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TERRITORIAL BEHAVIOR OF FLORIDA SANDHILL CRANES IN THE OKEFENOKEE SWAMP

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Abstract: Intraspecific and territorial interactions of adult Florida sandhill cranes (*Grus canadensis pratensis*) were studied in the Okefenokee Swamp, Georgia 1985-87. Adult pairs occupied exclusive and defended territories year round. We did not observe social behavior or flocking by adult cranes. Reproductive success did not influence the fidelity of pairs to their territories or aggressiveness toward other cranes. Females that lost mates retained their territories and eventually re-paired. Territoriality was most intense during fall and winter and may have been necessary to maintain feeding areas. Habitat conditions in the Okefenokee Swamp may dictate territoriality, not sociality, as a strategy for survival.

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Adult sandhill cranes are territorial during the breeding season, and defend nest sites and adjoining wetland habitats (Walkinshaw 1965, 1973; Littlefield & Ryder 1968; Drewien 1973). Nesting pairs can be very aggressive and often displace any other crane that lands within their established territories (Walkinshaw 1965). At the end of the breeding season, adult pairs abandon their nesting territories and assemble with other adults and subadults (Walkinshaw 1949). Sandhill cranes remain highly social throughout the fall and winter (Walkinshaw 1973). Social flocking is predominant among migratory bird populations, and is of survival value in locating food and roost sites (Welty 1975) and reaching wintering areas (Lincoln 1979). We suggest that social behavior may be less important for sedentary populations. Here we report on a nonmigratory crane population in which the adults exhibit territorial behavior throughout the year.

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STUDY AREA AND METHODS

The Okefenokee Swamp is a peat-filled depression or bog of 1,890 km² in southeastern Georgia. It is believed to have been formed during the Pleistocene by impoundment of ocean water behind a sandbar (Schlesinger 1978). Water chemistry and biology are influenced by low pH in the range of

3.8 to 4.2 (Bosserman 1981). The Okefenokee is a swamp-marsh complex comprised of a mosaic of freshwater wetland types including emergent 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). The Okefenokee Swamp exhibits a long hydroperiod frequently extending over several years, with a normal annual amplitude of 80 cm (Rykiel 1977). The climate of the region is humid subtropical and annual precipitation ranges from 100-150 cm. Marshes are heterogeneous and composed of a complex of forested, shrub and emergent wetlands. McCaffrey and Hamilton (1984) identified 2 major marsh vegetation types, (1) macrophyte marsh, vegetated by water lily (*Nymphaea odorata*), floating heart (*Nymphoides aquatica*), pickerel-weed (*Pontederia cordata*), neverwet (*Orontium aquaticum*) pipewort (*Eriocaulon compressum*) and hardhead (*Xyris smalliana*); and (2) herbaceous marsh, dominated by emergent graminoids, primarily maidencane grass (*Panicum hemitomon*), broom sedge (*Andropogon virginicus*), sedge (*Carex* spp.), chain-fern (*Woodwardia virginica*), red root (*Lacnanthes caroliniana*) and sphagnum moss (*Sphagnum* spp.). Scattered throughout the marshes are stands of trees and shrubs known locally as "houses". These "houses" are on hammocks of peat which are higher in elevation than the surrounding marsh.

Sandhill cranes were captured, equipped with radio transmitters and monitored using techniques and equipment described by Bennett (this Proceedings). One to three locations/week were obtained

for all cranes throughout the year. Home range-territory size was determined according to Odom & Kuenzler (1955). Observations of cranes were made from boats and elevated blinds using 25x45 power spotting scopes. Territorial behavior was illicit by placing pairs of commercially manufactured crane decoys (Carry-lite Milwaukee, WI) within the territories of marked pairs.

RESULTS

Twenty adult sandhill cranes were captured and radio-tagged. Transmitter failure during the first 90 days after capture reduced the sample size to 16. Only 1 crane (# 563) was unpaired at the time of capture but paired 9 months later. The mean monitoring time span for the radio-tagged cranes was 17 months ($r=9-29$ months). A total of 2,771 locations was obtained (\bar{x} 163 locations/crane), and visual observations were made on 31% of the locations.

All radio-tagged cranes occupied and defended territories throughout the year. The mean size of the 16 territories was 0.72 km² ($r=0.53 - 1.2$ km²). Territories were mutually exclusive and exhibited little overlap with neighboring pairs (Fig. 1). Extra-territorial movements were uncommon and detected for only 2 cranes, each during the winter of 1986-87 and involved pairs traveling 0.5 - 1.0 km outside their territories to feed during daytime. These movements coincided with extremely high water levels (40 cm above normal) and were probably due to the temporary unavailability of feeding habitat within their territories.

Territories included nesting, feeding and roosting divisions, as described by Hinde (1956). Because the Okefenokee marshes are heterogenous, these division were widely scattered throughout the territories and often changed seasonally due to water level fluctuations. An average of 40% of the territories were composed of unusable habitat (lakes, forested islands). Feeding and roosting divisions were core use areas which accounted for > 70% of the radio-locations, but often composed < 30% of the territories. Territory boundaries exhibited little seasonal or annual variation. A change in the boundary and configuration of 1 territory occurred after re-pairing and the immigration of a pair from an adjoining territory.

Although territorial behavior was observed throughout the year, aggressive interactions between pairs with adjoining territories were rare. Interactions along boundaries were subtle and pairs were often observed feeding within 100 m of

each other. Because the boundaries of many territories conformed to physical landmarks such as boat trails and tall stands of cypress (*Taxodium ascendens*), neighboring pairs were rarely able to see each other. Territory overlap was greatest in open marshes lacking extensive wooded areas.

Most territorial defense was directed at flocks of subadults or adults that did not have established territories. Pairs defended their territories with displays that included unison calling and directed walk threats. Aggressive behavior was initiated when pairs observed other cranes flying over or landing within their territory. Pairs also responded aggressively to cranes calling from within their territories. We observed 98 aggressive interactions in which a radio-tagged pair of adults displaced 1 or more cranes from their territories. The frequency of aggressive interactions exhibited a seasonal trend (Fig. 2). Fall and winter (Oct - Feb) accounted for 69.4% of the interactions. Defense of nest sites occurred in March, but was rarely observed during incubation (April - May).

During fall and winter, territorial defense was primarily directed at feeding areas. Defense of feeding areas intensified in early October and appeared to coincide with a dietary shift from live prey to the seeds and tubers of aquatic plants. When greater sandhill cranes (*G. c. tabida*) arrived in mid-November, several territories became saturated with migrant cranes. Under these conditions, resident pairs appeared to direct their aggressive behavior at maintaining feeding areas, and often ignored cranes in other portions of their territory.

Forty-three observations were made of tagged adults on overnight roosts. Paired adults roosted alone within their territories and interactions with other cranes were observed only twice, both involving a resident pair evicting other cranes that landed near their roost.

Where several territories converged, pairs often roosted within 250 m of each other and could see their neighbors flying to and from the roost. Pairs usually unison called when neighboring pairs were sighted. When decoys were placed on their roosts, pairs reacted by circling and diving at the decoys while emitting "guard" calls. Pairs would then land within 100 m of the decoys and walk-threat toward them. In one instance, a pair landed among and attacked the decoys.

Reproductive success during the course of this study did not influence the fidelity of pairs to their territory or intensity of aggressive behavior. Fifteen (93.7%) of the 16 pairs nested at least once, and 12 pairs (75%) constructed 3 or more nests. An aver-

age of 18% of the pairs reared broods each year. The frequency of aggressive interactions did not differ ($P > 0.05$) between successful and unsuccessful breeding pairs. However, pairs with chicks were slightly more effective at driving large groups of cranes from their territories.

Random observations of radio-tagged cranes were obtained on 860 occasions. Tagged cranes were alone or with their mate on 833 (96.8%) of the sightings. One pair of cranes briefly associated with a pair of subadults during the summer. Social behavior and flocking on roosts and feeding areas was not observed for any of the tagged adults.

Five pair members (4 female, 1 male) lost their mates due to predation or unknown causes. All 4 females retained their territories and eventually re-paired (Table 1). The male, which had a 70 day-old chick, abandoned his territory and paired with one of the 4 females on an adjoining territory. Season and reproductive status did not affect the fidelity of unpaired females to their territory.

DISCUSSION

Territoriality in birds is often centered around spatial habitat requirements (Hinde 1958; Brown 1969). In the Okefenokee Swamp, Florida sandhill cranes are exclusively dependent upon wetlands (Bennett, this Proceedings). Habitat resources required for reproduction, feeding, and roosting are evenly distributed. By establishing and defending territories, adult pairs can retain all the habitat requisites necessary during their life cycle.

The maintenance of annual territories has not been reported for other populations of sandhill cranes. Nonmigratory cranes in Mississippi and Florida normally abandon their breeding territories in late summer and become social (Walkinshaw 1973; Layne 1981; Valentine 1981; Nesbitt et al. in press). Social behavior is an advantage in locating food (Moriarty 1976) and may be important to cranes which follow a daily pattern of commuting between wetlands and uplands for feeding. Social behavior may also be of value to populations which occupy small or ephemeral wetlands that cannot support cranes throughout the year. In the Okefenokee marshes, where habitat availability remains relatively constant both seasonally and annually, holding and defending territories may be a better strategy for survival.

In fall and winter, territorial defense by Florida sandhill cranes was primarily directed at feeding areas. The tubers of red root are the major food in the winter diet of cranes in the Okefenokee Swamp

(Bennett this proceedings). Small monotypic beds of red root are scattered throughout the marshes and their availability is dependent on water levels. During periods of high water, availability of red root diminishes and competition for feeding sites intensifies. We have observed resident pairs driving > 35 greater sandhill cranes from small (< 0.3 ha) beds of red root. The feeding behavior of sandhill cranes in the Okefenokee Swamp might make territories necessary to prevent depletion of food resources, particularly during periods of stress. Whooping cranes (*Grus americana*) are also known to maintain and defend winter territories (Blankinship 1976; Stehn & Johnson 1987). Allen (1952) suggested that this behavior may stem from their winter diet, consisting mostly of blue crabs (*Callinectes sapidus*).

Territorial behavior in migratory crane populations primarily centers around establishing breeding territories (Walkinshaw 1973; Drewien 1973). In the Okefenokee Swamp, resident cranes did not initiate nesting until mid-March when most greater had migrated north. In marshes that did not support overwintering greater, pairs nested 1-2 weeks earlier. After migrant cranes had vacated their territories, defensive interactions were rarely observed during nest construction and incubation. In Florida, resident cranes begin nesting in January (Walkinshaw 1976) and are relatively tolerant of greater sandhills in the vicinity of the nest (Layne 1981). Because Okefenokee cranes maintain territories throughout the year, there may be little need for neighboring pairs to reaffirm territorial boundaries in spring. Movements and nesting habitat selection further reduce the potential for interaction with other cranes. Pairs were extremely sedentary while nesting, often using < 20% of their annual territory. Cranes often nest in small openings surrounded by flooded woody vegetation (Bennett, this Proceedings), where they are visually screened from the remainder of their territories. Archibald & Viess (1978) and Larue (1981) reported that territorial conflicts are uncommon when pairs are visually screened from each other by tall vegetation.

Territoriality results in pair spacing and excludes entry of other pairs which are seeking breeding sites (Brown 1969). We did not observe any instances of transient pairs entering and usurping an occupied territory. Transient adults, birds which did not have established territories, occasionally established temporary residence (< 30 days) within or between the boundaries of several established pairs. When evicted from 1 territory,

these birds moved into portions of adjoining territories which were temporarily unoccupied by the residents. Competition for territories appeared to occur throughout the year.

Because single adults retained their territories after loss of mates, pairing was the only means by which transient adults obtained a territory. Nesbitt (1987, 1989) found that adult male Florida sandhill cranes retained their territories after losing their mates, while females often abandoned their territories and joined flocks of non-breeders. In this population, single females successfully maintained their territories, reared chicks and eventually repaired. The absence of social behavior and the apparent survival advantage of territorial behavior may contribute to the fidelity of single adults to their territory. Additionally, cranes that retain their territory are more attractive to prospective mates and have a psychological advantage in defensive encounters (Welty 1975). The rate of mate loss and re-pairing among transient adult pairs was high. Occupying a territory appeared to be of great importance in maintaining a long term pair bond.

The defense of roost sites has not been observed in other nonmigratory sandhill crane populations. In south-central Florida, Walkinshaw (1976) observed families with young 3 months old foraging and roosting with other cranes. Valentine (1981) reported Mississippi sandhill cranes (*G. c. pulla*) communally roosting in estuarine ponds during fall and winter. In the Okefenokee Swamp, cranes roost on small floating batteries of peat (Bennett this proceedings). During high water conditions, roost sites are often in short supply and competition for roost sites occurs.

Territoriality often serves as an intrinsic limiting factor on population size (Brown 1969), and in the Okefenokee Swamp it may control the distribution of sandhill cranes. Chesser Prairie (12 km²) represents near optimum crane habitat, and supports the second highest crane density (4.8 km² marsh) including 14 territorial adult pairs (Bennett 1989). Ten pairs (71.4%) were radio-tagged and the remaining 4 pairs were color-marked or recognizable by behavior. Size and configuration of the existing territories in Chesser Prairie (Fig. 1) suggested that crane density may be at a saturation point. Between 1985-88 no new territories were established.

Numerous researchers have observed crane territory sizes decrease as population densities increase (Littlefield & Ryder 1968; Drewien 1973; Kuyt 1981; Stehn & Johnson 1987). However, density-related adjustments to territory size are often

dependent on habitat quality or the availability of unoccupied habitat (Brown 1969). Habitat quality varies dramatically between marshes in the Okefenokee Swamp and crane densities range from 0.3 to 6.1 birds/km² marsh (Bennett 1989). Where habitat quality is lower, the size of crane territories was larger. A minimum territory size threshold may exist in each marsh under which pairs cannot obtain the annual habitat requirements necessary for their survival.

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Table 1. Duration between re-pairing for single adult sandhill cranes, Okefenokee Swamp 1985-87.

Crane No.	Sex	Chicks	Days before re-pairing	Time of year
158	F	2	30	Nov - Dec
158	F	0	9	March - April
563	F	0	>270	
201	F	1	-	Dec - Feb
420	M	1	<60	July - August

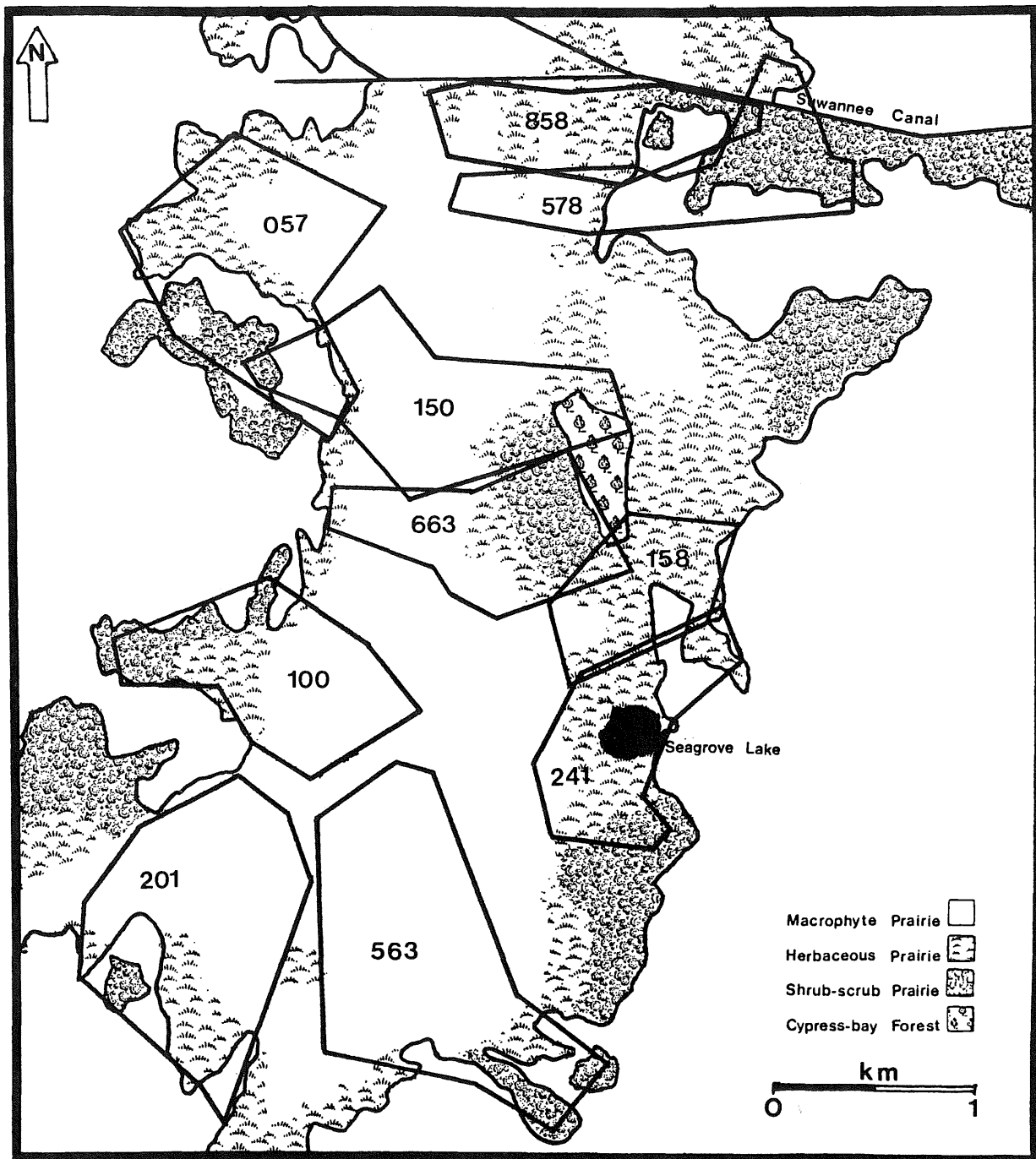


Figure 1. Configuration of 10 adult sandhill crane territories in Chesser Prairie, Okefenokee Swamp 1985-87 (see Bennett, this proceedings, for descriptions of habitat types).

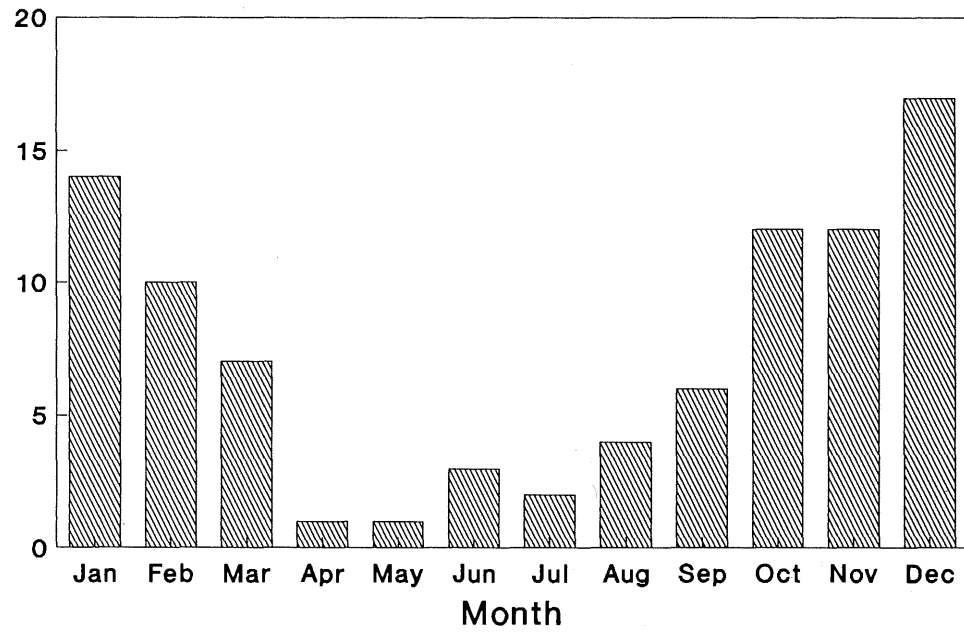


Figure 2. Monthly distribution of aggressive interaction observed among adult Florida sandhill cranes in the Okefenokee Swamp, 1985-87.