FACTORS AFFECTING REPRODUCTIVE SUCCESS OF WOOD STORKS (*MYCTERIA AMERICANA*) IN EAST-CENTRAL GEORGIA

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ABSTRACT.—From 1984 through 1989, we examined the reproductive success of Wood Storks (*Mycteria americana*) at the Birdsville colony in east-central Georgia. Average fledging success ranged among years from 0.33 to 2.16 fledglings per nest. For nests that produced fledglings, prey availability was an important factor affecting reproductive success. Yearly average prey densities at foraging sites were significantly correlated with the average number of fledglings produced from successful nests. Among 243 nests observed, all eggs or chicks were lost from 104 (43%) nests. Five factors were associated with the loss of entire clutches or broods. During the two driest years, 1985 and 1988, raccoon (*Procyon lotor*) predation eliminated almost all chicks. Many nests were abandoned early in 1989, following periods of cold weather when the parents appeared to be under stress. In 1985, the birds deserted the colony before egg laying when the area experienced freezing weather. Following nest abandonments within the colony, paired adults that presumably had abandoned their nests were involved in nest takeovers that also caused the loss of eggs and chicks. Three storms during the study caused the loss of a few nests. Some losses were due to unknown factors. The importance of these mortality factors varied from year to year. Nest abandonments and subsequent aggression seem to be related to cold periods early in the season. Raccoon predation seems to be related to drying out of the water under the colony. This suggests that the storks have a window in time when it is best to breed—after the winter and early spring cold weather and before the water dries under the colony in the summer. *Received 4 December 1991, accepted 15 November 1992.*

THE FACTORS THAT affect reproductive success in birds have been a main topic in studies of avian biology (Lack 1966, 1968, Perrins and Moss 1975, DeStevens 1980, Winkler and Walters 1983, and references cited within these papers). Reproductive success of wading birds may vary considerably among colonies and between years (Rodgers 1987b, Frederick and Collopy 1989a). The importance of food is one factor affecting reproductive success of wading birds (Kahl 1964, Clark 1979). In southern Florida, a positive relationship has been shown between the drying rate of wetlands and both numbers of nest attempts and reproductive success (Frederick and Collopy 1989a). Some wading birds had greatest reproductive success or began breeding in large numbers during years with faster drying rates than in years with slower drying rates (Kushlan et al. 1975). Other factors also affect reproductive success: predation (Rodgers 1987a, Frederick and Collopy 1989b), weather (Rodgers 1987b), and intraspecific aggression (Frederick

1986, Bryan and Coulter 1991). Birds may also abandon their nests (Frederick and Collopy 1989b). Moreover, the relative importance of the various factors is likely to differ between years.

The reproductive success of Wood Storks (*Mycteria americana*) was studied at a colony in east-central Georgia from 1984 through 1989 (Coulter 1988). We examined the relative importance of different factors affecting reproductive success and how these varied from year to year. We evaluated whether environmental conditions influence these processes and whether, by influencing reproductive success, these conditions could affect aspects of breeding biology such as phenology.

METHODS

We studied the breeding biology of Wood Storks at the Birdsville colony (32°52'N, 82°03'W) in Jenkins County, east-central Georgia from 1984 through 1989. The Birdsville colony was located in Big Dukes Pond in all years, except 1985 when the birds nested in Little Dukes Pond about 1 km from Big Dukes Pond. During these years, the colony has varied in size from

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a minimum of about 100 pairs in 1984 to a maximum of 193 pairs in 1987. We followed the fate of those nests that we could observe well each year ($n = 26$ to 65) from the period of egg laying (late March) through dispersal of young (early July through early September, varying among years). We made observations in the colony from 0630 to 1730 EST five days per week. Observations in Big Dukes Pond were made from a tower 18 m high in 1984 and from a 20-m tower in 1986-1989. In 1985, observations were made in Little Dukes Pond from a tree blind about 7 m high. We began following nests only after the nests contained eggs. The eggs and chicks were counted each day, and the causes of loss were determined when possible.

We were able to count eggs in the nests only in 1987-1989. We determined the clutch size for each nest and considered the maximum number of chicks counted during all observations as a measure of initial brood size. We calculated hatching success as initial brood size/clutch size. We determined the number of chicks fledging in each nest as the number of chicks alive at the time that the young could first fly.

In some years, we believed that the reproductive success among the nests that we followed intensively was not representative of the entire colony due to greater predation in some areas of the colony than in other areas. For all years we estimated the total number of nests lost to predation, and calculated an overall fledging rate for the colony.

When one or two chicks in a nest were lost but not the entire brood, it was usually difficult to determine the cause of mortality. On two occasions, we observed chicks thrown from their nests by intruding adults, and on one occasion we observed a raccoon (*Procyon lotor*) taking a chick. In most cases we were unable to determine the causes of these losses.

More often we could determine the cause of mortality when an entire brood was lost than when less than the entire brood was lost. Five sources of mortality were identified. We found entire nests missing immediately following two heavy thunderstorms, and attributed these losses to storm damage. We observed eggs and chicks thrown from nests by intruding storks (Bryan and Coulter 1991), and tallied these as intraspecific aggressions. During dry years when the swamp under the nest trees became dry, raccoons entered the colony (usually at night) and killed nestlings. After these invasions, the carcasses of dead young often were left in the nests. We attributed these losses to raccoon predation. To corroborate our identification of raccoon predation and examine the extent that these animals intruded into the colony, F. C. Depkin spent three nights observing the nests with a night scope from the tower. Some nests were occupied one day, but not occupied the next. There was no indication that the contents of the nests had been disturbed by predators, intraspecific interactions, or inclement weather. Some of these abandonments in the early

spring followed cold weather, when the storks appeared to be under stress. We attributed these losses to stress induced by the cold weather. In cases in which nests were found empty with no apparent cause, the failure was attributed to unknown causes.

It was not possible to examine directly the importance of food availability to reproductive success because our estimates of the numbers of fledglings produced were made visually, and we were unable to assess body condition. Therefore, we examined the relationship between the availability of potential prey at foraging sites (average yearly density and biomass) and average fledglings per nest through regression and correlation analyses. In these analyses we considered only nests from which at least one young fledged. Although some mortality in the successful nests may have been due to predation, intraspecific aggression, or harsh weather, any effects of food availability on reproductive success would be most apparent among these nests. We determined the availability of potential prey by sampling their density and biomass at foraging sites visited by storks of the Birdsville colony (Depkin et al. 1992, Coulter unpubl. data).

Data are summarized as $\bar{x} \pm 1$ SD. In most cases, parametric statistical tests were used. ANOVA was used to compare parameters among multiple years. When ANOVA results indicated significant differences, Scheffé's multiple-comparison tests were used to examine differences between specific years. When sample sizes were less than 10, nonparametric tests were used: Wilcoxon matched-pairs signed-ranks tests, chi-square test and Spearman rank correlations. All statistical tests were two-tailed and were considered significant at $P < 0.05$. Analyses were performed with the STATA computer statistical package of Stata Corporation.

RESULTS

CLUTCH SIZE AND HATCHING SUCCESS

The storks laid clutches of one to five eggs, with most clutches consisting of two or three eggs. From 1987 through 1989, the only years in which we could count eggs, the average clutch size was 2.9 ± 0.74 eggs per nest ($n = 48$; Table 1). Significant differences existed between years (ANOVA, $F_{2,45} = 5.99$, $P < 0.01$). The average clutch size in 1987 was significantly different from those in 1988 and 1989, but clutch sizes in 1988 and 1989 were not different (Scheffé's multiple-comparison test).

An average of 2.6 ± 0.71 (range 0-5) chicks hatched in 1987-1989 (Table 1). The numbers of chicks that hatched were significantly different between 1987 and 1988 (ANOVA, $F_{2,45} =$

TABLE 1. Clutch size and hatching success ($\bar{x} \pm$ SD) of Wood Storks at the Birdsville colony in east-central Georgia, 1987–1989.

Year	No. nests	Clutch size[a]	No. chicks hatched per nest	Hatching success (%)
1987	19	3.26 ± 0.65	2.95 ± 0.71	91
1988	14	2.23 ± 0.65	2.29 ± 0.47	93
1989	15	2.67 ± 0.72	2.47 ± 0.74	93
Total	48	2.85 ± 0.74	2.60 ± 0.71	92

[a] Eggs per nest.

4.54, $P < 0.05$; Scheffé's multiple-comparison test, $P < 0.05$), but other differences between years were not significant. Overall hatching success was 92%.

In addition to the nests in which we counted the eggs, there were other nests for which we could not count the eggs and in which all eggs were lost before hatching. These were not included in the above analyses because we were unable to count the eggs. These were lost either through aggression when intruding birds threw the eggs from the nests or abandonment, and are discussed below as mortality factors.

FLEDGING SUCCESS

The average initial brood size for 1984–1989 was 2.7 ± 0.74 ($n = 190$; Table 2). Brood sizes varied significantly among years (ANOVA, $F_{5,184} = 11.34$, $P < 0.001$). Initial brood sizes in 1986 were significantly larger than brood sizes in 1985, 1988, and 1989, and initial brood sizes in 1984 and 1987 were significantly larger than the sizes recorded in 1989 (Scheffé's multiple-comparison test, $P < 0.05$). Differences in initial

brood sizes between other years were not significant (Scheffé's multiple-comparison test, $P > 0.05$).

The storks produced an average of 1.37 ± 1.32 fledglings per nest. Fledging success varied significantly among years (ANOVA, $F_{5,184} = 27.76$, $P < 0.001$). Average fledging successes in 1984, 1986, and 1987 were greater than the averages in 1985, 1988, and 1989 (Scheffé's multiple-comparison test, $P < 0.001$).

We felt that mortality may not have been evenly distributed in the colony, and that the breeding success for the nests we followed may have been higher than the overall breeding success for the entire colony. Particularly in 1985, 1988, and 1989, there seemed to be much higher mortality in areas of the colony where we did not follow individual nests. Therefore, we calculated a reproductive success for the entire colony based on overall observations. Our estimates for reproductive success of the entire colony tended to be lower than fledging success for the followed nests, but the differences were not statistically significant (Wilcoxon matched-pairs signed-ranks test, $n = 6$, $P > 0.05$). The correlation between fledging rate in followed nests and the entire colony was significant (Spearman rank correlation = 0.94, $n = 6$, $P < 0.01$).

CAUSES OF MORTALITY

It was difficult to identify the causes of mortality of eggs and chicks except when the entire clutch or brood was lost. For 104 (43%) of the nests that we followed, the entire contents of the nests were lost and no chicks fledged. The numbers of nests from which no young fledged varied significantly among years ($X^2 = 60.75$, df

TABLE 2. Initial brood size and fledging success of Wood Storks at Birdsville colony in east-central Georgia.

Year	Initial brood size[a]	Fledglings per nest[a]	Percent success[b]	Fledglings per nest for entire colony[c]
1984	2.87 ± 0.80 (24)	2.23 ± 0.99 (26)	78	2.04
1985	2.26 ± 0.81 (23)	0.52 ± 1.05 (27)	23	0.33
1986	3.15 ± 0.59 (39)	2.65 ± 1.00 (40)	84	2.16
1987	2.82 ± 0.63 (49)	1.98 ± 1.13 (50)	70	1.96
1988	2.31 ± 0.48 (16)	0.09 ± 0.28 (35)	4	0.35
1989	2.23 ± 0.63 (39)	0.83 ± 1.01 (65)	37	0.63
Total	2.66 ± 0.74 (190)	1.37 ± 1.32 (243)	52	1.25

[a] Chicks per nest. $\bar{x} \pm$ SD (n).
[b] 100 (fledglings per nest/initial brood size).
[c] Estimated for entire colony (see Methods).

TABLE 3. Loss of entire nest contents due to different mortality factors for Wood Storks of Birdsville colony in east-central Georgia, 1984–1989.

	Nests lost (% nests lost)						
Mortality factor	1984 (26[a])	1985 (27)	1986 (40)	1987 (50)	1988 (35)	1989 (65)	Total (243)
Raccoon predation	0(0)	18(90)	0(0)	2(29)	13(36)	0(0)	33(32)
Intraspecific aggression	0(0)	0(0)	0(0)	2(29)	9(25)	5(14)	16(15)
Abandonment	0(0)	0(0)	0(0)	0(0)	0(0)	7(19)	7(7)
Inclement weather	0(0)	2(10)	0(0)	1(14)	0(0)	2(6)	5(5)
Unknown	3(100)	0(0)	2(100)	2(29)	14(39)	22(61)	43(41)
Total nests lost	3	20	2	7	36	36	104

[a] No. nests observed.

= 5, P < 0.001) and reflected the same rank order among years as the fledging success for the colony. Five factors in order of importance that were responsible for losses of entire nest contents were raccoon predation, unknown causes, intraspecific aggression, cold weather, and storm damage. The relative importance of these factors among followed nests varied among years (Table 3).

Raccoon predation.—Predation typically occurred late in the breeding season, and involved the loss of chicks. In almost all instances (87%), the entire brood was lost. Predation was very heavy in 1985 and 1988, accounting for 90 (43%) instances of mortality. Predation was not recorded in 1984 or 1986, and was recorded at low levels in 1987 and 1989. Both 1985 and 1988 were very dry years (Coulter unpubl. data), and the predation occurred in June and July. In 1985, the storks bred in Little Dukes Pond, where they nested in trees bordering the shoreline. While it never became dry under the trees, buttonbush (*Cephalanthus occidentalis*) growing among the trees allowed the raccoons to reach the nest trees from the shore with little risk of predation by alligators (*Alligator mississippiensis*).

At 1800 on 27 June 1985, predation of a chick by a raccoon was observed. A raccoon was seen climbing one of the trees that we monitored about 5 m from our observation post. The raccoon examined a dead chick in a nest that had been abandoned. When the raccoon was about 1 m below an active nest, the chicks became excited. The raccoon climbed to the nest and grabbed a chick, killing it with a bite at the base of the neck. The parent and two remaining chicks stayed near the far side of the nest (<0.5 m away) and snapped their bills a few times at the raccoon. The raccoon climbed down the tree with its prey.

We put up metal flashing (about 1 m high) at the base of this and all other nest trees to discourage the raccoons. However, on 1 July, a raccoon was again seen in the same tree. It climbed over the flashing and explored the tree, but killed no chicks.

During this period, the remains of chicks were observed in nests or nearby branches. The colony of 108 nests produced only about 36 chicks in 1985. Because most of the chicks were lost during this period and because we found remains of chicks in many of the nests, we felt that much of the loss was due to predation.

The flashing seemed to have little effect. Many nests were lost before we could erect the flashing. Once the flashing was put up, we suspect that the raccoons may have climbed over the flashing with or without the help of the buttonbush that was common throughout the colony.

In 1986, when the birds again nested in Big Dukes Pond, we recorded raccoons in the colony when it became dry in mid-June. We put up flashing on all nest trees, including trees with nests that we were not following. We recorded two dead chicks, with evidence that they had been killed by a raccoon, in a nest we were following with three chicks. The surviving chick subsequently fledged. We did not record other instances of predation among the nests we were following, but noted evidence of predation elsewhere in the colony.

In 1987, we observed raccoons in the colony late in the season, but recorded little predation. The water under the colony dried by late July and we saw raccoons shortly thereafter. By this time many of the chicks had fledged and only chicks in the very late nests suffered predation.

In 1988, a very dry year, we observed raccoons in the colony after the swamp had dried

underneath the nest trees in mid-June. F. C. Depkin spent a night in the blind and observed raccoons avoiding flashing by climbing trees without flashing and moving among trees above the flashing. We observed carcasses of stork chicks in the nests following the event. From the 101 nests in the colony (maximum count) with about 233 chicks, we estimated that only 35 chicks survived (0.35 fledglings per nest). The raccoon predation in each year was concentrated over a period of about a week.

Cold weather.—In mid-April (the incubation period) 1989, the area experienced a cold, wet period that appeared to alter the storks' nest-attendance behavior. The birds stayed on their nests for longer periods of time and, when they left to forage, they were gone for longer periods of time than we recorded for incubating birds at other times of year and in other years. During this cold spell, six nests with eggs among 19 nests that we followed were abandoned (Bryan and Coulter 1991).

There were other cases of what might be considered abandonment that occurred during the courtship and nest-building periods that occurred before egg laying. In 1985, we first recorded storks at the colony on 4 March, earlier than in other years. The numbers of storks increased to over 100 by 18 March. A cold front with freezing temperatures passed through the Birdsville area on 19 March. We counted 50 storks at the colony on that day. The numbers decreased and no storks were seen in the colony after 24 March. The storks had abandoned the colony during courtship and nest building, before any eggs had been laid and moved to Little Dukes Pond, about 1 km away, where they bred that year.

In 1988, the storks returned to the colony in mid-March. In late March, we noticed birds courting and beginning to build nests in an area of the colony where we did not follow individual nests. After a few days, the area was abandoned, and at the same time we noticed an increase in courting birds in another area. This happened twice more in late March and early April. These instances in 1985 and 1988 occurred before any eggs had been laid. They are not cases of abandonment according to the definition above, but could be considered analogous processes during the pre-egg stage.

Intraspecific aggression.—We recorded large groups of storks "mobbing" nest trees resulting in loss of nests and pairs of birds taking over

already occupied nests in 1987, 1988, and 1989. In the case of nest takeovers, the new pair threw the eggs or chicks from the nest and occupied the nests. This accounted for 30% of nest losses in 1988 and 14% in 1989. In 1989, we recorded nest abandonment prior to these nest takeovers. Previously paired birds from abandoned nests may have been involved in the aggression (Bryan and Coulter 1991). Nest abandonment also may have preceded the aggression observed in 1988, although the situation was less clear. We did not record nest takeovers in 1984, 1985, or 1986.

Aggression was primarily directed at adults on nests with eggs, although on two occasions (28 May 1987 and 2 June 1987) we observed chicks (13 and 38 days old) being thrown from nests that we were following. The chicks were thrown from their nests by males from adjacent nests while the parents were absent.

Storm damage.—We recorded five instances of nests lost during thunderstorms in 1985, 1987, and 1989. Following a severe thunderstorm during the afternoon and evening of 11 June 1985, one egg and six chicks were found in the water under the nest trees the next day. The storm caused mortality in two of the nests that we were following, but probably caused mortality in other nests as well. Again, following a severe thunderstorm on the afternoon of 22 June 1987, both chicks were missing from one of the followed nests. Other chicks in the colony may also have been lost during this storm. Following heavy rains on 8 and 9 June 1989, two of the nests that we were following were missing, presumably to destruction during the storms.

Unknown factors.—Many losses occurred for which we could not determine the causes (Table 3). Most of the losses due to unknown causes were recorded in 1988 and 1989. Some of these may have resulted from some of the factors discussed above.

IMPORTANCE OF FOOD AVAILABILITY

The ability of the parents to provide adequate food to their chicks may have affected reproductive success. None of the causes of entire-nest losses were obviously related to food availability, although there may have been indirect relationships. To determine the importance of food availability, we examined the relationship between average yearly prey density at foraging sites and the average number of young
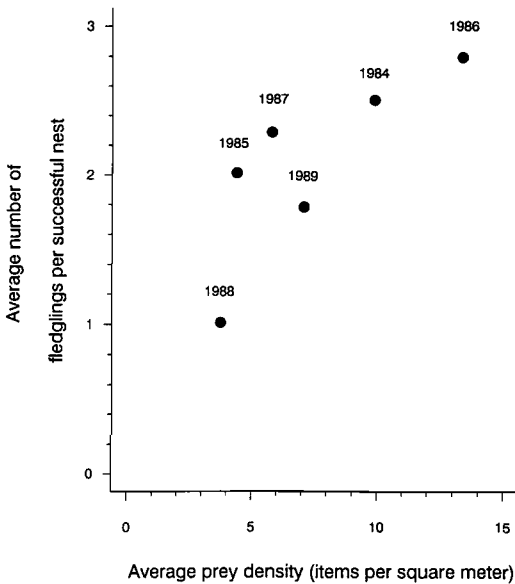
Fig. 1. Average number of Wood Stork fledging among for successful nests at Birdsville colony by year in relation to average density of potential prey at foraging sites.

fledged from successful nests (Fig. 1). The relationship was significant (Spearman rank correlation = 0.83, $n = 6$, $P < 0.05$).

DISCUSSION

Average annual reproductive success of Wood Storks at the Birdsville colony varied from 0.33 to 2.16 fledglings per nest from 1984 through 1989. Among nests that we followed, 4 to 84% of the chicks that hatched fledged each year. Prey availability was an important factor influencing fledging success, at least among those nests from which young fledged. No young fledged from 104 (43%) of the nests that we followed. Large numbers of nests were lost in 1985, 1988, and 1989, and the storks produced an average of less than one fledgling per nest. Few nests were lost in 1984, 1986, and 1987; the storks produced about two fledglings per nest in these years.

Factors that accounted for the loss of the entire nest contents included raccoon predation, stress induced by cold weather, intraspecific aggression, storm damage, and unknown factors. We have suggested that some of the abandonment and subsequent intraspecific aggression may be related to spring cold periods (Bryan

and Coulter 1991). Cold weather early in the season may stress the storks and lead to nest desertions. Although pairs do not stay together from year to year and pair bonds are established each year (Kahl 1972), pairs that have abandoned their nests may maintain their pair bonds within a season, and these birds subsequently may take over nests occupied by other birds.

Drying of the swamp under the nesting trees may be important in allowing raccoon predation. Although we put flashing around the base of the trees, raccoons got around the flashing, and it is unclear whether flashing had any effect on predation levels. Alligators in the water under the colony are probably a more effective deterrent to raccoons coming near the nests of Wood Storks. As long as there was water under the colony, alligators were present. They seem to be attracted to the colony, where they eat stork chicks and regurgitated food that occasionally fall from nests. Raccoons appear to be deterred from entering the colony by the presence of alligators, since we only recorded raccoon predation when the water under the nest trees was dry and alligators were absent. The swamp became dry under the nest trees in four of the six years of this study (Coulter unpubl. obs.). During these years, it became dry in June or July when chicks were still in the nests.

Cold temperatures and cold fronts passing through the area in February, March, and April may stress storks, leading to abandonment and/or nest takeovers. The winter and early spring cold may limit storks from breeding earlier than they do. However drying of the swamp under the colony appears to establish conditions enabling raccoon predation. Chicks from early nests are likely to avoid the raccoon predation by fledging before the water dries under the colony.

The potential impact of mortality from raccoon predation late in the season and cold temperatures early in the season suggests that these two phenomena form limits for the timing of breeding of storks in east-central Georgia. We suggest that the window for initiation of breeding is determined by the onset of drought and colony drying in June and July.

thusiastic, and hard-working crew: S. L. Coe (1986-1988), F. C. Depkin (1986-1988), T. L. Gentry (1988-1989), L. C. Huff (1984-1986), S. D. Jewell (1984-1985), W. B. Lee (1984), L. S. McAllister (1984), D. E. Manry (1989), K. L. Montgomery (1988-1989), L. A. Moreno (1988), M. A. Rubega (1986), D. J. Stangohr (1987), W. J. Sydeman (1985), N. K. Tsipoura (1987), J. M. Walsh (1985-1987), B. E. Young (1986) and D. P. Young (1989). J. Meyers, who directed the stork project from June 1983 through April 1984, laid the groundwork for sampling methods at foraging sites. L. Garrett of the Patuxent Environmental Science Center provided invaluable assistance in locating references. P. Frederick, H. W. Kale, and an anonymous reviewer made helpful comments on an earlier draft of this paper. We also thank M. H. Smith, J. W. Gibbons, and W. D. McCort for their indispensable support throughout this project. This research was supported by the United States Department of Energy, Savannah River Operations contract DE-AC0976SROO-819 with the University of Georgia, Institute of Ecology Savannah River Ecology Laboratory.

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