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# CHRONIC TIDALLY-INDUCED NEST FAILURE IN A COLONY OF WHITE IBISES[1]

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*Abstract.* Over five seasons, I censused an estuarine colony of White Ibises (*Eudocimus albus*) in South Carolina using aerial counts before and after tidal washovers. I found 61% of all nesting starts were abandoned during these tides; since not all washovers were monitored, this figure is conservative. An analysis of tide gauge data indicates these destructive tides were frequent, and predictable across seasons. This colony is growing in size, and there is circumstantial evidence of breeding site fidelity despite the washovers. This is surprising, since White Ibises are known for frequent colony shifts. Although egg predation at this colony was comparatively low, and clutch size comparatively high, breeders still suffered far more total nest loss than at other coastal colonies. I suggest White Ibises do not use nesting failure, or predictability of failure as cues for abandonment, but rely on environmental cues such as local food availability and frequency of nest-site predation instead.

*Key words:* *White Ibis*, Eudocimus albus; *nest failure; nest abandonment; nest predation.*

## INTRODUCTION

Breeding-site fidelity is common in many avian species, though the ultimate and proximate causes of this fidelity are poorly understood. Ultimately, reproductive success will mold the specific criteria used for nest-site choice and as cues for breeding dispersal. On a proximate level, nesting success itself could be a cue for breeding-site fidelity or abandonment. Many species are known to disperse to new sites following nesting failure, or to remain on nesting sites following successful breeding attempts (Darley et al. 1977, Newton 1982, Coulson and Thomas 1983, Shields 1984, see review by Rohwer 1986). However, breeding dispersal following reproductive failure is variable across species (see review in Rohwer 1986) and may often be initiated through signals other than reproductive failure.

Breeding-site fidelity is often striking in colonially nesting species. Though colony abandonment in response to predation has frequently been reported (Cullen 1960, MacDonald 1979, Buckley and Buckley 1980, Burger 1982), some colonies are known to continue despite chronic nest predation (Austin 1949, Southern and Southern 1979). In larids, colony abandonment in response to predation may vary with the timing in the reproductive cycle, and whether the predation was nocturnal or diurnal (Southern and Southern 1979). Similarly, degree of within-season breeding dispersal of Red-winged Blackbirds (*Agelaius phoeniceus*) following nest predation depends on the type of predator (Monnett and Rotterman 1980).

Other causes of large-scale nest failure may also not lead to colony abandonment. Though degradation of nesting substrate often leads to colony relocation (Weise 1978), Southern and Southern (1982) found complete bulldozing and filling of a portion of a Ring-billed Gull (*Larus delawarensis*) colony resulted in only a 12.2% reduction of nesting in that part of the colony.

Similarly, Burger (1982) found nest failure of entire colonies of Black Skimmers (*Rhynchops niger*) due to nest predation was a reliable predictor of colony site abandonment, whereas nest failure from tidal inundations was not. Since nest predators would probably return to a colony in ensuing years, future predation at once-predated colonies was predictable, but tidal washovers were unpredictable at any location in Burger's study area across years. Burger suggested that the degree of predictability of the source of nesting failure is an important criterion for colony site abandonment.

Here, I describe chronic mass nesting failure due to tidal inundations in a colony of White Ibises (*Eudocimus albus*) that has not led to colony abandonment. The predictability of these

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tidal events is examined in detail, and several explanations for such colony site tenacity are explored.

## MATERIALS AND METHODS

This study was conducted on Pumpkinseed Island (33°16'N, 79°12'W), an estuarine mixed-species wading bird colony in Georgetown County, South Carolina, for five breeding seasons (March through June, 1980, to 1984). This 8.9-ha island is covered primarily by a dense stand of needlerush (*Juncus roemarianus*). A thin band of shrubs (*Iva frutescens*) along the northeastern edge is the only elevated nesting substrate, usually occupied by nesting Great Egrets (*Casmerodius albus*) and other ardeids.

On Pumpkinseed, White Ibises nest only on matted-down clumps of living *Juncus,* and in many areas these clumps form a continuous mat. Nesting is therefore limited to one plane; heights of 64 nests averaged 0.32 m (±0.10 m) above the mud substrate. These *Juncus* nests are completely open, and have no vegetation above them.

In each season, I counted numbers of active ibis nests on slides taken of the colony from a fixed wing aircraft at approximately 150 m above ground level. The ibis nests were counted by projecting the slide onto a wall. White Ibises were the only white-plumaged species to nest in the *Juncus,* and counts of ibises were only made of areas in which the rather synchronous ibis nests were known to be in the incubation stage. Pairs usually took less than 35 sec to exchange incubation duties (pers. observ.) and the relieved member of the pair always left the island immediately. Thus numbers of white birds in the *Juncus*-covered areas were assumed to represent the number of ibis nests. This method is quite accurate for counting White Ibises at Pumpkinseed. In 1975, previous researchers compared similar aerial counts of marked quadrats visible from the air, with ground counts of the same areas. The two methods resulted in greater than 95% agreement (P. DeCoursey and T. Murphy, pers. comm.).

I timed aerial counts to document nest abandonments due to extremely high tides. The difference between counts immediately before and after such tidal events was taken to be the number of nests abandoned as a result of that tide. I was able to quantify only one case of tidally-induced nestling mortality, as attendance schedules of parental birds at this stage were usually too unpredictable to make aerial surveys accurate. Although I took data from most destructive tides, the aerial surveys did not encompass all of them.

In order to estimate the actual extent of tidal destruction, I examined daily high-tide data from a nearby tide gauge (NOAA #8662746 "South Island," 5 km from Pumpkinseed, established in 1975). I defined "destructive" tides as having a height greater than 0.80 m above mean sea level. This was the height of the tide from which I measured the least percent nest abandonment (21.9%) using the aerial method. Because destructive tides were often clumped in time, but only the first one actually destroyed nests, I defined a single destructive event as having more than five calendar days between it and the next destructive tidal event. I only considered tides during the normal ibis-nesting season (March 20 through June 30).

I then tested for a correlation between height of tide and percent loss of nests during that tide. For this test, I excluded any aerial counts that could have yielded ambiguous counts (low quality photographs, low angle of viewing, etc.). Percent nest abandonment figures were subjected to arcsine transformation before the correlation test to achieve homoscedasticity (Sokal and Rohlf 1969).

I also documented egg predation on Pumpkinseed. No terrestrial predators exist on Pumpkinseed, but Fish Crows (*Corvus ossifragus*) and occasionally Laughing Gulls (*Larus atricilla*) prey on ibis eggs. In 1984, I individually numbered 468 eggs in 178 nests with indelible ink at two locations on the island. These eggs were recounted 10 days later at one location, and nine days later at the other. These nests were known to have experienced no tidal inundation during this time, since the flocculent mud below nests retained old bird tracks. Daily egg mortality rates were then calculated as number of eggs lost/days exposed (Mayfield 1961, 1975). The two counts were made in the first week of incubation, when Fish Crow predation on White Ibis eggs is highest (Shields 1985).

Clutch size data were taken both from the above predation study in 1984, and from 83 nests at which mating patterns were observed intensively during 1982 and 1983 (Frederick 1985, 1987). In all cases, clutches were counted within three days of completion.

## RESULTS

### HIGH TIDE-INDUCED NEST MORTALITY

Extremely high tides occurred as a result of some combination of spring tides, strong and persistent northerly winds, and high estuary discharge. Over five nesting seasons, 61% of nesting starts were abandoned during or immediately following extremely high tides (Table 1). Tides high enough to wash over nests occurred at least once each season, and sometimes in a series, as in 1983. The minimum nesting mortality due to tides for any season was 42% (1984).

I documented the immediate effects of the tidal inundations and the responses of ibises from a blind 25 m from nests. Eggs often floated out of nests, or were washed out by wave action. Incubating adults usually left the nest when the water was 3 to 8 cm above the bottom of the nest cup, though some attempted to incubate while floating above their eggs. In some cases, I saw eggs transported from one nest to another, and later documented such transport with marked eggs. In several cases, marked eggs known to have been covered with brackish to salty water for more than 1 hr during early incubation later hatched.

### ACTUAL FREQUENCY OF TIDAL WASHOVERS

The correlation between height of a tide and percent abandonment of nests during that tide was significant ($r = 0.987$, $t = 15.05$, df = 3, $P < 0.001$, Fig. 1). The minimum nest abandonment I documented in any single tidal episode was 22% (1983). Using the corresponding tide height on that date as a minimum criterion for identifying washouts, I found an average of 7.36 (±1.804) destructive tidal episodes occurred per nesting season (March 20 through June 30) from 1975 to 1985. The average height of the highest tide in each event during this time was 0.948 m above Mean Sea Level (±0.1137 m, $n = 77$ events). This height is predicted by the above regression to lead to abandonment of 50.9% of the nests. The average of the highest single tide in each season was 1.143 m above MSL (±0.0936 m, $n = 11$ seasons), which is predicted to lead to 75.3% abandonment of nests.

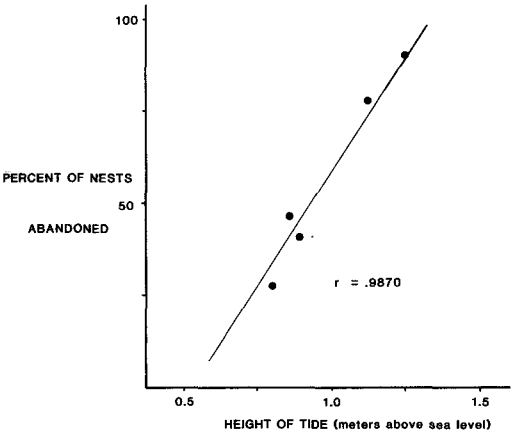


FIGURE 1. Regression of tide height and percent abandonment of nests at Pumpkinseed Island.

### EGG PREDATION

When the results of the two egg-predation study plots were combined (Table 2), 1.83 of the 468 marked eggs disappeared per day, and over the entire 21-day incubation period (Bent 1926, Rudegeair 1975, Shields 1985) 8.19% of all marked eggs are estimated to have been lost to aerial predators. Whole clutches disappeared due to predation at a rate of 0.575 per day; 6.78% of the 178 marked clutches are estimated to have

TABLE 1. Nest loss following tidal inundations.

| Year | Total nest starts | Tide | Nests before | Nests after tide | % Nest lost | |
|---|---|---|---|---|---|---|
| | | | | | Episode | Year |
| 1980 | 6,669 | 5/8 | 6,310 | 283 | 95.5 | 90.4 |
| 1981 | 7,887 | 5/16 | 7,887 | 3,807 | 48.3 | 48.3 |
| 1982 | 7,814 | 6/18 | 3,416 | 0 | 100.0 | 43.7 |
| 1983 | 10,035 | 4/20 | 10,035 | 7,849 | 21.8 | |
| | | 4/25 | 7,849 | 3,689 | 31.2 | |
| | | 6/12 | 3,689 | 1,586 | 88.2 | 84.2 |
| 1984 | 12,973 | 5/16 | 12,973 | 7,467 | 42.5 | 42.5 |
| Total | 45,378 | | 40,621 | 13,143 | | 60.6* |

* Percent of all nesting starts lost during washovers.

TABLE 2. Egg loss due to predation.

| | Study group | | |
|---|---|---|---|
| | SS | S. Central | Total |
| Eggs marked | 213 | 255 | 468 |
| Clutches marked | 80 | 98 | 178 |
| Days exposed | 10 | 9 | |
| Egg loss/day | 0.70 | 1.13 | 1.83 |
| Clutch loss/day | 0.20 | 0.38 | 0.56 |
| Egg loss/incubation* | 6.90% | 9.27% | 8.19% |
| Clutch loss/incubation | 5.25% | 8.04% | 6.78% |

* 21 days (Rudegeair 1975, Kushlan 1977, Shields 1985).

been lost to predators over the entire incubation period. Though predation was only measured in one season, numbers of Fish Crows and Laughing Gulls on the island did not change dramatically over the four seasons during which I was studying nesting ibises from a blind (Frederick 1985).

### BREEDING SITE FIDELITY?

White Ibises are known to have nested continuously on Pumpkinseed Island since 1967, and probably earlier. In the 10 years for which accurate estimates are available, the nesting population has grown steadily (Table 1). Pumpkinseed therefore seems to be a particularly stable White Ibis colony, especially since this species is noted for frequent colony shifts (Rudegeair 1975, Kushlan 1977, Ogden 1978). However, it is unknown whether the colony stability is primarily due to site fidelity of individuals. Sporadic sightings of banded and wing-flagged birds indicates some adults return in successive years, but these observations were incidental, and cannot be considered quantitative. More importantly, it is unknown whether these individuals experienced tidally-induced nest failure before returning.

### COMPARATIVE NESTING PARAMETERS

A comparison of clutch sizes at the Pumpkinseed colony with similar data from other colonies in the southeastern U.S. (Table 3) suggests that Pumpkinseed breeders have relatively large clutches.

Table 4 compares egg and nest mortalities during incubation of Pumpkinseed breeders with similar measures in other major coastal colonies. By comparison, ibises breeding on Pumpkinseed suffered far less egg predation.

## DISCUSSION

On the Pumpkinseed colony, nest destruction from tidal washovers is frequent, and by far the most important cause of nesting failure. My measures of tidally-induced nest loss are probably quite conservative. First, the aerial counts did not measure partial clutch loss due to washover, which frequently occurred in the higher nests without resulting in abandonment. Second, the aerial method did not attempt to quantify drowning of nestlings due to washovers, which was known to occur on several occasions. Finally, the aerial surveys were not made after every washover, and the data from the tide gauge indicate this may have led to considerable underestimation. The actual extent of tidally-induced nest mortality is difficult to estimate since it is unknown how many nests were vulnerable on each of the washover dates. It is clear, however, that destructive tides were quite likely in any nesting season.

TABLE 3. Comparison of primary clutch size of White Ibises at different coastal colonies.*

| Location | Number of clutches | Mean clutch size | Source |
|---|---|---|---|
| South Florida | 290 | 2.20 | Kushlan 1977 |
| West Central Florida | 208 | 2.07 | Rudegeair 1975 |
| Coastal Louisiana | 100 | 1.97 | Hammatt 1981 |
| Wilmington North Carolina | 312 | 2.23 | Allen-Grimes 1982 |
| | 755 | 2.53 | Shields 1985 |
| Pumpkinseed Island | 380 | 2.55 | This study |

* Inland colonies not included because they usually have significantly larger clutch sizes (Rudegeair 1975, Kushlan 1977).

These catastrophic tides have not caused complete abandonment of the colony. However, it is difficult to attribute the colony stability to breeding-site fidelity of individuals that experienced tidally-induced nest failure. Though a few individuals are known to have nested on the colony one year and returned the next, this is not necessarily indicative of the majority of the birds, or specifically of individuals that lost their nests to tides. The strongest circumstantial evidence comes from 1980 (Table 1). In that year, over 90% of all nesting starts failed due to high-tide washover. The following year showed no reduction of nesting and in fact an increase in the breeding population. So unless there was a 90% turnover of the island's population (12,054 birds) between 1980 and 1981, many of the same birds that were washed out returned to breed the next year. Though this level of turnover is not impossible, it would be surprising for such a stable colony. It seems more prudent to propose that a substantial proportion of the ibises were site faithful despite nest failure due to tides.

Why White Ibises may not abandon this colony in favor of a site not affected by tides is unclear. There are several possible explanations for such tenacity. First, the ibises may persist because local feeding conditions are especially favorable for the production of eggs and young. The relatively large clutch sizes at Pumpkinseed may reflect abundant local food sources, high prey availability, or short distances to food (Rudegeair 1975, Kushlan 1977). White Ibises breeding at Pumpkinseed are known to feed on a salt marsh 3 km from the colony, and in the rich bottomland swamps of two large freshwater rivers 15 to 20 km away (Bildstein 1983). However, Pumpkinseed is not the only nesting site that would allow the ibises to take advantage of those conditions. There are six other isolated islands within 3 km of Pumpkinseed in Winyah Bay, that are not washed over by tides, and that have vegetation quite similar to that of other coastal White Ibis colonies (Allen-Grimes 1982, Shields and Parnell 1986). A move to these islands would place the colony even closer to feeding areas.

Second, the Pumpkinseed colony may be attractive because there is so little egg predation. Indeed, the infrequent predation is probably a direct result of the low intertidal vegetation, which offers predators (Fish Crows) no surveillance perches, or nesting substrate. Pumpkinseed is one of only two islands in the bay offering such conditions. However, the benefits of such low egg predation would seem to be offset by the tidally-induced mortality. In fact, the Pumpkinseed colony experiences a greater loss of nests during incubation than any of the other colonies studied to date.

TABLE 4. Comparison of reproductive failure during incubation in White Ibis colonies.

| Egg predation (%) | | | |
|---|---|---|---|
| Egg loss | Nest loss | Total nest loss (%) | Source |
| 8.2 | 6.8 | >61.0* | This study |
| 40.7 | 42.4 | 43.0 | Shields 1985 |
| 27.4 | — | 41.0 | Allen-Grimes 1982 |
| — | — | 79.3** | Hammatt 1981 |

* Nest loss on Pumpkinseed probably an underestimate (see Discussion).
** Major source of nest loss in Hammatt's study was "mostly due to high tides."

Another hypothesis is that Pumpkinseed has only recently begun to experience these extreme tides as a result of sea-level rise, and that ibises continue to nest in what was once a much safer colony. In coastal South Carolina, sea-level rise since 1922 (0.25 cm/year) is considerably higher than the global average, due in part to a sinking coastal landmass (Hicks et al. 1983, Kana et al. 1984). This rate could have accounted for nearly 5 cm of increase in average height of high tides on Pumpkinseed since White Ibis began nesting there sometime in the 1960s. However, even if high tides were 5 cm lower then, mean highest tides of the season are predicted to have caused at least 69% abandonment of nests present, and mean highest tides in any tidal event are predicted to have led to a 44.6% loss of nests. Tidal inundation, then, has probably always been an important cause of nesting failure on Pumpkinseed.

Burger (1982) found that tidally-induced nest failure in Black Skimmers was not associated with colony desertion and suggested skimmers did not abandon in response because tidal washovers were unpredictable across years. The same reasoning is difficult to apply to the Pumpkinseed case. Although the exact timing of washovers was difficult to predict within any one season at Pumpkinseed, several washovers occurred there in each season. In fact, over 86% of nests are predicted to have been abandoned from the highest single tide alone. While reproductive success ultimately determines the evolution of abandon-

ment cues, the cues themselves may not be reliable in every situation. Though White Ibis will on occasion nest on grass clumps near the ground (Kushlan 1973, Hammatt 1981), they rarely nest in tidally-affected areas. It is therefore not surprising that they do not show adaptations to nest failure from tides. In the time frame of natural selection, most physical events such as storms and tides may be unpredictable, and Burger has probably correctly suggested predictability to be a key feature of abandonment cues. At a more proximate level, the Pumpkinseed example suggests that abandonment is not cued through a recognition of such predictability by individual birds.

The fact that White Ibises on Pumpkinseed did not apparently abandon the colony in the face of such continued nest failure is particularly interesting because this species is otherwise so prone to colony relocation. It seems clear that White Ibis do not rely on past nesting failure per se as a proximate cue for colony abandonment. Instead, they may rely on specific environmental cues such as local food abundance or predator activity when deciding where and when to nest (Kushlan 1976, Ogden 1978). Because breeding dispersal following nest failure is so variable among species (Rohwer 1986) and conditions (McNicholl 1975, Southern and Southern 1979, Monnett and Rotterman 1980), I suggest that many species of birds do not use breeding failure as a cue for breeding dispersal, but rather rely on specific stimuli that may often be related to breeding failure, such as food abundance or predator densities. Nest failure not accompanied by those stimuli may result in site fidelity.

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