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Conspecific aggression in a Wood Stork colony in Georgia.—The probability of interactions among conspecifics, including aggression, is increased in colonial nesting birds. Increased egg and nestling loss due to the presence or activities of conspecifics represents a potentially severe cost of coloniality in many species of birds (Wittenberger and Hunt 1985). Nest losses to late nesters can result if nest material or suitable nest sites are in short supply. Nest or territory takeovers can also result if birds attempt to return to previous breeding sites that are already occupied, if there is a lack of unoccupied suitable nesting habitat, or if the net value of the breeding site exceeds the cost of the takeover (Johnson and Kermott 1990). There have been few studies concerning conspecific aggression among colonially nesting Wood Storks (*Mycteria americana*) or their allies. Barthos (1908) observed a pair of intruding White Storks (*Ciconia ciconia*) dislodge the resident pair of storks from a nest, throw out the eggs, and use the nest structure themselves. Kahl (1964) reported that nest attendance by adult Wood Storks during the early nestling stage is necessary to protect the young from inclement weather and "marauding bands of un-mated storks, which will attack and destroy unguarded nests." Frederick (1986) also observed nest takeovers and egg destruction among White Ibises (*Eudocimus albus*).

In this paper, we report on observations of nest takeovers, group aggression, and adults killing nestlings in a colony of Wood Storks in east-central Georgia. We describe this aggression, examine the variation in frequency of aggression among years, and discuss the possible consequences of these incidents and reasons for their occurrence.

Methods.—The Birdsville colony is located in Jenkins County, east-central Georgia (32°52′N, 82°03′W), on the northern edge of the Wood Stork's range. From 1986–1989 the colony included between 100 and 200 pairs of Wood Storks and 30 to 80 pairs of Great Egrets (*Casmerodius albus*). They nested in the tops of Cypress trees (*Taxodium ascendens*) in densities of one to 20 nests per tree. Storks began arriving at the colony in March and began nesting in late March and April (Coulter 1990). Hatching occurred from April through mid-June, and birds began dispersing from the colony in June through August, with some interyear variation. The period of time for storks to lay and hatch eggs and raise young to fledging age is about four months.

Nesting pairs of Wood Storks were observed from an 18-m tower within the colony for 7–12 h/day, five days a week, throughout each breeding season from 1986 through 1989. Pairs were considered established when eggs were seen in their nests or when adult behavior and posture suggested they were incubating eggs. We monitored 31–68 nesting pairs in the colony each year, including 10–20 pairs in which the sexes had been determined during copulation. Individuals were identified by unique facial and bill characteristics. Pairs were observed until their nestlings began leaving the nests or until the nests failed. Occurrences of conspecific nest takeover, group aggression, and nestling killing were recorded. Rates of agonistic behavior (incidents per hour) also were calculated.

Results.—Most nest takeovers followed the same progression of events. Two or more intruding Wood Storks would attack the adult stork or storks attending eggs or young nestlings. Attending adults were usually bitten on the head and neck for several minutes by the intruders before being forced off the nest. The eggs or nestlings were thrown from the nest in each case, and the new pair copulated on the nest within 10–15 min. Courtship behavior by the new pairs was rare.

Nest takeovers were observed primarily in 1988 ($n = 12$) and 1989 ($n = 10$), a single takeover was observed in 1987, and none was witnessed in 1986. In all instances, two or more Wood Storks attacked the resident adult(s). A single bird was never observed trying to force another stork from its nest.

TABLE 1

AVERAGE NUMBER OF TRIPS TO GATHER NEST MATERIAL BY PAIRS OF WOOD STORKS AT TAKEOVER AND NON-TAKEOVER NESTS IN 1988 AND 1989

	Average number of nest material trips per hour			
	1988[b]		1989[b]	
Nest type[a]	N[c]	$\bar{x} \pm$ SD	N[c]	$\bar{x} \pm$ SD
Takeover	5 (121)	0.21 ± 0.23	5 (185)	0.17 ± 0.23
Non-takeover	8 (381)	0.32 ± 0.36	6 (300)	0.27 ± 0.37

[a] Takeover nests were acquired by conspecific aggression whereas non-takeover nests were initiated and maintained by the original pairs.

[b] Average nest material trips were significantly different between takeover and non-takeover pairs in 1988 (Wilcoxon Sum Rank test, $P < 0.01$) and in 1989 (Wilcoxon Sum Rank test, $P < 0.02$).

[c] N = Number of nests (number of nest-days of observation).

Eight nest takeovers occurred in which the sexes of the resident nesting individuals had been determined. In each of these cases, takeover attempts occurred when a single adult Wood Stork was in attendance. Seven of the eight attending adults at the time of the takeover were females. Resident pairs forced from their nests always attempted to drive the intruders away once their absent mates had returned. Only one pair regained its nest, but its young (1 nestling and 2 eggs) had already been thrown from the nest. This pair abandoned the nest site the following day. Two of the resident pairs that lost their nests were brooding at least one 1-week-old nestling, whereas the remaining six resident pairs were incubating eggs.

Nest takeovers should enable a pair of Wood Storks to spend less time and energy bringing material to the nest than would be required if they had initiated a nest themselves. To address this hypothesis, we compared the frequency of nest material trips made by intruding (takeover) pairs and resident (non-takeover) pairs in 1988 and 1989. Nest material trips per hour for all pairs varied significantly between years (Wilcoxon Rank Sum test, $P < 0.01$), and the data from the two years were analyzed separately. In both years, takeover pairs made significantly fewer trips than did resident pairs (Wilcoxon Rank Sum tests, $P < 0.02$; Table 1).

Only one of eight intruding (takeover) pairs successfully fledged young (3 fledglings). Six of the remaining seven intruding pairs produced eggs, and four of these pairs hatched young. However, all six breeding attempts failed either as a result of raccoon (*Procyon lotor*) predation or nest abandonment by the parents. The other attempt by an intruding pair resulted in one egg and was itself a victim of a nest takeover.

Group aggression involved more than four intruding Wood Storks fighting with one or more pairs of resident storks in nest trees and were frequently associated with nest takeovers. Group aggression began in at least two ways. First, intruding storks sometimes assembled in a tree containing nesting birds. Eventually, a resident stork or storks attempted to chase away an intruder and a fight ensued. The remaining intruding storks either participated in the fight or hovered near the nest tree.

Second, some group aggression followed other disputes, such as the theft of nest material. Within such disputes, resident Wood Storks responded to a threat with "bill-clattering" behavior (Kahl 1972). The snapping noise associated with this behavior seemed to attract storks from throughout the colony, resulting in group aggression.

We observed as many as 35 Wood Storks involved in a single group aggression. In that instance, three nests were taken over, and three new nests were later initiated by nonresident

TABLE 2

COMPARISON OF CONSPECIFIC AGGRESSION OBSERVED AMONG WOOD STORKS IN THE BIRDSVILLE COLONY, 1986 THROUGH 1989

Year	Hours (days) of observation[a]	Aggressive interactions observed[b]	Aggressive interactions/hour[c]	No. days aggression observed
1986	420 (40)	0	0.000	0
1987	433 (40)	3	0.008	3
1988	442 (43)	11	0.057	11
1989	520 (47)	45	0.086	20

[a] Observations in March, April, and May.
[b] Varied significantly among years (Kruskal-Wallis, $P < 0.01$)
[c] Varied significantly among years (Chi-square = 29.7, df = 7, $P < 0.01$).

birds that participated in the group aggression. We never observed lone parents abandoning their eggs or nestlings to join group aggression, but we observed adults that were attending incubating or brooding mates leave their mate to join the intruders.

Adult Wood Storks were observed throwing nestlings from neighboring nests on two occasions. In both cases, male storks were attempting to steal nest material from nests with young that were unattended by adults. On 28 May 1987, three nestlings were thrown from a nest within a 15-min period by a single neighboring male. An attack on 2 June 1987 resulted in the death of a single nestling from a brood of two nestlings.

Nest takeovers and group aggression were rare among Wood Storks in 1986 and 1987, but significantly more frequent in 1988 and 1989 (Kruskal-Wallis, $P < 0.01$; Table 2). Nest takeovers were also more frequent in 1988 and 1989, when they affected 13% (4/31) and 26% (18/69) of the observed nests, respectively, compared with 1986 and 1987, when they affected 0% (0/39) and 2% (1/51) of the nests, respectively. Numbers of days in which conspecific aggression was observed also were not evenly distributed among years (Chi-square = 29.7, df = 7, $P < 0.01$; Table 2).

Discussion.—Courtship behavior by storks is very important in the establishment of the pairbond and often occurs over a span of several hours to several days (Kahl 1971, 1972). However, there was a noticeable lack of courtship behavior in Wood Storks successful in takeover attempts, as well as in those storks initiating nests after incidents of group aggression. These intruding storks may have been paired prior to these nest takeover attempts. Ecological conditions conducive to early nest abandonment could result in paired storks that may attempt to acquire nests through agonistic behavior, an advantage of which is gaining an already built nest.

Early nest abandonments by Wood Storks were clearly linked to agonistic behavior with conspecifics. Abandonment of nests typically occurred only in the last half of the breeding season (June–August) in all years except 1989. These late-season abandonments were generally associated with increased predation as a result of drying conditions under the nest trees. In 1989, nests were abandoned as early as mid-April. Agonistic behavior in the colony peaked the week following these initial abandonments and continued into early May. Early abandonments in 1989 coincided with the week-long passage of a cold front in which temperatures dropped to 1°C and 9 cm of rain fell (Coulter 1990). The time budgets of nesting storks during this period indicated that they made fewer trips from the nest, stayed away for significantly longer periods on each trip when they did leave, and stayed at the

TABLE 3

COMPARISON OF AVERAGE DURATION OF TRIPS FROM AND STAYS AT THE NEST, AND THE NUMBER OF ACTIVITIES OF NESTING PAIRS IN THE BIRDSVILLE COLONY, 1986 THROUGH 1989[a]

Year	Duration of trips from the nest (min)[bc]			Stay at the nest (min)[bc]			Number of activities per day[de]		
	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD
1986	96	196.1	104.2	156	183.2	126.7	41	7.3	3.1
1987	52	79.9	42.9	202	149.9	107.7	35	7.8	4.0
1988	50	160.1	99.8	118	174.5	136.7	25	6.0	2.8
1989	25	297.8	115.2	68	333.8	152.1	37	3.4	5.6

[a] The time budgets analyzed here compare the trip length and number of activities of nesting pairs during the week-long passage of a cold front in 1989 to the time budgets of nesting pairs of a similar reproductive stage in the previous three years.

[b] Trips and stays at the nest less than 30 min in duration were not included in an effort to distinguish the longer foraging trips from the shorter trips to acquire nest material.

[c] Average duration of trips and stays at the nest were significantly different among years (Kruskal-Wallis tests, $P < 0.01$).

[d] Activities included any trip in which the bird returned to the nest.

[e] Average number of activities for nesting pairs in 1989 was significantly lower than that in 1986, 1987, or 1988 (Mann-Whitney U tests, $P < 0.01$). There were no other significant differences among years (Mann-Whitney U tests, $P > 0.05$).

nest for longer periods after returning (Kruskal-Wallis tests, $P < 0.01$; Table 3). Kahl (1964) suggested that cooler temperatures could hinder the storks energetically during the stressful courtship period and could negatively affect the availability of prey by making them less active and, presumably, more difficult to capture. Heavy rainfall can increase surface water levels at foraging sites and disperse prey. Thus, storks may have needed more time to locate and capture food during this period.

In 1988, another year with frequent nest takeovers and group aggression, abandonment of Wood Stork nests in the first half of the season was not noted. However, that year the storks arrived at the colony site about one week later than normal and in lower numbers than the previous two years (Coulter 1989). March and early April of 1988 was characterized by considerable movements of large groups of nest-building storks from one tree to another. These movements appeared to occur before any eggs were laid, but many birds may have been paired prior to abandonment. Storks may have arrived late in 1988 as a result of poor feeding conditions on their wintering grounds so that the birds may have needed more time to reach breeding condition. Also, the late arrival could have made the acquisition of an already built nest more advantageous.

Taking over an active stork nest can be beneficial to potential nesters if either nest material or suitable nesting sites are in short supply. Although not quantified in this study, nest material and suitable nest sites seemed abundant in the colony each year, and we could not discern a preference or advantage of a particular type of nest site. Also, neither nest density nor location in the colony affected the likelihood of predation when predators (raccoons) invaded the colony.

Wood Storks involved in nest takeovers were socially or behaviorally atypical. Mutual manipulation of nest material by nesting Wood Storks is a behavior that maintains the pairbond throughout the lengthy breeding season (Kahl 1972). Whereas the reduced number of nest material trips by takeover pairs was energetically beneficial, it also effectively reduced

the opportunity to reinforce the pairbonds of these birds and suggests a weakness in the pairs themselves.

Nest takeovers and group aggression at the Birdsville colony usually occurred from late March through May each year when most birds were building nests and laying eggs. Renesting by Wood Storks was occasionally successful. We observed a color-banded Wood Stork attempt to nest three times at different sites within the colony early in the same season and successfully raise young from the third attempt to fledging age. Most takeover pairs were not successful nesters. Nest takeovers seem to be attempts by paired birds from early abandonments to save time and energy by renesting as quickly as possible in already built nests. However, such attempts have a reduced likelihood of success because of increased risk of predation as a result of nesting later in the season and possible weaknesses in the pairbond of the takeover pairs.

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