raccoons are effective predators on ground nesting birds (Greenwood 1981) and are an important predator of crane nests in the eastern United States (Walkinshaw 1965, 1982). In the Okefenokee Swamp, cranes select nest sites that are drier and closer to wooded cover than cranes in Florida (Bennett 1990). Nests are usually constructed around perimeters of large marshes where herbaceous cover merges with stands of cypress and loblolly bay, or in small (<0.5 ha) shrub-scrub marsh openings. As a result, nests are often situated near travel corridors of raccoons.

At Paynes Prairie, Florida, Nesbitt (1988) found that later clutches were more successful than earlier clutches. However, in his study area predation is uncommon and most nest failures are due to flooding (S. Nesbitt, pers. comm.). In the Okefenokee Swamp, where nesting success is lower, renesting is important to population maintenance. Variables that lower the renest rate, such as drought, substantially reduce numbers of successful nests.

Brood survival and recruitment.—During 1985–1987, 34 (46%) of 74 broods survived to fledge; seven of 15 (47%) in 1985, 15 of 27 (55%) in 1986, and 12 of 32 (38%) in 1987. Survival rate of broods from first nests (40%) was lower ($P < 0.05$) than that of broods from second nests (56%).

Among 40 broods in which no chicks survived, 81% of the losses occurred ≤21 d after hatching. The major cause of brood loss was not determined. Two chicks in a brood died at the nest from a leg deformity that prevented them from standing or walking. A 1-day-old chick was killed by a raccoon and a 40-day-old chick was eaten by an alligator when it swam across a canal. Bobcats (*Felis rufus*) killed two adults during the nesting season and were observed stalking pairs with flightless chicks. Chick mortality from drowning and pneumonia was suspected in 1987 when prolonged rainfall and high water levels coincided with the peak in hatching. Because water levels normally recede during spring while height and density of concealment cover increases (Bennett 1990), habitat conditions may favor survival of broods from second nests.

Recruitment rates during 1985, 1986, and 1987 were 7.7, 11.6, and 8.9%, respectively. Recruitment rates were lowest during those seasons when water levels fluctuated above or below normal. Reproductive con-

TABLE 2. Comparison of nest success and recruitment among Sandhill Crane populations in North America.

Subspecies and location	% Nest success	Brood size at fledging	% Young fall populations	Reference
Eastern greater (*G. c. tabida*)				
Michigan	74	1.35	—	Walkinshaw (1965)
Wisconsin	84	1.36	11.1	Bennett (1978)
Indiana	—	—	12.0	Lovvorn & Kirkpatrick (1981)
Western greater (*G. c. tabida*)				
Idaho, Grays Lake NWR	78	1.35	13.0–14.0	Drewien (1973)
New Mexico	—	—	11.5	Drewien (1973)
Oregon, Malheur NWR	44	—	6.6	Scholorff et al. (1983)
Mississippi (*G. c. pulla*)				
MS Sandhill Crane NWR	64	—	—	Valentine (1981)
Florida (*G. c. pratensis*)				
Kissimmee Prairie	77	—	—	Walkinshaw (1981)
Central Florida	—	1.25	12.3	Bishop (1988)
Paynes Prairie	48	—	—	Nesbitt (1988)
Okefenokee NWR	57	1.12	9.4	(this study)

ditions were most favorable in 1986 when water levels were high at the onset of nesting (March) and steadily receded throughout incubation and brood rearing.

Bishop (1988) reported a mean annual recruitment of 12.3%, range 6.0 to 27.2%, and mean brood size at fledging of 1.25 for three sites in central Florida. Layne (1983) reported an average recruitment rate of 27.7%, range 18.6 to 56.5% for cranes in southcentral Florida during 1973–1979. However, this estimate is exaggerated because Layne (1983: 118) only counted "family groups" in determining his ratio and did not count unsuccessful breeders, adults that did not breed, and subadults. Mean brood size at fledging and annual recruitment for the Okefenokee Swamp population are lower than those reported for eastern and western Greater Sandhill Cranes (*G. c. tabida*) (Table 2).

Drewien (1973) suggested that recruitment of 13–14% among Sandhill Cranes in Idaho characterized an increasing population whereas Littlefield and Ryder (1968) considered a population in southeastern Oregon to be stable with annual recruitment of 8–10%. However, annual survival rates for adult Sandhill Cranes have not been established and survival rates may differ between migratory and nonmigratory subspecies. Additional data are needed on long-term productivity and adult survival before the status of the Okefenokee Swamp population can be determined.

ACKNOWLEDGMENTS

We thank the Georgia Department of Natural Resources and pilots B. A. Vaughn and J. Hill for providing helicopter support. We are grateful to the staff of the Okefenokee National Wildlife Refuge for their cooperation in this study. R. A. Hunt and R. M. Windingstad made helpful comments on earlier versions of this manuscript. This study was funded by the U.S. Fish and Wildlife Service Contract No. 14-16-0009-1551, Endangered Species Research Program, and the Georgia Cooperative Fish and Wildlife Research Unit, the U.S. Fish and Wildlife Service, Georgia Department of Natural Resources, University of Georgia, and Wildlife Management Institute, cooperating.

LITERATURE CITED

BENNETT, A. J. 1978. Ecology and status of greater sandhill cranes in southeastern Wisconsin. M.S. thesis, Univ. Wisconsin, Steven Point. 110 pp.

———. 1989. Population size and distribution of Florida sandhill cranes in the Okefenokee Swamp, Georgia. J. Field Ornithol. 60:60–67.

———. 1990. Habitat use by Florida sandhill cranes in the Okefenokee Swamp, Georgia. *In* D. Wood, ed. Proc. 1988 crane workshop. Fla. Game and Freshwater Fish Comm., Tallahassee, Florida. In press.

BENNETT, L. A., AND A. J. BENNETT. 1990. Territorial behavior of Florida sandhill cranes in the Okefenokee Swamp. *In* D. Wood, ed. Proc. 1988 crane workshop. Fla. Game and Freshwater Fish Comm., Tallahassee, Florida. In press.

BISHOP, M. A. 1988. Factors affecting productivity and habitat use of Florida Sandhill cranes: an evaluation of three areas in central Florida for a nonmigratory population of whooping cranes. Ph.D. thesis, Univ. Florida, Gainesville. 190 pp.

COHEN, A. D. 1973. Possible influences of subpeat topography and sediment type upon the development of the Okefenokee Swamp–marsh complex of Georgia. Southeast. Geol. 15:141–151.

DREWIEN, R. C. 1973. Ecology of Rocky Mountain greater sandhill cranes. Ph.D. thesis, Univ. Idaho, Moscow. 152+ pp.

GIRARD, G. L. 1939. Life history of the shoveler. Trans. N. Am. Wildl. Nat. Resour. Conf. 4:364–371.

GREENWOOD, R. J. 1981. Nocturnal activity and foraging of prairie raccoons in North Dakota. Am. Midl. Nat. 107:238–243.

HAMILTON, D. B. 1977. Vegetation mapping in Okefenokee Swamp using LANDSAT multi-spectral data and conventional aerial photography. Bull. Ecol. Soc. Am. 58:36.

LAYNE, J. N. 1983. Productivity of sandhill cranes in south central Florida. J. Wildl. Manage. 47:178–185.

LITTLEFIELD, C. D., AND R. A. RYDER. 1968. Breeding biology of the greater sandhill crane on Malheur National Wildlife Refuge, Oregon. Trans. N. Am. Wildl. and Nat. Res. Conf. 33:444–454.

LOVVORN, J. R., AND C. M. KIRKPATRICK. 1981. Roosting behavior and habitat of migrant greater sandhill cranes. J. Wildl. Manage. 45:842–857.

MCCAFFERY, C., AND D. B. HAMILTON. 1984. Vegetation mapping of the Okefenokee Swamp ecosystem. Pp. 201–211, *in* A. D. Cohen, ed. The Okefenokee Swamp: its natural history, geology and geochemistry. Wetland Surv., Los Alamos, New Mexico.

NESBITT, S. A. 1982. The past, present, and future of the whooping crane in Florida. Pp. 151–154, *in* J. C. Lewis, ed. Proc. 1981 crane workshop. Natl. Audubon Soc., Tavernier, Florida.

———. 1988. Nesting, renesting, and manipulating nesting of Florida Sandhill Cranes. J. Wildl. Manage. 52:758–763.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. SPSS: statistical package for the social sciences. McGraw Hill Book Co., New York. 675 pp.

REARDON, J. D. 1951. Identification of waterfowl nest predators. J. Wildl. Manage. 15: 336–395.

RYKIEL, E. J., JR. 1977. The Okefenokee Swamp watershed: water balance and nutrient budgets. Ph.D. thesis, Univ. of Georgia, Athens. 139 pp.

SCHOLORFF, R. W., G. HERRON, G. KAISER, C. KEBBE, G. W. KRAMER, AND C. D. LITTLEFIELD. 1983. Pacific flyway management plan for the Central Valley population of greater sandhill cranes. U. S. Fish Wildl. Serv., Portland, Oregon. 28 pp.

THOMPSON, R. L. 1970. Florida sandhill crane nesting on the Loxahatchee National Wildlife Refuge. Auk 87:492–502.

VALENTINE, J. M. 1982. Breeding ecology of the Mississippi sandhill crane in Jackson county, Mississippi. Pp. 63–72, *in* J. C. Lewis, ed. Proc. 1981 Crane Workshop. Natl. Audubon Soc., Tavernier, Florida.

WALKINSHAW, L. H. 1949. The sandhill cranes. Cranbrook Inst. Sci. Bull. 29. Bloomfield Hills, Michigan. 202 pp.

———. 1965. One hundred thirty-three Michigan sandhill crane nests. Jack-Pine Warbler 43:136–143.

———. 1973. Cranes of the world. Winchester Press, New York. 370 pp.

———. 1982. Nesting of the Florida sandhill crane in central Florida. Pp. 53–62, *in* J. C. Lewis, ed. Proc. 1981 Crane Workshop. Natl. Audubon Soc., Tavernier, Florida.

WILLIAMS, L. E., JR., AND R. W. PHILLIPS. 1972. North Florida sandhill crane populations. Auk 89:541–548.

Received 10 Feb. 1989; accepted 24 Oct. 1989.