

FISH CROW PREDATION ON EGGS OF THE WHITE IBIS AT BATTERY ISLAND, NORTH CAROLINA

MARK A. SHIELDS¹ AND JAMES F. PARNELL

Department of Biological Sciences, University of North Carolina,
Wilmington, North Carolina 28403 USA

ABSTRACT.—We studied predation by Fish Crows (*Corvus ossifragus*) on eggs of the White Ibis (*Eudocimus albus*) during the 1983 and 1984 nesting seasons at Battery Island, southeastern North Carolina. Crow predation accounted for the loss of 32% ($n = 223$) of ibis eggs in 1983 and 44% ($n = 538$) in 1984. Crows usually took all eggs in a clutch. An estimated 6 pairs of Fish Crows nested on the island each year. We believe these individuals were responsible for most egg loss. The predation rate of ibis clutches was highest in plots nearest crow nests and lowest in two plots that contained observation blinds. Results of experiments using simulated ibis nests suggested that crows were wary of the blinds. Predation declined with nest age, apparently due to increased nest attentiveness by adult ibises during the last week of incubation. The overall predation rate in 1984 was significantly higher than in 1983. Greater nest densities and less synchronous breeding by ibises in 1984 may have contributed to the higher predation rate. Ibis productivity was estimated at 1.22–1.30 fledglings per pair in 1983 and 1.05–1.12 in 1984. This level of reproduction appeared sufficient for maintenance of the population. Thus, egg predation by Fish Crows during our study did not appear to be a serious threat to the productivity of this White Ibis population. Received 24 June 1985, accepted 22 January 1986.

CROWS (*Corvus* spp.) are well known as predators of birds' eggs. Upon finding an unguarded nest, a crow typically flies off with an egg, eats or caches it, and then returns to the same area to steal another egg (Tinbergen et al. 1967, Croze 1970, Montevecchi 1976). Because crows often return to sites of previous prey capture, their predation success increases with increasing prey density (Tinbergen et al. 1967, Göransson et al. 1975, Montevecchi 1977). Thus, predation on eggs of colonial nesters, particularly wading birds (Ciconiiformes) that do not exhibit group-mobbing antipredator behavior, may be severe (Krebs 1978). Crow predation on eggs of wading birds is documented thoroughly (e.g. Bent 1926, Baker 1940, Meanley 1955, Dusi and Dusi 1968, Rudegeair 1975, Burger and Hahn 1977, Maxwell and Kale 1977, Tremblay and Ellison 1979, Allen-Grimes 1982, Frederick 1985). We can find no detailed studies, however, of the extent of egg predation during more than one breeding season, factors affecting the rate of predation, or the impact of this egg loss on wading bird populations.

The White Ibis (*Eudocimus albus*) reaches its northern limit of regular breeding in coastal North Carolina (A.O.U. 1983). White Ibis breeding biology was studied by Allen-Grimes (1982) at Battery Island, site of the largest White Ibis colony in North Carolina. She found nesting success to be significantly lower than in Florida populations (Rudegeair 1975, Kushlan 1977) and attributed this, in part, to high egg loss. Allen-Grimes frequently saw Fish Crows (*C. ossifragus*), which also nested on the island, carrying off eggs. She suggested that crow predation may have been a major reason for low nesting success of this ibis population. We initiated our study specifically to examine Fish Crow predation on ibis eggs at Battery Island.

Our objectives were to determine the extent of Fish Crow predation on White Ibis eggs, to examine temporal and spatial patterns of predation, and to evaluate the impact of predation on ibis productivity.

STUDY AREA AND METHODS

We conducted the study from April to August 1983 and 1984 at Battery Island (33°54'N, 78°01'W), a National Audubon Society sanctuary located in the Cape Fear River estuary 1 km southeast of Southport, Brunswick Co., North Carolina. This island has sup-

¹ Present address: Wyoming Cooperative Fishery and Wildlife Research Unit, Box 3166, University Station, Laramie, Wyoming 82071 USA.

ported a mixed-species heronry since at least 1938 (Brimley 1938). Recently it has held the largest heronry in North Carolina (Parnell and Soots 1979, Parnell and McCrimmon 1984) and the northernmost large (>100 pairs) breeding colony of White Ibises in North America (Allen-Grimes 1982, Shields and Parnell 1983).

Comprising an area of about 40 ha, Battery Island is mostly salt marsh dominated by *Spartina alterniflora*. Two wooded uplands, North (1 ha) and South (7 ha) colonies, provide nesting habitat for the large wading bird assemblage. White Ibises nest only in the South Colony.

The South Colony site, created by deposition of dredged material (Funderburg 1960), is a grass/forb-covered dome fringed by a maritime thicket. The thicket vegetation is composed of red cedar (*Juniperus virginiana*), yaupon (*Ilex vomitoria*), Hercules'-club (*Zanthoxylum clava-herculis*), wax myrtle (*Myrica cerifera*), groundsel-tree (*Baccharis halimifolia*), marsh elder (*Iva frutescens*), and several other woody species. Trees and shrubs are also scattered in clumps across the dome. Woody vegetation on the dome is dominated by red cedar, with lesser numbers of yaupon, wax myrtle, Hercules'-club, cherry (*Prunus* sp.), red mulberry (*Morus rubra*), and buckthorn (*Bumelia lycioides*).

In 1983 the South Colony contained an estimated 3,737 White Ibis nests and 637 nests of eight other wading bird species (*Casmerodius albus*; *Bubulcus ibis*; *Egretta thula*; *E. caerulea*; *E. tricolor*; *Butorides striatus*; Black-crowned Night-Heron, *Nycticorax nycticorax*; and *Plegadis falcinellus*). The South Colony held 4,849 White Ibis nests and 852 nests of the other eight species in 1984. At least 2 pairs of Fish Crows nested in the South Colony in 1983. We located 6 nests during extensive searches in 1984. Other potential egg predators in the South Colony included Black-crowned Night-Herons, Boat-tailed Grackles (*Quiscalus major*), Norway rats (*Rattus norvegicus*), and snakes (*Elaphe obsoleta quadrivittata* and *E. g. guttata*). No large mammals inhabited the island.

We determined the fates of White Ibis nests in ten 15 × 15 m plots selected randomly from a pre-established grid. We used the same plots in both years; White Ibises did not nest in one plot (R15) in 1984, however, and another (J28) was chosen to replace it. White Ibis nests comprised over 95% of all wading bird nests in the plots used each year. We attempted to individually mark all ibis nests and eggs in each plot. The highest nests in most plots could not be reached easily without endangering lower nests and therefore were excluded from study. Unmarked nests accounted for about 15% of all ibis nests in the study plots. We marked nests with inconspicuous plastic tags wired beneath the nest bowl. Eggs were numbered on both ends using waterproof India ink. We did not mark empty nests.

We usually visited nests every 3–4 days to record contents. To minimize colony disturbance and thermal stress to eggs and young, visits were made as quickly as possible (<30 min/plot) during 0700–1200. If eggs were missing, we searched the area immediately surrounding the nest for the presence of eggshells. In addition, we regularly collected all eggshells and shell fragments within each plot. We recorded a predation loss if an egg was punctured in the manner characteristic of crows (Rearden 1951) or if the disappearance of an egg could not be attributed to the egg hatching or falling from the nest (Burger and Hahn 1977, Montevecchi 1977, Gottfried and Thompson 1978, Miller and Burger 1978).

We computed a daily predation rate (DPR) by dividing the number of clutches predated (partial clutch loss was small) by the amount of nest exposure (in nest-days) (Mayfield 1961, 1975). The data were grouped by plot into 1-week periods, with the first week beginning on the date of our first visit, to examine spatial and temporal patterns in DPR each year. We compared DPRs between two groups of nests using the variance estimator and statistical test described by Hensler and Nichols (1981). When more than two groups were compared, we employed the Bonferroni multiple comparison method (Miller 1966).

We estimated ibis nesting success using the Mayfield method to evaluate the impact of egg predation on ibis productivity. We calculated nest success separately for the egg and nestling stages. We defined the egg stage as the period from the day the first egg in a clutch was laid to the day before hatching of the first egg. The nestling stage extended from the day the first egg hatched to 10 days after that date, at which time nestling ibises began to leave their nests upon our approach and no longer could be associated with specific nests (cf. Custer et al. 1983).

If the first clutch is destroyed, many wading birds will lay a replacement clutch, often using the original nest (Jenni 1969, Milstein et al. 1970, Maxwell and Kale 1977). Failure to take renesting into account will result in an underestimate of nesting success (Custer and Pitelka 1977). We estimated the extent of renesting by ibises to reduce this bias. Because unattended White Ibis nests are quickly (often within one day) dismantled by neighboring birds (Rudegeair 1975, Shields pers. obs.), we considered a clutch to be a replacement if the nest was not dismantled between the time of original egg loss and subsequent laying (Schreiber 1979).

RESULTS AND DISCUSSION

We individually marked 694 eggs in 262 clutches in 1983 and 1,213 eggs in 493 clutches in 1984. We marked 98% of the nests during the first week of incubation.

TABLE 1. Fates of White Ibis eggs in sample clutches at Battery Island.

Fate	1983		1984	
	n	%	n	%
Hatched	410	59.0	596	49.1
Predated	223	32.1	538	44.3
Survived incubation, but did not hatch	43	6.2	59	4.9
Abandoned	8	1.2	4	0.3
Unknown ^a	8	1.2	0	0.0
Dump egg ^b	2	0.3	8	0.7
Other ^c	0	0.0	8	0.7
Total	694	100.0	1,213	100.0

^a The outcome of 3 clutches in 1983 could not be determined.

^b Egg laid in another ibis's nest. All dumped eggs were laid well after hosts' clutches were completed; no dumped eggs hatched due to inadequate incubation.

^c Includes 6 eggs cracked or dented, 1 egg dropped during handling, and 1 runt egg in 1984.

Extent and sources of predation.—Predation was the most important source of egg mortality and accounted for the loss of 223 (32.1%) eggs in 1983 and 538 (44.3%) eggs in 1984 (Table 1). We believe that Fish Crows were responsible for most, if not all, egg predation. Other potential avian predators were common in the colony, but during >150 h of observation logged over three nesting seasons (1982–1984) we saw only Fish Crows preying on ibis eggs. We observed only one snake each year. The effect of Norway rats is unknown.

Crows took eggs from 100 (38.2%) clutches in 1983 and 244 (49.5%) clutches in 1984. All eggs were removed from 89 (89.0%) clutches in 1983 and 231 (94.7%) in 1984. Loss of all eggs in a clutch is typical of crow predation (Rearden 1951). Fish Crow predation accounted for 97.3% of all clutch losses in 1983 and 99.1% in 1984.

Estimated predation loss of ibis eggs in 1981 (calculated from Allen-Grimes 1982) was 5% lower than in 1983 and 17% lower than in 1984. Predation rates at Battery Island were comparable to those at some other wading bird colonies where Fish Crows also nested (e.g. Burger and Hahn 1977, Miller and Burger 1978), but were more than double the rate of crow predation at another White Ibis colony in which crows did not nest (Frederick 1985).

Resident crows appeared to be the primary predators. We observed a maximum of 14 adult crows in the South Colony each year during

our visits. Based on the 6 crow nests found in the South Colony in 1984, we assumed that the resident population was composed of 12 adults. The 2 additional crows may have been nest helpers (McNair 1985) or nonresident crows. We frequently saw 2–3 crows perched together near two known crow nests, but rarely saw crows flying between the South Colony and the mainland (a distance of 1 km) or between the South and North colonies (a distance of 0.5 km). Fish Crow pairs tolerate helpers at nest sites and food caches, but vigorously defend these areas against intrusion by other Fish Crows (McNair 1985). We therefore believe that the major egg predators were resident pairs, some perhaps with helpers, and that territorial behavior limited the number of nonresidents foraging on the island.

Spatial patterns of predation.—The overall DPR of ibis clutches varied considerably among study plots in each year (Table 2). However, trends in relative predation intensity among plots were quite similar in both years (Spearman's rank correlation, $r = 0.78$, $n = 9$, $P < 0.01$) despite the higher DPRs in 1984 (Table 2). For example, plots K23, M21, and F16 had the lowest DPRs in both years, while plots K15 and N24 had the highest. This similarity between years suggests that the intensity of predation was related to some characteristic(s) of the plots that remained relatively stable over both years.

Nesting habitat did not appear to be related to predation intensity as the three plots with the lowest DPRs in both years had quite different vegetative structures: M21 consisted of a low (<2 m), dense growth of yaupon; K23 was made up of a 3.4-m-high red cedar and a 2.4-m-high Hercules'-club; and F16 was composed of a tall (6.5 m) red cedar with an understory of yaupon and buckthorn. Plots K15 and N24 consisted of tall (>5 m) cedars similar to F16, yet these two plots had the highest DPRs in both years (Table 2). The degree of nest concealment did not differ significantly between predated and nonpredated clutches (Shields 1985).

The location of a plot within the colony, however, was related to predation intensity. In general, overall DPR declined with increasing distance from a Fish Crow nest (Fig. 1). Despite weekly variation, the DPRs in K15, N24, and H11 (the three plots nearest crow nests in 1984)

TABLE 2. Daily predation rate (DPR) of White Ibis clutches by study plot and year. n = amount of nest exposure (in nest-days) during the egg stage.

Plot	1983		1984	
	DPR \pm SD	n	DPR \pm SD	n
K23	0.0000 \pm 0.0698	205	0.0268 \pm 0.0062	672
M21	0.0043 \pm 0.0030	466	0.0104 \pm 0.0039	674
F16	0.0057 \pm 0.0033	529	0.0262 \pm 0.0055	839
H11	0.0144 \pm 0.0059	415	0.0375 \pm 0.0080	560
I28	0.0173 \pm 0.0070	347	0.0281 \pm 0.0064	676
R15	0.0234 \pm 0.0087	299	—	—
E13	0.0247 \pm 0.0065	567	0.0318 \pm 0.0074	566
K27	0.0322 \pm 0.0112	248	0.0271 \pm 0.0109	221
K15	0.0403 \pm 0.0073	720	0.0715 \pm 0.0085	909
N24	0.0478 \pm 0.0125	293	0.0539 \pm 0.0096	557
J28	—	—	0.0326 \pm 0.0064	765
Overall	0.0217 \pm 0.0023	4,089	0.0358 \pm 0.0023	6,439

were consistently higher than the rates in the other seven plots (Fig. 2). A similar pattern was observed in 1983, with K15, N24, and E13 consistently having the highest DPRs (Fig. 2). Corvids often obtain much of their food from within their territories (Goodwin 1976), and several authors (Jones and Hungerford 1972, Loman and Göransson 1978, Erikstad et al. 1982) similarly reported decreasing rates of nest predation as distance from corvid nests increased. Such a spatial pattern of predation may be expected because it would be less energetically expensive for crows to forage as close as possible to their nests (Loman and Göransson 1978).

Although we did not obtain complete data on Fish Crow nest locations in 1983, we believe that crows occupied the same territories in 1983 and 1984. Northwestern Crows (*C. caurinus*) maintain one or more feeding stations within their territories and use the same sites year after year (Verbeek 1982). We found a Fish Crow feeding station at the study site about 5 m from K15 (which contained a crow nest in 1984) in the 1982–1984 breeding seasons. This suggests that a Fish Crow territory also encompassed plot K15 in 1982 and 1983. In 1984 we found a crow nest about 20 m from the site of the one known crow nest in 1983. In 1983 we observed a recently fledged crow from an undiscovered nest perched in the same cedar in which the nest closest to N24 was located in 1984. We frequently saw several adult crows perched in this tree during the 1983 breeding season. Two crow nests were located within 30 m of H11 and within 50 m of E13 in 1984. H11 had the third

highest overall DPR in 1984, while E13 was one of the three plots with consistently high DPRs throughout the 1983 breeding season. We believe that nesting by crows in the same territories, but not necessarily the same nest sites, in successive years (see Butler et al. 1984) accounted for the similarity of predation patterns among plots in 1983 and 1984.

The DPRs in plots K23 and M21 were lower in 1984 than might be expected based on the proximity of these plots to crow nests (Fig. 1). These plots also had the lowest DPRs in 1983 (Table 2), when only two clutches were predated in both plots combined. The presence of a small cloth-covered observation blind in each plot may have contributed to the lower than expected DPRs. Preliminary studies conducted in May 1982 indicated that Fish Crows were wary of the blind in M21. We placed 10 simulated ibis nests, each containing two chicken eggs colored to resemble White Ibis eggs, within this plot. The nests survived three days with only one loss, while 12 similar nests placed in areas of the thicket where blinds were absent were predated within 24 h. We observed crows from the blind in M21 for 9 h on the first day of the experiment. Crows frequently flew over the plot and perched in nearby trees but made no attempt to land near the nests, all of which were 5–10 m from the blind and in full view of the crows. Montevecchi (1976) also reported that Fish Crows were wary of a blind, although he felt that crows were wary because of his presence in the blind. The loss of only one nest in three days in our experiment suggests that

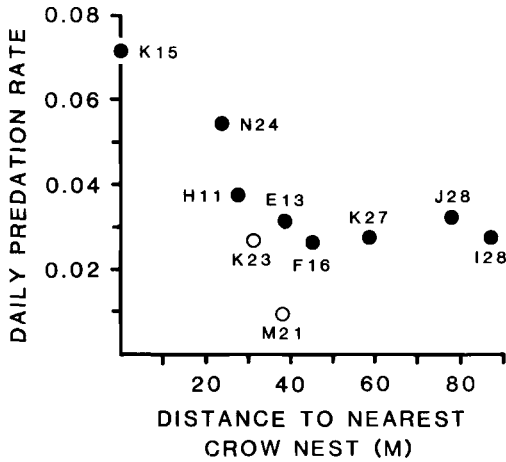


Fig. 1. Daily predation rate of White Ibis clutches in relation to the distance from the study plots to the nearest Fish Crow nest in 1984. Open circles denote plots that contained observation blinds.

the crows may have learned to associate the blind with human presence and therefore exhibited caution whether or not we were present.

Temporal patterns of predation.—Throughout the breeding season DPR remained higher in the three plots closest to crow nests than in the other seven plots (Fig. 2). DPR increased from the first to second weeks in both groups of plots in both years. Egg predation might be expected to be lower in the first week of study than in the second while the crows develop a searching image for new prey items (Croze 1970). However, we do not believe the development of an egg-specific searching image by Fish Crows can completely explain the dramatic peak in DPR during the second week in 1984 (Fig. 2). Weather during this period was cloudy and windy. Our observations during the two years of study indicated that ibises tended to flush from their nests more readily and with greater frequency, even in the absence of human disturbance, during windy conditions than when the air was calm. Such behavior would result in increased exposure of eggs to predators and may account for the high rate of predation. Windy conditions facilitated American Crow (*C. brachyrhynchos*) predation on Double-crested Cormorant (*Phalacrocorax auritus*) eggs, by causing cormorants to readily leave their nests (Ellison and Cleary 1978).

The DPR in the three plots nearest crow nests

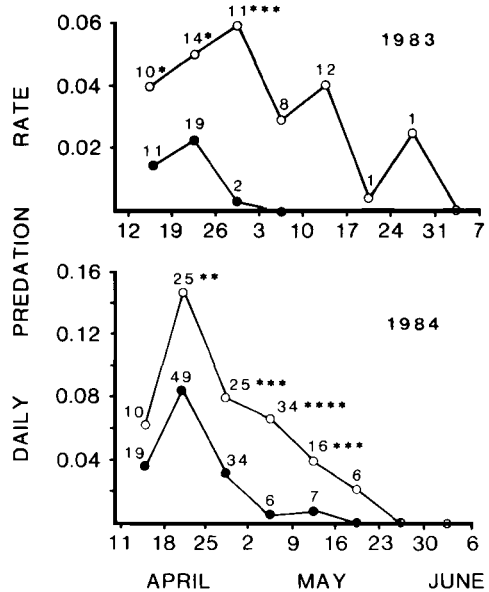


Fig. 2. Weekly variation in the daily predation rate of White Ibis clutches. Open circles denote the 3 study plots nearest Fish Crow nests; solid circles denote the other 7 plots. The number of clutches predated each week in both groups of plots is shown. Significance levels for comparisons of the DPRs between the two groups of plots by week are indicated by asterisks: * $0.05 < P < 0.10$, ** $P < 0.05$, *** $P < 0.005$, **** $P < 0.0001$.

remained relatively high through the first 4–5 weeks in both years (Fig. 2). The DPRs in the other plots, however, declined sharply after the second week, although predation in these plots in 1984 was still fairly high through the third week (Fig. 2). The declines in DPRs in the two groups of plots came during or just before the week of peak hatching of clutches in both years (Shields 1985). White Ibises appeared to flush less readily and to return to their nests more quickly late in incubation and when small young were present. For example, early in incubation all adults flushed from their nests as we approached to within 10–15 m of a plot. Toward hatching and when small (<10-day-old) young were in nests, adults usually did not flush until we were within 5 m, and often several adults remained perched in the tops of trees in which we were working (see also Skutch 1962, Ellison and Cleary 1978). This increased nest attentiveness probably accounts for the rapidly declining DPRs near the period of peak hatching.

To examine quantitatively the relationship between age of nest and predation, we divided the egg stage into three 7-day age groups and calculated the DPR for each group. We estimated the date of initiation of each clutch by back-dating, allowing two days for each egg laid (Rudegear 1975, Kushlan 1977). In 1983 clutches in the 15–21-day-old group had a lower overall DPR (0.0120 ± 0.0030) than clutches in either the 1–7-day-old group (0.0258 ± 0.0044) or the 8–14-day-old group (0.0270 ± 0.0042), although the differences among groups were not significant statistically ($P > 0.05$). In 1984, 15–21-day-old clutches had a significantly ($P < 0.05$) lower overall DPR (0.0096 ± 0.0022) than 1–7-day-old clutches (0.0506 ± 0.0047) and 8–14-day-old clutches (0.0434 ± 0.0042). This supports the observation that, as hatching nears, adult ibises become more attentive and thereby reduce egg losses to Fish Crows.

Breeding extended later into the season in the three plots nearest crow nests in both years because high initial levels of predation resulted in few early clutches surviving to hatch and in the laying of many replacement clutches. In addition, most late-arriving ibises nested within these three plots in 1983 (Fig. 3), perhaps attracted by the availability of abandoned nest sites or the activities of renesters, or both. Thus, many clutches in the more vulnerable early stages of incubation were available throughout the first 5–6 weeks of each season, and predation rates remained high. Lower levels of predation in the other seven plots allowed more early clutches to hatch, and fewer replacement clutches were laid. Thus, young clutches were available for a shorter period, and predation rates in these plots declined earlier in both years (Fig. 2).

Comparison of predation between years.—Although trends in relative predation intensity among plots were similar in both years, the overall DPR in 1984 was significantly ($z = 4.33$, $P < 0.0001$) higher than in 1983 (Table 2). The difference may have been due to changes in Fish Crow or White Ibis nest densities between years. Although the total number of Fish Crow nests in the South Colony in 1983 was unknown, our observations of crow activity did not indicate an increase in crow numbers in 1984. More than 1,100 more ibis nests were counted in 1984 than in 1983, however, and

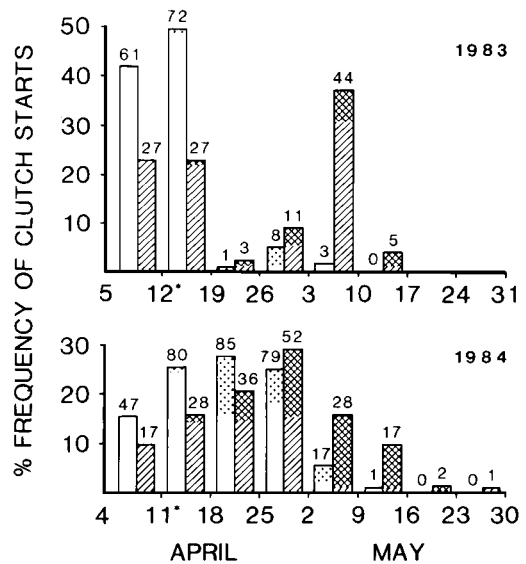


Fig. 3. Frequency distribution of White Ibis clutch initiations by week. First nests and renests in the 3 study plots nearest Fish Crow nests are denoted by hatched and cross-hatched bars, respectively; first nests and renests in the other 7 plots are denoted by open and dotted bars, respectively. The number above each bar is the number of clutches initiated. The dates of initiation of 3 clutches in 1984 could not be determined. Asterisks denote the dates of our first visits to the plots. Mean \pm SD age of clutches present on our first visit was 2.0 ± 0.8 days ($n = 88$) in 1983 and 2.6 ± 1.3 days ($n = 64$) in 1984.

maximum nest densities in all but one of our study plots were greater in 1984 than in 1983. Because predation success of crows increases with increasing prey density (Tinbergen et al. 1967, Croze 1970, Göransson et al. 1975, Montevocchi 1977), the greater density of ibis nests in 1984 may have accounted for the higher predation rate.

Synchrony of nesting is often cited as an antipredator adaptation of colonial nesting in birds (Darling 1938, Patterson 1965, Nisbet 1975). Differences in ibis breeding synchrony between years also may have contributed to the difference in overall DPR. Nesting in all plots was less synchronous in 1984 (Fig. 3). The availability of many young clutches throughout much of the breeding season may have increased predation above the rate in 1983, when overall nesting was more synchronous.

Impact of predation on ibis productivity.—Nesting-success data for White Ibises at Battery Is-

TABLE 3. Nesting success of White Ibises in study plots at Battery Island. Nest success estimated using Mayfield (1961, 1975) method.

	1983	1984
Nest success—egg stage (A)	0.6302	0.4645
Hatching success (B) ^a	0.8801	0.8801
Nest success—nestling stage (C)	0.9630	0.9214
Nestling success (D) ^b	0.9220	0.9361
Egg success (A × B × C × D) ^c	0.4925	0.3526
Mean clutch size (E)	2.64	2.44
Number of 10-day-old young/nest (A × B × C × D × E)	1.30	0.86
Number of clutches/pair (F)	1.11	1.44
Number of 10-day-old young/pair (A × B × C × D × E × F)	1.44	1.24

^a The probability of an egg hatching given that the nest survives the 21-day egg stage.

^b The probability of a young surviving to 10 days of age given that the nest survives the 10-day nestling stage.

^c The probability of an egg producing a 10-day-old young.

land in 1983 and 1984 are given in Table 3. All clutch losses were used in the calculations, but because Fish Crow predation accounted for over 97% of clutch losses in both years, success rates for the egg stage reflect primarily the effects of predation. The probability of an egg surviving to hatch (A × B, Table 3) was 55.5% in 1983 and 40.9% in 1984. Survival of nestlings to 10 days of age (C × D, Table 3) was much higher (88.8% in 1983 and 86.3% in 1984). Thus, egg loss, due mainly to predation by Fish Crows, was the primary cause of nest failure.

A mean of 1.30 10-day-old young was raised per nest in 1983 and 0.86 in 1984 (Table 3). Taking renesting into account, we estimated the number of 10-day-old ibises raised per pair at 1.44 in 1983 and 1.24 in 1984. Because White Ibises fledge at 40–50 days of age (Kushlan 1977), fledging success at Battery Island was undoubtedly lower due to nestling mortality after the age of 10 days. Most nestling losses in the coastal Florida colonies studied by Kushlan (1977) occurred in the first 20 days of age; the mortality rate of young between the ages of 20 and 40 days was only 10%. Similar trends in nestling mortality rates have been noted in other wading bird colonies not subject to predation by large mammals (e.g. Wolford and Boag 1971, Miller and Burger 1978). Assuming a 10–15% mortality rate of young between 10 days of age and fledging, 1.22–1.30 fledglings

would have been produced per pair of White Ibises in 1983 and 1.05–1.12 in 1984.

Productivity of ibises in our study plots was comparable to that reported for the other White Ibis colonies (e.g. Kushlan 1977). Because human disturbance may facilitate Fish Crow predation (Bent 1926, Schreiber and Risebrough 1972, Montevecchi 1977, Shields 1985) and because most of the South Colony was undisturbed by our activities, we believe that the nesting success of the colony as a whole was higher than indicated by our sample. Production of young at a level above that needed for replacement may explain the steady increase in the breeding population of White Ibises at Battery Island since the early 1960's (Parnell and Soots 1979) and also may account for the recent northward expansion of nesting by ibises in coastal North Carolina (Shields and Parnell 1983). Thus, at present crow and ibis densities, egg predation does not appear to be a serious threat to the productivity of the Battery Island White Ibis population.

ACKNOWLEDGMENTS

Dargan Frierson, Jr., Paul E. Hosier, and Donald A. McCrimmon, Jr., provided valuable suggestions on methodology and data analysis, and also made helpful comments on an earlier version of the manuscript. Many people aided us in the field. We particularly thank Robin D. Bjork, Peter B. Colwell, W. Walker Golder, and Jennifer E. Slack for their help on numerous occasions. The comments of Thomas Wray II and two anonymous reviewers greatly improved the manuscript. Major funding for this study was provided by the Sanctuary Department, National Audubon Society; the New Hope and Forsyth Audubon societies; and the University of North Carolina at Wilmington through its Department of Biological Sciences and Biology Trust Fund.

LITERATURE CITED

- ALLEN-GRIMES, A. W. 1982. Breeding biology of the White Ibis (*Eudocimus albus*) at Battery Island, North Carolina. Unpublished M.S. thesis, Wilmington, Univ. North Carolina.
- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. Washington, D.C., Amer. Ornithol. Union.
- BAKER, R. H. 1940. Crow predation on heron nesting colonies. *Wilson Bull.* 52: 124–125.
- BENT, A. C. 1926. Life histories of North American marsh birds. U.S. Natl. Mus. Bull. 135.

- BRIMLEY, H. H. 1938. The Battery Island rookery near Southport, N.C. *Chat* 2: 41-43.
- BURGER, J., & D. C. HAHN. 1977. Crow predation on Black-crowned Night Heron eggs. *Wilson Bull.* 89: 350-351.
- BUTLER, R. W., N. A. M. VERBEEK, & H. RICHARDSON. 1984. The breeding biology of the Northwest-ern Crow. *Wilson Bull.* 96: 408-418.
- CROZE, H. 1970. *Searching image in Carrion Crows.* Berlin, Paul Parey.
- CUSTER, T. W., G. L. HENSLER, & T. E. KAISER. 1983. Clutch size, reproductive success, and organo-chlorine contaminants in Atlantic coast Black-crowned Night-Herons. *Auk* 100: 699-710.
- , & F. A. PITELKA. 1977. Demographic fea-tures of a Lapland Longspur population near Barrow, Alaska. *Auk* 94: 505-525.
- DARLING, F. F. 1938. *Bird flocks and the breeding cycle.* London, Cambridge Univ. Press.
- DUSL, J. C., & R. T. DUSI. 1968. Ecological factors contributing to nesting failure in a heron col-ony. *Wilson Bull.* 80: 456-466.
- ELLISON, L. N., & L. CLEARY. 1978. Effects of human disturbance on breeding Double-crested Cor-morants. *Auk* 95: 510-517.
- ERIKSTAD, K. E., R. BLOM, & S. MYRBERGET. 1982. Ter-ritorial Hooded Crows as predators on Willow Ptarmigan nests. *J. Wildl. Mgmt.* 46: 109-114.
- FREDERICK, P. C. 1985. Mating strategies of White Ibis (*Eudocimus albus*). Unpublished Ph.D. disserta-tion, Chapel Hill, Univ. North Carolina.
- FUNDERBURG, J. B. 1960. The breeding birds of Bat-tery Island, North Carolina. *Chat* 24: 19-20, 36.
- GOODWIN, D. 1976. *Crows of the world.* Ithaca, New York, Cornell Univ. Press.
- GÖRANSSON, G., J. KARLSSON, S. G. NILSSON, & S. ULFSTRAND. 1975. Predation on birds' nests in relation to antipredator aggression and nest den-sity: an experimental study. *Oikos* 26: 117-120.
- GOTTFRIED, B. M., & C. F. THOMPSON. 1978. Experi-mental analysis of nest predation in an old-field habitat. *Auk* 95: 304-312.
- HENSLER, G. L., & J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bull.* 93: 42-53.
- JENNI, D. A. 1969. A study of the ecology of four species of herons during the breeding season at Lake Alice, Alachua County, Florida. *Ecol. Monogr.* 39: 245-270.
- JONES, R. E., & K. E. HUNGERFORD. 1972. Evaluation of nesting cover as protection from magpie pre-dation. *J. Wildl. Mgmt.* 36: 727-732.
- KREBS, J. R. 1978. Colonial nesting in birds, with special reference to the Ciconiiformes. Pp. 299-314 in *Wading birds* (A. Sprunt VI, J. C. Ogden, and S. Winckler, Eds.). Natl. Audubon Soc. Res. Rept. No. 7.
- KUSHLAN, J. A. 1977. Population energetics of the American White Ibis. *Auk* 94: 114-122.
- LOMAN, J., & G. GÖRANSSON. 1978. Egg shell dumps and crow *Corvus cornix* predation on simulated birds' nests. *Oikos* 30: 461-466.
- MAXWELL, G. R., II, & H. W. KALE II. 1977. Breeding biology of five species of herons in coastal Flor-ida. *Auk* 94: 689-700.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255-261.
- . 1975. Suggestions for calculating nest suc-cess. *Wilson Bull.* 87: 456-466.
- MCNAIR, D. B. 1985. An auxiliary with a mated pair and food-caching behavior in the Fish Crow. *Wilson Bull.* 97: 123-125.
- MEANLEY, B. 1955. A nesting study of the Little Blue Heron in eastern Arkansas. *Wilson Bull.* 67: 84-99.
- MILLER, L. M., & J. BURGER. 1978. Factors affecting nesting success of the Glossy Ibis. *Auk* 95: 353-361.
- MILLER, R. G. 1966. *Simultaneous statistical infer-ences.* New York, McGraw-Hill.
- MILSTEIN, P. LE S., I. PRESTI, & A. A. BELL. 1970. The breeding cycle of the Grey Heron. *Ardea* 58: 171-257.
- MONTEVECCHI, W. A. 1976. Egg size and the egg predatory behaviour of crows. *Behaviour* 57: 304-320.
- . 1977. Predation in a salt marsh Laughing Gull colony. *Auk* 94: 583-585.
- NISBET, I. C. T. 1975. Selective effects of predation in a tern colony. *Condor* 77: 221-226.
- PARNELL, J. F., & D. A. MCCRIMMON, JR. 1984. 1983 supplement to atlas of colonial waterbirds of North Carolina estuaries. Univ. North Carolina Sea Grant Publ. UNC-SG-84-07.
- , & R. F. SOOTS, JR. 1979. Atlas of colonial waterbirds of North Carolina estuaries. Univ. North Carolina Sea Grant Publ. UNC-SG-78-10.
- PATTERSON, I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. *Ibis* 107: 433-459.
- REARDEN, J. E. 1951. Identification of waterfowl nest predators. *J. Wildl. Mgmt.* 15: 386-395.
- RUDEGEAIR, T. J., JR. 1975. The reproductive behav-ior and ecology of the White Ibis (*Eudocimus al-bus*). Unpublished Ph.D. dissertation, Gaines-ville, Univ. Florida.
- SCHREIBER, R. W. 1979. Reproductive performance of the eastern Brown Pelican, *Pelecanus occiden-talis*. *Contrib. Sci. Nat. Hist. Mus. Los Angeles Co.* 317: 1-43.
- , & R. W. RISEBROUGH. 1972. Studies of the Brown Pelican. *Wilson Bull.* 84: 119-135.
- SHIELDS, M. A. 1985. An analysis of Fish Crow pre-dation on eggs of the White Ibis at Battery Is-

- land, North Carolina. Unpublished M.S. thesis, Wilmington, Univ. North Carolina.
- , & J. F. PARNELL. 1983. Expansion of White Ibis nesting in North Carolina. *Chat* 47: 101-103.
- SKUTCH, A. F. 1962. The constancy of incubation. *Wilson Bull.* 74: 115-152.
- TINBERGEN, N., M. IMPEKOVEN, & D. FRANCK. 1967. An experiment on spacing-out as a defence against predation. *Behaviour* 28: 307-321.
- TREMBLAY, J., & L. N. ELLISON. 1979. Effects of human disturbance on breeding of Black-crowned Night Herons. *Auk* 96: 364-369.
- VERBEEK, N. A. M. 1982. Egg predation by Northwestern Crows: its association with human and Bald Eagle activity. *Auk* 99: 347-352.
- WOLFORD, J. W., & D. A. BOAG. 1971. Distribution and biology of Black-crowned Night Herons in Alberta. *Can. Field-Natur.* 85: 13-19.
-

ERRATUM

The American Robin (*Turdus migratorius*) should be deleted from Table 1 of "The function of singing in female Black-headed Grosbeaks (*Pheucticus melanocephalus*): family-group maintenance" by Gary Ritchison (1983, *Auk* 100: 105-116).