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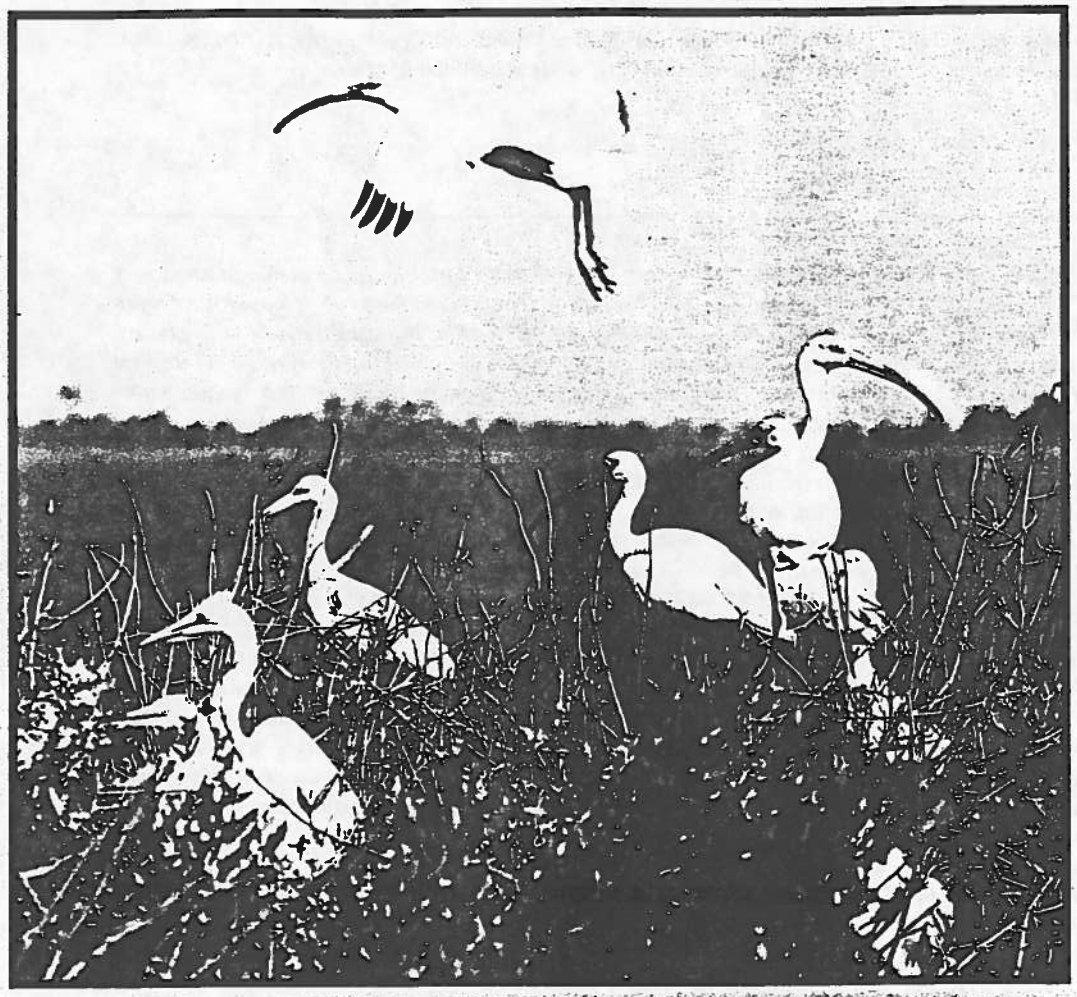

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Conservation of Large, Nomadic Populations of White Ibises (*Eudocimus albus*) in the United States

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Abstract: *We compiled published and unpublished records of large nestings of White Ibises (*Eudocimus albus*) in the United States between 1930 and 1993. The resulting database provides evidence of at least four major geographic shifts of the breeding population of White Ibises during the period. Banding returns and colony histories demonstrate that the movements were not migratory. The extremely fast growth of most White Ibis breeding colonies indicates that local recruitment could not have fueled the large increases in breeding numbers in colonized areas. Ibises seem to colonize wetland areas that have good feeding resources and to abandon areas that lose the ability to supply this resource. Mechanisms of attraction to new sites and repulsion from degraded ones may work alone or in tandem. Degradation of breeding sites frequently occurs through natural processes, such as hurricanes, stochastic weather patterns, and wetland conditions, and the nomadic behavior of White Ibises appears to be an obligate life-history feature. Although surveys throughout the range of the U.S. population of White Ibises have never been comprehensive, available records indicate minimum breeding populations of 125,000 pairs in 1933, 170,000 pairs in 1976, and 51,000 pairs in 1991. The U.S. population as a whole appears to be decreasing. White Ibises share a suite of population, social, and movement characteristics with a number of nomadic species. Conservation strategies for these species may differ fundamentally from those targeting more sedentary species. Nomadic species may typically depend on large populations to find food and to stimulate breeding and are therefore likely to decline abruptly and unpredictably as habitat is lost or degraded. Rapid population declines may occur at population levels well above those predicted by genetic and minimum viability models. Because of its nomadic habit, the survival of this species may depend on a regional planning approach. To conserve this species we recommend a continuing commitment to the monitoring, assessment, and preservation of a mosaic of fresh and estuarine wetlands in the southeastern U.S.; the maintenance of natural disturbances needed to produce pulses of food in these wetlands, and the coordination of management efforts throughout the U.S., as well as between the U.S. and Cuba.*

La conservación de grandes poblaciones nómadas de Ibises Blancas (*Eudocimus albus*) en los Estados Unidos

Resumen: *En el presente trabajo compilamos registros, publicados y sin publicar, sobre grandes anidamientos de Ibises Blancas en los Estados Unidos entre 1930 y 1993. Las bases de datos resultantes proveen evidencia de por lo menos cuatro grandes cambios geográficos de la población reproductiva de Ibises Blancas durante este periodo. Los datos sobre la recuperación de bandas de marcado y las historias de las colonias demuestra que estos movimientos no fueron migratorios. El crecimiento extremadamente rápido de la mayoría de las colonias reproductivas de Ibises Blancas indica que el reclutamiento local no fué el responsable de los grandes incrementos en el número de reproductores en las áres colonizadas. Las Ibises parecen colonizar áreas de humedales que tienen buenos recursos alimenticios y abandonan áreas que pierden la habilidad para proveer estos recursos. Los mechanismos de atracción a los nuevos sitios y repulsión de los sitios*

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degradados podrían actuar por si solos o en secuencia. La degradación de los sitios de crianza ocurre frecuentemente mediante procesos naturales tales como huracanes, patrones climáticos estocásticos y condiciones de los humedales. Es así que el comportamiento nomádico de las Ibises Blancas parece ser una característica forzosa de su historia natural. Si bién los estudios a lo largo del área de distribución de la población de Ibises Blancas de los EEUU nunca han sido comprendidos, los registros disponibles indican que el tamaño mínimo de las poblaciones reproductivas fue de 125,000 parejas en 1933, 170,000 parejas en 1976 y 51,000 parejas en 1991. La población de los EEUU parece estar decreciendo. Las Ibises Blancas comparten una serie de características poblacionales, sociales y de movimiento con varias especies nomádicas. Las estrategias de conservación para estas especies podrían diferir fundamentalmente de aquellas que estan destinadas a especies más sedentarias. Las especies nomadas podrían depender típicamente de grandes poblaciones para encontrar comida y estimular la crianza y son por lo tanto más susceptibles a declinar abruptamente e impredeciblemente a medida que el hábitat se pierde o se degrada. Declinaciones poblacionales muy rápidas pueden ocurrir a niveles poblacionales mucho mayores que aquellos predichos por los modelos genéticos y de viabilidad mínimos. Dado su hábito nomádico, la supervivencia de esta especie podría depender de una estrategia de planeamiento a nivél regional. Con la finalidad de conservar esta especie nosotros recomendamos un compromiso continuo de monitoreo, evaluación y preservación de los mosaicos de humedales estuarinos y de agua dulce en el sudeste de EEUU; el mantenimiento de las perturbaciones naturales necesarias para producir los pulsos de recursos alimenticios en estos humedales y la coordinación de los esfuerzos de manejo a lo largo y ancho de los EEUU, así como también entre EEUU y Cuba.

Introduction

Long-legged wading birds (order Ciconiiformes) show great variation in degree of breeding-site fidelity, ranging from year-round territoriality to a near-complete lack of philopatry (Ogden et al. 1980; Hancock & Kushlan 1984; Bancroft et al. 1988; Hancock et al. 1992; Lopez Ornat & Ramo 1992; Bildstein 1993). The frequent lack of breeding site fidelity in these birds has been interpreted as an adaptation to unpredictable local breeding conditions, in turn tied to variable weather events and foraging conditions in nearby wetlands (Kushlan 1986; Hancock et al. 1992; Bildstein 1993; Frederick & Loftus 1993).

Given sufficient uncertainty in breeding conditions, nomadism can evolve in colonial-nesting species and may frequently include life-history, social, and reproductive adaptations (Bucher 1992). The resulting suite of adaptations may be unique to nomadic animals and may produce population responses to habitat loss that are quite different from those of more sedentary or even migratory species. The White Ibis (*Eudocimus albus*) appears to be such a nomadic species.

The breeding range extends from coastal Colombia and northeastern Brazil in South America, along both coasts of Mexico, along both Gulf and Atlantic coasts of North America to Virginia, and likely Cuba and Hispaniola. The overwhelming majority of the breeding population of White Ibises is found in North America, although many now believe the species to be conspecific with the Scarlet Ibis (*Eudocimus ruber*), which becomes numerous in northern South America (Spaans 1975; Ramo & Busto 1987, 1988; Hancock et al. 1992).

The White Ibis exhibits extremely low breeding-site fidelity. A number of authors have described considerable inter-annual variation in breeding numbers at specific sites (Kushlan 1976*a*; Bildstein et al. 1990; Spaans 1990; Bildstein 1993) and apparent shifts in major breeding sites within and among ecosystems (Ogden 1978; Kushlan et al. 1984; Spaans 1990; Bildstein 1993; Fleury & Sherry in press). Within the United States observations of interregional shifts in breeding have become consistent enough to suggest that large-scale movements of large segments of the breeding population are common and that, within the U.S., the species may be represented by a single, relatively panmictic population (Ogden 1978; Bildstein 1993; Fleury & Sherry in press), an idea supported by genetic evidence (Stangel et al. 1991). Our ability to assess this possibility directly has been hampered by a lack of synchronous breeding censuses of the species over its entire southeastern United States breeding range. It is also unclear whether such large-scale movements are typical of the species' natural breeding ecology or are the result of human-induced disturbance and habitat degradation (Ogden 1978; Bildstein 1993).

We summarize the evidence for and consistency of interregional shifts of the North American White Ibis population to examine trends in the total number of breeders within this portion of the range, to examine the conditions and mechanisms that contribute to abandonment of nesting sites and initiation of nesting in others, and to offer management recommendations appropriate to the highly mobile and unpredictable nesting characteristics of this still-numerous species.

Methods: Summary of Breeding Information

White Ibises are conspicuous, social, and highly colonial nesters, frequently occurring in aggregations of several thousands to tens of thousands of nests (Kushlan & Bildstein 1992). The conspicuousness of these large breeding aggregations has prompted numerous counts or

Table 1. Sources of records of ibis nesting in the southeastern United States.

State	*Region or colony*	*Period of effort*	*Source(s)**
Florida	Everglades	1930–1977	Ogden 1978; Frohring et al. 1988
		1930–1980	Kushlan et al. 1984
		1930–1990	Bancroft 1989; Frohring et al. 1988
		1990–1994	Frederick 1993, 1994*a*
		1930–1978	NAS unpublished
		1974–1975	Kushlan & White 1977
	Cedar Keys	1950–1990	Lower Suwannee National Wildlife Refuge, unpublished records
	Alafia Banks	1948–1992	NAS unpublished; R. Paul, personal communication
	Atlantic coast	1976–1977	Osborn & Custer 1978
	statewide	1978–1980	Nesbitt et al. 1982
		1986–1989	Runde 1991; Runde et al. 1991
		1930–1977	Ogden 1978; NAS unpublished
Georgia	Okefenokee Swamp	1971–1977	Ogden 1978; Stinner 1980, 1983
	statewide	1930–1977	Ogden 1978; Osborn & Custer 1978
		1980–1993	Georgia Department of Natural Resources, unpublished; U. S. National Wildlife Refuges records
South Carolina	Pumpkinseed Island	1950–1993	Bildstein 1993
	Drum Island	1984–1986	Post 1990
	statewide	1975–1977	Osborn & Custer 1978
		1930–1977	Ogden 1978
North Carolina	Battery Island	1950–1992	Shields & Parnell 1986; J. Parnell, personal communication
	statewide	1930–1977	Ogden 1978
	statewide	1975–1977	Osborn & Custer 1978
Alabama	statewide	1930–1977	Ogden 1978; NAS unpublished; Keeler 1956
		1952–1986	Dusi et al. 1971; Dusi & Dusi 1987
Louisiana	statewide	1930–1977	Ogden 1978; NAS unpublished; Lowery 1949; Keller et al. 1984; Spendelow & Patton 1988
		1989–1991	Martin & Lester 1991; Keller et al. 1984; Spendelow & Patton 1988
Texas	statewide	1930–1977	Ogden 1978; NAS unpublished
		1979–1982	Texas Colonial Waterbird Society 1982; Spendelow and Patton 1988
		1979–1992	Lange 1993, Spendelow & Patton 1988

**Other sources searched for references to ibis breeding aggregations include Bent (1926), Oberholser (1938), Sprunt (1954), Lowery (1955), Hopkins and Dopson (1967), Hopkins (1969), Sprunt and Chamberlain (1970), Oberholser and Kincaid (1974), and all issues of four state bird journals:* Chat *(North and South Carolina),* Oriole *(Georgia), and* Florida Field Naturalist *from 1930 through 1993.*

surveys, often with a written record. These counts sometimes have become regular, occurring over a period of consecutive years. The white plumage and local dominance of ibises within nesting aggregations makes them suitable for aerial counts. Where systematic and comprehensive surveys have been conducted over large areas, between 73 and 96% of the total number of nests have been found in colonies of over 1000 nests (Spaans 1975; Kushlan & White 1977; Osborn & Custer 1978; Nesbitt et al. 1982; Texas Colonial Waterbird Society 1982; Martin & Lester 1991; Runde et al. 1991). Thus, large influxes of breeding ibises into a previously unoccupied area, as well as the disappearance of formerly large colonies, are likely to have been detected, reported, and often counted with an accuracy of at least an order of magnitude. This level of accuracy is appropriate for our analysis, which is intended to detect major shifts in the location of the breeding population.

We searched the literature for all credible records of White Ibises nesting in Florida, Georgia, South Carolina, North Carolina, Alabama, Mississippi, Louisiana, and Texas between 1930 and 1993. Major sources of nesting information are listed by state and location in Table 1. The resulting database is too large to publish here, but electronic copies are available from the authors.

We picked 1930 as our starting date because interest in the fate of colonially nesting ciconiform birds in the United States seems to have arisen during the 1920s and 1930s, often prompting surveys both within and outside of heavily used areas (Ogden 1978, 1994). In addition, the use of aerial survey techniques was uncommon before that period.

In many core nesting areas, such as the Everglades, Cedar Keys, and Tampa Bay in Florida and the coasts of North and South Carolina and Texas, breeding colony counts and surveys have been regular and sufficiently thorough to establish demographic trends. Nesting aggregations of White Ibises in the coastal regions of the Florida Everglades have been sought and counted at least sporadically since the 1930s and regularly since the 1970s (Kushlan et al. 1984); freshwater and coastal areas have received comprehensive surveys during the 1970s

as well as annually since 1986. Annual counts are also available from Alafia Banks in Tampa Bay (1973 to the present) and the Cedar Keys on the Gulf Coast of Florida (1953 to the present). The relative importance of the Everglades and the two latter areas as breeding sites within Florida has been confirmed during three statewide surveys (Ogden 1978; Nesbitt et al. 1982; Runde 1991; Runde et al. 1991).

We also gleaned considerable information from annual statewide searches for Wood Stork (*Mycteria americana*) colonies from 1975 to 1986 (unpublished records of National Audubon Society files on record at Everglades National Park Library, Homestead, Florida, referred to collectively from here on as NAS unpublished).

Several large coastal colonies in North and South Carolina (Pumpkinseed and Drum Islands in South Carolina, Battery Islands in North Carolina) have been surveyed annually since the mid-1970s (Parnell & Soots 1979; Post 1990; Bildstein 1993; J. Parnell, personal communication). The overwhelming numerical importance of these colonies within the states of North and South Carolina has been verified through several comprehensive coastal surveys.

In Louisiana and Texas we relied upon unpublished National Audubon Society reports and surveys conducted during the 1940s and 1950s (NAS unpublished) and upon statewide and coastal surveys for waterbirds during the 1970s and 1980s (Portnoy 1977, 1978; Texas Colonial Waterbird Society 1982; Martin & Lester 1991; Lange 1993). In addition, we have used unpublished data from the Louisiana Department of Fish and Game, the Fish and Wildlife Service Refuge system, and anecdotal accounts of breeding colonies.

We analyzed all resighting and recapture records for White Ibises banded or color-marked in the United States between 1926 and 1985, available from the Bird Banding Laboratory, National Biological Service, Laurel, Maryland. Banding and resighting locations are accurate to 10 minutes of latitude and longitude. This database provided information on 18,173 birds banded as nestlings with U.S. Fish and Wildlife Service aluminum bands, 458 birds banded as nestlings with USFWS bands and orange patagial marks, and 82 birds banded as adults with both USFWS bands and patagial marks. First-year, second-year, and adult White Ibises are distinguishable from one another on the basis of plumage (Kushlan & Bildstein 1992).

Results

Regional Breeding Population

Historical data suggest substantial changes in the total population breeding in the United States during the twentieth century. During several years in the early and late 1930s, exceptionally large numbers of ibises were found in several colonies in the coastal Everglades. A balanced and conservative interpretation of the original accounts suggests approximately 125,000 nesting pairs during the highest counts in 1933 (Ogden 1994). During this time White Ibises rarely were reported nesting in large numbers outside of Florida, and anecdotal information suggests that drought in other parts of Florida had forced nearly all the ibis to breed in south Florida in 1933 (Holt 1933; R. P. Allen in Ogden 1978).

In 1976, surveys of the coastal regions of Louisiana, Texas, Florida, and the Atlantic Coast states, including interior Florida (Osborn & Custer 1978; Nesbitt et al. 1982; Texas Colonial Waterbird Society 1982; Kushlan et al. 1984; NAS unpublished) yielded an estimated total of 170,000 breeding pairs. Most recently, surveys of the largest colony sites in Florida, Georgia, South and North Carolina, Texas, and Louisiana yielded estimates of approximately 51,000 and 43,000 pairs in 1990 and 1991, respectively.

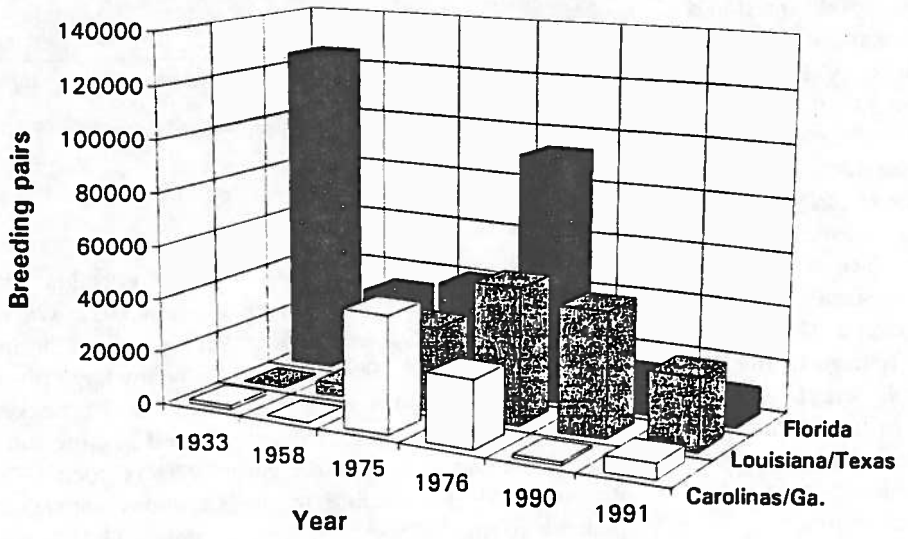

Figure 1. Numbers of breeding pairs of White Ibises by region in the southeastern United States, shown for years in which substantial survey efforts have been made throughout most of the range.

Because survey efforts were never complete throughout the breeding range during any of these surveys, each of these "total" population sizes represents a minimum estimate. Nonetheless, we believe these estimates include the majority of breeding ibises and closely reflect total numbers of pairs breeding during those periods. A summary of breeding records, coupled with existing literature, shows evidence for a number of broad patterns (see Fig. 1).

FLORIDA

Within Florida, declines of at least 90% of breeding ibises between the 1930s and the 1980s are well documented for the Everglades region (Kushlan et al. 1984; Bancroft 1989; Frederick & Spalding 1994; Ogden 1994). The exact timing of these declines is difficult to pinpoint because of a long hiatus in survey efforts between the 1950s and the late 1960s, and because large variation in inter-annual breeding effort is likely to have been typical of the pre-degradation Everglades (Ogden 1994). It seems obvious that declines of at least 50% had occurred by the early 1970s.

The number of breeding pairs at two colonies in the Gulf coast of central Florida (Alafia Banks and Cedar Keys) increased from 5000 in 1938 to well over 100,000 pairs by the mid 1970s (NAS unpublished, Lower Suwannee National Wildlife Refuge records, Richard Paul, personal communication; see Table 2). At Cedar Keys the number of nesting White Ibises crashed in 1979 following a series of freezes that killed all of the mangrove nesting vegetation; since then the number has never exceeded 8000 pairs (Ridell 1978). Since 1975 the Alafia Banks colony has fluctuated between 4000 and 11,000 pairs.

A comparison of a three-year statewide survey of White Ibis colonies in Florida in the late 1970s (Nesbitt et al. 1982) with surveys conducted during three years in the late 1980s (Runde 1991; Runde et al. 1991) suggests a minimum statewide decline of 55% during the intervening 10 years (90,000 to 40,000 pairs, measured from peak annual counts in both surveys). Rainfall patterns, increased survey effort, and slight differences in the survey methodology of the two studies all bias the estimates of the 1980s upward compared with the 1970s (Frederick 1994*b*). Because fewer birds were actually found in the later surveys despite more effort, the conclusion that a decline has taken place is conservative. Since the end of the second set of surveys in 1990, new survey information in selected parts of Florida suggests no evidence of reversal in the pattern of decline (Frederick 1993; 1994*a*; NAS unpublished; Lower Suwannee National Wildlife Refuge records). In addition, Runde et al. (1991) found that between the 1970s and 1980s surveys in Florida, large colonies (>1000 pairs) had declined in absolute numbers by over 70%.

Table 2. Numbers of breeding pairs of White Ibises recorded at Tampa Bay and Cedar Keys on the Gulf coast of Florida between 1938 and 1993.

Year	*Tampa Bay*[a]	*Cedar Keys*[b]
1939–1946	5000	
1948–1952	30,000	
1953		1800
1954		
1955		
1956		4700
1957		10,000
1958	22,000	10,000
1959		7500
1960		8100
1961		3250
1962		60
1963		900
1964		4000
1965		10,000
1966		11,000
1967		70,000
1968		
1969		75,000
1970		55,000
1971	500	20,000
1972		100,000
1973		40,000
1974		20,000
1975	5000	15,000
1976	5000	50,000
1977	8000	15,000
1978	1000	45,000
1979		25
1980		37
1981	4900	100
1982	5750	125
1983	11,000	
1984	6760	
1985	3300	200
1986	4895	5000
1987	6455	8500
1988	4660	2000
1989	4340	797
1990	4703	2700
1991	5605	3800
1992	4150	3600
1993	7400	3600

[a] *Data for Tampa Bay are from National Audubon Society unpublished records.*
[b] *Data for Cedar Keys are from Lower Suwannee National Wildlife Refuge.*

NORTH AND SOUTH CAROLINA

Breeding records for South and North Carolina date from 1922 and 1950, respectively (Sprunt 1922; Wayne 1922; Stephens 1950). Sporadic survey efforts during the 1950s and early 1960s did not show any large population increases (Quay 1947; Cutts 1955, 1959, Beckett 1965). Indeed, the species did not breed in large numbers in the Carolinas until the early 1970s (Ogden 1978; Bildstein 1993). Breeding in the Carolinas apparently peaked by the 1975 survey (Fig. 1), when 41,104 pairs

were found there, dominated numerically by three coastal colonies at Battery Island, North Carolina and Drum and Pumpkinseed Islands, South Carolina. Although numbers of breeding pairs at the former site have increased steadily, those at Drum Island have decreased substantially in response to heavy predation (Post 1990) and, possibly, a rediversion of the Santee River; at Pumpkinseed Island the population has decreased substantially since 1989 as a result of the effects of Hurricane Hugo on feeding habitat (Bildstein 1993).

LOUISIANA AND TEXAS

Between the start of our study period and 1940, White Ibises were uncommon as breeders in Texas and Louisiana (Oberholser 1938, NAS unpublished; Fig. 1). By the late 1940s, however, over 20,000 pairs were discovered breeding in Louisiana (Lowery 1949), and small but consistent increases were reported in Texas. By 1976, over 40,000 pairs were found breeding in Louisiana (Portnoy 1977). Between the late 1970s and 1993, Texas totals fluctuated between 4000 and 12,000 pairs (Texas Colonial Waterbird Society 1982; Lange 1993). There may have been large increases in breeding pairs in Louisiana between 1985 and 1993. Several extremely large colonies have been reported in south-central Louisiana during the early 1990s (R. Martin, B. Fleury, personal communication). Rough estimates of the size of these colonies indicate several tens of thousands of pairs in total. Fleury and Sherry (in press) report dramatic increases in numbers of White Ibises found on Christmas Bird Counts and Breeding Bird Surveys in Louisiana during the same time period and suggest that the increases are related to a rapidly growing crayfish aquaculture industry (Fleury 1994). Freshwater crustaceans are a principal food item for ibises (Nesbitt et al. 1974; Kushlan & Kushlan 1975). The timing and order of magnitude of these more recent increases in Louisiana (several tens of thousands of pairs) is similar to the timing and magnitude of decreases in Florida and the Carolinas during the late 1980s.

Newly Colonized and Deserted Sites

Observers of huge colonies (several hundred thousand pairs) in the Everglades during the 1930s suggested that these large colonies were unusual and may have been caused by drought conditions in most of peninsular Florida, coupled with excellent foraging conditions in the Everglades (R. P. Allen in Ogden 1978; Robertson & Frederick 1994). Similarly, conditions at large coastal colonies in South and North Carolina during the 1970s were apparently quite productive (Frederick 1987). The large colonies in southcentral Louisiana during the early 1990s have been centered around a rich food source, the rapidly growing commercial crayfish aquaculture industry (Fleury 1994).

On the other hand, we were unable to isolate characteristics of the central Florida Gulf coast area that would make it particularly attractive to ibises, although both Alafia Banks and Cedar Keys are offshore islands with few ground predators and productive freshwater wetlands nearby. Although they appear to be a prerequisite for ibis nesting (Bildstein et al. 1990; Kushland & Bildstein 1992), such conditions would not have been unique to these locations at the time of colonizations.

Abandoned areas appear to have undergone some type of habitat degradation. Habitat degradation in the Everglades between 1960 and 1993 has made it difficult or impossible for an entire suite of ciconiform birds to nest on a regular basis (Bancroft et al. 1994; Frederick & Spalding 1994; Ogden 1994). Rapid declines in numbers of ibises breeding at Drum Island have been linked to concurrent increases in Fish Crow (*Corvus ossifragus*) populations and subsequent predation on ibis eggs (Post 1990), as well as to the effects of a rediversion of outflow of the Santee River from the drainage basin in which the colony is located (P. Wilkinson, personal communication). At Pumpkinseed Island, hurricane-induced salinization of essential freshwater foraging habitat is the likely source of dramatic declines (Bildstein 1993). Salinization of the Caroni Swamp in Trinidad has been linked with the cessation of breeding by the closely related Scarlet Ibis (*Eudocimus ruber*; Bildstein 1990). We could find no obvious reason why the Cedar Keys colonies had been reduced from several tens of thousands of pairs in the 1970s to one or a few thousand during the 1980s. Declines in nesting in Florida during the 1980s were widespread and may be linked to a combination of reduced habitat suitability in the Everglades (Ogden 1994) and to pervasive changes in land use statewide (Fernald & Purdum 1992).

Movements of Marked Individuals

We identified 150 recoveries or resightings of White Ibises banded as young (n = 18,631) or as adults (n = 82). Recovery locations (Fig. 2) suggest regular movements among breeding colonies, south Florida, and Cuba. Both adults and juveniles moved large distances (up to 1300 km) within annual periods (Fig. 3). First-year birds showed a marked tendency toward inland and northward dispersal, but third-year and older birds did not (Fig. 4). Overall, the proportion of recoveries to the north of the banding location declined with age at recovery (Fig. 5). Ibises were most often recovered within 200 km of the colony at which they were banded as nestlings and so may be either weakly philopatric or tend to die close to the colony during the first year of life (Fig. 3). The large proportion of recoveries from

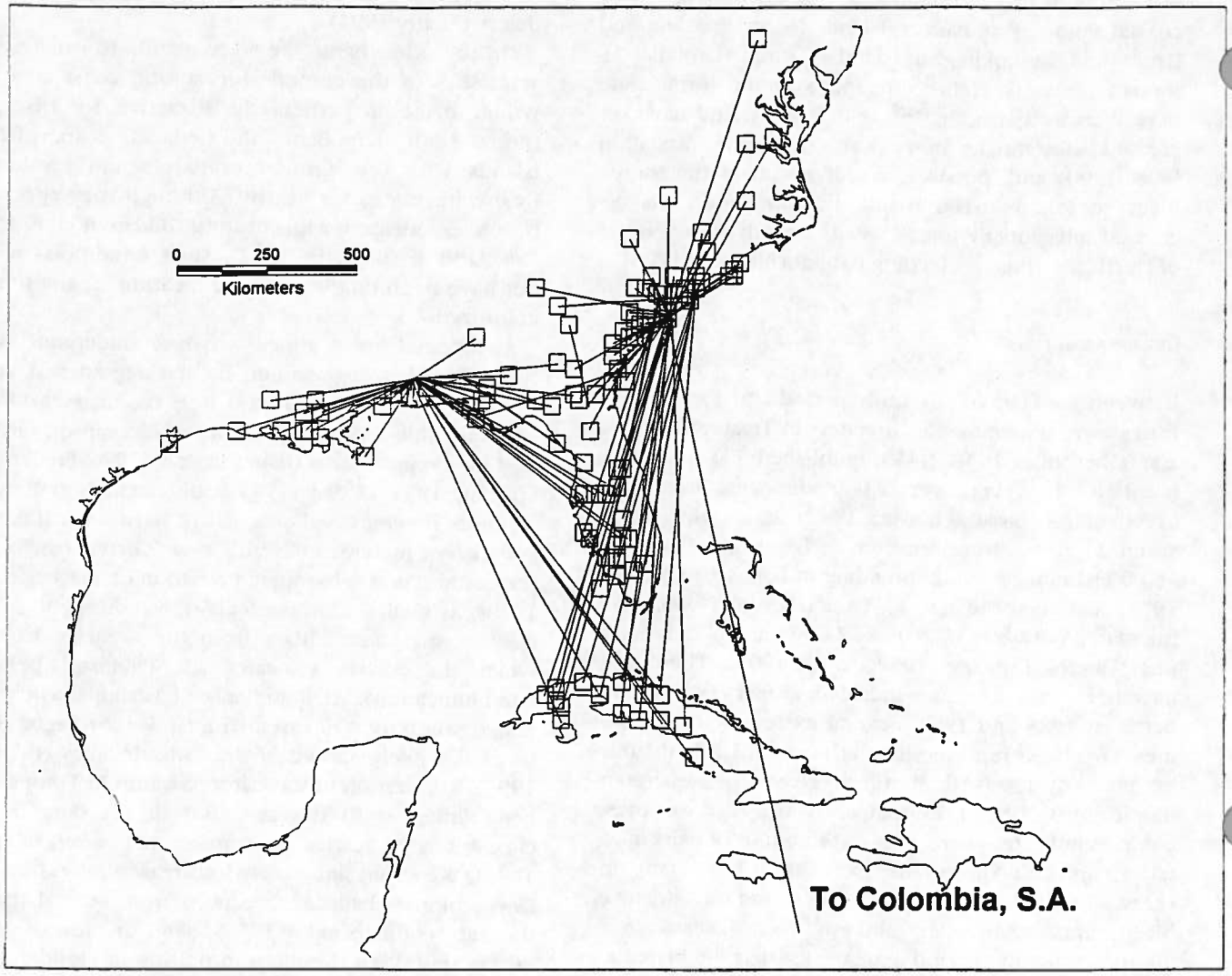

Figure 2. Locations of recoveries (squares) of all ibises banded in the United States between 1926 and 1989. The one recovery off the map is in northern Colombia.

Cuba (see increase for adults at approximately 1200 km in Fig. 3) may be overrepresented because a high proportion of Cuban returns were killed by hunters.

Discussion

The overall picture that emerges from our analyses is one of large-scale population shifts of White Ibises breeding within the United States. The database we present suggests the numbers of breeding birds in south Florida declined by at least 90% between the mid-1940s and the early 1970s; that there was a marked increase in breeding in the central Gulf coast of Florida between the late 1950s and the mid 1970s; and that populations in Florida as a whole have declined by over 50% between the late 1970s and late 1980s. Populations in North and South Carolina increased rapidly in the 1970s and decreased during the 1980s. Breeding numbers in Louisiana and Texas increased markedly beginning in the 1940s, with a second identifiable increase during the late 1980s.

Although the growth of breeding numbers in areas at the edges of the range (North Carolina, Texas) is slow enough to result from local reproductive recruitment, most large increases and decreases in other areas appear to be due to nomadic relocations of large numbers of breeders. In several specific cases the disappearance of colonies or large numbers of birds in one area was closely matched by increases in others (Ogden 1978). In other instances colonies of many thousands of pairs have appeared de novo. The first recorded nesting in Alabama was of 7000 pairs (Keeler 1956), and the large nesting of 15,000 pairs in Okefenokee Swamp in 1976 was unprecedented. The first nesting record in North Carolina was 1500 pairs (Stephens 1950).

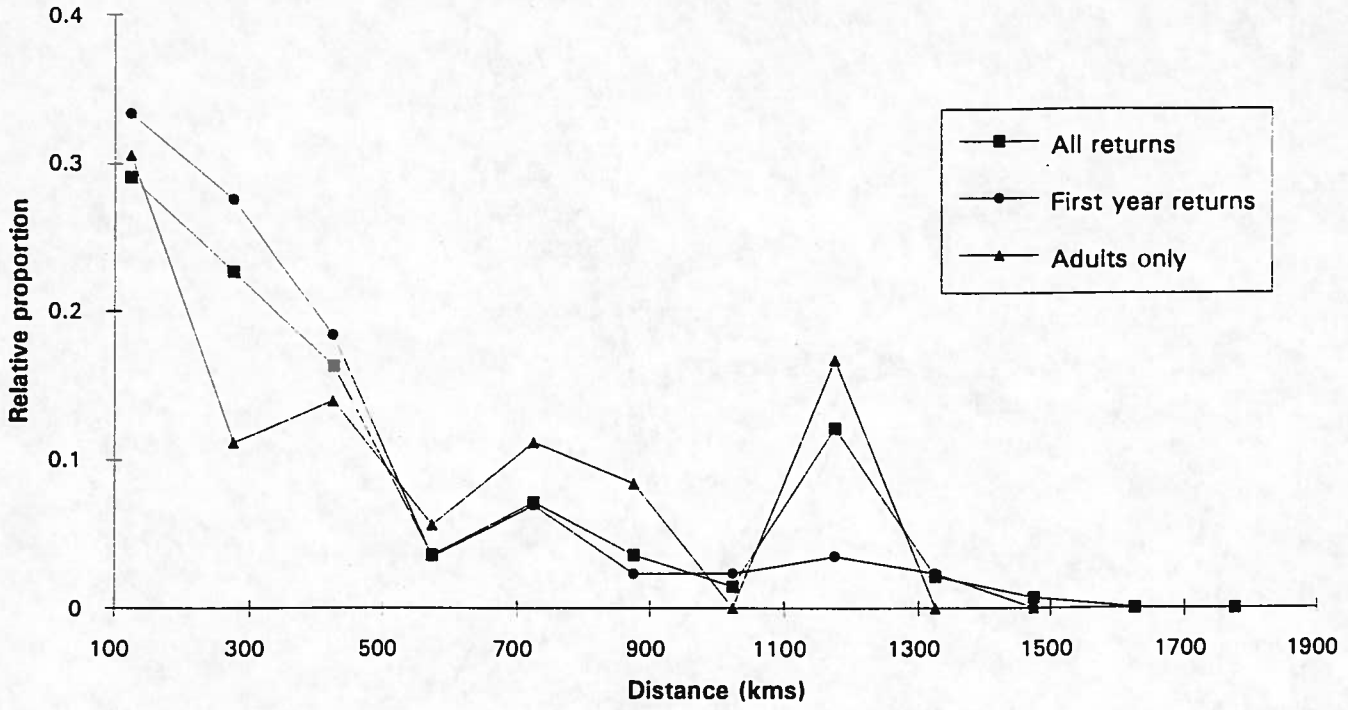

Figure 3. Frequency distribution of distances moved by banded birds. Although many returns are close to the natal colony, ibises are capable of moving several hundreds of kilometers between years during their first year and later as adults.

Other, less dramatic examples are also unlikely to have resulted from local recruitment. The increase at the Cedar Keys from 1800 to between 40,000 and 100,000 pairs took place in less than 22 years. For this to have been due to recruitment from the founding population, annual growth would have had to have been between 14 and 18%. Such population growth is virtually impossible without emigration, given the reproductive and population characteristics of the species (Bildstein 1993; Frederick 1994). The likelihood of mass movements is further supported by the records of marked adult and juvenile birds, which typically move over large areas within and among years.

Although it is difficult to match population changes among regions, several instances of reciprocal increase and decrease are suggestive. During the late 1980s, the numbers of birds breeding on the South Carolina coast and in Florida decreased at the same time that numbers of breeders increased dramatically in Louisiana. But, the absolute magnitude of increase in Louisiana is unknown because the largest colonies were not accurately estimated. The increases in both the Carolina coast and the Florida Gulf Coast occurred somewhat contemporaneously and could have resulted from Everglades birds moving northward. Unfortunately, the lack of surveys in the Everglades during the 1950s and 1960s makes the match of reciprocal movements untestable. Although these examples provide support for the notion that birds departing one location approximate those appearing in another, the data are simply too imprecise to be more than suggestive.

White Ibises are known to abandon locations en masse when breeding and feeding opportunities become degraded. Alteration of flooding regimes (Everglades), increases in nest predation, diversion of rivers (Charleston), or increased salinity in foraging habitat (South Carolina, Trinidad, West Indies) are all examples of degradation and can be natural or anthropogenic in origin.

Extensive breeding in new locations also seems to be stimulated by especially rich food sources; this feature is probably a prerequisite. Kushlan (1976a) provides several examples of ibises breeding outside the normal season in south Florida in response to unseasonal pulses of food. A case can also be made that food sources were particularly abundant in the Everglades during the 1930s, in the coastal South Carolina colonies during the 1970s and early 1980s, and recently in southcentral Louisiana (Frederick 1987; Bildstein 1993; Robertson & Frederick 1994; Fleury & Sherry (in press).

These data suggest that White Ibises are nomadic breeders, adapted to take advantage of food resources that are highly unpredictable at large spatial scales and at annual time scales. The ability to locate these resources is critical at two different spatial scales, when ibises are looking for wetland landscapes in which to breed and when they are looking locally for food from a given colony. The propensity of this species to disperse

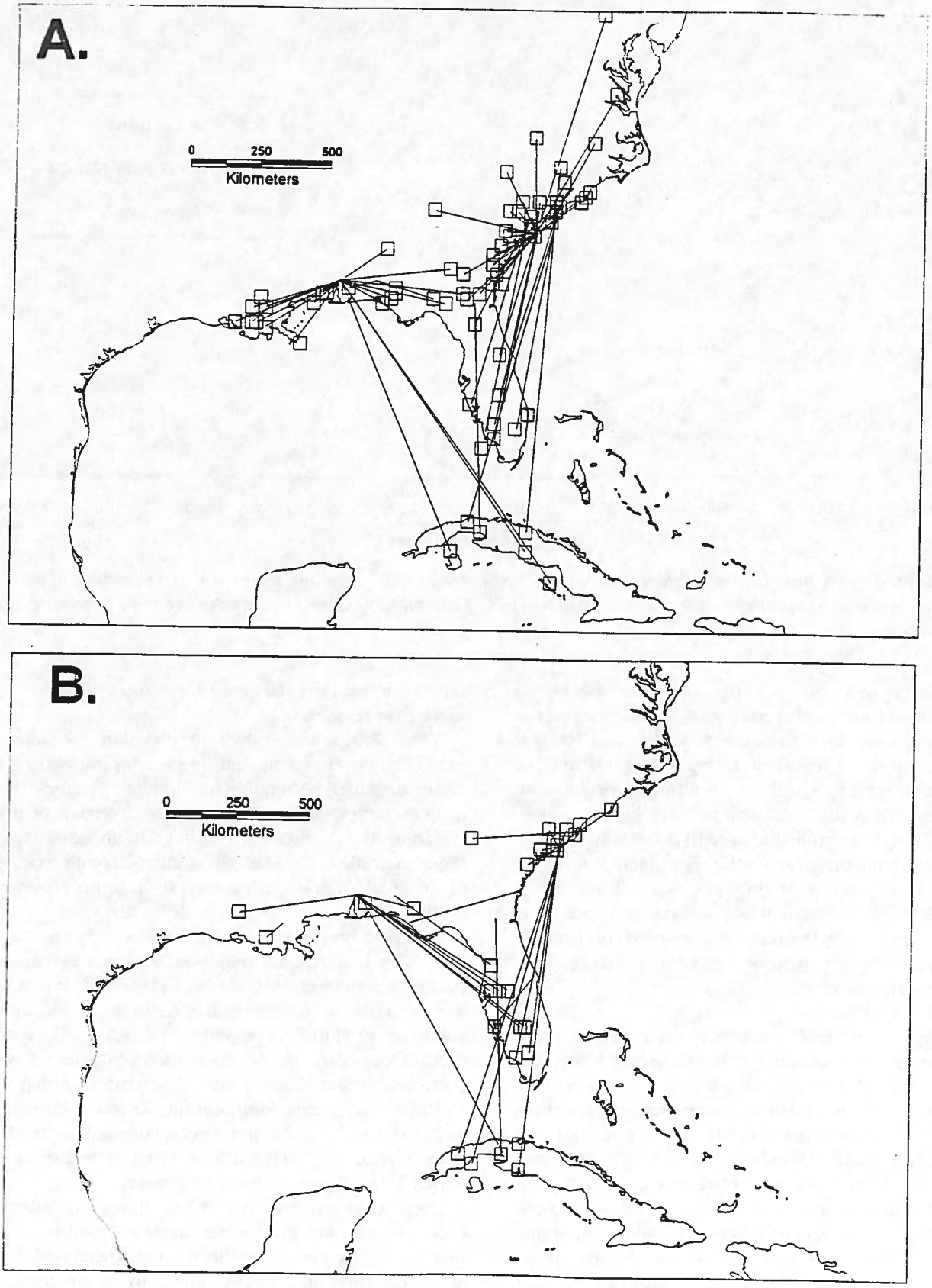

Figure 4. Locations of recoveries of birds in the first year of life (a) and in third and later years (b).

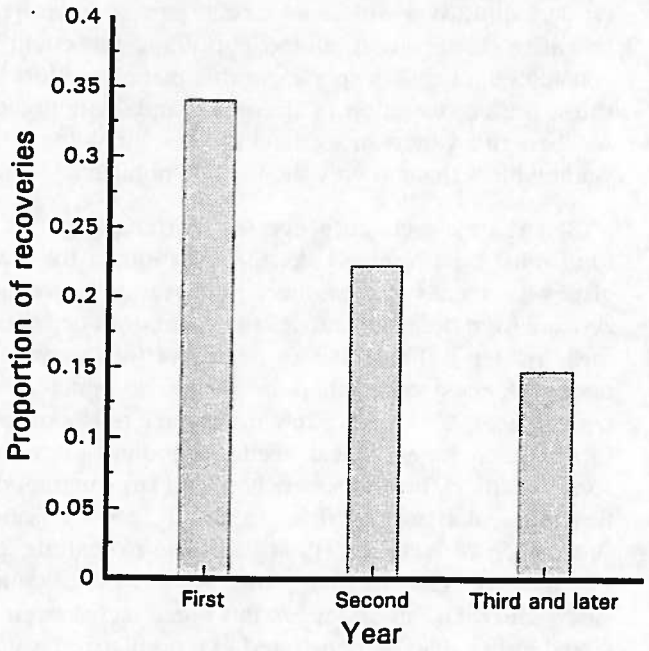

Figure 5. Proportion of recoveries to north of banding location, shown by age at recovery.

widely as juveniles, to travel long distances within and among years, and to search socially for food and feed in large flocks seems likely to facilitate such food finding at these large spatial scales (Kushlan & Bildstein 1992; Bildstein 1993; Fleury & Sherry (in press). The ability of ibises to breed in response to rapidly changing seasonal and geographic conditions may well be facilitated by highly synchronized courtship displays (Rudegeair 1975; Bildstein 1993). The existence of these adaptations to nomadic breeding and the documented movements in response to natural disturbance suggest that the occurrence of nomadism is not an artifact of twentieth-century human activity but an evolved feature of the life history of White Ibises. This is not surprising in light of other species of ibises that show nomadic habits (Spaans 1975; Bildstein 1993; Hancock et al. 1992).

Conservation Implications of a Nomadic Habit

White Ibises are clearly declining as breeders in Florida, and a more widespread decline may also be in progress throughout the U.S. range. Currently, White Ibises appear to be far better surveyed than at any point in the past, yet the maximum counts are now less than half the estimates from either the 1970s or the 1930s (Fig. 1). At the same time the average size of colonies may also be shrinking.

The effects of reduced population size are difficult to predict for nomadic species normally characterized by large population size. Bucher (1992) suggested that in Passenger Pigeons (*Ectopistes Migratorius*) the social and behavioral adaptations to nomadism functioned efficiently only in the context of large population size. Although populations of Passenger Pigeons were primarily decimated by habitat destruction, Bucher suggests that reduced populations ceased to breed entirely because smaller groups of birds had difficulty locating distantly spaced habitat patches and because they were inappropriately stimulated by social context.

It is unclear whether White Ibis populations will behave the same way as those Passenger Pigeons at low population size. It is not obvious, for instance, that ibis breeding aggregation size directly influences nesting effort or success of reproduction. It is likely that reduced colony size will affect local ecosystems. Large colonies of White Ibises are known to affect local prey populations (Kushlan 1976*b*; Bildstein et al. 1982), nutrient cycling (Stinner 1983; Bildstein et al. 1991), and vegetative and faunal composition in the vicinity of colonies (Onuf et al. 1977; Powell et al. 1991; Frederick & Powell 1994). Smaller ibis colonies considerably dilute or remove the perturbatory function of large nesting events.

If large populations of ibises depend upon food patches that are large and unpredictable in space and time, then the conservation of ibises will depend on preserving the conditions that create those flushes of food and, particularly, their time and space dynamics. Although information exists on the patchiness of wetland prey densities at fine spatial (tens of kilometers) and temporal (monthly or annual) scales (Loftus et al. 1986, 1992; Chick 1992), there is little information on the patchiness of prey at a spatial scale of hundreds of kilometers or a time scale of decades. It does seem clear that nomadism is an integral part of the ibis's breeding ecology and that the population is declining in large parts of the range if not overall. It is therefore of considerable concern that wetland habitat destruction and degradation is proceeding at a rapid rate within the southeastern U.S. (Tiner 1984).

We reiterate Bucher's (1992) assertions that nomadic species have population and social behavior characteristics that are quite different from most endangered, threatened, and insular species, and that they will require different approaches to conservation. We emphasize that nomadism is quite distinct from migratory behavior or from a population that is gradually shifting range. Nomadic species are unlikely to be insular and easily protected, they are likely to be habitat generalists rather than specialists, their nomadic habit is likely to be inextricably linked with other aspects of reproduction and survival, and their populations may show abrupt declines in the face of reduction or degradation of habitat. Most important, the ability of nomadic species to locate ephemeral breeding conditions may depend in part on large population size. Many nomadic species like the White Ibis may be dependent upon ephemeral abundances of food, which are often the product of distur-

bances of various types that are highly unpredictable in space and time. These flushes of food may prove difficult to reproduce in a managed situation.

Monitoring and management of nomadic species is unlikely to be well served in the U.S. by current state or federal systems, in the former because the range of the species is too large and in both because populations of any species must be reduced to the point of endangerment before remedial action can be started. Because the fate of colonial, nomadic animals may well be driven by the social phenomena of large populations and the benefits of movement itself, it will be necessary to focus conservation strategies on the preservation of these characteristics in order to preserve large populations.

Management Recommendations

Because the effect of large White Ibis populations on ecosystems and prey populations differs fundamentally from that of small populations, and because there may be feedback effects of population size, we suggest that priority be given to the conservation of large White Ibis populations—at minimum, present levels. We emphasize that this is a fundamentally different goal than ensuring that sufficient numbers of animals exist to maintain genetic diversity. Specifically, we suggest the following steps be taken to maintain large populations of White Ibises and to assure the survival of this species:

(1) Extensive and repeated monitoring of the North American breeding population. Monitoring is central to assessing the effect of any conservation effort and in this case may also give advance warning of possible abrupt population declines. The evidence suggested in this paper as well as the work of Spaans (1990) in South America indicate that such an effort can be undertaken only with synchronous surveys throughout the breeding range of the species. In addition, the large inter-annual fluctuations in breeding numbers suggest that surveys will be meaningful only if conducted for several consecutive years. Comprehensive surveys are now conducted in a nonsynchronous fashion in North Carolina, South Carolina, Florida, and Texas, and surveys in Louisiana have not been comprehensive. The formation of a regional council is recommended to accomplish this objective and could serve to oversee an integrated conservation plan.

(2) Assessment and preservation of wetlands. White Ibis populations apparently depend on pulses of food that are sporadically created by a population of geographically dispersed wetlands. Regions that have been or are core breeding areas are the Everglades, the Florida Gulf coast wetlands, the coastal and interior wetlands of Louisiana, the Okefenokee Swamp, and the freshwater riverine marshes of coastal North and South Carolina. To plan for wetlands conservation, documentation and use classification of the existing wetlands of the southeastern U.S. and Cuba will be needed as part of an effort to prioritize conservation efforts. The White Ibis could be considered a flagship species in this planning effort because the conservation of these wetlands undoubtedly will benefit a variety of wetland species, including other wading birds that are only slightly less nomadic.

(3) Dynamic wetland processes that create pulses of food must be preserved. As the situation in the Everglades has clearly shown, mere preservation of wetland acreage from drainage and development does not necessarily preserve the processes necessary for the maintenance of ecosystem functions (Davis & Ogden,1994; Ogden 1994). Processes likely to produce pulses of food for ibises include cyclical events (flooding, tides, seasonal weather), habitat succession, and large natural disturbances such as fires, drought, floods, and hurricanes (Robertson & Frederick 1994). But the magnitude and timing of the resulting food pulses are so far poorly measured, and their importance to ibis breeding has been inferred rather than demonstrated in a predictive fashion. An understanding of these two relationships would be of great benefit to the conservation of this species and should be research priorities.

These pulses of prey seem to be mimicked by crayfish farming in Louisiana. Crayfish farmers view ibises as agricultural pests, however, and are trying various methods to exclude the birds from their ponds. If an exclusion method is found, the loss of this food source will likely result in a sharp drop in the ibis population and another regional population shift. If exclusionary methods fail, the U.S. Department of Agriculture will come under increasing pressure to issue permits for killing large numbers of White Ibis under its Animal Damage Control Program. This is not desirable in light of the declining population overall.

(4) A large-scale mosaic of freshwater and coastal marshes must be maintained. Bildstein (1993) and Bildstein et al. (1990) have shown that access to fresh water is critical to ibis breeding because young ibises are intolerant of high-salt diets. The preservation of fresh and estuarine wetlands to achieve the necessary feeding habitat will require proactive strategies, because rising sea level and subsidence are expected to salinize or drown large portions of coastal wetlands within the next century, particularly in coastal South and North Carolina, Louisiana, and the Florida Everglades (Wanless et al. 1994).

(5) Coordination of conservation efforts with Cuba. Banding returns indicate that Cuba is an important wintering ground for White Ibises hatched in the U.S. The wetlands of this Caribbean island are likely to play an integral part in the ecology of the North American population of White Ibises. The extent of this linkage needs to

be documented, and Cubans must be included in the conservation process.

(6) Research on demographic parameters. Although there is adequate information on the movements, longevity, and reproductive success of the White Ibis, there is no information available on survival rates for this species. Until that can be supplied it is impossible to predict the fate of this species with any accuracy. We recommend a study specifically designed to measure the survival of juvenile and adult White Ibises.

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