# NESTING SUCCESS OF FIVE CICONIIFORM SPECIES IN RELATION TO WATER CONDITIONS IN THE FLORIDA EVERGLADES

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ABSTRACT.—In 1986 and 1987, we studied the nesting success of five species of wading birds (Ciconiiformes) through repeated visits to a total of 1,609 marked nests in 18 colonies in the Florida Everglades. Abandonment was the most common cause of nesting failure for all species and usually occurred following heavy rainfall and periods of rising surface water. Using stepwise logistic regression, we found that rapid surface water drying rate was associated most strongly with White Ibis (*Eudocimus albus*) nesting success, and that amount of rainfall was directly associated with failure of Great Egret (*Casmerodius alba*) nests. From records of 32 past surveys of White Ibis nesting numbers in two different water management areas, we found that years with high nesting numbers had significantly faster spring drying rates than years with low nesting numbers. There was no significant difference in amount of spring rainfall, autumn/winter drying rate, or water depth. Abandonments by ibises appeared to be closely related to prey densities, which probably were directly affected by water-level fluctuations. *Received 6 September 1988, accepted 8 May 1989.*

IN FRESHWATER wetlands, the location and success of foraging by wading birds (Ciconiiformes) is highly dependent on both present and past surface water conditions, which influence the distribution, demographics, and availability of prey species (Kushlan 1976a, 1978; Powell 1987). These factors influence food intake and may determine the timing, location, and success of reproductive efforts by wading birds. Several studies have found direct relationships between numbers of breeding attempts and amount of rainfall preceding the breeding season (Ogden et al. 1980, Bancroft et al. 1988, Bildstein et al. in press). Kahl (1964) found that the timing of initiation and abandonment of Wood Stork (*Mycteria americana*) breeding attempts in southwest Florida was predictable from surface water levels in freshwater marshes. Kushlan et al. (1975) found that the success, magnitude, and timing of Wood Stork breeding attempts were directly associated with rapid winter/spring recession of water levels (drying rate) in the Florida Everglades marshes. Kushlan (1979) also suggested that rapid recession of water levels was associated with the location and nesting chronology of White Ibis (*Eudocimus albus*) colonies in the Everglades.

Interactions between the timing, magnitude, and success of breeding attempts, and rainfall and surface water conditions involve a variety of mechanisms. While many marsh-dwelling fish and invertebrate species can survive periods of drought, prolonged periods without surface water may result in complete die-offs of prey species, followed by slow recolonization. Conversely, prolonged periods without drought may increase individual fish size, skew species composition towards larger, predatory species, and reduce both standing crop and biomass of prey species (Kushlan 1976b). Foraging success of particular wading-bird species also may rely on specific aspects of water-level fluctuation, such as depth (Kushlan 1978, Powell 1987), or concentration and entrapment of prey through water-level recession. Wood Storks, for example, are limited to the highly specialized "grope-foraging" method (Kahl 1964) which relies to some extent on prey being concentrated by drying conditions.

Previous studies (Kahl 1964, Kushlan et al. 1975, Clark 1978) have established clear relationships between surface water dynamics and Wood Stork breeding in freshwater wetlands; there has been no detailed study of this relationship in other wading-bird species. White Ibises often forage using primarily tactile means (Kushlan 1979), but may not be as dependent as Wood Storks on receding water to mechanically concentrate and entrap prey. Kushlan (1974) observed that ibises feeding in the Everglades just prior to breeding were equally

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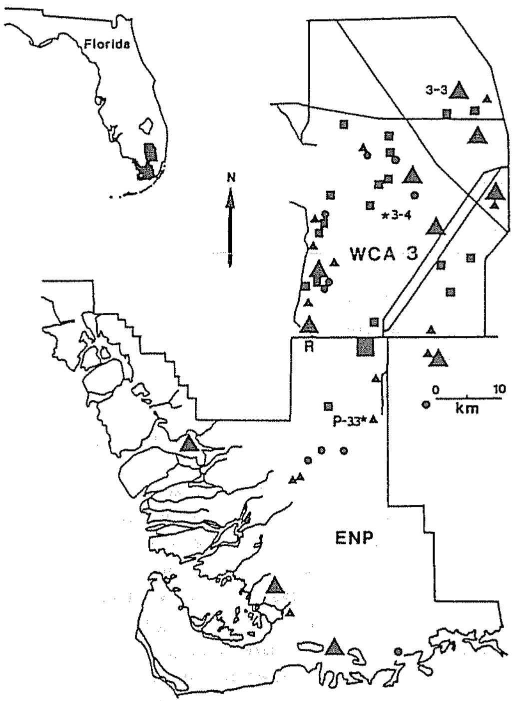

Fig. 1. The study area and colony locations in Everglades National Park (ENP) and Water Conservation Area 3 (WCA 3). Large symbols indicate colonies with >100 nest starts; circles represent colonies active only in 1986, squares are those active only in 1987, and triangles are those active in both years. Locations of water and rainfall gauging stations are indicated (3-3, 3-4, P-33, and R).

concentrated in areas with appropriate water depths during both rising and falling water trends, suggesting that mechanical concentration is not important for reproductive feeding. Many ardeids utilize stationary or stalking hunting techniques (Recher and Recher 1969; Kushlan 1976a; Kent 1986a, b). The success of these foraging strategies is not dependent on highly concentrated prey sources and, as a result, most ardeids may not rely on receding water conditions to initiate or maintain successful reproduction.

We studied the nesting success of five species of wading birds in the Everglades, and we analyzed nesting success and the number of breeding pairs in relation to variation in rainfall and surface water conditions.

## METHODS

We studied reproduction of White Ibises, Great Egrets (*Casmerodius albus*), Tricolored Herons (*Egretta tricolor*), Little Blue Herons (*Egretta caerulea*), and Snowy Egrets (*Egretta thula*) in the freshwater marshes of southern Florida (Dade, Broward, and Monroe counties; Water Conservation Area 3 [WCA 3]; East Everglades; and Everglades National Park [ENP]; see Fig. 1). These areas currently are separated by a network of canals and dikes, and they have markedly different water depths, hydroperiods, and water management goals.

Mixed-species breeding colonies of wading birds were located systematically between 15 January and 30 July in both 1986 and 1987. While many wading-bird species nest nearly year-round in nearby Florida Bay (Kushlan and White 1977), this period included the vast majority of nesting attempts of the species studied in the freshwater marshes (Kushlan et al. 1984). Fixed-wing aircraft surveys were made bi-weekly along east-west transects, spaced ca. 2 km apart throughout the study area, at 250–300 m above ground level and 160 km per hour airspeed. Information on colonies located in the mangrove region of ENP was supplied to us through similar surveys conducted by ENP and the National Audubon Society Research Department in Tavernier, Florida.

To quantify foraging dispersion, we used fixed-wing aircraft to follow unmarked birds from active colonies to the first location where the birds landed on the marsh surface. Individuals and flocks were selected on a first-out-of-the-colony basis, and followed at a vertical distance of at least 150 m. Foraging flights were conducted during the nestling phase of the species being followed. Position of foraging sites and distances from the colony were determined using an aviation-grade LORAN C navigational unit, accurate to 0.18 km.

We measured reproductive success in selected colonies in the freshwater marshes of the Everglades (11 in 1986, 7 in 1987) by visiting marked nests every 4 days and recording their contents. We considered nests to be active with the laying of the first egg, and successful if at least one young was raised to an age at which they were capable of escape by walking (14 days of age for White Ibises, Tricolored Herons, Little Blue Herons, and Snowy Egrets; and 21 days for Great Egrets). We expressed reproductive success as the probability of a nesting attempt resulting in one or more young surviving to the ages mentioned above, as calculated by the Mayfield method (Mayfield 1961, 1975; Hensler and Nichols 1981; Hensler 1985). Because rates of nest mortality are likely to vary with nesting stage, we calculated reproductive success separately for laying (0–6 days), incubation (7–21 days for White Ibises, 7–22 days for *Egretta* species, and 7–28 days for Great Egrets), and nestling periods (as above). An overall success term was calculated by combining these period-specific estimates (Hensler 1985). Losses due to hatching failure were included in the incubation period. Because eggs and nests of the three *Egretta* species are indistinguishable until young hatch (Hammatt 1981), we combined reproductive success for these three species at any one colony or location during the egg-laying and incubation periods. The overall success estimate for each *Egretta* species was derived by combining both the genus-wide success estimate for the egg-laying and incubation periods, and the species-specific success estimate for the nestling period.

We collected data on surface water and rainfall at or near each colony before and during the nesting period. Because breeding birds usually foraged within 5 km of the colony and with few exceptions within the same water management basin (Frederick and Collopy 1988), measurements of these parameters at colony sites probably were indicative of the foraging areas as well. We measured water level on marked poles or at permanent water level recording stations, and indexed these values to local marsh depths at each location by averaging 20 standardized depth measurements in the two *Eleocharis*-dominated prairies closest to the colony. We measured rainfall at the colony using nearby (within 2 km) existing continuous recorders or open-topped wedge-type rainfall collectors at the colonies. The latter were read every 4 days and rainfall was averaged over those 4 days to give daily values.

We compared several hydrological and rainfall parameters as predictors of the probability of nest success for White Ibises and Great Egrets using stepwise logistic regression (SLR; see Lachenbruch 1975 for a detailed discussion of model development and applicability). The same analysis was not carried out for the three *Egretta* species because we would have had to combine data from all three species as a result of the egg identification problem.

Hydrological and rainfall values were assigned to individual nests during a standardized period (30 days prior to the success or failure of each nest). Hydrological variables were net change in water level (drying rate), mean daily water depth, mean daily rise in water level, and number of days of rising water. Date of nest initiation (date of first egg) also was used as a variable in these analyses.

We followed the SLR procedures described in Harrell (1980), using the LOGIST package available through SAS software. SLR regresses each of the independent variables individually on a log-linearized probability of nest success. The variable with the highest correlation value is then selected as the most important. This is then confirmed by adding the other variables in stepwise fashion. During this latter procedure, variables may enter or leave the analysis as significant predictors based on a tolerance level of 0.05, and interactive effects may change the initial relationships considerably. In cases where one or more pairs of initially significant variables showed high correlation with each other (Pearson correlation coefficient > 0.80), the data were reanalyzed with each of the correlated variables in the absence of the other. The nonsignificant parameter was then discarded as a predictive variable in the reported results. Separate analyses were performed for Great Egrets and White Ibises, and data from both years of study were combined within species.

We also compared hydrological conditions in the study area during years that were reported to have large and small numbers of White Ibis nesting attempts. This type of analysis has previously been performed for Wood Storks (Kushlan et al. 1975); the only other species for which adequate data existed was the White Ibis. The records of nesting numbers we used in our analyses were compiled from a number of sources (Kushlan 1977; Kushlan and White 1977; Ogden 1978; Kushlan et al. 1984; Everglades National Park Research Center data base; National Audubon Society files, Tavernier, Florida). Records were divided into two geographical categories: nesting sites within ENP and those within the boundaries of WCA 3. This division was justified because water dynamics have been independent and dramatically different in the two areas, and because surveys have historically been specific to one or the other area. We used only the results of surveys in which it was clear that the major potential colony sites in each of the two areas had been visited at least once during the period from 15 March through 30 May. Because of potential inaccuracies in nest counts and in the timing of surveys relative to the actual peak in nesting, we categorized records of nesting during spring seasons simply as "attractive" if >2,000 nests were initiated and "unattractive" otherwise. Records prior to 1962 were available only within ENP; the P-33 water gauging station (see Fig. 1) was used as an indicator of surface water conditions in this area. WCA 3 became a functional water management entity after 1962, so we used the 3-4 water gauging station as the indicator of surface water conditions in this area. Consequently, any year after 1962 could potentially be represented in the analysis by two entries: one for ENP and one for WCA 3. The analysis of initial water level was performed only for records from ENP because water elevation cannot be compared between sites, and because water gauging stations in WCA 3 were too often inoperative on 1 January to support a similar comparison.

## RESULTS

*Nesting population and nesting success.*—We found 35 active colony sites in 1986 and 46 active colony sites in 1987 (see Fig. 1). Colony turnover rate between the two seasons was 36.3% (Erwin et al. 1981). Overall, we estimated that 8,292 nests of all species were initiated in 1986 and 10,283 were initiated in 1987 (Table 1).

Nesting success of wading birds varied con-

TABLE 1. Breeding attempts and nesting success of wading birds in the Everglades in 1986 and 1987.

| Species | Year | Total nest starts | Nests studied (colonies) | Probability of nest success[a] | SD | Mean no. fledglings/ successful nest (SD) |
|---|---|---|---|---|---|---|
| Great Egret | 1986 | 1,751 | 208 (8) | 0.1480 | 0.025917 | 1.87 (0.515) |
| | 1987 | 2,005 | 237 (5) | 0.2064 | 0.273560 | 1.89 (0.610) |
| White Ibis | 1986 | 2,503 | 245 (3) | 0.2038 | 0.025732 | 2.11 (0.657) |
| | 1987 | 4,130 | 227 (2) | 0.4887 | 0.038429 | 1.11 (1.100) |
| Tricolored Heron | 1986 | 1,033 | 173 (7) | 0.4613 | 0.038069 | 2.67 (0.704) |
| | 1987 | 1,383 | 342 (6) | 0.6610 | 0.028121 | 2.72 (0.730) |
| Little Blue Heron | 1986 | 437 | 99 (4) | 0.7284 | 0.044032 | 2.38 (0.728) |
| | 1987 | 723 | 63 (3) | 0.7164 | 0.037749 | 2.71 (0.853) |
| Snowy Egret | 1986 | 1,319 | 15 (1) | 0.7117 | 0.044032 | 2.78 (0.786) |

[a] Probability that any nesting attempt will produce one or more fledged young, as calculated by the Mayfield method (see Hensler 1985).

siderably with species and year (Table 1). Little Blue Herons had consistently high nesting success under all conditions, whereas nests of Great Egrets and White Ibises were much more likely to fail. Snowy Egrets and Tricolored Herons nesting success was intermediate compared with the other species.

*Causes of nest failure.*—An empty nest was the most common evidence of nest failure (57.2% in 1986, and 78.1% in 1987; see Table 2). It was difficult to distinguish between failure due to predation and failure due to abandonment followed by scavenging of nest contents. Abandonment was assigned only when a complete set of cold eggs, or dead or moribund nestlings, was found (42% in 1986, and 18.2% in 1987; Table 2). Both direct and indirect evidence suggested nest predation by birds (<2% of nests), and mammals and snakes (<12% of nests) was relatively low (Frederick and Collopy in press). Nest abandonment, often followed by post-abandonment scavenging, was the major source of nest failure.

Nest abandonments often were synchronized, particularly in Tricolored Herons and White Ibises, and to a lesser extent in Great Egrets. Synchronized nest abandonments were strongly associated with periods of heavy rainfall (Table 3). South Florida has a pronounced dry season during the winter and spring months, and periods of heavy rainfall occurred only during the passage of late winter frontal systems (through March of both years) and during the onset of summer rains (late May in 1986, and mid-July of 1987).

White Ibises and Tricolored Herons typically

TABLE 2. Sources of nest failure.

| Year | Species | Total failed nests | Primary cause of failure: Abandonment | Predation | Other[a] | Total failures identified (% of failures) |
|---|---|---|---|---|---|---|
| 1986 | White Ibis | 168 | 67 | 0 | 1 | 68 (40.4) |
| | Great Egret | 187 | 72 | 0 | 0 | 72 (38.5) |
| | Tricolored Heron | 78 | 60 | 0 | 0 | 60 (76.9) |
| | Little Blue Heron | 7 | 1 | 0 | 0 | 1 (14.3) |
| | Snowy Egret | 2 | 0 | 0 | 0 | 0 (0.0) |
| | Annual Total | 496 | 206 | 0 | 1 | 207 (41.7) |
| 1987 | White Ibis | 90 | 45 | 8 | 3 | 56 (62.2) |
| | Great Egret | 147 | 6 | 9 | 0 | 15 (10.2) |
| | Tricolored Heron | 66 | 18 | 2 | 2 | 22 (33.3) |
| | Little Blue Heron | 21 | 0 | 0 | 1 | 1 (4.8) |
| | Unidentified small herons[b] | 60 | 1 | 2 | 5 | 8 (13.3) |
| | Annual Total | 384 | 70 | 21 | 11 | 84 (21.9) |
| Grand total | | 880 | 276 | 21 | 12 | 291 (33.1) |

[a] Handling by observers, wind damage, or nest usurpation by other species.

[b] Unidentified nests of three *Egretta* species.

TABLE 3. Association between failure of entire colonies and periods of heavy rainfall.

| | Heavy rainfall[a] | No heavy rainfall[b] |
|---|---|---|
| Failure[c] | 20 | 1 |
| Success[d] | 10 | 26 |

$\chi^2 = 23.48$, df = 1, $P \ll 0.001$

[a] More than 2.5 cm/day within 5-km radius: for failed colonies, within 10 days before abandonment; for successful colonies, at any time during the period the colony was active.

[b] No rainfall events accumulating >2.5 cm/day during the period of colony activity.

[c] More than 80% of nests abandoned within 1 week.

[d] Colonies with no major abandonments and with substantial numbers of fledged young.

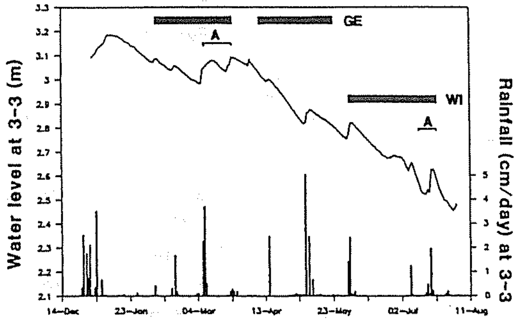

Fig. 2. Timing of synchronized abandonments (A) by Great Egrets and White Ibises at Alley North colony in 1987, in relation to water level (fluctuating line), daily rainfall (bars at bottom) and duration of nesting activity of Great Egrets (GE) and White Ibises (WI).

abandoned nesting synchronously during or immediately following periods of heavy rainfall. Great Egrets usually took longer than a week to abandon nests after heavy rainfall (for examples, see Fig. 2). In contrast, Little Blue Heron nests and the few Black-crowned Night Heron nests we recorded rarely were abandoned, even in the same colonies and at the same time and stage of the nest cycle as synchronized White Ibises and Great Egrets.

We compared foraging dispersion of White Ibises before and during a period of synchronized abandonments at the largest single colony in the study area in both years. White Ibises flew significantly farther during the abandonment period than they had during the previous three weeks (Table 4). During visits to this colony in 1986, we noted a distinct change in prey fed to nestlings at the time of abandonments. Prior to abandonment, regurgitated boluses and feces contained predominantly crayfish parts; during the period of abandonment, the few young that were fed produced boluses and feces that were dark brown, very liquid, and often contained mud and insect parts.

*Hydrological correlates of nest failure.*—For both White Ibises and Great Egrets, the date of initiation was the most significant correlate of nesting success (Table 5); however, the relationship was not in the same direction for both species. Early Great Egret nests were most likely to fail, whereas early White Ibis nests were least likely to fail. For Great Egrets, rainfall was the only other variable significantly associated with nest failure, showing a positive correlation. For White Ibises, rainfall was not a significant variable; however, nest failure was negatively correlated with drying rate.

Years with high numbers of White Ibis nesting attempts (>2,000 nests) had significantly faster spring (January–March) drying rates than years with low numbers of attempts (Table 6). There was no significant difference between the two groups in winter drying rates (November and December), January water depth (analyzed only within ENP), or February–March rainfall.

## DISCUSSION

Compared with estimates made in Everglades National Park (<50% of the size of the current study area) in the 1930s and 1940s, the numbers of breeding birds we found were reduced by

TABLE 4. Distances flown by White Ibises from Alley North colony to foraging sites before and during abandonments (week of June 27 in 1986; week of July 21 in 1987).

| Year | | $n$ | $\bar{x}$ distance (km) | SD | $Z$[a] | $P$ |
|---|---|---|---|---|---|---|
| 1986 | Before abandonments | 28 | 1.50 | 0.850 | 7.26 | $\ll 0.001$ |
| | During abandonments | 47 | 33.00 | 0 | | |
| 1987 | Before abandonments | 96 | 4.46 | 3.412 | 3.12 | $<0.001$ |
| | During abandonments | 5 | 10.41 | 4.770 | | |

[a] Mann-Whitney $U$-test.

TABLE 5. Discrimination of successful and unsuccessful nesting attempts using stepwise logistic regression analysis with failure as the dependent variable. Data from 1986 and 1987 were pooled.

| Species (successful/failed) | Residual $\chi^2$ ($P$) | Variable[a] | Coefficient | SE | $R$ | $P$ |
|---|---|---|---|---|---|---|
| Great Egret (74/124) | 16.46 (0.003) | Eggdate | 0.030 | 0.0069 | −0.247 | <0.0000 |
| | | Rainfall | 0:993 | 0.3845 | 0.134 | 0.0098 |
| White Ibis (127/149) | 2.41 (0.300) | Eggdate | 0.073 | 0.1141 | 0.319 | <0.0000 |
| | | Dryrate | 0.698 | 0.1468 | 0.232 | <0.0000 |

[a] Variables: Eggdate = date first egg was laid in nest; rainfall = net daily rainfall (mm); dryrate = mean daily change in water level (positive or negative). Variables not contributing significantly are not listed; these included water depth (mean daily depth), duration of rising water trend (days), and rising component of water level change.

1-2 orders of magnitude, or >90%, for all species except Great Egrets (Robertson and Kushlan 1974, Ogden 1978, Kushlan et al. 1984, Kushlan and Frohring 1986). Moreover, the total number of nesting attempts we found was <25% of the number estimated in the most recent survey (1974-1975) of the same area (Kushlan and White 1977).

Nesting success is difficult to compare in the same fashion because it has not been measured previously for these species in this area. Abandonment of entire colonies has been recorded in the past (Ogden pers. comm.), but it is not clear if previous studies were temporally intensive enough to document the rate of abandonments we observed. The two years of our study were not comparable to previous years of generally successful nesting in the area (Kushlan 1977, Kushlan and White 1977, Kushlan et al. 1984, Kushlan et al. 1975).

The SLR analyses of nesting success generally supported the observation that failure was strongly associated with changes in weather and surface water. The strong association of date of nest initiation with nest failure (both positively and negatively) can reasonably be attributed to an interaction of the nesting phenology of each species and the seasonality of rainfall patterns. For example, Great Egrets nested relatively early in the season in both years and were exposed to rainfall only from winter frontal systems (Fig. 3). Because rainfall became much less likely during the latter part of the spring season, date of initiation was an excellent predictor of the probability of encountering heavy rains and water level rise. In contrast, the earliest White Ibis nests were initiated after 1 May in both years and were exposed to rainfall only during the onset of the rainy season (June-July). Consequently, White Ibises never nested at the time of winter frontal weather systems. Thus, the last White Ibis nests would be the most likely to encounter rainfall and water level rise. In both species, the period of greatest nest abandon-

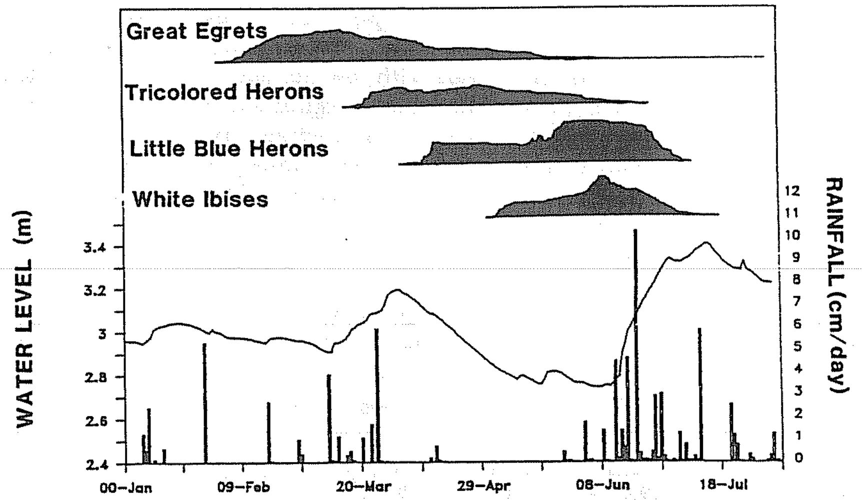

Fig. 3. Nesting chronology of 4 wading bird species in 1986, in relation to water level fluctuations (fluctuating line) and rainfall (bars). Shaded areas represent numbers of active nests of each species.

TABLE 6. Comparison of hydrological factors and rainfall in years of high (>2,000) and low (<2,000) numbers of White Ibis nest initiations in two water management entities of the Everglades freshwater marshes (Everglades National Park and Water Conservation Area 3).

| Year | Nest starts ($n$) | Area | Early drying rate$^{a}$ (cm/day) | Late drying rate$^{b}$ (cm/day) | Rainfall$^{c}$ (cm) | Water level$^{d}$ |
|---|---|---|---|---|---|---|
| 1953 | >2,000 | ENP | 1.35 | 1.82 | 11.4 | 6.2 |
| 1959 | 5,000 | ENP | 1.38 | 1.09 | 20.1 | 6.13 |
| 1967 | 5,000 | ENP | 4.87 | 0.88 | 14.9 | 5.86 |
| 1969 | 6,750 | ENP | 3.21 | −1.00 | 18.0 | 6.04 |
| 1971 | 400 | ENP | 2.41 | 1.78 | 5.1 | 5.99 |
| 1972 | 6,700 | ENP | 1.39 | 1.29 | 11.8 | 5.96 |
| 1973 | 3,600 | ENP | 0.84 | 2.60 | 15.2 | 6.29 |
| 1974 | 892 | ENP | 1.69 | 1.27 | 0.8 | 5.94 |
| 1975 | 890 | ENP | 1.62 | 9.90 | 6.3 | 6.02 |
| 1976 | 0 | ENP | 0.54 | 0.36 | 1.3 | 6.02 |
| 1977 | 0 | ENP | 0.03 | 1.58 | 8.8 | 6.26 |
| 1978 | 100 | ENP | 0.54 | 0.10 | 22.6 | 6.17 |
| 1979 | 250 | ENP | 1.58 | 1.17 | 9.5 | 6.56 |
| 1980 | 0 | ENP | 1.47 | −2.40 | 13.0 | 6.48 |
| 1981 | 465 | ENP | 2.58 | 1.37 | 12.3 | 6.55 |
| 1982 | 188 | ENP | 2.15 | 1.42 | 14.2 | 6.37 |
| 1986 | 250 | ENP | 2.15 | 0.28 | 18.2 | 6.16 |
| 1987 | 200 | ENP | 1.68 | 0.00 | 28.6 | 6.07 |
| 1972 | 17,800 | WCA3 | 3.27 | 2.54 | 15.4 | |
| 1973 | 15,500 | WCA3 | 3.20 | 3.39 | 9.3 | |
| 1974 | 8,100 | WCA3 | 4.60 | 3.30 | 2.0 | |
| 1975 | 11,000 | WCA3 | 4.70 | 6.81 | 0.3 | |
| 1976 | 14,500 | WCA3 | 4.88 | 1.70 | 5.3 | |
| 1977 | 8,300 | WCA3 | 3.60 | 2.34 | 5.0 | |
| 1978 | 0 | WCA3 | 2.35 | −2.18 | 5.3 | |
| 1979 | 0 | WCA3 | 4.72 | −0.30 | 13.5 | |
| 1980 | 0 | WCA3 | −0.78 | 0.30 | 9.0 | |
| 1981 | 1,500 | WCA3 | 2.10 | 1.22 | 14.3 | |
| 1982 | 12,050 | WCA3 | 5.08 | 2.83 | 7.8 | |
| 1986 | 1,442 | WCA3 | 1.92 | 0.81 | 18.2 | |
| 1987 | 4,100 | WCA3 | −2.08 | 1.77 | 28.6 | |

[a] Net change in water level, 1 November through 1 January. Mann-Whitney $U = 75$, $P > 0.05$, comparing drying rates in years of high and low numbers of nesting attempts.

[b] Net change in water level, 1 January through 31 March. Mann-Whitney $U = 48$, $P < 0.02$, comparing drying rates in years of high and low numbers of nesting attempts.

[c] Net rainfall, 1 January through 31 March. Mann-Whitney $U = 118$, $P > 0.10$, comparing rainfall in years of high and low numbers of nesting attempts.

[d] Water level on January 1, at P-33 station in ENP. Mann-Whitney $U = 46$, $P > 0.10$, comparing water levels in ENP in years of high and low numbers of nesting attempts.

ment coincided with the time of greatest rainfall and water level rise within the nesting period of the species. We believe that the strong date effects we found were an artifact of sampling. We hypothesize that if any of the species had nested throughout the spring period, date of initiation would probably not have been a significant variable. This argument, of course, does not explain why date of nest initiation was more significant than other water variables. Presumably, there are other variables associated with date of initiation (e.g. temperature, prey activity, and reproductive cycles) that contribute to the strength of association.

The remaining significant variables imply mechanisms by which failure is related to changes in weather and surface water. For Great Egrets, the effects of rainfall, and not its subsequent effects on surface water, were most strongly associated with nest failure. Potential direct effects include strong winds, temperature drop, and heavy rainfall. Fewer than 6% of Great Egret nests suffered obvious damage by wind or rainfall. Simmons (1959) reported that very low spring temperatures (−6°C) and snowfall did not lead to the abandonment of nests with eggs in a Louisiana colony. Cold weather in the Everglades temporarily halted the initiation of new courtship and nest building. The fact that the Great Egrets we studied typically took a week or more to abandon nests after a major rainfall event suggests there are other factors associated with rainfall that were not discovered by our analyses.

The SLR analysis confirmed that rainfall was not associated strongly with nesting failure of White Ibises, despite the apparently immediate and synchronous abandonments after heavy rains. Rapid increases in water level were associated with failures, which implies that the indirect effects of rainfall on surface water were causally related to White Ibis abandonments.

Although we could not perform the SLR analysis with *Egretta* herons, it appeared that Tricolored Herons responded to rainfall events in the same way as White Ibises. Little Blue Heron abandonment probably was not induced by the same conditions, which suggests that important differences exist in the foraging and nesting ecology of the three *Egretta* species.

The two breeding seasons studied were particularly wet (Frederick and Collopy 1988), with relatively slow spring drying rates, and results drawn solely from these seasons may not represent the long-term variability in this area. The analysis of White Ibis nesting from 31 nesting events indirectly supported the results found in our analysis of individual nests. Spring drying rate was strongly associated with numbers of nesting attempts, but rainfall, water depth, and prebreeding season drying rate were not. We summarize that drying rate is important both as a short-term prerequisite for White Ibis nest initiation (as previously suggested by Kushlan 1976c) and as a determinant of nesting success.

The relationship between initiation and success of breeding, and surface water dynamics seems robust for White Ibises. The mechanism that influences breeding is unclear. The abrupt changes in foraging locations and prey items taken during abandonments suggest that abandonments result from an inability to gather enough food or food of an appropriate type. The increase in distance flown to foraging locations probably did not affect nest abandonment by itself, because the locations were well within the range of distances flown by successfully breeding ibises elsewhere (Bateman 1970, K. Bildstein unpubl. data). Similarly, ibises were not forced to change foraging locations by water depth alone, because at the time of abandonments, pre-abandonment foraging sites were well within the 5–20 cm range reported by Kushlan (1974) as suitable for ibis foraging. Water depth also was not an important correlate of nesting success in the SLR analysis. We believe that nesting success is affected directly by availability of prey, which is affected by the rate of surface water recession.

Crayfish (*Procambarus alleni*) are the main prey item of White Ibises in the Everglades and fish are eaten rarely (Kushlan and Kushlan 1975, Kushlan 1979). Two potential mechanisms might account for the observed relation of water recession rate to nesting success and numbers of nesting ibises. First, crayfish might be concentrated by rapidly receding water and so become more available. Although fish become concentrated by falling water levels (Kushlan et al. 1975, W. Loftus unpubl. data), it is not clear whether crayfish follow (and are concentrated by) receding water or if they burrow in place as the water recedes. Second, if crayfish are not concentrated by receding water, local depletion of crayfish through predation may require the constant exposure of new areas of appropriate foraging depth for sustained foraging by ibises. This could be accomplished only by steadily and rapidly receding water. Falling levels would expose areas where crayfish presumably are active, but rising levels would only make previously dry areas available to ibises. Previously dry areas probably are depauperate in crayfish.

Our results on White Ibises closely parallel those for Wood Storks (Kahl 1964, Kushlan et al. 1975). Timing and success of both White Ibises and Wood Storks are highly dependent on surface water conditions. Fast winter-spring drying rates tend to produce early nesting and fewer colony failures (Wood Storks), and greater numbers of nest initiations and greater nesting success (White Ibises). Even though these relationships for Wood Storks are directly attributable to the dependence on mechanically concentrated prey, it is not clear that ibises are dependent on the same factor for reproductive feeding. Although our results for the ardeid species are less conclusive, it seems clear that nest success of Great Egrets is linked to some effect of weather on surface water dynamics. Because Great Egrets forage on some of the same prey as ibises and storks, some of the same mechanisms may be involved for this species.

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