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Source: *Colonial Waterbirds*, Vol. 20, No. 2 (1997), pp. 316-323
Published by: Waterbird Society
Stable URL: http://www.jstor.org/stable/1521699
Accessed: 06/10/2009 15:45

# Philopatry and Nomadism: Contrasting Long-term Movement Behavior and Population Dynamics of White Ibises and Wood Storks

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**Abstract.**—We compare long-term movement behavior, breeding site philopatry, population dynamics and prey choice of White Ibises (*Eudocimus albus*) and Wood Storks (*Mycteria americana*) in order to illustrate (1) differences in strategies for exploiting spatially and temporally unpredictable food resources in wetlands of the southeastern U.S., and (2) the temporal and geographic scale at which conservation strategies for these species must be targeted. Since the 1930s, the U.S. White Ibis population has made a series of long-range (>400 km) shifts in the center of its breeding range. Very large colonies seem to exist for less than 15 years, and to be supported by at least 800 km$^2$ of wetlands. Movements may be prompted either by degrading breeding conditions caused by both man-made and natural disturbances, or by attraction to abnormally high concentrations of prey. Wood Storks have also undergone large scale shifts in the center of breeding, but are much more philopatric to breeding sites (often >25 yr). They may be locally buffered from the unpredictability of food resources by the ability to forage at large distances from their colonies, and by being associated with more permanent wetlands. Preservation of specific colony sites and associated wetlands may well aid in conserving Wood Stork populations. In contrast, nomadic ibises require a different conservation approach, one that protects a geographically widespread network of wetland ecosystems.

**Key words.**—Conservation, Everglades, *Eudocimus albus*, movement behavior, *Mycteria americana*, nomadism, philopatry, population dynamics, White Ibis, Wood Stork.

Colonial Waterbirds 20(2): 316-323, 1997

Studies of the movements and metapopulation dynamics of animal populations are key tools in the conservation of ecosystems, communities, and species (Soule and Kohm 1989). Such information can be especially important for developing conservation strategies for organisms that are long-lived, have weak philopatry, and make long-distance movements, because these organisms may need particularly large, often disjunct ranges during their long lifetimes. Many colonial-nesting waterbirds exhibit several of these characteristics, yet long-term studies are only just beginning to reveal the true spatial scale of movements over the lifetime of individual birds, the time scales of population dynamics, and of interactions with habitat and prey animal populations.

In this paper, we contrast the long-term movement behavior and breeding strategies of 2 ciconiiform species, White Ibises (*Eudocimus albus*) and Wood Storks (*Mycteria americana*), both of which live and breed almost exclusively in wetlands. These habitats are typically highly dynamic in terms of hydropattern, nutrient cycling, aquatic animal communities, vegetative communities, and disturbance ecology (Loftus *et al.* 1986, Mitsch and Gosselink 1993, DeAngelis and White 1994). The seasonal and annual variability in these environments presents aquatic predators like wading birds with food resources that are highly unpredictable in space and time. Uncertainty in prey availability may occur both at the scale of days and weeks for particular foraging sites within any wetland ecosystem, and at annual time scales, for breeding birds choosing among a mosaic of wetlands distributed over hundreds of km$^2$. We have chosen to examine these 2 species in detail because they have been studied for long enough periods and over large enough areas that their long-term movements and population fluctuations can be summarized over periods of decades throughout their North American range (Kahl 1964, Kushlan 1974, Rudegair 1975, Ogden 1978, Kushlan 1986, Frederick *et al.* 1996). We feel that the comparison is of interest because these species are faced with similar environmental unpredictability, over similar geographic ranges. The differences and similarities in adaptation may shed light on the degree to which their life history strategies are constrained by the unpredictable wetland environment (Holling 1992). A synthesis of the geographic and temporal scale of movements and population dynamics of these species also may allow insight into the necessary scale of conservation strategies for populations and perhaps, the wetland habitats upon which the birds depend.

## RESULTS

### Population Sizes and Trends

White Ibis population sizes in the U.S. were summarized by Frederick *et al.* (1996), based on a survey of all published and many unpublished records of nesting in the U.S.A. this century. In addition to published accounts, this survey benefited from several long runs of information made possible by the U.S. Fish and Wildlife Service, statewide surveys, the National Park Service, and the National Audubon Society. Figure 1 shows a summary of the regional population counts, for years between 1930 and 1992 in which population estimates were made possible either through regional systematic counts, or through unusual circumstances concentrating the population in a single area (e.g., Everglades during the early 1930s). Total population sizes in the southeastern U.S. fluctuated between 51,000 and 169,000 breeding pairs during this period, with evidence of a decline of up to 50% during the period 1976 and 1992. In Florida, the species declined by 50% between the survey periods 1978-1980, and 1989-1991 (Nesbitt *et al.* 1982, Runde 1991), and by over 90% since 1930 in the Everglades region of southern Florida (Ogden 1994).

Population histories of the Wood Stork have been summarized by Ogden (1994), relying on a similar survey of historical and recent information. The population during the early part of this century probably numbered in the range of 15,000-25,000 breeding pairs. The population has exhibited a marked decline (Table 1), especially between 1960 and the mid-1970s, when the population appears to have been reduced by approximately half.

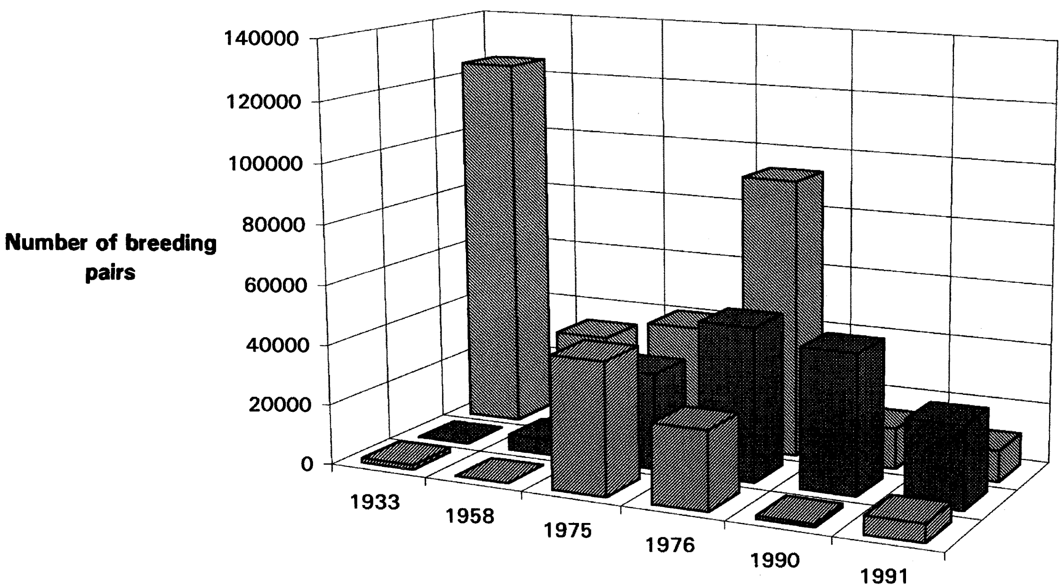


**Figure 1. Numbers of breeding pairs of White Ibises in three sub-areas of the southeastern United States during six years selected as times when comprehensive or indicative surveys of the population were undertaken throughout the U.S. breeding range.**

**Table 1. Numbers of pairs of Wood Storks nesting in the southeastern United States during the period 1930-1990. These data are summarized from Ogden and Nesbitt 1979, Ogden *et al.* 1987, and U.S. Fish and Wildlife Service 1996.**

| Region | 1960 | 1976 | 1986 | 1995 |
|---|---|---|---|---|
| South Florida | 8,500 | 3,575 | 640 | 1,096 |
| Central and North Florida | 1,560 | 1,679 | 4,355 | 4,427 |
| Georgia | 0 | 0 | 648 | 1,501 |
| South Carolina | 0 | 0 | 120 | 829 |
| Totals | 10,060 | 5,270 | 5,763 | 7,853 |

### Regional Shifts in Breeding Location

Prior to the 1940s, White Ibises were known to have nested in large numbers only in Florida, and most of the reports within Florida were from the Everglades (see review by Frederick *et al.* 1996). During the 1940s large breeding colonies (7,000-40,000 breeding pairs) were discovered in Alabama (Keeler 1956), and Louisiana (Frederick et al. 1996), and during the 1950s, large colonies (>1,000 pairs) were found in North Carolina, South Carolina, and the Central Gulf coast of Florida. By the 1970s, the majority of nesting was found north of the Everglades, with very large (>10,000 pairs) colonies in Gulf coastal Florida, South Carolina, North Carolina, Louisiana, and Texas. Thus White Ibises had moved their breeding range into the coastal plain regions of at least 5 southeastern states during a period of only 35 years. Between the late 1970s and the early 1990s, ibises declined in Florida by 50%, declined in coastal South Carolina, and increased dramatically in south-central Louisiana. These most recent movements are perhaps the most accurately documented, and provide the best evidence for declines in 1 area being matched by increases in another (see also Ogden 1978).

Although the historic annual breeding range of the U.S. population of Wood Storks includes the southeastern coastal plain from South Carolina west to eastern Alabama (Bent 1926, Palmer 1962), regular nesting occurred only in Florida prior to the mid-1970s, and was concentrated in south Florida. Between 1976 and 1995, Wood Storks expanded their breeding range into Georgia and South Carolina (Table 1), and the proportion breeding north of Lake Okeechobee increased substantially. Colonies in south Florida accounted for 84% of the breeding population in 1960, but only 14% by 1995. Conversely, colonies in Georgia and South Carolina accounted for <1% of the breeding population in 1976, and 30% by 1995.

### Philopatric Tendencies

White Ibises show the ability to move breeding location rapidly, with large colonies disbanding and new ones forming, often in the space of 1 or 2 years (Ogden 1978). This is evidenced both by the often rapid regional shifts noted above, and by the movements of individual colonies. For instance, the first breeding record for the species in Alabama was a colony of 7,000 pairs (Keeler 1956), and the colony at Cedar Keys, Florida went from 20,000 pairs to over 100,000 pairs in the space of 2 years during the mid-1970s (Frederick *et al.* 1996). The very large colonies (>10,000 pairs) at Pumpkinseed Island and Drum Island, South Carolina, declined to near extinction in the space of 1 and 4 years, respectively (Post 1990, Bildstein 1993). Thus, these dramatic fluctuations were not demographically controlled, and can only be explained by movement behavior. This evidence also defines the philopatric tendencies of ibises as weak, and the species is probably best classified as a nomad (Kushlan 1977, Kushlan and Bildstein 1992, Frederick *et al.* 1996).

Wood Storks are, by contrast, much slower to abandon colonies and to establish new ones, and the process seems to proceed in a gradual, rather than threshold fashion. For example, the increase in numbers of pairs nesting in Georgia between 1976 and 1995 was at an annual increase rate of only 12%. During this same 20-yr period, the average stork colony size in Georgia increased from 54 pairs (1976-1980) to 115 pairs (1991-1995), and the maximum colony size increased from 125 pairs (1981) to 511 pairs (1993) (Harris 1994, U.S. Fish and Wildlife Service 1996). By comparison with ibises, these changes are quite gradual, and can be explained either by reproductive recruitment, or by relatively small proportions of the population moving between colony sites.

## Colony Longevity and Relationships with Foraging Habitat

Longevity of ibis colonies was derived from the ibis nesting database described in Frederick *et al.* (1996). It should be emphasized that Fig. 2 shows considerable uncertainty in the measurement of size of wetland area associated with colonies of various longevities. The straight-line length of the largest dimension of various wetlands used by the birds were measured from U.S. Geological Survey maps (usually 1:100,000). Locations of wetlands used for foraging were taken from published descriptions (Kushlan 1974; Frederick 1985, 1987; Frederick and Collopy 1988), unpublished descriptions (National Audubon Society files available at Everglades National Park, Homestead Fl.; Frederick, unpubl. data), or personal communications with local researchers (Cedar Keys, Florida, southwest Louisiana). Descriptions were usually general, and the wetland ecosystem or watershed was often the only information available. To standardize the metric used, we measured the largest dimension of the entire wetland ecosystem referred to on 1:100,000 U.S. Geological Survey maps.

Large colonies (>1,000 pairs) of White Ibises existed (maintained at least 1,000

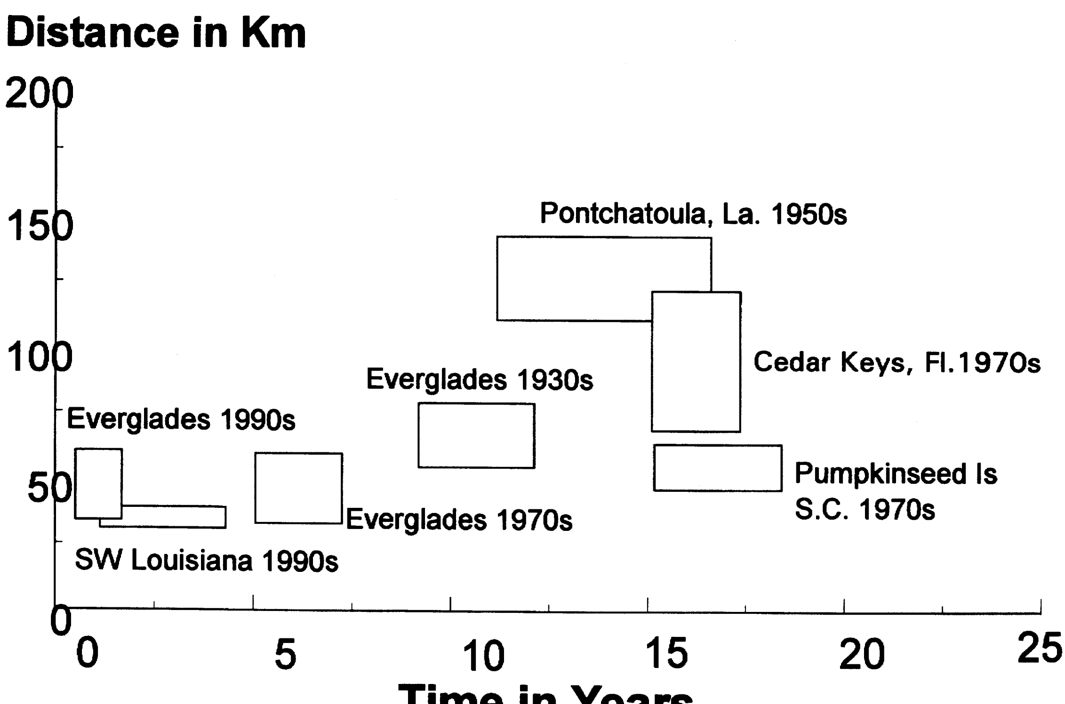


**Figure 2. Plot of longevity of White Ibis colony (number of years of occupancy during which the population remained at or above 1,000 pairs) vs. straight-line length of the largest dimension of wetland used by the birds. The center of each rectangle is the intersection of longevity and size of wetland. The bounds of the rectangle represent the uncertainty in measurements on both axes.**

pairs) for between 1 and 17 years, and there may be a relationship between size of wetland area associated with the colony and colony longevity (Fig. 2). Colonies of greatest longevity (up to 15 yr) were associated with relatively large wetlands (to 150 km greatest dimension); all colonies in existence for less than 10 yr were associated with wetlands of less than 10 km largest dimension. If size of wetland is conservatively estimated, wetlands of at least 800 km$^2$ seem to be associated with the more long-lived of White Ibis colonies.

Abandonment of colonies seems to be associated with degraded breeding conditions, such as increased predation (Post 1990), salinization of foraging habitat (Walters *et al.* 1992, Bildstein 1993,), drainage and changes in water management (Frederick and Spalding 1994, Ogden 1994), and destruction of nesting vegetation from freezing temperatures (Frederick *et al.* 1996). Large, new colonies are generally associated with abnormal abundances of food and exceptional breeding conditions (Kushlan 1976, Frederick 1987, Frederick *et al.* 1996).

Wood Stork colonies tend to be long-lived, and tend to be used by varying numbers of pairs each year, regardless of local breeding conditions. Of 17 Florida colony sites occupied in 1959 and 1960, 6 (35%) were still being used in 1 or more years during the period 1991-1995. During the 11 yr period 1976-1986, 9 large colonies in Florida were used by storks an average of 7.8 years. Of the original nine, 6 (67%) were still active in 1 or more years during the period 1991-1995. Some colonies are extremely persistent; the Cuthbert Lake colony in Everglades National Park was used for nesting by storks in almost all years between 1940 and 1992, although the number of pairs varied between 100 and 1,000 pairs. Similarly, the Big Duke's Pond colony in east-central Georgia has been occupied annually or has shifted only locally between 1980 and 1996, varying between 60 and 330 pairs.

## Prey Characteristics

Ibises are predominantly tactile foragers, and the bulk of the diet is invertebrates (Kushlan and Bildstein 1992). Much of the prey is crayfish, but shrimps, crabs and insects also are commonly taken. Fishes are generally not captured unless they are small, and concentrated in shallow water (Kushlan 1974, Kushlan and Kushlan 1975).

Wood Storks are also tactile foragers, but select for large-bodied fish (Ogden et al. 1976, Depkin *et al.* 1992, see also Table 2). Typically, much of the diet of Wood Storks is made up of centrarchid fishes, which tend to be large omnivores or carnivores.

## DISCUSSION

The characteristics of ibises and storks presented here indicate that the 2 species are almost at opposite ends of continua of several life history characteristics. White Ibises have weak breeding site philopatry, and tend to abandon colonies, often permanently, whenever breeding conditions are inappropriate. They also show the ability to begin breeding in large numbers in completely novel locations. Thus, their colony turnover rates are very high, and the predictability of breeding location is low, even on an ecosystem-wide scale. Wood Storks, by contrast, show a tendency to remain at the same sites despite poor breeding success, and often attempt breeding there even during poor breeding conditions. Change in colony location is gradual, and may take decades, as in

**Table 2. Sizes (cm total length) of Wood Stork prey items.**

| Location | Mean | Range | Source |
|---|---|---|---|
| Georgia | 9.9 | 2.5-25 | Depkin *et al.* 1992 |
| Everglades | 4.1/5.4 | 1.5-22 | Ogden *et al.* 1976 |
| Pelican I. Florida | 6.1 | 2.6-30 | Ogden unpubl. data |
| El Clair, Florida | 6.24 | 2.5-12.2 | Ogden unpubl. data |
| Lane River Florida | 9.34 | 2.1-19 | Ogden unpubl. data |

the case of the movement of storks from south Florida to more northerly locations.

These differences are probably related to other differences in adaptation to unpredictable food sources. Wood Storks tend to eat large fishes, most of which take 1 or more years to grow, and which are likely to occur in relatively permanent wetlands, or at least those which have semi-permanent sources of water. We hypothesize that the Wood Stork's breeding site fidelity is possible in part because of this tendency to associate with wetlands which include areas of long hydroperiod, and which have high inter-annual predictability. Wood Stork philopatry is also possible because of the long-distance foraging flights (up to 130 km one way, with distances of 50 km common) that this species is capable of making (Browder 1978, Clark 1978, Kushlan 1986, Bryan and Coulter 1987, Ogden, unpubl. data). The large range allows this species to exploit even distant wetlands from their breeding colonies.

White Ibises tend to forage in very shallow water (5-25 cm, Kushlan and Bildstein 1992) and to specialize on invertebrate prey. Therefore, ibises are frequently associated with short-hydroperiod, shallowly inundated wetlands, many of which may not have a permanent source of water, or which may be distant from a permanent source. The foraging habitat is therefore quite unpredictable on an annual basis, especially for freshwater wetlands. Further, ibises are singularly dependent upon freshwater habitats for foraging because of the inability of young ibises to excrete the salt from estuarine and marine invertebrate prey (Bildstein *et al.* 1990, Bildstein 1993). Ibises do not show the same long-distance foraging flight abilities as Wood Storks, and most of their flights are limited to under 40 km (Bancroft *et al.* 1994). These characteristics make nomadism a viable, or perhaps necessary strategy for ibis breeding.

The most striking difference between the two species is in the longevity of colonies. Even the most durable of ibis colonies does not last more than 17 years, while many stork colonies are occupied for over 25 years. Similarly, ibises seem to be much more reactive to local breeding conditions than are storks, with essentially immediate responses to poor or excellent breeding conditions.

These features have profound implications for the design of conservation strategies for the 2 species. It would be inappropriate to spend large amounts of money to purchase specific ibis colony locations, if even the best sites have a useful life of less than 20 yr. What is needed instead, is a reserve network across the southeastern U.S. that targets wetlands that are likely to include areas of short hydroperiod.

For Wood Storks, however, the relative longevity of colony sites makes protection of colony locations a partial and feasible conservation strategy. However, it is important to note that the long-distance foraging abilities of Wood Storks only serves to buffer them against environmental variability if the foraging range contains a variety of types of wetlands, including those of long and short hydroperiod, and those that are likely to come into production in a sequential fashion. Thus the protection of colony sites must also include the preservation and or management of a mosaic of surrounding wetland types.

For both species, the temporal scale at which the regional population and its movements is viewed is also critical for conservation efforts. Prior to 1940, the preservation of the Everglades colonies was deemed sufficient for the conservation of both species. Yet the picture viewed from the vantage of the 1990s suggests that sites throughout the southeast region are very important for the existence of both species. Certainly human-induced degradation of the Everglades and human enhancement of foraging and nesting habitat through impoundments, aquaculture and construction of feeding ponds (Coulter 1990, Ogden 1991) has contributed to the range expansions and regional movements of both species. But it is important to note that natural catastrophes frequently occur in wetlands (hurricanes, fires, floods, river course changes), and that some of the ibis movements can be traced directly to ecological changes that were natural in origin. Even in a landscape devoid of humans, it seems likely that both species would need, over the course of decades or at least centuries, a variety of wetland ecosystems distributed over a landscape that is hundreds of kilometers in any dimension.

ACKNOWLEDGMENT

We thank A. L. Bryan for comments on earlier drafts of this manuscript. This is Journal Series R-05802 of the Florida Agricultural Experiment Station.

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