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STEPHEN A. NESBITT

Florida Fish & Wildlife Conservation Commission

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AGE, SEX, AND AGGRESSION IN FLORIDA SANDHILL CRANES

STEPHEN A. NESBITT, Florida Fish & Wildlife Conservation Commission, Wildlife Research Laboratory, 4005 South Main Street, Gainesville, FL 32601, USA

Abstract: Individually directed aggressive interactions were recorded for sandhill cranes in Florida over a 9-year period. Charges and stabs were the most frequently observed aggressive behaviors. Paired adults initiated most of the encounters. Males directed 67% of aggressive interactions toward other males and 84% of female aggressive interactions were directed toward other females. The sex of initiator was significantly correlated with the sex of the receiver ($P = 0.001$). Paired adults directed most aggression (64.7%) toward other paired adults. Aggression initiated by subadult cranes was directed toward adults and subadults with equal frequency. The aggressiveness in males as an indicator of territoriality may be a means that females may use to assess suitability of potential mates.

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Key words: age, aggression, cranes, Florida, *Grus canadensis pratensis*, mate selection, pairing, sandhill cranes, sex.

Intraspecific aggression is a conspicuous aspect of most vertebrate societies (Collias 1944). In sandhill cranes (*Grus canadensis*) aggressive displays are components of many social interactions. Aggressive behaviors in sandhill cranes can range from antiphonal calling (Nesbitt and Bradley 1997) and subtle postures to dramatic frontal kicking and active pursuit flights (Ellis et al 1998). I recorded aggressive interactions within a population of known-age, known-sex Florida sandhill cranes (*G. c. pratensis*). These data were collected adventitiously during investigations of questions pertaining to the possible reintroduction of whooping cranes (*G. americana*) to Florida (see Nesbitt et al. 1997).

Florida sandhill cranes are perennially monogamous with reproductively successful pairs remaining together for several years. A pair typically frequents the same nesting territory as long as the pair bond persists (Nesbitt and Tacha 1997). And while on the territory, the pair will actively defend it against other cranes.

The interaction of aggression and submission between males and females may be an aspect of potential mate assessment and pair bond initiation. Nesbitt and Wenner (1987) observed aggressive posturing followed by appeasement, and offered this as one method that a female could use to attract the attention of a potential mate. Knowing what influence sex and age has in determining initiator or receiver during aggressive encounters could provide insights into what role, if any, aggression plays in mate selection.

METHODS

Observations were made from 1986 through 1995 on and around Paynes Prairie State Preserve in Alachua County, in north central Florida. Paynes Prairie is an area of 7,300 ha, managed by the Florida Department of Environmental Protection. The preferred crane habitat is emergent palustrine wetlands (Cowardin et al. 1979) dominated by pickerelweed (*Pontederia cordata*) and maidencane (*Panicum hemitomom*) grading

to open grassland and pasture. A wooded rim borders these extensive open areas (see Nesbitt and Williams 1990 for more detailed description).

Cranes were captured with the use of oral tranquilizers (Bishop 1991). Each bird was banded and individually color marked with colored plastic leg bands (Nesbitt et al. 1992). Sex was determined after banding with karyotyping of blood samples (Goodpasture et al. 1992), or by unison call displays (Archibald 1976) observed following release. Wing molt patterns were used to assign birds into juvenile, subadult, or adult age classes (Nesbitt 1987). Whether the bird was paired or unpaired was recorded at the time each interaction was observed.

Some aggressive displays are not obviously directed at a specific individual. Direct Walk, for example, may be directed at a pair of adults and it is not always apparent which member of the pair is the object of the aggression. I only recorded aggressive interactions where the targeted individual was obvious (see Fig. 1). In some cases an encounter could involve more than one aggressive behavior, for example a stab could lead to an aerial pursuit, in such case the final (which was often the most intense) display was the one recorded.

Aggressive interactions were monitored during territorial interactions, or at feeding sites, roost sites, and other areas where cranes gathered. Observations were made from a blind or other inconspicuous location with binoculars or 25x telescopes. In addition to date and type of aggression, I recorded the giver and receiver. If sex and age were not known at the time the observation was made they were added later, after checking the bird's records. Only birds of known age and known sex were used for this study.

Each aggressive encounter was analyzed using a weighted linear mixed model, with sex modeled as a between-subject fixed effect. Age was modeled as a within-subject fixed effect. Since there was frequently more than one observation per individual bird, within-bird as well as between-bird variations needed to be accounted for during analysis. To accomplish this each bird and the interaction between age and bird were

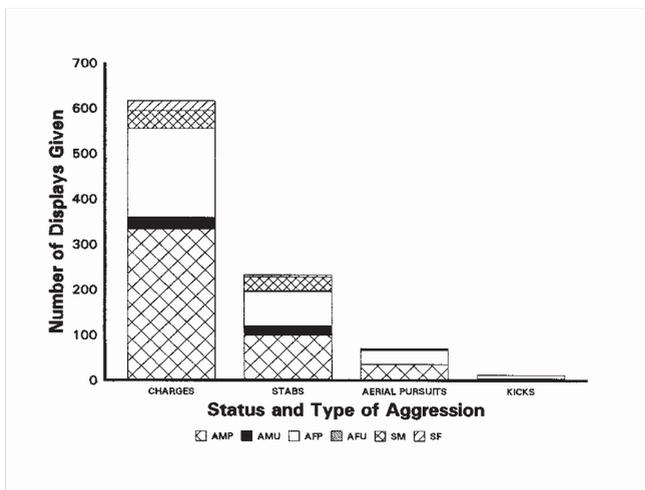


Fig. 1. Age, sex, social status and type of aggression in Florida sandhill cranes, 1986-1995 (paired adult males [AMP], unpaired adult males [AMU], paired adult females [AFP], unpaired adult females [AFU], subadult males [SM], and subadult females [SF]).

nested within sex and then modeled as a random effect. By doing this the potential for confounding that might result from the differential number of observations for a few individuals was avoided. Observed proportions of aggressive interactions that were with males were arcsine-square root-transformed prior to analysis to stabilize variance. Total number of male and female interactions per bird per age was used as weights in the analysis.

RESULTS

Banding and color marking resulted in 309 uniquely marked Florida sandhill cranes. I recorded 930 aggressive interactions of 94 aggressors where sex, age, and paired status of the aggressor and the receiver were known. Two of the birds in the sample were unmarked, but their age, sex and social status could be determined because they were paired with a marked bird whose status was known.

Adult Florida sandhill cranes are relatively sedentary and usually stay within a predictable year-round home range (Nesbitt and Williams 1990). This made it possible to observe the same individual over a period of years. Approximately half of the 94 birds were sampled just once; the remaining 45 were sampled multiple times over a period of a few days to 12 years. The mean duration of observations was 1.43 years (± 2.4 years SD). This extended period of observation made it possible to observe several individuals (N=13, 10 males and 3 females) as they matured and changed social status. The mean number of observations for a single individual in a single age class averaged 8.64 ± 19.92 (SD, range 1 to 183). The individual with the largest number of observations was a male that was seen over a period of 12 years. He was observed first as a subadult, then

Table 1. Sex, age and social status of crane and number of aggressive interactions in Florida, 1986-1995.

Initiator	Receiver						Total
	Paired adult		Unpaired adult		Subadult		
	Males	Females	Males	Females	Males	Females	
Paired adults males	253	105	41	16	32	24	471 (50.9)
Paired adult female	35	149	0	69	15	41	309 (33.2)
Unpaired adults males	19	3	2	0	20	3	47 (5.1)
Unpaired adult females	0	0	0	0	0	2	2 (0.2)
Subadult males	13	13	8	0	9	30	73 (7.9)
Subadult females	4	10	2	4	0	8	28 (3.0)
Total	324	280	53	89	76	108	930

later as a member of a pair.

Adults initiated 89.2% of the 930 observed aggressive encounters and subadults the remaining 10.8%. Males were the initiator in 63.7% and females in 36.3% of the encounters. Paired birds initiated 83.9% and unpaired birds 16.1% of the encounters (Table 1).

Males directed more aggression (397/194) toward other males than toward females. Females directed aggression toward other females more often (283/56) than to males. Among adults aggression was directed toward other adults more often than toward subadults (692/141). Aggression in subadults was directed almost equally (54/47) between adults and other subadults. Paired birds most often directed aggression (604/333) toward other paired birds. Among unpaired cranes the direction of aggression was more equally divided (62/88) between paired and unpaired cranes (Table 2).

I recorded 930 aggressive incidences with a known initiator

Table 2. Sex, age and social status of crane initiating and receiving with % frequency of aggression in Florida, 1986-1995.

	Receiver				
	Male	Female	Adult	Subadult	
Aggressor	Male	67.2	32.8		
	Female	16.5	83.5	Adult	Subadult
			Adult	83.1	16.9
		Subadult	53.5	46.5	Paired
			Paired	64.7	35.3
			Unpaired	41.3	58.7

and a known receiver, 66.3 % were charges, 24.9 % stabs, 7.5 % aerial pursuits, and 1.3 % kicks. There were differences in the frequency of aggression displayed by status of the initiator (Fig. 1). Charges were given more in all the status categories than the other 3 displays. Paired adult males gave proportionally more stabs (20.8%) than kicks (.08%), whereas paired adult females gave more kicks (24.3%) than stabs (2.6%). Kicks were not seen in any unpaired birds and aerial pursuits were most frequently seen in paired adults.

The weighted linear mixed model analysis showed sex had a significant effect on the receiver of aggression in sandhill cranes. The likelihood of a male directing aggression at another male was greater than for him to direct aggression toward a female ($P=0.0011$). Sex had a significantly greater influence on the direction of aggression in adults ($P=0.0002$) than in subadults ($P=0.0596$).

DISCUSSION

The statistically significant rate of same-sex directed aggression is evidence that Florida sandhill cranes are able to recognize the sex of other cranes. If cranes had no ability to differentiate sex, it would be expected that aggression direction would be sex neutral. Males or females would direct aggression towards other cranes with sexual equity, since sex ratios are nearly equal in the wild (Nesbitt et al 2001). Determination of the sex in Florida cranes cannot be based on relative size alone, since there is overlap in size between males and female Florida sandhill cranes (Nesbitt and Moore 1992). Posture or subtle behaviors may be more reliable than size for cranes to differentiate between sexes.

In Florida sandhill cranes males exhibit greater philopatry than females. Males secure and are the primary defender of the territory while females are the dispersers (Nesbitt and Schwikert 2002). Females are more actively engaged in seeking out and selecting a prospective mate. The level of aggressive response in the male could be one factor used by females to evaluate a possible mate. A female's mate choice decision could be based on her assessment of a potential mate's ability to secure and maintain a territory. I have seen unpaired females eliciting aggression from males, even when the male was already paired (though without chicks), (Nesbitt 1987). The female would assume an erect posture and in response the male directed his attention to this potential challenger. As the male approached she would lower her head to a subordinate position. This sequence could be repeated several times and if the encounter lasted long enough eventually the female might assume a precopulation posture. In two instances the males were subsequently seen paired with the interloping females. Male sexual mimicry by females as strategy for pair formation may explain why males directed aggression toward females almost twice as often as females directed aggression toward males (table 2). Even if sex mimicry has nothing to do with mate choice, it is apparent that Florida sandhill cranes are able to identify sex and social status

of other cranes. This ability to assess status of other cranes at a distance reduces the need to interact aggressively, risking potential injury, with another crane that poses little or no threat.

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