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The significance of mate loss in Florida Sandhill Cranes.—Monogamy, in which “one male and one female join to rear at least a single brood” (Wilson 1975), is the most common mating system among birds. In perennial monogamy the pairbond is persistent, even during the non-breeding season (Brown 1975) and is common in species with prolonged parent/offspring involvement. Established adult pairs of Sandhill Cranes (*Grus canadensis*) i.e., those with a history of fledging young, are perennially monogamous (Walkinshaw 1973, Nesbitt and Wenner 1987). Re-pairing of adults following separation or the death of a mate has been reported (Littlefield 1981; Nesbitt and Wenner 1987; Bishop 1988; Bennett and Bennett, in press) although the circumstances preceding and following these cases of mate loss were not usually known.

Florida Sandhill Cranes (*G. c. pratensis*) captured as part of a long-term study were individually color banded beginning in 1977 (Nesbitt 1981). Each bird was aged at banding as adult (> 3 years), subadult (1–3 years), or juvenile (< 1 year), based on plumage characters (Lewis 1979, Nesbitt 1987). Sex of pair members was determined, in the field, during episodes of unison calling. The territories of these pairs were in Paynes Prairie and Kanapaha Prairie (Fig. 1), areas of freshwater marsh and improved pasture in southern Alachua County in north central Florida. Twenty-one nesting pairs were monitored for a total of 122 crane-pair years between 1977 and 1988 (Table 1). Seven pairs (33%) remained together while 14 (67%) changed mates (1 four times) for a total of 17 re-pairings. Nine of 17 (53%) re-pairings followed the known death of a pair member, three (18%) resulted from “divorce” (separation of a pair that had nested previously), in five (29%) the fate of the missing pair member was unknown.

Minton (1968) observed a 14% divorce rate among breeding pairs of Mute Swans (*Cygnus olor*). In the Black-legged Kittiwake (*Rissa tridactyla*), Coulson and Thomas (1983) found a higher divorce rate among younger breeding pairs that was “correlated with the failure of the pair to rear young.” Prior to the three recorded divorces in Florida Sandhill Cranes, although the pair nested and the female laid fertile eggs, they never fledged young. Pair #113, for example, hatched two young in 1986, failed to fledge either, then separated briefly during summer 1986. In 1987, after one nesting attempt with his first mate (a 4-year-old female), the male (a 3-year-old) paired with a new (3-year-old) female and made two additional nesting attempts with her in 1987. His former mate remained within the vicinity of the territory and associated with a mixed flock of adult and subadult cranes before leaving the area.

Unproductive pairs did not necessarily always divorce. The KSE pair remained together between 1984 and 1988 without fledging young, though they nested several times and hatched young three times. It is possible they produced young prior to 1984. Pairs with a reproductive history have remained together for several years without producing young. The first YEL

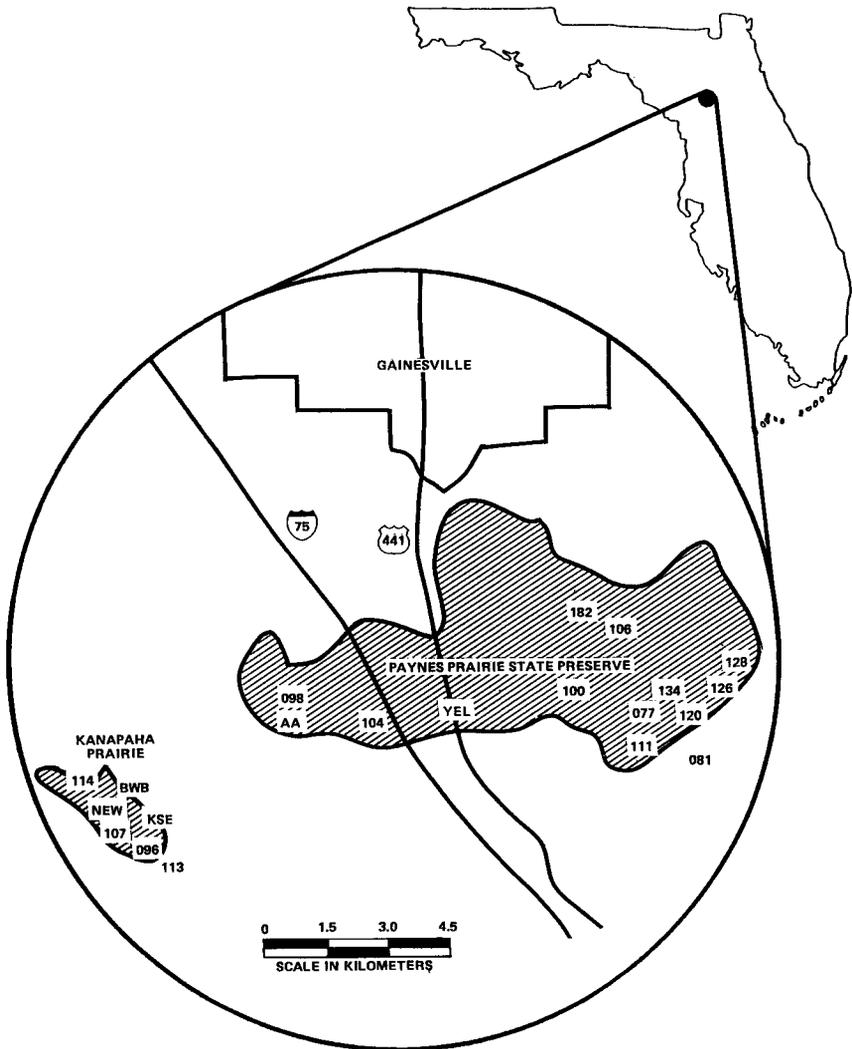


FIG. 1. Study area and relative location of nesting territories for 21 pairs of Florida Sandhill Cranes.

pair fledged young at least three times prior to 1981 then remained together from 1981 until the death of the female in 1985, although they produced no young.

Retention of the territory subsequent to mate loss was related to the sex of the surviving bird. Males retained the territory eight of nine times (89%), surviving females only four of ten times (40%). In three of the four instances that females retained a former territory, the bird re-paired with a younger, inexperienced male (a first-time nester) that had no established

TABLE 1
PAIRING HISTORY FOR TWENTY PAIRS OF FLORIDA SANDHILL CRANES

Pair	Years of contact	Did pair fledge young	Fate
126	1982-1988	Yes	Male b—Female d
128	1982-1988	Yes	Male b—Female e
106 first	1984-1985	Yes	Female b—Male e
106 second	1985-1986	No	Female b—Male e
106 third	1986-1987	No	Female c—Male e
106 fourth	1987-1988	Yes	Male b—Female d
100	1981-1984	Yes	a
077	1983-1988	Yes	a
111	1983-1988	Yes	Female c—Male e
134	1977-1988	Yes	Male b—Female e
081	1983-1985	No	Female d—Male e
YEL	1977-1985	Yes	Female b—Male e
104	1985-1988	Yes	Female c—Male e
098	1985-1988	Yes	Female c—Male e
114	1984-1988	No	Male b—Female e
113	1985-1988	No	Female d—Male e
096	1984-1988	Yes	a
107	1983-1988	Yes	a
NEW	1985-1988	No	Male d—Female e
BWB	1984-1988	Yes	a
KSE	1984-1988	No	a
AA	1981-1988	Yes	a
182	1982-1988	No	Male c—Female d
120	1982-1984	No	Male b—Female d

a—Pair remained together.

b—Died.

c—Fate unknown.

d—Left territory and re-paired.

e—Remained on territory and re-paired.

territory. In the fourth instance, following the death of #114 male in August 1986, #114 female re-paired in January 1987 with the "NEW" pair male. In 1986, the "NEW" pair (a 2-year-old male and 3-year-old female) failed in their first-ever nesting effort on a small, newly established territory adjoining the 114 territory. His former mate retained the original territory and re-paired with an inexperienced male that made a first nesting attempt with her in 1987. In four of the six instances when females lost their mates and did not retain the territory, the territory was quickly appropriated by neighboring pairs. In the other two instances, occupation of the vacant territory was not immediately apparent.

Successful reproduction was a major factor in perpetuating a newly initiated pairbond. Without a successful reproductive history, a pair would likely separate. The consequences of mate loss were more significant for females than males. Following mate loss, established males usually retained the territory, secured another mate and attempted nesting, often successfully, the following season. Surviving females usually (6 of 10 times) left the territory

following mate loss and in four instances it was 2–3 years before they re-paired and attempted to nest again. Females that retained former territories and re-paired usually paired with younger, often inexperienced, males. Males that retained their territories re-paired with females that were as old or older than themselves. It is apparently more difficult for single females to defend a territory and resist the pressure from neighboring pairs to appropriate the territory. These patterns are consistent with a male-dominated resource defense system (Greenwood 1980) in which the male has a higher investment in securing and maintaining the resource (territory) and the females' mate choice is imposed upon that mating system. The consequence of mate loss that I have observed may be reflective of a particular population density of this non-migratory subspecies. Mate loss among another subspecies, especially one that is migratory, may not have the same significance.

LITERATURE CITED

- BENNETT, L. A. AND A. J. BENNETT. Territorial behavior of adult Florida Sandhill Cranes in the Okefenokee Swamp. Proceedings 1988 Crane Workshop. Lake Wales, Florida. In press.
- BISHOP, M. A. 1988. Factors affecting productivity and habitat use of Florida Sandhill Cranes (*Grus canadensis pratensis*): an evaluation of three areas in central Florida for a nonmigratory population of Whooping Cranes (*Grus americana*). Ph.D. diss., Univ. Florida, Gainesville, Florida.
- BROWN, J. L. 1975. The evolution of behavior. W. W. Norton, New York, New York.
- COULSON, J. C. AND C. S. THOMAS. 1983. Mate choice in the Kittiwake Gull. Pp. 361–376 in *Mate choice* (P. Bateson, ed.). Cambridge Univ. Press, Cambridge, England.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28:1140–1162.
- LEWIS, J. C. 1979. Field identification of juvenile Sandhill Cranes. *J. Wildl. Manage.* 43: 211–214.
- LITTLEFIELD, C. D. 1981. Mate-swapping in Sandhill Cranes. *J. Field Ornithol.* 52:244–245.
- MINTON, C. D. T. 1968. Pairing and breeding of Mute Swans. *Wildfowl* 19:41–60.
- NESBITT, S. A. 1981. The past, present and future of the Whooping Crane in Florida. Pp. 151–154 in *Proceedings 1981 Crane Workshop* (J. C. Lewis, ed.). Nat. Audubon Soc., Tavernier, Florida.
- . 1987. A technique for aging Sandhill Cranes using wing molt—preliminary finding. Pp. 224–229 in *Proceedings 1985 Crane Workshop*. Platte River Whooping Crane Maintenance Trust (J. C. Lewis, ed.). Grand Island, Nebraska.
- AND A. S. WENNER. 1987. Pair formation and mate fidelity in Sandhill Cranes. Pp. 117–122 in *Proceedings 1985 Crane Workshop*. Platte River Whooping Crane Maintenance Trust (J. C. Lewis, ed.). Grand Island, Nebraska.
- WALKINSHAW, L. H. 1973. *Cranes of the world*. Winchester Press, New York, New York.
- WILSON, E. O. 1975. *Sociobiology*. Belknap Press, Cambridge, Massachusetts.
- STEPHEN A. NESBITT, *Florida Game and Fresh Water Fish Commission, Wildlife Research Laboratory, 4005 South Main St., Gainesville, Florida 32601. Received 18 Oct. 1988, accepted 15 Feb. 1989.*