

In—*Everglades: The Ecosystem and  
Its Restoration*, edited by S. Davis &  
J. Ogden, 1994, 848 pp., St. Lucie Press,  
Delray Beach, FL (407) 274-9906

## 26

---

# FACTORS AFFECTING REPRODUCTIVE SUCCESS of WADING BIRDS (CICONIIFORMES) in the EVERGLADES ECOSYSTEM

Peter C. Frederick  
Marilyn G. Spalding

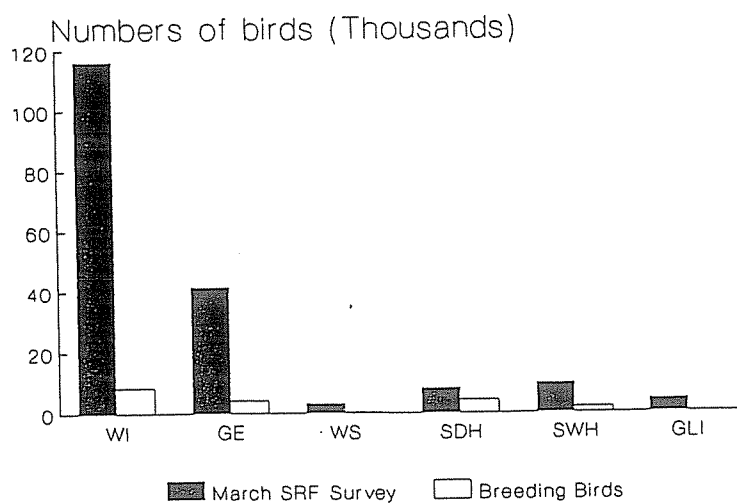
### ABSTRACT

This chapter analyzes over 40 years of inquiry into the factors which affect reproductive success of wading birds in the Everglades system, with a focus on the past 20 years. It is unlikely that reproductive success has been limited by human disturbance (in the post-plume-hunting era), a depauperate potential nesting population, or lack of suitable colony substrate. Predation of nest contents usually has a minor effect on reproductive success, although predation is clearly a correlate of other stresses, such as drying of the marsh surface, human disturbance, or changes in food availability. The majority of reproductive failures instead appear to be associated with the availability and quality of food and with disease agents. For wood storks and white ibises both the initiation and abandonment of nesting can be associated indirectly with the recession rate of surface water in Everglades marshes. This relationship is almost certainly the result of increased prey availability through entrapment during drying phases. Tricolored herons, snowy egrets, and great egrets all show some susceptibility to abandon nesting during winter storms and reversals in the drying trend, although the mechanism may not entirely be related to dilution of prey. Rising water levels do not apparently contribute to the abandonments in great egrets, while the effects of cool temperatures on prey do.

blue herons (*Egretta caerulea*), great blue herons (*Ardea herodias*), and tricolored herons (*Egretta tricolor*). Great egrets (*Casmerodius albus*) appear to be the only species whose nesting numbers have remained relatively stable (Kushlan et al., 1984).

The decline is of interest from a number of perspectives. First, the near complete loss of breeding birds is disturbing on philosophical and aesthetic grounds. Second, the birds play a central role in the food web through predation and nutrient transport (Kushlan, 1976a; Christy et al., 1981; Stinner, 1983; Bildstein et al., 1990; Frederick and Powell, 1994), suggesting that their loss may have already had feedback effects on the ecosystem. Third, because of their position in the food web, the decline of wading birds probably signifies that the health of wetland species upon which the birds depend is in question. Finally, the Everglades is a geographically strategic component of the suite of habitats still utilized by wading birds during the winter and on migration (Hoffman et al., 1991; Bancroft et al., 1992); the management and fate of Everglades habitat could therefore have direct effects on wading bird populations of the entire southeastern United States.

Several lines of evidence suggest that degradation of nesting conditions has played a central role in the decline of Everglades breeding birds. First, the reductions in breeding birds in the Everglades was not matched by similar reductions in nesting in the southeastern United States (Ogden, 1978; Custer and Osborn, 1977), implying that breeding reductions were not unilateral. Second, the declines in Everglades breeding populations have occurred despite the fact that the Everglades region continues to be an important wintering ground for nearly all of the wading bird species concerned. The wintering populations are currently one to two orders of magnitude larger than breeding populations (Figure 26.2) (Bancroft



**Figure 26.2** Comparison of breeding and wintering wading bird population sizes in 1987. Wintering population estimate is from Systematic Reconnaissance Flight results (Bancroft et al., 1987) in March, which usually represents peak numbers in the winter. Breeding censuses were as reported by Frederick and Collopy (1988).

**Table 26.1** Comparison of Nest Success Estimates  
Derived from Traditional and Mayfield Methods, Using the Same Data

Year	Species	Traditional <sup>a</sup>	Mayfield <sup>b</sup>	Percentage-point difference
1986	Great egret	0.3846	0.1481	23.7
	White ibis	0.3061	0.2039	10.2
	Tricolored heron	0.7036	0.4613	24.2
	Little blue heron	0.9487	0.7284	22.0
	Snowy egret	0.8925	0.7117	18.1
1987	Great egret	0.3475	0.2064	14.1
	White ibis	0.6035	0.4887	11.5
	Tricolored heron	0.7632	0.6652	9.8
	Little blue heron	0.7941	0.7164	7.77
	Great blue heron	0.2857	0.1766	10.9

*Note:* All data are from colonies in the freshwater Everglades marshes (see Frederick and Collopy, 1988).

<sup>a</sup> Number of nests that succeed per number of nests monitored.

<sup>b</sup> Probability of success, prorated over the entire period; see Mayfield (1975) and Hensler and Nichols (1981).

habit, has given this group the potential of being accurate (and easily assessed) biological indicators of aspects of the food web which supports them, such as demographics of prey animals, pollutant load, and degree of parasitism (Custer and Osborn, 1977).

However, the reproductive parameters of birds are often quite removed in space and time from environmental parameters (Temple and Wiens, 1989), and caution must be used in assigning indicator relationships (Morrison, 1986). For example, the use of wading bird reproductive parameters as biological indicators of prey abundance, density, or availability is often implicitly assumed, yet it rests heavily on the assumption that food is the major factor controlling reproductive success. Wading bird reproduction is in fact likely to be strongly affected by intense predation by a variety of mammals, reptiles, and birds (Baker, 1940; Burger and Hahn, 1977; Shields and Parnell, 1986; Rodgers, 1987), as well as human disturbance (Tremblay and Ellison, 1979; Parsons and Burger, 1982) and disease (Wiese, 1977). In addition, the methods used to measure or estimate reproductive success can strongly affect the resulting picture of nesting success (for example, see Table 26.1). It is therefore essential that the factors which actually affect reproductive parameters be identified before reproductive parameters are used as bioindicators of environmental conditions. This must be done on a case by case basis. In addition, different measures of reproductive success may reflect different factors in the environment (fecundity versus nestling health, for example), and some definitions of the most commonly used parameters may be of use to the reader in this regard.

### Definitions of Reproductive Parameters

Reproductive effort is defined as the number of nesting attempts (usually those progressing to egg laying) in a given location or year and is the only useful figure

by humans. The exception to this rule has been researchers, who have monitored colony activity and breeding success using methods which vary widely in their intrusiveness. Researcher disturbance cannot be invoked to explain the general decrease in nesting success and breeding numbers in the Everglades, because researcher disturbance has only been common during the last two decades of the decline; further, much of the monitoring has been remotely done using aircraft. Overflights by single-engine reconnaissance aircraft (Kushlan, 1979) and military jets (Black et al., 1984) have not been found to result in reduced reproductive success or in behaviors likely to lead to reduced success.

Entry of researchers into colonies, however, can strongly affect nesting success of herons (Tremblay and Ellison, 1979), especially if colonies are entered during the sensitive courtship and egg-laying stages. This is of particular importance because the very act of entering colonies to monitor success may affect the measurement of reproduction itself. In the freshwater Everglades, Frederick and Collopy (1989a) found no differences in five measures of reproductive success between paired colonies of tricolored herons visited frequently (4-day interval) and infrequently (8-day interval). The latter result suggests that there was little frequency-of-visit effect. Because success was high in both colonies, it was concluded that carefully conducted nest checks during the post-egg-laying period may not strongly affect nesting success. However, until completely undisturbed nesting success (monitored remotely from a tower or vantage point) can be compared with the effects of a single-disturbance event, it is impossible to determine the effects of visits themselves (at any frequency). Similarly, effects of human disturbance are likely to vary considerably with species and location.

One of the most common effects of researcher disturbance is to increase predation and scavenging of nest contents, usually while researchers are in the colony (Milstein et al., 1970; P. C. Frederick and M. G. Spalding, personal observation). In a North Carolina colony, Shields and Parnell (1986) found that over 40% of all white ibis eggs were taken by fish crows (*Corvus ossifragus*), perhaps largely as a direct result of researcher intrusions. Predation by common crows (*C. brachyrhynchus*) on eggs of herons during researcher visits has been a recurrent problem in colonies in the coastal mangrove region of Everglades National Park, where crows are abundant (Bancroft and Jewell, 1987; Bancroft et al., 1991) and in Florida Bay (G. V. N. Powell, personal communication). The magnitude of the effect of crow predation in the absence of researcher disturbance has never been estimated because it requires (as above) measuring nest success remotely at control sites. A key question in this regard is whether crows can force attending parental waders off their nests in order to steal eggs or young. If not, crows must normally be scavengers in colonies, rather than primary predators. Nest attendance is nearly continuous during egg laying and incubation in several species of wading birds (Jenni, 1969; Rudegeair, 1975; Wiese, 1975; Rodgers, 1978, 1980a; Frederick, 1985), suggesting that the effect of crows might only be important during periods of food stress, abandonment, and disturbance or when crows occur in extremely large numbers (Post, 1990).

Other important disturbance effects include thermal stress on eggs and young and the premature departure of young from nests (Parsons and Burger, 1982). While careful timing of visits can presumably take care of the former problem, the

effect of the latter on survival of young has not been systematically investigated for any of the wading bird species which nest in the Everglades. Interestingly, Parsons and Burger found that early habituation of nestlings significantly reduced the early fledging problem, suggesting that frequent visits starting when chicks are small will have less impact than single-time censuses.

### Disease and Parasites

Disease, including parasitic disease and those resulting from toxins, is one of the most poorly understood factors which affect reproductive success of ciconiiforms, particularly in the Everglades. This neglect has a variety of sources. Diseases in wading birds are unlikely to be reported, given the vastness and inaccessibility of much of the area and the fact that most diagnoses are difficult without detailed necropsy procedures. Disease in nestlings in particular is likely to be overlooked because wading bird young often die in large numbers, and it is generally assumed that a large percentage of these deaths must be from starvation, intersibling aggression (Lack, 1968; Powell, 1983; Clark and Wilson, 1981; Mock, 1984), and predation.

Despite these popular beliefs, thorough necropsy, parasite screening, histopathologic examination, and metal and toxin analysis are necessary to identify (or rule out) disease as a contributor to death. For example, a major epizootic of eustrongylidosis (described in detail later) in the Everglades during 1986–90 would have gone unnoticed by professional ornithologists if complete necropsy examinations by a pathologist had not been made (Spalding et al., 1993). Disease also may be obscured as a cause of death because the dead or moribund chick has subsequently been evicted from the nest, scavenged, fallen into the water, or even eaten by a nestmate.

In addition to the lack of reporting, the specific effects of diseases are also extremely difficult to isolate. Diseases almost always occur in conjunction with many other disease agents and toxins commonly found in "healthy" birds, along with the nutritional and environmental stresses with which they live. These factors may alter the response and thus the outcome of the "primary disease" as compared with single-factor experimental infection results. Lesions compatible with the initial illness may no longer be present at the time of death because they were obscured by a secondary disease process, thus resulting in an inaccurate assessment of the importance of the primary disease. Aside from mortality, diseases in general might have a number of other effects of note for wading bird species. One is the abandonment of colony sites by adults. There is evidence that severe ectoparasitism causes abandonment by adults in other colonial nesters (King et al., 1977). Abandonments in a small colony in central Florida occurred when nestlings (and possibly adults) were very severely infected with *Eustrongylides* larvae (Spalding et al., 1993; N. Edelson, personal communication). On the other hand, there is evidence that some colonies will reform the following year even though a devastating disease agent is still active (Wiese, 1977; Spalding et al., 1993). Finally, sublethal diseases or contaminants may have subtle effects on wading bird individuals but dramatic effects on foraging and reproductive success or effort; these effects are likely to be quite difficult to demonstrate. For example, the



western states and only rarely occurs in the eastern United States. Conditions necessary for mortality from this disease are poorly understood (Brand, 1984).

Enterotoxemia, or mortality due to enteritis and toxin produced by *Clostridium perfringens* type C, was responsible for the death of at least 104 adult wading birds of 7 species near Lake Okeechobee in 1971. This epizootic occurred during the late nesting season, although the effect of the disease on nestlings was not mentioned. The source of the infection was unknown (Jasmin et al., 1972).

Botulism, resulting in mortality due to a toxin produced by *C. botulinum* type C, has occurred in northern Florida (Forrester et al., 1980). Although primarily a disease of waterfowl, one snowy egret was involved in this die-off. It is believed that the conditions produced in a phosphate mining operation in conjunction with high temperatures were responsible for this outbreak, which would otherwise be unexpected in Florida.

Salmonellosis, chlamydiosis, and avian pox occasionally occur in adult and nestling wading birds in the Everglades (Conti et al., 1986; M. G. Spalding, unpublished) and have the potential to cause widespread mortality. No large die-offs due to these diseases have been reported.

Dermestid larvae occasionally cause lesions on nestlings in the Everglades, but the number of affected birds is usually small (Snyder et al., 1984; M. G. Spalding, unpublished). Blood parasites and tumors are relatively insignificant in Florida wading birds (Telford et al., 1992; Spalding and Woodard, 1992).

A number of experimental studies have shown effects of contaminants on the immune system of birds and increased susceptibility to disease (Goldberg et al., 1990; Trust et al., 1990; Rocke and Samuel, 1991); however clear evidence of increased susceptibility in free-flying birds has not been demonstrated.

In the early 1970s a great flurry of work focused on the analysis of pesticide concentrations in birds along the east coast of North America (Ohlendorf et al., 1978, 1981). Occasionally wading birds were included in these analyses. DDE, TDE, DDT, dieldrin, heptachlor epoxide, oxychlordan, *cis*-chlordan, *trans*-nonachlor, *cis*-nonachlor, endrin, toxaphene, mirex, and PCB residues have all been reported in Florida great blue herons (Ohlendorf et al., 1981). In only one case was mortality attributed directly to pesticide intoxication (dieldrin). With the exception of *cis*-nonachlor and heptachlor epoxide, the same array of pesticides was found in black-crowned night heron eggs in Florida (Ohlendorf et al., 1978). Both heavy metals and pesticides in eggs were found to be lower in the southern states when compared to northern states in the early 1970s (Ohlendorf et al., 1978). In black-crowned night heron colonies outside Florida, Custer et al. (1984) found an effect on hatching success in colonies with higher pesticide concentrations, but little effect on overall reproductive success. Embryonic mortality and congenital defects (common symptoms of some contaminants) do not appear to be a severe problem in southern Florida at present. Several authors reported that at least 80% and usually more than 90% of all eggs present in active nests at the expected time of hatching do hatch (Girard and Taylor, 1979; Shields and Parnell, 1986; Rodgers, 1980a, 1980b; Rodgers, 1987; Black et al., 1984; Frederick and Collopy, 1988). Congenital defects were present but uncommon in a preliminary survey of 562 nestlings (M. G. Spalding, unpublished).

Ohlendorf et al. (1981) measured concentrations of mercury in black-crowned

also may have become more attractive because they were more reliably flooded than previously due to the creation of the water conservation impoundments.

The location of colonies within the Everglades ecosystem appears to have a strong effect on clutch size. Kushlan (1977) found significantly larger white ibis clutch sizes at inland sites than at coastal sites within the Everglades. A comparison of data collected during the late 1980s shows a similar result for tricolored herons (Frederick et al., 1992). This phenomenon has also been reported from other sites for white ibises (Rudegeair, 1975; Frederick, 1987) and *Egretta* herons (Jenni, 1969; Maxwell and Kale, 1977). While the coastal "depression" of clutch size might be a result of differences in food availability (Kushlan, 1977), the phenomenon might also arise as a function of distances traveled to foraging sites (Rudegeair, 1975; Kushlan, 1977) or of physiological stress due to the ingestion of salty prey (Bildstein et al., 1990; Johnston and Bildstein, 1990) (see next section). Kushlan (1977) found that significant geographic differences in white ibis clutch sizes within the Everglades did not result in differences in numbers of young produced during the two breeding seasons in which he studied reproduction; he suggested that clutch size was not very important in determining production of young in white ibises. The possibility exists that at a longer time scale, clutch size differences have an effect on production.

As discussed in the final section, distance from colony to foraging sites can have important energetic consequences for production of young. The location of colonies may be determined by a number of processes which vary between species. White ibises often change colony sites to take advantage of locally abundant food sources and have been considered almost nomadic nesters (Kushlan, 1977; Ogden, 1978; Frederick, 1987). Actual location of white ibis colony sites in any year probably involves an assessment of nearby food sources, photoperiod, and reproductive condition (Kushlan, 1974). At the opposite end of the spectrum are wood storks, which are much more site faithful, a condition probably enabled by their use of low-energy flight techniques, allowing exploitation of a very large foraging range (Kahl, 1964; Kushlan, 1986). Great and snowy egrets appear to be slightly less nomadic than white ibises and often use old colony sites when nesting, although the same sites may not be used every year. Bancroft and Jewell (1987) have shown that within a season, individual tricolored herons may attempt to nest in several different, traditionally occupied colony sites along the Everglades gulf coast. Frederick and Collopy (1988) and Bancroft et al. (1988) found high colony turnover rates within the freshwater Everglades marshes and Big Cypress regions of southern Florida. These results imply that some fidelity may pertain at the regional level for these species, but not for a single colony site.

### Past Nesting Success

Does past nesting success (or failure) at a site influence future nesting site selection or nesting success for waders? The answer probably depends on the causes of nest failure. Over 5 years, annual destruction of an average of 61% of white ibis nests through tidal inundation at a colony in South Carolina did not result in decreased use of the colony, even following seasons in which over 90% of nests were destroyed (Frederick, 1987). Similarly, at a Delaware River colony repeated

appears to be the habit of nesting in vegetation surrounded by water (Rodgers, 1987).

Raccoons are notorious nest predators, and raids by one or a few animals can cause the disruption and abandonment of entire colonies, often through excess killing (Lopinot, 1951; Rodgers, 1987; Coulter, 1987; Post, 1990). In most colonies, raccoon predation has only been noted when the surface water surrounding the colony has receded (Jenni, 1969; Coulter, 1987; Rodgers, 1987; Frederick and Collopy, 1989c) or the colony island is large enough to permanently support a number of raccoons (Post, 1990).

In the relatively long-hydroperiod marshes of Water Conservation Area 3, raccoons are quite uncommon. Frederick and Collopy (1989c) found that only 2 baited tracking stations were visited by raccoons or other potential mammalian nest predators out of a total of 341 tracking station nights at 27 locations. Almost half of these stations were placed in shallow, drying marshes of less than 5 cm depth, so that even shallowly inundated areas were not visited. The collection of six raccoons for mercury assay in Shark River Slough during 1990 proved extremely difficult (O. L. Bass, personal communication). These findings suggest either that mammalian use of long-hydroperiod marshes is severely limited by even very shallow water or that nest-predatory mammals are quite rare in Everglades freshwater marshes. Further, it is not clear if this sparse distribution is typical of a natural situation or if raccoon populations are currently reduced by mercury contamination or disease.

Frederick and Collopy (1989c) found that colonies in Water Conservation Area 3 experienced very little predation from mammals during 1986 and 1987 (estimated at between 1 and 12% of nests). Because colonies are depredated most often by mammals when dry, it follows that both drought years and drying of the colony during the middle of the nesting season would lead to much more regular nest destruction by raccoons than has been documented in the Water Conservation Areas.

In mangrove regions of the Everglades, raccoons are probably more numerous. Nesting by wading birds is entirely on islands well-separated from the mainland, and W. Robertson (personal communication) has noted that roseate spoonbills (*Ajaia ajaja*) nest only on the few islands in Florida Bay that do not have raccoons on them, suggesting a strong potential effect of predation on nesting success. The island nesting strategy may work. Bancroft et al. (1991) and G. V. N. Powell III and R. D. Bjork (unpublished) have never found evidence of raccoon nest predation at any of the estuarine colonies they studied in the Everglades and Florida Bay.

Jenni (1969) proposed that raccoons might also be deterred from entering Florida wading bird colonies by the alligators (*Alligator mississippiensis*) that usually frequent colonies for scraps and fallen chicks. However, no statistical association was noted between alligator activity at freshwater colonies and lack of visits by raccoons (Frederick and Collopy, 1989c). Many of the freshwater tree island colonies have long perimeters and dense surrounding vegetation. These conditions may make raccoons difficult to detect in freshwater colonies. A case cannot be made at present for alligator deterrence of mammalian predators in Everglades wading bird colonies.

Rat snakes (*Elaphe* spp.) are frequently reported as egg predators in wading



depredations probably are limited to this short period. Because black-crowned night herons are relatively infrequent nesters in Everglades colonies, their overall contribution to nestling losses probably is quite small.

Southern bald eagles (*Haliaeetus leucocephalus*) often prey upon waders and occasionally their nestlings (Rudegear, 1975; Frederick et al., 1993; M. G. Spalding, R. B. Bjork, and G. B. V. Powell III unpublished), although eagles have never been reported at Everglades colonies outside of Florida Bay. Similarly, great horned owls (*Bubo virginianus*) can be very destructive in bird colonies, although the rather characteristic evidence of predation by owls (Pratt, 1972; Nisbet, 1975) has not been reported from Everglades colonies. Red-shouldered hawks (*Buteo lineatus*) are common residents throughout the Everglades and are a potentially important predator of nestling waders. These raptors are known to take nestling birds frequently (Sherrod, 1978). While they have not been reported as predators of wading birds, they would probably not leave telltale evidence at the preyed upon nest.

The emerging picture is that predation on nest contents is usually a minor component of nest failure in Everglades marshes, if colonies remain inundated and if food stress and weather (see later) do not affect parental tenacity and attendance. This picture can be substantially altered if the colony dries out during the nesting period, if food or weather conditions deteriorate, if crows are present during researcher visits, and if mammalian predators increase substantially in abundance. It is suggested here that mammalian nest predation usually leads to episodic, catastrophic losses, rather than the regular, low-frequency predation by arboreal snakes or the opportunistic predation by most birds.

Nest predators could both increase or decrease as an eventual result of the compression and compartmentalization of the Everglades ecosystem. Raccoons and other "meso-mass" mammals are hypothesized to become more abundant in response to a reduction of populations of large predators such as the Florida panther (*Felis concolor coryi*) (Harris and O'Meara, 1989), a shortening of hydroperiods, and an increase in available human garbage. Similarly, the intrusion of roads and accompanying human refuse probably helps crows to seasonally exploit wading bird colonies. Populations of raccoons and nearly all marsh-dwelling nest predators could be considerably reduced by mercury contamination or increased exposure to disease agents with human encroachment (Bigler et al., 1973; Hoff et al., 1974).

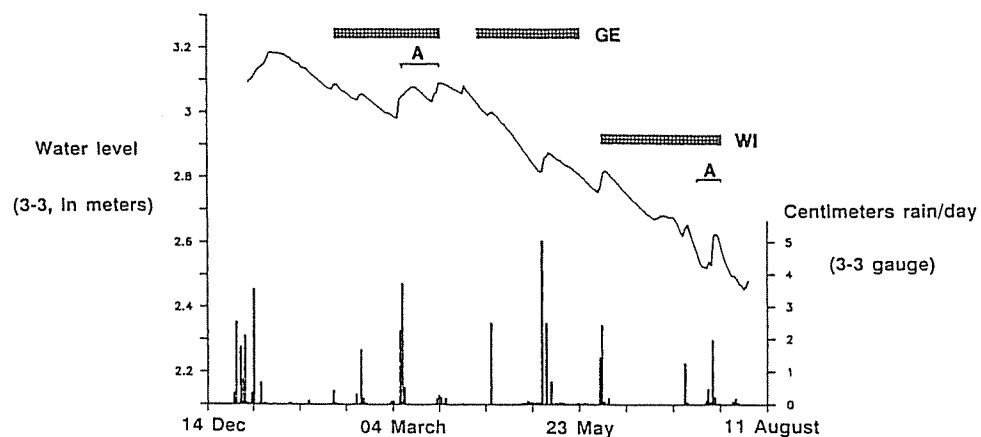
### Drought

Effects of drought on nesting success have rarely been documented, in large part because droughts have been difficult to define in the Everglades, where partial drying of the marsh is a seasonal event. The most obvious effect of drying of the marsh surface is that freshwater colony sites will lose their protection from mammalian predators, and nest losses will undoubtedly increase. Drying of the colony site may result in immediate abandonment by wood storks, especially if during the early stages of nesting or if accompanied by nest predators (Coulter, 1987; Rodgers, 1987). White ibises do not seem as prone to abandonment during colony drying. During the drought associated with the late onset of summer rains

related to specific water levels in the surrounding marshes, but did not examine correlations with water recession rates. Similarly, Clark (1978) found both nest initiation dates and numbers of young produced by wood storks at a Merritt Island, Florida colony to be associated with water levels and water recession rate in the nearby St. Johns River basin. Finally, wood storks have been found to abandon nesting attempts in Everglades National Park in response to strong rainfall events which abruptly reverse regional surface water recession trends (Bancroft and Jewell, 1987; Frederick and Collopy, 1988; J. C. Ogden, personal communication).

This relationship of stork nesting behavior and success with surface water recession rate has been explained as a dependence of storks on the prey which are concentrated into ponds and gentle depressions by falling water levels; during even short periods of rising water, prey presumably disperse and densities are too low for energetically demanding nesting activities. Although many species feed with storks and consume similar prey species, wood storks are presumed to be particularly vulnerable to prey density effects because of their specialized gape foraging technique (Kahl, 1964).

Nesting initiation and abandonment in several other wader species in the Everglades also may be related to hydrological or weather parameters, although the effect and the mechanism does not seem as obvious as with the storks. During three concurrent studies of wading bird nesting success in southern Florida, relatively synchronous colony failure events were noted in great and snowy egrets, tricolored herons, and roseate spoonbills following strong winter frontal weather patterns during which large amounts of rain often (but not always) fell, marsh surface water levels frequently rose, and temperatures dropped (Figure 26.4) (Bancroft and Jewell, 1987; Frederick and Collopy, 1989b; G. V. N. Powell III and R. B. Bjork, unpublished; Frederick et al., 1992). Similarly, white ibises, tricolored herons, little blue herons, and wood storks abandoned nesting synchronously following the onset of the summer rainy season (Frederick and Collopy, 1989b; Bancroft and Jewell, 1987; P. C. Frederick, unpublished data).



**Figure 26.4** Large-scale synchronous abandonments of great egrets and white ibises (A) in relation to surface water dynamics (fluctuating line), rainfall (thin bars), and period of breeding activity (hatched horizontal bars) at Alley-North colony in Water Conservation Area 3 in 1987.

to modify the thermal responses of marsh fishes as well, especially previous experience of the fish with cold weather events (Frederick and Loftus, 1993).

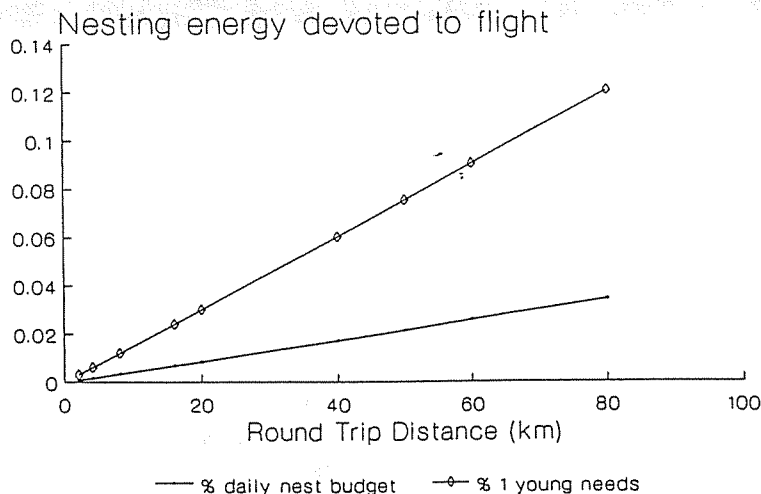
Neither low temperatures nor sustained high winds are likely to explain abandonments by white ibises, tricolored herons, and wood storks, which typically abandoned during the onset of summer rains. Using a multivariate analysis of environmental conditions at the conclusion of successful and unsuccessful white ibis nests, Frederick and Collopy (1989b) found that nest success was related to early nesting and rapid rates of surface water recession. Interestingly, amount of rainfall was not picked as a significant variable, despite the close timing of abandonments with onset of heavy summer rainfall. These results strongly implied that abandonments by white ibises were directly linked to changes in the rate of water level fluctuation, probably by affecting prey availability. Certainly, it appeared that young ibises were not getting very much to eat during the abandonments (Frederick and Collopy, 1988), and adults flew significantly farther in search of food during the period of abandonments. A parsimonious explanation for all these results is that reversals in surface water recession trends make food difficult to obtain for ibises over large parts of the ecosystem, enough so as to result in nesting failure.

Rate of water level recession also seems to predict the timing and numbers of ibis nesting attempts. Kushlan (1976b) gave several convincing examples of large numbers of white ibises initiating breeding apparently in response to artificial or unseasonal water level recessions. Frederick and Collopy (1989b) analyzed nesting records from 31 foci of nesting and found that those with large numbers of nesting attempts (>2000) had significantly faster water recession rates than did those with small numbers of nesting attempts (<2000), but no difference was found in amount of spring rainfall or initial water level. These results suggest that rapid recession rates both stimulate ibis nesting and are associated with nest success.

### The Role of Hydrodynamics in Food Availability

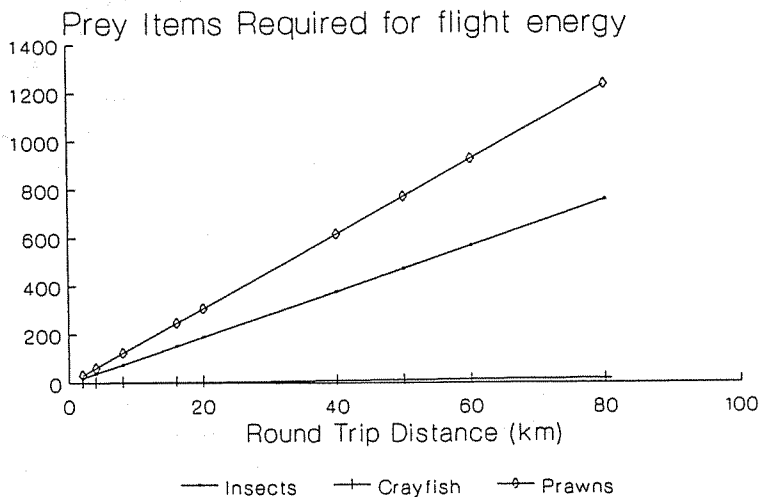
The timing of nest initiations and failures in relation to weather-induced water levels therefore appears to be similar for both wood storks (prior to the decade of the 1980s) and white ibises in the Everglades. Both seem likely to begin nesting during periods of rapid surface water recession and, conversely, may delay initiation in response to slow water recession rates. Both abandon nesting in response to relatively small reversals in receding water trend. For both species, the relationship seems to be the immediate result of food availability. Wood storks feed primarily on small fishes (Ogden et al., 1976), which are known to become concentrated during the dry season in pools and depressions (Kushlan, 1974; W. Loftus, unpublished).

Ibises are primarily demersal, tactile foragers (Kushlan, 1978), which feed largely on crayfish (*Procambarus alleni*) and freshwater shrimp (*Palaemonetes paludosus*) in the Everglades (Kushlan and Kushlan, 1975). Fish become an important food item for ibises only during extremely rapidly receding water trends (Kushlan, 1976b). It is not known whether crayfishes become concentrated during receding water in the same fashion as fishes, because they may burrow in place as surface water recedes. While long-term throw trap data suggest that crayfishes



**Figure 26.5** Daily energy required by a pair of breeding ibises to fly various distances as a proportion of the total daily nest energy requirements (diamonds) and daily energy requirements of one young (dots). Note that even at a round-trip distance of 80 km, the energy required for flight takes up less than 10% of the energy of either a whole nest or one young.

Little blue herons, however, forage less on fish and more on invertebrates and anurans than any of the other wading bird species (Frederick and Collopy, 1988; Telfair, 1981). This dietary difference may explain why little blue herons were found in several instances breeding successfully in colonies where great egrets, white ibises, and tricolored herons were abandoning (Frederick and Collopy, 1988; Bancroft and Jewell, 1987).



**Figure 26.6** Daily energy required by a pair of breeding ibises as a function of distance, expressed as the numbers of prey items required to make up the energy deficit.

tions, wading birds might be far less constrained by weather, hydrological variables, and season in their breeding attempts.

### Factors Affecting Survival of Fledglings

The preceding discussion has focused largely on effects on initiation and success of nesting attempts, which end with fledging by definition. It should be remembered that first-year mortality in juvenile ciconiiforms is likely to be high and that several species may not breed until their second spring (Palmer, 1962; Bent, 1926). J. C. Ogden (personal communication) estimated over 50% mortality among first-year wood storks during years with poor foraging conditions. Kahl (1963) found over 75% first-year mortality in great egrets, and G. V. N. Powell III and R. B. Bjork (unpublished) found that 86% of great blue herons (*Ardea herodias*) radio-tagged in Florida Bay died within their first year of life. An analysis of over 150 band recoveries of white ibises estimated first-year mortality to be 62% (P. C. Frederick, unpublished data).

In general, fledglings are relatively inefficient foragers. Bildstein (1984) found a steady increase in foraging success with age among first-year, second-year, and adult white ibises foraging in the same place and at the same time. Similarly, Recher and Recher (1969) and G. V. N. Powell III (unpublished) found that juvenile little blue herons and great blue herons, respectively, had significantly lower foraging success than adults. It is likely that young ciconiiforms will require excellent foraging conditions to compensate for their developing abilities, perhaps as dense as is required for nesting. Rodgers and Nesbitt (1979) hypothesized that the high prey densities in the immediate vicinity of colonies were important for the development of juvenile heron foraging skills and critical for the survival of young. Certainly fledglings begin foraging on their own directly under nest trees and gradually expand their hunting to nearby marshes surrounding the colony (Rodgers and Nesbitt, 1979; Rudegeair, 1975; DeSanto et al., 1990; P. C. Frederick, personal observation).

Very few studies have focused on post-fledging survival, despite the fact that mortality during this period appears to have a very large effect on recruitment. It seems that an understanding of the factors which affect survival of juveniles is every bit as important as an understanding of factors affecting nesting.

### Summary of Factors Affecting Reproductive Success

In summary, there is reasonable evidence to propose that nesting success of wading birds in the Everglades has not been limited severely by human disturbance, a depauperate potential nesting population, or lack of suitable colony sites. In addition, it is probable that in the absence of other stresses, predation of nest contents usually is a relatively minor component of nesting success. The majority of reproductive failures instead appear to be associated with the availability and quality of food and with disease agents. For wood storks and white ibises, both the initiation and abandonment of nesting can be associated indirectly with the recession rate of surface water in Everglades marshes. This relationship is almost certainly the result of increased prey availability as a result of entrapment during



present system is certainly large enough to accumulate the energy needed for large populations of nesting birds (Frederick and Powell, 1994; Loftus and Eklund, 1994), the number, size, and consistency of food concentrations will increasingly depend upon hydroperiods as the system grows effectively smaller.

Compartmentalization and controlled water flow have probably had large effects on the prey of wading birds. The compartmentalization of long- (Water Conservation Areas) and short- (much of Everglades National Park, Northeast Shark River Slough, Big Cypress National Preserve) hydroperiod marshes has had measurable effects on aquatic fauna populations (Loftus and Eklund, 1994), and the barriers between them must serve to inhibit normal emigration and seasonal recolonization. The barrier effect is likely to be most extreme following periods of extended and severe drought, when the only populations of fishes surviving will be found within these long-hydroperiod impoundments bordered by deep canals. If this results in increased recolonization times, large sections of the marsh may be rendered inactive, even well into periods when aquatic fauna populations should be rapidly reproducing.

Reductions in spatial scale and resilience are also likely to affect wading birds in less direct ways. The severe reductions in Florida panther populations that resulted from reduction in spatial scale may lead to increases in small mammal populations, which prey on wading birds. Similarly, reductions in the aquatic prey base may tend to further focus predatory efforts by marsh mammals on wading bird colonies.

The reduction in numbers and changes in locations of colonies of breeding birds has in turn probably had effects on the heterogeneity of aquatic flora and fauna within the marsh, because wading bird colonies are islands of heavy nutrient enrichment within an otherwise highly oligotrophic marsh (Frederick and Powell, 1994).

Decreased resilience in wading bird reproduction in the Everglades cannot be seen as an effect isolated to southern Florida. The Everglades is an important overwintering site and concentration point for the breeding population of wading birds in the southeastern United States (Bancroft et al., 1992) and poor conditions for breeding could easily extend to the wintering population if unchecked. Further, the Everglades until recently hosted a substantial part of the southeastern United States breeding population of wading birds (Ogden, 1978; Kushlan, 1977; Osborn and Custer, 1977; Nesbitt et al., 1982), and it is not clear that the new nesting locations farther north can take the place of the Everglades. Every wading bird species that was numerically important in the Everglades now has the distinction of having some kind of federal or state protected status (Florida Game and Fresh Water Fish Commission, 1993). The white ibis, for example, remains the most numerous wading bird in Florida, yet has decreased so markedly as to warrant a suggested threatened status (Frederick, in review). Just as a variety of habitats and sites within the Everglades were important to the resilience of wading bird breeding, the Everglades was probably a very important component in the array of sites available for a regional breeding population (Ogden, 1978). Clearly, decreases in local resilience can cascade up to a regional level.

## LITERATURE CITED

- Baker, R. H. 1940. Crow predation on heron nesting colonies. *Wilson Bull.*, 52:124-125.
- Bancroft, G. T. and S. D. Jewell. 1987. Foraging Habitat of *Egretta* Herons Relative to Stage in the Nesting Cycle and Water Conditions, 2nd Annual Report to South Florida Water Management District, West Palm Beach, 174 pp.
- Bancroft, G. T., W. Hoffman, and R. Sawicki. 1987. Wading Bird Populations and Distributions in the Water Conservation Areas of the Everglades, Report to the South Florida Water Management District, West Palm Beach, 166 pp.
- Bancroft, G. T., J. C. Ogden, and B. W. Patty. 1988. Colony formation and turnover relative to rainfall in the Corkscrew Swamp area of Florida during 1982 through 1985. *Wilson Bull.*, 100:50-59.
- Bancroft, G. T., S. D. Jewell, and A. M. Strong. 1991. Foraging and Nesting Ecology of Herons in the Lower Everglades Relative to Water Conditions, Final Report to South Florida Water Management District, West Palm Beach, 156 pp.
- Bancroft, G. T., W. Hoffman, and R. Sawicki. 1992. The importance of the Water Conservation Areas in the Everglades to the endangered wood stork (*Mycteria americana*). *Conserv. Biol.*, 6:392-398.
- Bateman, D. L. 1970. Movement-Behavior in Three Species of Colonial-Nesting Wading Birds: A Telemetric Study, Ph.D. dissertation, Auburn University, Auburn, Ala., 233 pp.
- Bent, A. C. 1926. Life histories of North American marsh birds. *U.S. Nat. Mus. Bull.*, No. 135, 490 pp.
- Bigler, W. J., R. G. McLean, and H. A. Trevino. 1973. Epizootiologic aspects of raccoon rabies in Florida. *Am. J. Epidemiol.*, 98:326-335.
- Bildstein, K. L. 1984. Age-related differences in the flocking and foraging behavior of white ibises in a South Carolina salt marsh. *Colon. Waterbirds*, 6:45-53.
- Bildstein, K. L. 1990. Scarlet ibises and salt tolerances of nesting in the Caroni Swamp of Trinidad. *Biol. Conserv.*, 54:61-78.
- Bildstein, K. L., W. Post, J. Johnston, and P. Frederick. 1990. Freshwater wetlands, rainfall, and the breeding ecology of white ibises (*Eudocimus albus*) in coastal South Carolina. *Wilson Bull.*, 102:84-98.
- Bjork, R. B. and G. V. N. Powell III. 1990. Studies of Wading Birds in Florida Bay: A Biological Assessment of the Ecosystem, Comprehensive report to the Elizabeth Ordway Dunn Foundation, National Audubon Society, New York.
- Black, B. B., M. W. Colopy, H. F. Percival, A. A. Tiller, and P. G. Bohall. 1984. Effects of Low Level Military Training Flights on Wading Bird Colonies in Florida, Tech. Rep. #7, Florida Cooperative Fish and Wildlife Research Unit, School of Forest Resources and Conservation, University of Florida, Gainesville.
- Borg, K. S. 1969. Alkylmercury poisoning in terrestrial Swedish wildlife. *Viltrevy*, 6:301-379.
- Brand, C. J. 1984. Avian cholera in the central and Mississippi flyways during 1979-80. *J. Wildl. Manage.*, 48:399-406.
- Browder, J. A. 1978. A modeling study of water, wetlands and wood storks. in *Wading Birds*, A. Sprunt IV, J. C. Ogden, and S. Winckler (Eds.), Res. Rep. #7, National Audubon Society, New York, pp. 325-346.
- Burger, J. 1982. The role of reproductive success in colony site selection and abandonment in black skimmers (*Rhynchops niger*). *Auk*, 99:109-115.
- Burger, J. and C. Hahn. 1977. Crow predation on black-crowned night heron eggs. *Wilson Bull.*, 89:350-351.
- Christy, R. L., K. L. Bildstein, and P. DeCoursey. 1981. A preliminary analysis of energy flow in a South Carolina salt marsh: Wading birds. *Colon. Waterbirds*, 4:96-103.
- Clark, E. B. 1978. Factors affecting the initiation and success of nesting in an east-central Florida wood stork colony. *Colon. Waterbirds*, 2:178-188.
- Clark, A. B. and D. S. Wilson. 1981. Avian breeding adaptations: Hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.*, 66:253-277.

- Frederick, P. C., R. B. Bjork, G. V. N. Powell IV, and G. T. Bancroft. 1992. Comparative reproductive parameters of herons in three southern Florida habitats. *Colon. Waterbirds*, 15:192-201.
- Frederick, P. C., M. G. Spalding, and G. V. N. Powell. 1993. An evaluation of methods for measuring nestling survival in colonially-nesting tricolored herons (*Egretta tricolor*). *J. Wildl. Manage.*, 57:34-41.
- Girard G. T. and W. K. Taylor. 1979. Reproductive parameters for nine avian species at Moore Creek, Merritt Island National Wildlife Refuge, Florida. *Fla. Sci.*, 42:94-102.
- Goldberg, D. R., T. M. Yuill, and E. C. Burgess. 1990. Mortality from duck plague virus in immunosuppressed adult mallard ducks. *J. Wildl. Dis.*, 26:299-306.
- Gunderson, L. H. 1994. Vegetation of the Everglades: Determinants of community composition. in *Everglades: The Ecosystem and Its Restoration*, S. M. Davis and J. C. Ogden (Eds.), St. Lucie Press, Delray Beach, Fla., chap. 13.
- Hammatt, R. B. 1981. Reproductive Biology in a Louisiana Heronry, M.Sc. thesis, Louisiana State University, Baton Rouge, 93 pp.
- Harris, L. D. and T. E. O'Meara. 1989. Changes in Southeastern Bottomland Forests and Impacts on Vertebrate Fauna. in *Freshwater Wetlands and Wildlife*, R. R. Sharitz and J. W. Gibbons (Eds.), DE90005384, National Technical Information Service, Springfield, Va., pp. 755-772.
- Hensler, G. L. and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: A model, estimators, and simulation results. *Wilson Bull.*, 93:42-53.
- Hoff, G. L., W. J. Bigler, S. J. Proctor, and L. P. Stallings. 1974. Epizootic of canine distemper virus infection among urban raccoons and gray foxes. *J. Wildl. Dis.*, 10:423-428.
- Hoffman, W., G. T. Bancroft, and R. W. Sawicki. 1991. Wading Bird Populations and Distribution in the Water Conservation Areas of the Everglades: 1985-1988, Report to South Florida Water Management District, West Palm Beach, 173 pp.
- Holling, C. S., L. H. Gunderson, and C. J. Walters. 1994. The structure and dynamics of the Everglades system. in *Everglades: The Ecosystem and Its Restoration*, S. M. Davis and J. C. Ogden (Eds.), St. Lucie Press, Delray Beach, Fla., chap. 29.
- Jasmin, A. M., D. E. Cooperrider, C. P. Powell, and J. N. Baucom. 1972. Enterotoxemia of wildfowl due to *Cl. perfringens* type C. *J. Wildl. Dis.*, 8:79-84.
- 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.
- Johnston, J. and K. L. Bildstein. 1990. Dietary salt as a physiological constraint in white ibises breeding in an estuary. *Phys. Zool.*, 63:190-207.
- Kahl, M. P., Jr. 1963. Mortality of common egrets and other herons. *Auk*, 80:295-300.
- Kahl, M. P. 1964. Food ecology of the wood stork (*Mycteria americana*). *Ecol. Monogr.*, 34: 97-117.
- King, K. A., D. R. Blankinship, and R. T. Paul. 1977. Ticks as a factor in the 1975 nesting failure of Texas brown pelicans. *Wilson Bull.*, 89:157-158.
- Klukas, R. W. and L. N. Locke. 1970. An outbreak of fowl cholera in Everglades National Park. *J. Wildl. Dis.*, 6:77-79.
- Krebs, J. R. 1978. Colonial nesting in birds, with special reference to the ciconiiformes. in *Wading Birds*, A. Sprunt IV, J. C. Ogden, and S. Winckler (Eds.), Res. Rep. #7, National Audubon Society, New York.
- Kushlan, J. A. 1974. The Ecology of the White Ibis in Southern Florida: A Regional Study, Ph.D. dissertation, University of Miami, Coral Gables, Fla.
- Kushlan, J. A. 1976a. Wading bird predation in a seasonally fluctuating pond. *Auk*, 93:86-94.
- Kushlan, J. A. 1976b. Site selection for nesting colonies by the American white ibis (*Eudocimus albus*) in Florida. *Ibis*, 118:590-593.
- Kushlan, J. A. 1977. Population energetics in the American white ibis. *Auk*, 94:114-122.
- Kushlan, J. A. 1978. Feeding ecology of wading birds. in *Wading Birds*, Res. Rep. #7, A. Sprunt IV, J. C. Ogden, and S. Winckler (Eds.), National Audubon Society, New York.
- Kushlan, J. A. 1979. Effects of helicopter censuses on wading bird colonies. *J. Wildl. Manage.*, 43:756-760.

- Ogden, J. C., D. A. McCrimmon, Jr., G. T. Bancroft, and B. W. Patty, 1987. Breeding populations of the wood stork in the southeastern United States. *Condor*, 89:752-759.
- Ohlendorf, H. M., E. E. Klass, and T. E. Kaiser. 1978. Environmental pollutants and eggshell thinning in the black-crowned night-heron. in *Wading Birds*, Res. Rep. #7, A. Sprunt IV, J. C. Ogden, and S. Winckler (Eds.), National Audubon Society, New York, pp. 63-82.
- Ohlendorf, H. M., D. M. Swineford, and L. N. Locke. 1981. Organochlorine residues and mortality of herons. *Pestic. Monit. J.*, 14:125-135.
- Osborn, R. G. and T. W. Custer. 1977. Herons and Their Allies: Atlas of Atlantic Coast Colonies, 1975 and 1976, Biological Report FWS/OBS 77/08, U.S. Fish and Wildlife Service.
- Palmer, R. S. 1962. *Handbook of North American Birds*, Vol. 1. Yale University Press, New Haven, Conn.
- Parsons, K. C. and J. Burger. 1982. Human disturbance and nesting behavior in black-crowned night herons. *Condor*, 84:184-187.
- Pennycuik, C. J. and T. De Santo. 1989. Flight speeds and energy requirements for white ibises on foraging flights. *Auk*, 106:141-143.
- Pierce, C. W. 1962. The cruise of the bonton. *Tequesta*, 22:3-63.
- Post, W. 1990. Nest survival in a large ibis-heron colony during a 3-year decline to extinction. *Colon. Waterbirds*, 13:50-61.
- Powell, G. V. N. 1983. Food availability and reproduction by great white herons *Ardea herodias*: A food addition study. *Colon. Waterbirds*, 6:139-147.
- Powell, G. V. N., R. D. Bjork, J. C. Ogden, R. T. Paul, A. H. Powell, and R. B. Robertson, Jr. 1989. Population trends in some Florida Bay wading birds. *Wilson Bull.*, 101:436-457.
- Powell, G. V. N., J. W. Fourqurean, W. J. Kenworthy, and J. C. Zieman. 1991. Bird colonies cause seagrass enrichment in a subtropical estuary. *Estuarine Coastal Shelf Sci.*, 32:567-579.
- Pratt, H. W. 1972. Nesting success of common egrets and great blue herons in the San Francisco Bay region. *Condor*, 74:447-453.
- Recher, H. F. and J. A. Recher. 1969. Comparative foraging efficiency of adult and immature little blue herons (*Florida caerulea*). *Anim. Behav.*, 17:320-322.
- Rocke, T. E. and M. D. Samuel. 1991. Effects of lead shot ingestion on selected cells of the mallard immune system. *J. Wildl. Dis.*, 27:1-9.
- Rodgers, J. A., Jr. 1978. Breeding behavior of the Louisiana heron. *Wilson Bull.*, 90:45-59.
- Rodgers, J. A., Jr. 1980a. Little blue heron breeding behavior. *Auk*, 97:371-384.
- Rodgers, J. A., Jr. 1980b. Reproductive success of three heron species on the west coast of Florida. *Fla. Field. Nat.*, 8:37-40.
- Rodgers, J. A., Jr. 1987. On the antipredator advantages of coloniality: A word of caution. *Wilson Bull.*, 99:269-270.
- Rodgers, J. A., Jr. and S. A. Nesbitt. 1979. Feeding energetics of herons and ibises at breeding colonies. *Colon. Waterbirds*, 3:128-132.
- Roffe, T. J. 1988. *Eustrongylides* sp. epizootic in young common egrets (*Casmerodius albus*). *Avian Dis.*, 32:143-147.
- Rosen, M. N. and A. I. Bischoff. 1949. The 1948-49 outbreak of fowl cholera in birds in the San Francisco Bay area and surrounding counties. *Calif. Fish Game*, 35:185.
- Rudegeair, T. J. 1975. The Reproductive Behavior and Ecology of the White Ibis (*Eudocimus albus*, Ph.D. dissertation, University of Florida, Gainesville.
- Sherrod, S. K. 1978. Diets of North American Falconiformes. *Raptor Res.*, 12:49-121.
- Shields, M. H. and J. Parnell. 1986. Fish crow predation on eggs of the white ibis at Battery Island, North Carolina. *Auk*, 103:531-539.
- Simmons, E. M. 1959. Observations on effects of cold weather on nesting common egrets. *Auk*, 76:239-241.
- Snyder, N. F., J. C. Ogden, J. D. Bittner, and G. A. Grau. 1984. Larval dermestid beetles feeding on nesting snail kites, wood storks, and great blue herons. *Condor*, 86:170-174.
- Spaan, J. W., R. G. Heath, J. F. Kreithzer, and L. N. Locke. 1972. Ethyl mercury *p*-toluene sulfonanilide: Lethal and reproductive effects of pheasants. *Science*, 175:328-331.