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Abstract: From 1980–98 we captured and uniquely marked more than 400 Florida sandhill cranes (*Grus canadensis pratensis*). Age ratios of the marked population, excluding juveniles, was 66% adult and 33% subadult, and the sex ratio was 49% male and 51% female. Average clutch size for 210 nests checked from 1983–97 was 1.78 ± 0.18 (SD) and frequency of 1-egg clutches varied among years. Average post-fledging brood size from 1991 to 1997 was 1.27 ± 0.17 (SD), included a 3-chick brood. Average percent of young from 2 study areas, 1991–97 was 11.9 ± 3.23 (SD). We observed renesting up to 3 times, even after chicks had been hatched and reared for up to 16 days. Re-pairing following death or divorce was documented and was particularly noteworthy in a female that oscillated between 2 males during 4 years of observation.

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Reintroduction of the whooping crane (*Grus americana*) to Florida, began in 1993 (Nesbitt et al. 1997) and was preceded by studies of Florida sandhill cranes and greater sandhill cranes (*G. c. tabida*) starting in December 1980. Results derived from some aspects of these earlier studies were published previously (Nesbitt 1988*a*, 1992; Nesbitt and Carpenter 1993). These data presented here were incidental to those previous studies.

Sandhill cranes and whooping cranes exemplify k-selected species. They are both long-lived species (>20 yr) that exhibit deferred sexual maturity, low annual fecundity, and a high level of parental investment. They are perennially monogamous, and the pair members typically remain together year round.

The Florida sandhill crane has the longest recorded nesting season for any subspecies of sandhill crane, extending from December to early June, and occasionally into August (Tacha et al. 1992, Nesbitt 1996). This long nesting window and perennially monogamous pair bonds afford the opportunity for up to 3 renestings in a single nesting season (Nesbitt 1988*a*). The average interval between nests was reported as 19.5 ± 1.19 (SE) days and ranged from 14–39 days (Nesbitt 1988*a*). First attempted breeding occurs at 22 months of age for males and 34 months for females. First successful breeding in Florida sandhill crane males and females has been reported at 3 and 4.7 years of age respectively (Nesbitt 1992). In this paper we are reporting data collected since the publication of comprehensive papers on the sandhill crane (Drewien et al. 1995, Tacha et al. 1992). Other observations are reported that expand our understanding of the parameters associated with pairing and reproduction in Florida sandhill cranes.

STUDY AREA AND METHODS

These studies were conducted in north-central and south-central Florida (Alachua and Osceola Counties, respectively). In Alachua County, study sites were on Paynes (7,300 ha) and Kanapaha (650 ha) Prairies. Both supported a similar mixture of freshwater aquatic habitats that graded to open pastures and natural grasslands. Predominant aquatic vegetation in the shallower areas was maidencane (*Panicum hemitomon*), pickerel weed (*Pontederia cordata*), and smartweeds (*Polygonum spp.*) with stands of woodier vegetation including water willow (*Decodon verticillatus*), willow (*Salix spp.*), and button bush (*Cephalantus occidentalis*). Deeper water sites supported spatter-dock (*Nuphar luteum*) and white water-lily (*Nymphaea odorata*). Open pastures were dominated by Bahia grass (*Paspalum notatum*) and carpet grass (*Axonopus affinis*), with live oaks (*Quercus virginiana*) prominent at the pasture edges. For a more detailed description of the area see Nesbitt and Williams (1990). The southern Osceola County study site included the Three Lakes Wildlife Management Area and adjacent private lands.

Pre-fledged Florida sandhill cranes were captured by hand as they foraged with their parents. Post-fledging cranes

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were captured with the use of oral tranquilizers applied to whole corn bait (Bishop 1991). All birds were banded and marked with unique color combinations of plastic bands to facilitate field identification (Nesbitt et al. 1992). Some individuals were also instrumented with leg-band-mounted radio transmitters (Melvin et al. 1983).

Nest sites were located from fixed-wing aircraft, by walking in on radio-instrumented birds that were suspected of incubating, or by observing single adults until a nest exchange occurred. We recorded clutch size, vegetative characteristics at the nest, and nest habitat. Nests were visited once and only during the cooler part of the day to reduce the chance of egg loss. Because post-fledging mortality is about the same as for adults (Nesbitt 1992), reproduction was considered successful if young were fledged. We evaluated productivity, the number of young of the year that survived to 1 year of age. In both study areas, we observed ≥100 birds each year between August (after all chicks had fledged) and mid-October (when migrant greater sandhill cranes begin arriving). Cranes were inventoried as family groups or small foraging flocks. Groups were also counted at communal roosts. The number of juvenal plumage birds was recorded and the percent of juveniles calculated.

Sex of individually marked paired adults was determined from unison calling posture and voice (Archibald 1976). In younger, unpaired birds, sex could not be determined unless by chromosome examination of blood or feather pulp (Van Tuinen and Valentine 1987) taken at time of capture. Age was based on plumage (Lewis 1979) or wing feather molt patterns (Nesbitt 1987). Birds were aged as adults (>3 yr), subadults (>1 but <3 yr), or juveniles (<12 months).

Cranes were released in the capture area after they had recovered from the effects of the drug. Observations of marked birds were made with 20–60x spotting scopes and 7x binoculars, usually from vehicles, but occasionally nesting birds or birds that were not easily accessed otherwise were observed from blinds.

RESULTS AND DISCUSSION

Population Structure

We captured and individually color marked 126 Florida sandhill cranes in Alachua County. Additional birds were captured and marked in Osceola County (Folk and Schmidt unpublished reports), and some marked birds remaining from a previous study (Bishop 1988). Most of the observations were of birds in Alachua County. Thirty-four summer flocks of ≥10 birds were checked from 1983–88, and ≥40% had been marked and were of known age. Paired adults accounted for 46.8% of the population, unpaired adults accounted for 19.2% of the population, and subadults comprised 34.0% of the population (Nesbitt 1988*b* unpublished). The sex ratio among 94 known birds was 49% males and 51% females.

Nesting and Renesting

The average clutch size for 210 nests from 1983–97 was 1.78 ± 0.18 (SD) (99 of these nests were reported earlier, Nesbitt 1988*b* unpublished). This is below the average of 1.90 reported for several subspecies or populations and above 1.76 reported for Alaska (Tacha et al. 1992), but it is not significantly distinct from either. Mean annual clutch size ranged from 1.60 to 2.00 for the 11 years that ≥10 nests were checked. Frequency of 1-egg clutches varied annually (Table 1), but there was no obvious reason for such wide variation. Although 3-egg clutches have been reported elsewhere (Tacha et al. 1992), we found none in Florida.

Renesting, with the laying of fertile eggs was observed even after the loss of chicks. In 1991, pair 098 hatched and reared a single chick for 16 days: it disappeared 3 April from an unknown cause. The pair laid a second nest 8 April, only 5 days after the first chick disappeared. They successfully raised a chick from this second nesting effort.

Table 1. Surveys of nests and clutch sizes in Florida sandhill cranes in Alachua and Osceola Counties Florida, 1983–97.

Year	No. of nests	No. of eggs	$\bar{x}$ clutch size	% 1-egg clutches
1983	8	14	1.75	25.0
1984	9	12	1.33	66.6
1985	15	27	1.80	20.0
1986	25	44	1.76	24.0
1987	32	57	1.78	28.0
1988	14	27	1.93	7.1
1989	13	24	1.85	7.7
1990	15	30	2.00	0.0
1991	17	28	1.65	35.3
1992	15	28	1.87	13.3
1993	12	19	1.58	41.7
1994	10	16	1.60	40.0
1995	6	11	1.83	16.7
1996	12	23	1.92	8.3
1997	7	14	2.00	0.0
Total/ Average	210	374	1.78	23.8

Parental Investment

Renesting following the loss of chicks could be interpreted to demonstrate minimal consequence to chick mortality. The parents are quickly able to make the physiological adjustments necessary to begin the nesting process again. However, Florida sandhill crane chicks stay with their parents for an average of 327 days (Nesbitt and Schwikert unpublished data). This long-term parental investment represents a substantial amount of energy, and it might be expected there would be a concomitant level of parental loyalty to a chick.

One example of a degree of parental loyalty seemed unusual. We captured and banded a pair and their only chick near Cross Creek in Alachua County on 18 July 1996. The 55-day-old chick had a 6-cm diameter lesion on the left elbow with associated swelling of the joint, perhaps the result of being injured in a fence. The bird's wing drooped, and it was unlikely the bird would ever be able to fly without our intervention. We took the bird to the University of Florida School of Veterinary Medicine that afternoon for treatment. On 27 July the wing had healed and we returned the chick to the natal area. The parents were together in the area feeding at 0930. They walked off 150 to 200 m at our approach. The chick was released where parents had been feeding in the open live oak understory, 100 m from the edge of Orange Lake. The chick immediately began walking toward the parents; no calling from the chick or the parents was heard. Within 10 minutes, the chick was back with its parents and they were seen to feed the chick. The chick remained in close proximity to the parents, as was typical for cranes of that age, while we observed them for the next 30 minutes. It was as though the chick had never been missing. The chick remained with its parents for the rest of that year. Unfortunately, the bird was never able to fly and was hit and killed by a car the following winter. It is interesting that the parents were able to recognize their chick and immediately began caring for it again after an absence of 9 days.

Productivity

We monitored 317 nesting efforts of 262 nesting pairs from 1983–97. Data for all aspects of nesting (e.g., clutch size, hatching date) were not obtained for every nesting effort.

First breeding efforts by inexperienced birds were usually unsuccessful (Nesbitt 1992). We observed a 23-month-old female paired with a male of unknown age successfully fledge 1 young in Osceola County in 1994 on her first breeding effort. This is the youngest known successful reproduction in a female Florida sandhill crane known to us.

Mean brood size (Fig. 1) from 1991–97 was 1.27 ± 0.17 (SD) and is equivalent to the mean (1.26) for previous years

Fig. 1. Florida sandhill crane with chick, Alachua County, Florida, 1990. (Photo by Stephen A. Nesbitt.)

we reported in Drewien et al. (1995). Average Florida crane brood size was comparable with the highest averages reported for any population of sandhill cranes (Drewien et al. 1995). We never documented a 3-egg clutch in Florida for >300 nests. There was a 3-chick brood recorded 14 September 1995 in Osceola County. Drewien et al. (1995) found only 17 cases (0.14%) of triplets in 12,239 broods surveyed.

Drewien et al. (1995) summarized production in Florida sandhill cranes from 6 studies covering an 8-year interval (1984–91) and found an average of 9.8% young in the population. We have recorded production by year for Alachua and Osceola Counties from 1991–97, and it averaged 11.9% ± 3.23% (SD) (Table 2). The average for Osceola County was 12.4% ± 3.5%1 (SD), and 11.3% ± 3.07% (SD) for Alachua County. Annual production of Florida cranes ranged from 6.8% to 17.8% young (Table 2). Years of lowest production were years when rainfall associated with the nesting seasons was below normal. Years with the highest production were years of average or above average water levels during the nesting and post-nesting season. This apparent correspondence of reproductive success in sandhill cranes and water levels has been reported before (Littlefield and Lindstedt 1992, Drewien et al. 1995).

Table 2. Production of Florida sandhill cranes in Alachua and Osceola Counties Florida, 1991–97.

Year	% juveniles Alachua Co. (*n*)	$\bar{x}$ brood size	% juveniles Osceola Co. (*n*)	$\bar{x}$ brood size
1991	10.2 (127)	1.31	11.5 (234)	1.06
1992	12.5 (72)	1.30	14.3 (189)	1.54
1993	13.9 (36)	1.67	14.5 (179)	1.33
1994	8.8 (81)	1.17	6.8 (250)	1.13
1995	9.5 (84)	1.14	17.8 (258)	1.34
1996	7.9 (63)	1.25	11.6 (215)	1.14
1997	16.4 (116)	1.19	10.4 (308)	1.23

Pair Formation

Pair formation in cranes is a subtle, sometimes protracted, process (Bishop 1984, Stehn 1997). The mechanism of pair formation is not understood but may involve an extended period of association and synchronized behavior with both birds doing the same or compatible behaviors (Nesbitt and Wenner 1987). Reproduction is the purpose of the pair bond, and without it, the pair bond does not persist (Nesbitt and Tacha 1997). We observed several pairs form and disintegrate during the course of this study; the close association between successful reproduction and an enduring pair bond was apparent. Pairs that fail to successfully reproduce in their first year often separate before the next nesting season. Pairs with a history of successful reproduction separated after a few years (3–5) without reproductive success.

There have been several examples of divorce and repairing in Florida sandhill cranes. We observed 1 exceptional case of an oscillating pair bond involving a female and 2 males. The female, 024, was first captured as an adult 12 October 1995. Her first mate, 134, was initially captured as a subadult (hatch year 1986) on 1 June 1987. Her alternate mate, 106, was initially captured as a subadult (hatch year 1985) on 2 October 1986. During the 1996 breeding season, she nested with male 134 without success. On 2 October 1996, 134 and 024 were seen unison calling, indicating a pair bond, with the other male (106) nearby. The 2 males were aggressive toward each other, and 2 days later 024 was unison calling with the 106 male, while her former mate, 134, was nearby but uninvolved. On 18 November she was back with 134 male, and 106 was not seen. Four days later she was back with 106, and 134 was not seen. That pair remained together into January 1997. The other male (134) was seen several times alone in the area. Then on 22 January, male 106 was seen alone without 024. In April 1997, 106 paired with an unmarked female, while his former mate, 024, nested that spring with 134. They produced a chick which disappeared after 7 May. On 12 May, female 024 was back with 106 male displaying dominance toward other cranes in the area. Her former mate (134) was in the area and seen within 50 m of the new pair, but did not associate with 024. However, on 9 June, female 024 and male 134 were together acting as if paired. Then on 12 June, she was back with male 106 (134 was with an unmarked bird). Three days later, she again appeared to be paired with male 134, and they were all 3 together by mid-August. The trio persisted into October 1997.

During this single year, female 024 switched no fewer than 20 times between these 2 males. She alternately unison called with each of the males, in 1 case only 2 days apart. Had these birds not been uniquely marked, these mate changes would have gone unnoticed. The constant disruption of the pair bond may have been symptomatic of an underlying physical or behavioral problem in 1 or more of these birds but ultimately no young were fledged from these pairings. The female died in 1998, and the 2 surviving males paired with other females and have subsequently both nested.

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