

SURVIVAL, MOVEMENT PATTERNS, AND HABITAT USE OF JUVENILE  
WOOD STORKS, *Mycteria americana*

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL  
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT  
OF THE REQUIREMENTS FOR THE DEGREE OF  
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2004

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## ACKNOWLEDGMENTS

I received tremendous support and encouragement from many friends and colleagues along the way, and sincerely appreciate their tireless efforts in helping this project run smoothly. My advisor, Peter Frederick, was ever supportive and patient in guiding me to trust my instincts, think outside the box, and pursue my goals. His perceptiveness and spirit were always inspiring, and I thank him for his candor and belief in my abilities.

I especially want to thank my mother and the following friends for listening, brainstorming, and sharing their lives with me, as they made this journey worthwhile: Christa Zweig, Erin Slusser, Jamie Duberstein, Janell Brush, Jenifer Hilburn, Matthew Bokach, and Zach Welch.

My previous experiences in the Everglades helping Julie Heath, John David Semones, and Martin Ruane were all extremely influential in making this research a success. In addition, I thank everyone who helped me drag ladders through the swamp, capture unwilling quarry, crouch in muck for hours every day, maintain cranky boats and trucks, keep money in the coffers, and laugh off all the critters that used us for breakfast. These wonderful folks include Jamie Cloninger, Matthew Bokach, Jenifer Hilburn, John David Semones, Eric Weis, Jeff Sloan, Madeline Schickel, Jody Bartz, Dawn Reding, Ben Wollenzien, Laura Hayes, Sam Jones, Caprice McRae, Monica Lingberg, Janell Brush, Sean O'Conner, Ricardo Zambrano, Paul Miller, and Samantha Musgrave. My

pilots (Matt Alexander and Romke Sikkema) always kept flying fun, despite my stomach's insistence that I remain on the ground.

I thank Peter Frederick, Ken Meyer, Marilyn Spalding, and Teresa de la Fuente for their guidance and assistance with field techniques and blood analysis. Marinela Campanu's statistical assistance was immensely appreciated, as was the GIS advice of Matthew Bokach, Christa Zweig, and Tom Hocht. I thank my committee members Peter Frederick, Ken Meyer, and Graeme Cumming for their thoughtful comments and revisions.

I thank Billy Brooks, Ricardo Zambrano, and John Ogden for always being very helpful and supportive of this research. Finally, I want to thank Everglades National Park for allowing me to conduct research on their premises; and the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service, for funding this project.

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Abstract of Thesis Presented to the Graduate School  
of the University of Florida in Partial Fulfillment of the  
Requirements for the Degree of Master of Science

SURVIVAL, MOVEMENT PATTERNS, AND HABITAT USE OF  
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By

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August 2004

Chair: Peter Frederick

Major Department: Wildlife Ecology and Conservation

I used satellite telemetry to analyze the survival, habitat use, and movement patterns of 72 juvenile Wood Storks (*Mycteria americana*) in the southeastern United States in 2002 and 2003. Survival of juvenile storks varied significantly between years during all periods (incubation, nestling, fledging, 6 month, 1 year), indicating large year effects. In the first year, which was largely successful, 88% of the tagged young ( $n = 33$ ) survived to fledge, with a 41% first-year survival rate for fledglings ( $n = 29$ ). In contrast, tagged birds in second year were largely unsuccessful, with only 50% fledging success ( $n = 39$ ), and a 6% first-year survival rate for fledglings ( $n = 17$ ). The survival rate for birds 2 years old was 75%.

Using Cox's proportional hazard model, I found white blood cell count of nestlings to be consistently the best health indicator of postfledging survival. The models showed that gender (when combined with health parameters) also played a significant role in predicting survival, with males being most at risk.

In both years, storks initially dispersed from the Everglades, Florida natal colony into southern Florida wetlands, but quickly spread north across Florida and the coastal plains of Georgia, South Carolina, Alabama, and Mississippi. Three strong movement patterns were identified in both years: rapid dispersal from south/central Florida in June; a return to central and southern Florida in September/October; and establishment of individually consistent summer and winter ranges. Results showed that Wood Storks can exhibit migratory behavior, as the birds demonstrated rapid, predictable, circannual movement patterns, with 88% of tagged birds showing fidelity to specific summer ranges as second-year birds.

Storks used cultivated lands, herbaceous uplands, and wetlands significantly more than other habitat types in relation to availability. The storks' heavy use of landscapes dominated by cultivated lands offers a challenging conservation problem, since foraging within flooded agricultural lands or along drainage ditches may pose serious health risks to the birds through exposure to agricultural contaminants.

Considering the high variability in annual survival, and the high mobility of this species, conservation strategies should focus on long-term monitoring efforts that include a focus at the landscape level. Continuing similar research with juvenile and adult storks will enable biologists and managers to fully understand interannual variability in survival rates, and the factors affecting survival.

## CHAPTER 1 INTRODUCTION

Wood Storks (*Mycteria americana*, Ciconiiformes) are large, highly mobile wading birds found only in the Americas, ranging from the southern United States to Northern Argentina (Hancock et al. 1992). The U. S. population of breeding Wood Storks, located in the southeastern states, is federally endangered and is considered genetically panmictic (Stangel et al. 1990). The wetlands of southern Florida were once the stronghold of this species (Ogden and Nesbitt 1979). However, habitat degradation through increased agricultural and urban land development, and subsequent drainage of freshwater wetlands have probably driven both the storks' population decline and breeding range expansion into northern Florida, Georgia, and South Carolina (Ogden 1994).

Appropriate foraging conditions for Wood Storks are ephemeral and are irregularly distributed across the landscape both spatially and temporally due to dramatic changes in water levels and pulses of prey availability (Hoffman et al. 1994). As appropriate foraging conditions are often short-lived, storks typically require a large home range because they must frequently change foraging locations (Erwin 1983, Fleming et al. 1994, Hoffman et al. 1994).

Identifying landscape-level behaviors and survival information for this mobile species has historically been challenging due to limitations in tracking technology. Survival during nonbreeding periods has been particularly difficult to quantify, but is known to significantly influence population fluctuations in many other wading bird

species (North 1979, Kanyamibwa et al. 1990, Cezilly et al. 1996, Saether et al. 1996, Cezilly 1997). Understanding space-use patterns and population dynamics of storks is necessary for developing successful conservation strategies across broad geographical regions (Ims et al. 1993, Turchin 1998, Wiens 1989, Lima and Zollner 1996).

My study was the first attempt to closely follow a robust sample of individual Wood Storks at the landscape scale, over multiple seasons, by using satellite telemetry. I followed the nesting success of storks for 2 years and obtained postfledging survival estimates for juvenile storks up to 2 years of age. I also examined the impact of nestling health on the postfledging survival of tagged storks. Finally, I described the general movement patterns of tagged birds, and analyzed their habitat use at multiple scales. The information on juvenile survival will serve as the first step toward filling in a demographic picture for this species, which can later be coupled with future research on adult storks. Overall, this knowledge will be instrumental in enhancing the management of the broader southeastern U.S. population and the habitats on which the population depends.

CHAPTER 2  
FACTORS AFFECTING THE SURVIVAL OF JUVENILE WOOD STORKS, *Mycteria  
americana*, FROM THE EVERGLADES, FLORIDA

**Introduction**

In a multi-species analysis of avian demography, Saether and Bakke (2000) found high variability in the ability of adult survival rate to explain population growth rates among long-lived species such as owls, wading birds, and seabirds. For Grey Herons, *Ardea cinerea*, the size of the breeding population was closely regulated by juvenile survival rates (North 1979). Similarly, in some long-lived ungulates (Gaillard et al. 1998) and turtles (Crowder et al. 1994), juvenile survival affected variation in population growth rates more than did adult survival. However, for those species that delay breeding until at least 3 years of age, there are relatively few survival estimates for the period between fledging and breeding. Immatures of these species often spend the prebreeding period away from their natal areas, making reliable survival estimates difficult to obtain.

Little information is available for the survival of birds during nonbreeding periods regardless of age class. Survival during the nonbreeding season is typically difficult to quantify, but is known to have a significant influence on population fluctuations in many species (North 1979, Cezilly et al. 1996, Saether et al. 1996, Cezilly 1997). For example, in the temperate zone, survival rates and population trends have been significantly linked to the severity of winter conditions (Den Held 1981, Kanyamibwa et al. 1990, Hafner et al. 1994, Cezilly et al. 1996), particularly for first-year birds (Lack 1966, Stafford 1971, North 1979, Reynolds 1979, Butler 1994).

Although there is considerable information about the fecundity of adult Wood Storks (Palmer 1962, Rodgers et al. 1997, Coulter et al. 1999), there is very little information of any kind on the survival or even life history of this species during nonbreeding periods. In particular, there is almost nothing known about the time between fledging and first reproduction, a significant period of 2-3 years (Coulter et al. 1999). This time after fledging is when wading birds often suffer the highest mortality rates of their lifetime (Cezilly 1997, Frederick 2001), with mortality rates often estimated to be 2-3 times greater than that of adults (Lack 1949, Kahl 1963). I will refer to young birds less than one year old as juveniles, and prebreeding birds older than one year as immatures.

Although Wood Storks are considered a long-lived species with delayed breeding, very little is actually known about age at first breeding or survival after fledging. Of 1,589 nestlings color-marked in Florida, 4 were subsequently seen in colonies at 3 years of age with immature plumage, while 3 were seen in colonies displaying adult plumage when 4 years of age (Coulter et al. 1999). An additional bird color-marked in Georgia was reported breeding at three years of age (J. Robinette unpubl. data). Most breeding birds are therefore likely to be at least three years old (Coulter et al. 1999). The White Stork (*Ciconia ciconia*) begins breeding on average at 3.4 years (range 2-7 years) (Barbraud et al. 1999).

R.P. Allen (in Palmer 1962) suggested a 60% survival rate in the first 12 months of life for juvenile storks and 80% annually thereafter. However, there were no data given to support these estimates, and they may have been guesses based on information from other large Ciconiiforms. Little useful information on survival was gained from Ogden's

study either, despite the large number of young tagged (Coulter et al. 1999). The greatest recorded longevities are 11.7 y for a wild Wood Stork (Hancock et al. 1992) and 27.5 y for a captive bird (Brouwer et al. 1992).

The health status of birds at the nestling stage is known to have a significant effect on postfledging survival (Sagar and Horning 1990, Gaston 1997, Naef-Daenzer et al. 2001, Keedwell 2003). Hematological analysis is commonly used to characterize the health of wild birds, and blood composition is strongly influenced by the bird's nutritional state (Latshaw 1991, Brown 1996, Svensson and Merila 1996, Merino and Potti 1998).

My first objective was to follow the survival of tagged storks across multiple seasons and years. I predicted that the highest levels of mortality would occur during the first 6 months after fledging, when birds are first learning to forage for themselves, and are moving across unfamiliar landscapes. I also predicted that survival would be lower in the first year of life, compared to the second year.

My second objective was to compare nestling health and postfledging survival. I predicted that the body condition, hematological parameters, stress index, and mercury levels of nestlings would significantly affect their survival postfledging. Specifically, I predicted that nestlings with lower immune parameters, higher stress indices, and poorer body condition would have lower rates of postfledging survival.

## **Methods**

### **Reproductive Success**

I worked in the Tamiami West colony (TW) (N25°45.31, W80°31.90), a mixed-species wading bird colony located in Everglades National Park, Miami-Dade County, Florida. Approximately 400 and 350 Wood Stork nests were initiated in TW in

2002 and 2003, respectively. To monitor nest success, I marked nests (120 in 2002, 108 in 2003) with orange surveyor flagging along looping or roughly north-south transects within the tree island. In both years, only nests within approximately five meters of transects were marked to avoid focusing efforts in a single area. Although nests were not randomly selected, I believe I studied a representative cross-section of the nesting population by traveling throughout much of the total area. At minimum, this design produced a sample with both edge and center-located nests, which are known to have different characteristics and risks (Coulson 1968, Brown and Bomberger-Brown 1987, Simpson et al. 1987, Brunton 1997).

Nests in the Tamiami West colony were almost entirely built in the canopy (2-4m above ground) of Pond Apple (*Annona glabra*), although a few nests were in Willow (*Salix caroliniana*). I used three-meter long extension poles with attached mirrors to view nest contents and determine numbers of eggs and young. I conducted nest checks every 4-7 days throughout the nesting season to determine nest contents and age of nestlings. I waited 12 days between one pair of successive nest visits, in late April 2002, to avoid disturbing the large numbers of other nesting wading bird species during critical egg-laying and incubation periods (Frederick and Collopy 1989).

I used the Mayfield Method (Mayfield 1961, 1975) to estimate nest survival rates, which pro-rates survival on a daily basis. I calculated success rates separately for the incubation and nestling periods, as well as an overall nesting success rate (probability that a nest would survive both periods and produce at least one fledgling) (Hensler and Nichols 1981). I pro-rated nest initiation dates in cases where a full clutch had yet to be completely laid, or a chick in a nest was hatching on the nest check date. Nests were

successful if they produced at least one young to 55 days of age. The incubation period extended from the lay date of the first egg to 27 days after the first egg was laid (Coulter et al. 1997). The nestling period began on the day the first egg hatched. Brood size was measured during the second week of the nestling period, after all eggs had hatched (8-14 days).

Only nests visited more than once before termination (failure or success) were included in the analysis. Nests were considered failed when nest contents were completely missing, depredated, abandoned (eggs cold to touch), or where all nestlings were dead. The nest failure date was estimated as the midpoint between the ultimate and penultimate visits (Mayfield 1961, 1975). The nestling period was truncated at 55 days after hatching, as birds were typically capable of flying by this time and had become independent of their nest sites. On average, however, juvenile storks remained associated with the colony and continued to be fed by their parents until at least 80 days old. Nestlings were considered fledged only when they permanently left the colony.

### **Nestling health**

Nestling storks were randomly selected for inclusion in the health and telemetry studies between late April and early June in both years. Starting from the northern-most section of the transects and moving southward on subsequent visits, I selected the first marked nests I approached that had chicks of the appropriate age. Only one chick from each nest was marked to avoid the nonindependence effect of siblings and to control for biases related to hatching order (Mock 1984, Magrath 1990). Earliest-hatched nestlings were preferred over later-hatched nestlings. In one case in 2002, the earliest-hatched chick was too mobile for capture, and its later-hatched sibling was used instead. Hatch order was determined by visually assessing relative culmen lengths among siblings.

Chicks were fitted with satellite transmitters and had health exams at 4-5 weeks of age. In cases where nestling age was not known from hatch date, the approximate age of chicks was based on size, feather growth, and presence of flight feathers (Kahl 1962). Storks were considered to be at least 4 weeks of age when they had visible white contour feathers on the back and coverts, and primaries 508cm in length. All nestlings were caught by hand on the nest and were immediately hooded to reduce stress. I worked in colonies only during early morning hours, when thermal stress was lowest and when I was least likely to interrupt feedings by adults.

I fitted a United States Fish and Wildlife Service individually numbered aluminum leg band to the tibiotarsus of each bird and recorded culmen and tarsus lengths (nearest mm), and mass (nearest g). Each health assessment also included a physical examination for oral parasites and ectoparasites (Forrester and Spalding 2003), and palpation for *Eustrongylides* nematodes in the abdomen (Spalding et al. 1994). In addition, 4-6 growing scapular feathers were collected from each bird and analyzed within 2-3 months for total mercury by the Florida Department of Environmental Protection Chemistry Section (see Frederick et al. 2004 for detailed analysis methodology).

Blood was collected to determine gender, packed cell volume (PCV), leukocyte counts, and the presence of blood parasites and diseases. I collected up to 2mL of blood by venipuncture from the brachial vein. Blood samples were collected for sexing by storing drops of whole blood in ethanol in 2002, and in 2003 by smearing a thin layer of blood across a Zoomark card. Blood was analyzed for sexing purposes by Zoogen Services, Inc., Davis, California. Two-four blood smears of whole, nonanticoagulated blood were prepared for each bird in the field using a 2-slide method (Campbell 1988),

and preserved with a thorough wash of methanol. The remaining blood was transferred to lithium heparin tubes (100 units/cc).

Hematological evaluations were performed within 4 hours of blood collection using whole blood from the lithium heparin tubes. Blood was transferred to heparinized microcapillary tubes and centrifuged at 12,000 rpm for 5 min to obtain PCV. PCV was measured with a ruler as the percent cellular fraction of total whole blood volume. Total white blood cell counts (WBC) were performed manually using the eosinophil Unopette (Becton-Dickinson, Rutherford, NJ, USA) technique by counting the average number of leucocytes observed within five fields under 50 X power (Campbell 1988).

Within four months of preparation, blood smears were stained with Wright-Geisma stain (ACROS Organics, Morris Plains, NJ, USA) and examined for hemoparasites at the University of Florida School of Veterinary Medicine, Gainesville, FL. Differential leukocyte counts were determined for each bird from the blood smears by multiplying the WBC counts by the percentage of each cell type in the differential. The differential count included relative percentages of lymphocytes, heterophils, monocytes, basophils and eosinophils based on descriptions by Hawkey and Dennett (1989). The H/L ratio is the number of heterophils divided by the number of lymphocytes.

### **Satellite Telemetry**

Following the health exam, each bird was fitted with a backpack harness that carried a 10g VHF radio transmitter with a motion/mortality detector (2002: American Wildlife Enterprises, Monticello, FL, USA; 2003: Model A1120, Advanced Telemetry Systems, Isanti, MN, USA) and a 35g solar-powered Argos certified PTT for satellite tracking (Microwave Telemetry, Inc., Columbia, MD, USA, 10 h on/24 h off duty cycle) (see Chapter 3 and Appendix). The Teflon harness (Bally Ribbon Mills, Bally, PA,

USA), VHF transmitter and PTT weighed approximately 48g. In 2002, I experienced problems with vultures separating the VHF transmitters from the PTTs on carcasses of dead birds, so in 2003 I further secured the VHF to the PTT using 2 small screws. Location information for all PTTs was obtained daily by email from Service Argos, Inc. (Landover, MD, USA).

I determined the survival of tagged birds by monitoring VHF frequencies daily from a position near the colony prior to fledging, and by monitoring satellite transmitter signals after fledging. Postfledging mortalities were suspected when I stopped receiving data or when birds did not move from a location for multiple days. To confirm a mortality, I averaged the last PTT-derived locations for that bird as a guide for a ground or aerial search, and then used VHF signals to hone in on the precise location of the carcass.

### **Statistical Analysis**

I used a Z-test to compare Mayfield nest success rates between years (Hensler and Nichols 1981). For bivariate analyses, Mann-Whitney *U*-tests were used with a Z-approximation. Values are reported as mean  $\pm$  SE, and a significance level of  $P \leq 0.05$  was set *a priori* for all statistical tests.

I used Cox's proportional hazards model (Cox 1972, 1975) to determine the effects of nestling health variables on the survival rate of postfledging storks (White and Garrott 1990, Lee and Wang 2003). Explanatory variables included WBC, eosinophil, lymphocyte, basophil, heterophil, monocyte, H/L ratio, body condition, tarsus, culmen, mass, PCV, and gender. The model was run independently for each year of study, because survival rates were significantly different between years.

I derived an index of body condition (body mass corrected for variation in body size, Johnson et al. 1985) using principle component analysis (PROC PRINCOMP, SAS Institute 2000) of tarsus and culmen lengths (Alisauskas and Ankney 1987, Dufour et al. 1993). The first principal component (PC1) accounted for 71% of the overall variation. I then regressed body mass on PC1 to give an index of body condition (PROC GLM; SAS Institute 2000).

Cox's proportional hazard model was run using PROC PHREG in SAS (SAS Institute 2000, see Yoder et al. 2004 for a thorough description of this method). This procedure yielded estimated regression coefficients for the hazard function using a partial likelihood function that only included probabilities for birds that died within six-months of fledging. All birds that remained alive on a given day in the model were considered the at risk population. The threshold for stepwise inclusion of a specific variable into the model was arbitrarily set at  $P < 0.20$ . The Wald test statistic, which uses a chi-square distribution, was used to determine if the estimated regression coefficients were significantly different from zero. I also used the Pearson correlation coefficient (PROC CORR; SAS Institute 2000) to examine the relationship between white blood cell counts and survival.

Table 2-1. Mean ( $\pm$  SE) clutch and brood sizes of Wood Storks in Tamiami West colony

Year	Average clutch size	Average brood size
2002	3.09 $\pm$ 0.08 ( $n = 46$ )	2.81 $\pm$ 0.09 ( $n = 26$ )
2003	3.56 $\pm$ 0.08 ( $n = 84$ )	2.97 $\pm$ 0.15 ( $n = 38$ )
Florida average (1875–1967)	3.28 $\pm$ 0.05 ( $n = 199$ )	—

Average historic clutch size in Florida as reported in Rodgers (1990).

Table 2-2. Nesting success of Wood Storks in Tamiami West colony in 2003

Year	Traditional Method of Success (%) *	Mayfield Method of Success (%)		
		Incubation Period **	Nestling Period **	Combined
2002	77.39 ( <i>n</i> = 115)	49.66 ± 1.02 ( <i>n</i> = 54)	89.29 ± 1.63 ( <i>n</i> = 97)	44.34 ± 0.62
2003	24.07 ( <i>n</i> = 108)	19.04 ± 0.57 ( <i>n</i> = 84)	23.28 ± 0.76 ( <i>n</i> = 69)	4.43 ± 0.17

Traditional nesting success is number of nests fledging at least one young / number of nests studied. Mayfield method pro-rates survival on a daily basis. An asterisk (\*) indicates a significant difference of  $P < 0.01$  between years and a double asterisk (\*\*) indicates a significant difference of  $P < 0.001$ .

## Results

### Reproductive Success

At the time of initial nest-marking in early March, 57% of 115 nests were in the early nestling stage in 2002 compared with only 4% of 84 nests in 2003; the remainder of nests were being incubated. Thus the nesting in 2003 was initiated considerably later than in 2002. The average clutch size of nests marked during the incubation period was significantly smaller in 2002 at 3.09 compared to 3.56 in 2003 ( $z = 4.02$ ,  $P < 0.0001$ ) (Table 2-1). The average brood size when chicks were 8-14 days old was 2.81 in 2002, compared with 2.97 in 2003, and was not significantly different between years ( $z = 0.99$ ,  $P = 0.16$ ).

Nesting success was significantly different between years for all stages of nesting (Table 2-2). The proportion of nests studied with at least one young 55 days old for this colony was 77.4% in 2002 and 24.1% in 2003 ( $\chi^2 = 64.7$ ,  $P < 0.01$ ). The 2003 success rate was 31% lower than in 2002. Mayfield nest success during the incubation stage was 61% lower in 2003 (19.04%) than in 2002 (49.66%,  $\chi^2 = 14.15$ ,  $P < 0.001$ , Table 2-2). Survival during the nestling period was also significantly lower in 2003 (23.28%) than in 2002 (89.29%,  $\chi^2 = 73.84$ ,  $P < 0.001$ ). The overall, combined Mayfield nesting success

for these two periods in 2002 was 44.34%, while the combined overall nesting success rate for 2003 was 4.43%.

### **Survival of Tagged Nestlings**

Of the 33 birds tagged with satellite transmitters in 2002, 6 mortalities occurred within the borders of the colony prior to the birds fledging (82% survival prior to fledging). Two of these mortalities were of flighted birds that were still dependent on the colony. Of the 34 birds tagged in the Tamiami West colony in 2003, 17 (50% survival) died prior to fledging.

### **Fledgling Survival**

Twenty-seven birds tagged with satellite transmitters fledged in 2002. The survival rate for the first 6 months after fledging (June–Nov) was 63.0% ( $n = 27$ ) (Figure 2-1, Table 2-3). There were no mortalities in the 2002 cohort between February and July 2003. Second-year survival rate (75%,  $n = 12$ , Mar 2003–Feb 2004) was significantly higher than first-year postfledging survival rate (41.4%,  $n = 29$ , Mar 2002–Feb 2003) for 2002 birds ( $\chi^2 = 4.23$ ,  $P < 0.05$ ). Overall, a young bird from the 2002 cohort that became independent of the colony had a 31.0% chance of surviving to 24 months of age. Of the 19 postfledging mortalities that occurred by two years of age, 14 occurred in Florida (74%), 2 in Georgia (11%), 1 in Alabama (5%), 1 in Mississippi (5%), and 1 in South Carolina along the Georgia border (5%).

Seventeen birds tagged with satellite transmitters fledged in 2003. The survival rate after the first 6 months for the 2003 cohort (23.5%, Figure 2-1, Table 2-3) was significantly lower than survival in the same period for the 2002 cohort (63.0%,  $\chi^2 = 6.15$ ,  $P < 0.02$ ). Satellite data suggest that only 1 of the 17 fledglings in the 2003 cohort was still alive after a year, resulting in a 5.9% first-year survival rate. First-year survival rate

Table 2-3. Percent survival rates for juvenile Wood Storks in 2002 and 2003

Year	Survival Rates (%)		
	6 months (1-6 months)	1st year (1-12 months)	2nd year (13-24 months)
2002	63.0	41.4	75.0
2003	23.5	5.9	—

Six-month survival indicates survival within the first six months of fledging. First year survival rates are for the first 12-month period after hatching (March-February). The second-year survival rate is for period of 13-24 months after hatching (March-February).

in 2003 was significantly lower than that of the 2002 cohort ( $\chi^2 = 4.22, P < 0.05$ ). The study ended in March 2004 after the 2003 cohort reached 1 year of age, so the 2<sup>nd</sup> year survival rate for the 2003 cohort was not available for comparisons. The majority of deaths of the fledged 2003 cohort occurred in Florida (13 birds, 81%), while 3 birds died in Georgia (19%).

I considered using the Kaplan Meier product limit estimator (Kaplan and Meier 1958) as an additional method for estimating survival rates for the juvenile birds. This estimator requires that birds of ambiguous fates be censored from the sample. My inability to relocate most grounded transmitters from fledged birds resulted in few known

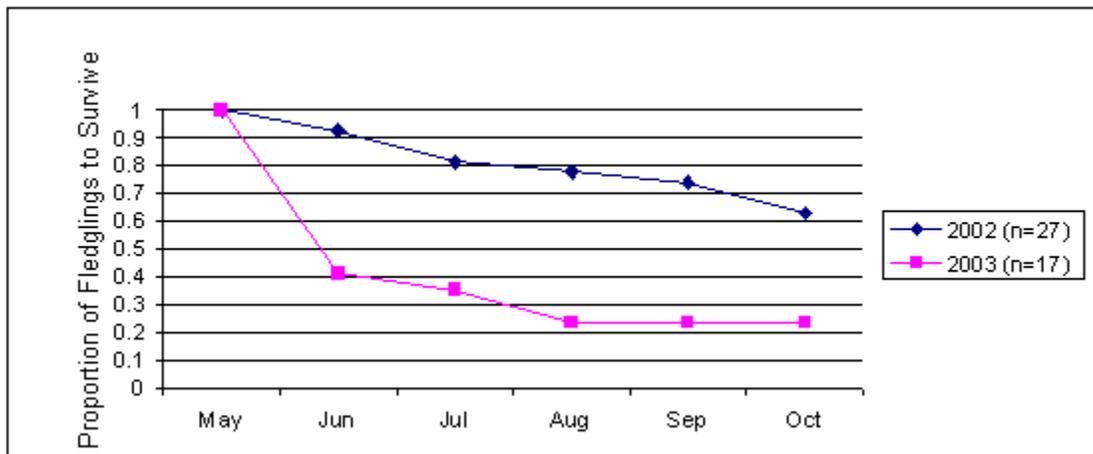


Figure 2-1. Survival curves of tagged storks in the 2002 and 2003 cohorts for the first 6 months after fledging. As survivorship is based on known outcomes, not estimates, error bars are not available. Fledging occurred in May in both years.

mortalities ( $n = 3$  in 2002;  $n = 4$  in 2003) and an inadequate sample size. One other way to deal with the uncertainty of mortality due to potential tag loss is to express the upper limit of survival by considering only mortalities that were unambiguous (i.e., transmitters were relocated with the carcass). Within the fledged 2002 cohort, first year survival rate of these birds was 75.0% ( $n = 16$ ), as compared to 41.4% ( $n = 27$ ) estimated when including all assumed mortalities. Using only birds with known fates within the fledged 2003 cohort, first year survival rate was 28.6% ( $n = 7$ ), as compared to 5.88% ( $n = 17$ ) estimated when including all assumed mortalities.

### Analysis of Health Factors

Multivariate regression analysis using Cox's proportional hazard model revealed that year ( $P = 0.0007$ ) and white blood cell counts ( $P = 0.0035$ ) significantly affected the 6 month postfledging survival of juvenile storks (Table 2-4). There was a significant negative correlation between WBC counts and survival ( $r = -0.37$ ,  $P = 0.0335$ ,  $n = 33$ ). For the 2002 cohort, white blood cell counts ( $P = 0.0071$ ) and eosinophil counts ( $P = 0.0311$ ) were significant risk factors. Both lymphocytes ( $P = 0.0679$ ) and gender

Table 2-4. Multivariate analysis of the risk factors on overall survival in juvenile Wood Storks (Cox's proportional hazards test)

Variable	Model		
	Years combined <i>P</i>	2002 Cohort <i>P</i>	2003 Cohort <i>P</i>
Year	0.0007	—	—
White Blood Cell (WBC)	0.0035	0.0071 (+)	0.0398 (-)
Lymphocyte	—	0.0679 (-)	0.0271 (+)
Eosinophil	—	0.0311 (-)	0.1151 (+)
Gender (M/F)	—	0.0981 (+)	0.0265 (+)
Heterophil/Lymphocyte ratio	—	—	0.0187 (+)
Body condition	—	—	0.1126 (-)
Mercury	—	—	0.1775 (-)

A dash (—) indicates the variable did not meet the  $P < 0.2$  threshold for entry into the model. Model fit in 2003 was not significant at the 0.05 level. The signs (+/-) indicate the direction of the variable's relationship to survival.

( $P = 0.0981$ ) also showed marginally significant power to explain survival rates in 2002. When considering all model components together, females were  $2.0 \pm 1.2$  times as likely as males to survive to 6 months of age. The survival rate for the 2003 cohort was not consistent throughout the 6 month period as there was a large decline in survival during the first month after fledging, followed by a survival rate similar to that of the 2002 cohort (Figure 2-1). Although the inconsistency in survival rate over the six-month period resulted in a less accurate fit to the Cox Proportional Hazards Model ( $\chi^2_7 = 9.81$ ,  $P = 0.1997$ ), the model for the 2003 cohort still had explanatory value.

Gender ( $P = 0.0265$ ), WBC levels ( $P = 0.0398$ ), and lymphocyte levels ( $P = 0.0271$ ) all significantly affected the survival rate of juvenile storks in the 2003 cohort. Controlling for health factors, females were  $5.0 \pm 2.3$  times as likely to survive 6 months compared to males. Unlike in the 2002 cohort, eosinophil levels ( $P = 0.1151$ ) were not related to survival risk in the 2003 cohort. The H/L ratio, an indicator of stress levels, was a significant factor in predicting survival rates in 2003 ( $P = 0.0187$ ). Neither variation in mercury ( $P = 0.1775$ ) nor body condition ( $P = 0.1126$ ) influenced survival in the 2003 cohort. Descriptive statistics for the body measurements, mass, mercury levels, and health factors are in Appendix B.

## Discussion

There were large differences in survival rates for all of the developmental periods of young storks between the two years of study, despite average to above average clutch and brood sizes in both years. Nesting success was significantly higher in 2002 than 2003 during both the incubation and nestling periods than in 2003. In 2003, heavy rains in early March preceded a large abandonment event involving approximately half the

nesting storks in Tamiami West. Rapid water level increases throughout the nesting period were likely the cause of additional abandonments during the nestling phase (Kahl 1964, Kushlan et al. 1975, Ramo and Busto 1992). Similar abandonments were seen in other stork colonies in the Everglades ecosystem during this period (Gawlik and Crozier 2003), so it seems unlikely that my own activities in the colony resulted in the abandonments, and the synchrony of abandonments is in keeping with a weather-related cause.

Although there were large differences in the survival rates of storks during the two years, the general patterns that emerged largely matched my predictions. First, the wide range in survival values exhibited by juvenile storks is fairly typical for first-year wading birds, with high productivity and survival in some years and little to none in others (Freeman and North 1990, Hafner 1998, Barbraud et al. 1999). Second, the survival rates of first-year birds are typically lower and more variable than those of older birds. For example, annual survival of banded juvenile White Storks has been highly variable across years (0-100%), although adult survival has been relatively constant, averaging 78% (Barbraud et al. 1999). Little Egrets (*Egretta garzetta*) are also estimated to have a higher, less variable adult survival rate of 71.4% (range = 69-86%) compared to first-year birds (7-55%) (Hafner et al. 1998).

The pattern of significantly lower survival in first-year birds compared to older birds is common and is usually attributed to relative experience levels (Lack 1954, Botkin and Miller 1974). The greatest mortality in birds occurred during the first six months after fledging in both years. This is the period when birds are first developing their foraging skills and independently making decisions regarding habitat selection and

predator avoidance. Juvenile storks often initially forage at inappropriate sites where adults are not present and prey are unavailable (i.e., flooded lawns and rainwater depressions) (Coulter et al. 1999). Limited prey availability, when coupled with inexperience, could have a strong negative impact on survival in some years.

It is extremely unlikely that any birds from the 2003 cohort will reach breeding age. Even in 2002, which saw significantly higher fledging and survival rates, a fledgling had only a 31.03% chance of surviving to 24 months of age. If the fledglings do not begin breeding until their 4th year, only approximately 5 of the 29 fledglings (17%) from the 2002 cohort will reach adulthood if the annual survival rate of 75% continues each year as seen in other Ciconiiformes (Palmer 1968, Hafner et al. 1998, Barbraud et al. 1999). The high initial mortality of fledglings is an important limiting factor for recruitment to the breeding population, even in successful years. Characterizing only the nesting and fledging success of storks may yield inaccurate and limited understanding of actual stork population dynamics.

The survival estimates of juvenile Wood Storks in my study are based on several assumptions: 1) losses of telemetry devices were due to mortality, 2) PTT failure was due to mortality, and 3) attachment of transmitters did not affect survival. There is no evidence to suggest that grounded transmitters were the result of harness failure or detachment from the harness. Although harnesses were not always found attached to carcasses, particularly in the colony where scavenging rates were high, all of the harnesses found were intact. The relocated harnesses were never torn or frayed, and the stitchings were intact. The only visible wear on the harness was color fading from sun and weather.

There was also no evidence that PTTs simple stopped working. The solar power source for the PTTs used in my study was designed to exceed the lifetime of battery-powered PTTs (3 years minimum design lifetime). There are limited studies of failure rate for PTTs due to the inherent difficulty in tracking highly mobile individuals by other means. Britten et al. (1999) found only a 4.7% failure rate in 42 Peregrine Falcons (*Falco peregrinus*) wearing 30g battery-powered PTT-100s (Microwave Telemetry) that was not attributable to battery exhaustion. K. Meyer (unpubl. data) reported that losses of PTT signals for Swallow-tailed Kites (*Elanoides forficatus*) and Short-tailed Hawks (*Buteo brachyurus*) were space/time clumped, suggesting localized sources of bird mortality and not radio/harness failure. The PTTs of 9 tagged storks were still operating after 2.25 years as of 1 July 04, and all grounded PTTs ( $n = 24$ ) were still working upon recovery. I had no indication that PTT failure was not due to mortality.

Assumption 3, attachment of transmitters did not affect survival, was not tested in my study, though there is some evidence to support it. Survival estimates of the 42 PTT-tagged peregrines in the Britten et al. (1999) study were not significantly different from previous survival estimates based on a mark/resighting study of banded peregrines. K. Meyer (unpubl. data) reported no significant difference between survival estimates of Swallow-tailed Kites from PTT-tagged and VHF-tagged birds, where PTTs were almost twice as heavy as VHF's. The maximum migration distance flown for a PTT-tagged peregrine was also comparable to that of a resighted, banded bird (Ambrose and Riddle 1988, Britten et al. 1999). Transmitter loads for these raptors were >3% of the birds' mass, as they were in my study.

Although many studies of the effects of PTTs on albatrosses and petrels show an increase in foraging trip duration and lowered nesting success, transmitter loads usually exceeded 3% of adult mass, and adults were often tagged during sensitive nesting periods (see Phillips et al. 2003). Phillips et al. (2003) did not find a significant increase in foraging trip duration, meal mass, breeding success, or rate of return in adult albatrosses and petrels when transmitter loads were less than 3% of adult mass and when birds were tagged during less sensitive nesting periods. I tagged young storks 3-5 weeks prior to fledging, which allowed for a period of recovery from handling and habituation to the transmitter package prior to flight and fledging. In light of the existing knowledge about transmitter effects, it seems unlikely that bird handling and transmitter attachment affected postfledging survival.

The hazard model results indicated the importance of the lymphatic system to survival. WBC were negatively correlated with survival rates in 2003 and, but were positively correlated in 2002. Eosinophil levels were also negatively correlated with survival rates in 2002. High WBC and eosinophil counts are often indicative of infections or blood disorders, while low WBC counts may indicate poor immunocompetency (Campbell 1994, Svensson and Merila 1996, Howlett et al. 2002). Thus it seems consistent that poor survival would be associated with both high and low WBC counts. Similarly, the heterophil/lymphocyte ratio was a significant factor in 2003, with high ratios negatively correlated with survival.

Although a sex bias was not apparent from the raw survival data, females were twice as likely as males to survive in 2002 and five times more likely to survive in 2003, when the effects of other model variables were taken into account. In many vertebrates,

males are negatively affected more often than females by adverse conditions during growth (Clutton-Brock 1991). As male birds (including Wood Storks) are often larger and have greater energy requirements than females (Slagsvold et al. 1986), males may have greater sensitivity to adverse conditions (Clutton-Brock et al. 1985).

There are numerous effects of mercury on birds that may affect survival directly or indirectly, depending heavily on dose, species and the effects of other stressors (Eisler 1987, Wolfe et al. 1996, Thompson 1996, Frederick 2000). Although mercury did not appear to affect survival of the young storks in my study, the conditions may not have resulted in an adequate test of the effect. I measured mercury during a period when extremely rapid feather growth can effectively depurate body burdens of mercury in young birds (Honda et al. 1986, Spalding et al. 2000, Sepulveda et al. 1999). In addition, the young birds may have encountered widely varying levels of mercury exposure during the postfledging period (Spalding et al. 2000). Thus the contaminant levels I measured during the late nestling period may not have been representative of the burdens at fledging or later.

In general, the results of my study support my prediction that prefledging health can significantly affect postfledging survival, although the variation in results makes specific interpretations difficult. Overall, 2002 was a much more successful year for juvenile storks than 2003. During 2003, health factors and gender were more closely associated with survival, suggesting they may play a role in regulating survival during years where storks are scarce. White blood cell count, an indicator of an organism's ability to fight infection, was consistently the best health indicator of survival. The variation in response of survival to high and low hematological values demonstrates the sensitivity of

blood chemistry to perturbations and the variability of health issues in different years. Although I found that hematological factors were significantly correlated with survival, there may be many other ecological or physiological factors that also directly impacts survival.

According to the characterizations described by Saether et al. (1996), storks seem to follow a “bet-hedging” life strategy, in which long-lived species tend to live in generally favorable breeding and survival habitats, but in which the quality of the breeding habitat may vary annually. A bet-hedging life-history strategy may be an adaptation to living in variable environments, allowing for high productivity in occasional favorable years. Bet-hedging strategies are common in waders, owls and terns with large clutch sizes and early maturation (<3-yr-old) (Saether et al. 1996). In these species, however, Saether and Baake found large variation in the contribution of adult survival rate to population growth rate (2000).

Apart from telling us about the life history strategy of this species, the large variation in survival rates and effects of health on survival between years and age-classes demonstrates the importance of interannual effects, and therefore the necessity of long-term monitoring this species. Continuing similar research with juvenile storks will enable us to fully understand the interannual variability in survival rates and the factors affecting survival. Conducting similar studies with adult storks would also provide much needed information on longevity, age at first breeding, and variability in survival rates. Long-term monitoring and a functional demographic model will allow managers and biologists to understand the population dynamics of Wood Storks, enabling the development of better conservation strategies.

CHAPTER 3  
HABITAT USE AND MOVEMENT PATTERNS OF JUVENILE WOOD STORKS  
(*Mycteria americana*) IN THE SOUTHEASTERN UNITED STATES

**Introduction**

Conservation and management of highly mobile animals that have large home ranges requires an understanding of space use patterns at an appropriately large scale (Wiens 1989, Hansen et al. 1993, Ims et al. 1993, Frederick et al. 1996, Lima and Zollner 1996, Turchin 1998, Roshier et al. 2002, Graham 2001). The pattern of spatial movements may be at least as critical as the scale for identifying successful conservation strategies. For example, an accepted approach for seasonally migratory species is to identify and protect high-use habitat patches and the corridors connecting these patches (Noss et al. 1996, Wikramanayake et al. 1998, Poiani 2000, Mech and Hallett 2001, Wikramanayake et al. 2004). Alternatively, a more nomadic species relying on unpredictable resources might benefit little from such an approach; efforts instead might focus on preserving ecosystem function that creates the temporary habitat, or on preserving a mosaic of geographically widespread sites for use (Woinarski et al. 1992, Frederick et al. 1996, Roshier et al. 2002). While an understanding of spatial behavior and habitat use is generally recognized as important to conservation, this has proved to be technically challenging for vagile animals with large spatial requirements (Mauritzen et al. 2001, Roshier et al. 2002).

Wood Storks (*Mycteria americana*, Ciconiiformes) are large, highly mobile wading birds that capture aquatic prey that pass through their open bills as they slowly wade

through shallow water (Kahl and Peacock 1963). The stork's foraging technique is effective in shallow water where prey are concentrated, but works less well in deeper water where prey are dispersed (Kahl 1964, Gawlik 2002). Appropriate foraging conditions for Wood Storks are therefore highly dependent upon the interplay of water depths and prey densities, and are by nature ephemeral and irregularly distributed across the landscape both spatially and temporally (Hoffman et al. 1994). Because appropriate foraging conditions are often short-lived (days to weeks), storks typically require a large home range and must frequently change foraging locations (Erwin 1983, Fleming et al. 1994, Hoffman et al. 1994).

Adult Wood Storks are generalists, commonly use a variety of wetlands for foraging, including impoundments and inundated agricultural fields (Sykes and Hunter 1978, Browder 1984, Gawlik 2002). Coulter and Bryan (1993) found that adult storks from the Birdsville colony in east-central Georgia foraged more frequently than expected in open habitats such as ponds and marshes compared to hardwood and cypress swamps. Pearson et al. (1992) and Gaines et al. (1998) found that foraging storks in coastal Georgia used freshwater habitats more frequently than palustrine habitats compared to availability. Pearson et al. (1992) also found that upland habitats were used less frequently compared to availability. Each of these habitat-use studies were conducted during the breeding season.

Little is known about habitat-use outside the breeding season, particularly for juvenile storks. The lack of information is largely due to the high mobility and low re-sighting potential for banded birds across their large range (Bancroft 1992, Coulter et al. 1999, Saether and Bakke 2000). In other wading birds, survival during nonbreeding

periods has been shown to play an integral role in population regulation (North 1979, Kanyamibwa et al. 1990, Cezilly et al. 1996, Cezilly 1997). Understanding the behavioral responses of Wood Storks to local environmental conditions during nonbreeding periods is essential, as habitat use is probably important for survival.

An intensive color-marking of storks in the 1970s showed that juvenile storks fledging from southern Florida colonies exhibited rapid postfledging dispersal across Florida, Georgia, Alabama, and South Carolina upon the onset of the rainy season (May–June). Juveniles from the Everglades were found to disperse further north than conspecifics hatched in central and north Florida, with most Everglades storks resighted in central Florida, coastal Georgia and South Carolina. Only 2 of 1589 marked juveniles (<0.01% of all resightings) were relocated outside these states, with one bird resighted in west-central Alabama and subsequently seen in east-central Mississippi with another tagged conspecific. Banded storks then returned to south and central Florida during winter months (Nov–Feb). Despite the large sample, little information was gained about the migratory nature of this species, their movement patterns, or the general mechanisms they use to make movement decisions.

Although Kushlan (1981) identified storks as migratory, the evidence was only that they left southern Florida after breeding. More recently, Coulter et al (1999) did not consider Wood Storks to be a true migratory species, and their movements were thought to be defined only as a response to local environmental conditions (Coulter et al. 1999). Adult storks have been identified as moving north from the Everglades after large nesting failures when no nests are initiated, and prior to the beginning of the summer rainy season (Coulter et al. 1999). Although large northward movements by juveniles were

identified in the 1970s, they were considered an example of postfledging dispersal that is typical of many birds, including ciconiiform species.

In my study I focused on the movements and habitat use of juvenile storks using satellite telemetry. Since storks do not begin breeding until their third or fourth year (Hancock et al. 1992, Coulter et al. 1999), and so the young birds I studied here were not constrained to remain in one location for breeding purposes. I hypothesized that juvenile Wood Storks would exhibit predictable seasonal movement patterns as seen in the banding study, not just track resources at the local level.

First, I predicted that storks would initially move into local wetlands upon leaving the natal colony. Local foraging areas near the colony are likely important during the first weeks when storks are learning to fly and forage on their own. Local foraging areas for the tagged birds included the wet prairies within Everglades National Park and the nearby Water Conservation Areas. Second, I predicted that storks would move north into northern Florida, Georgia, Alabama, and South Carolina for the summer, as was recorded for banded storks in the 1970s (Coulter et al. 1999). Finally, I predicted that storks would leave their summer locations and spend the winter months in southern Florida as previously described (Bancroft et al. 1992, Coulter et al. 1999).

Based on the information known for adult storks, I also hypothesized that juveniles would exhibit nonrandom use of habitat, and would prefer shallow, periodically inundated wetland sites more often than upland or residential habitats. Habitats that are at least periodically inundated include wetlands, agricultural and cultivated areas. Of these inundated habitat types, I predicted that storks would use wetlands more often than cultivated habitats.

## Methods

### Study Area

I studied movements of young birds originating from the Tamiami West (TW, N25°45.31, W80°31.90, Figure 3-1) colony, in Everglades National Park, Miami-Dade County, Florida as this colony was most accessible of all colonies in the Everglades ecosystem, and had consistently hosted a large number of nesting Wood Storks (>400 pairs) in recent years. Nearly all nests in TW were built in the canopy of Pond Apple (*Annona glabra*), although a few nests were located in Willow (*Salix caroliniana*). I visited colonies on foot during early morning hours between March (majority of nests incubating) through the end of all nesting in July.

After high levels of abandonment and mortality in TW in 2003, I placed an additional 5 transmitters on juvenile storks in late May in the Martin County Spoil Island 2 colony MC2, N27 11.40, W80 11.27), located along the Atlantic coast of Florida just south of Sewalls Point, Martin County, Florida (Figure 3-1). In 2003, MC2 was a mixed-species wading bird colony with approximately 50 storks nesting in red mangrove (*Rhizophora mangle*) and sea grape (*Coccoloba uvifera*). Satellite transmitters were deployed in late May on five juvenile storks hatched in this colony.

Nestling storks are capable of flying by approximately 55 days after hatching. However, juvenile storks typically remain in or in close proximity to the natal colony and continue to be fed by their parents until at least 80 days (Coulter et al. 1999). Nestlings were considered fledged only when they permanently left the colony. I refer to storks aged 55-80 days as flighted.

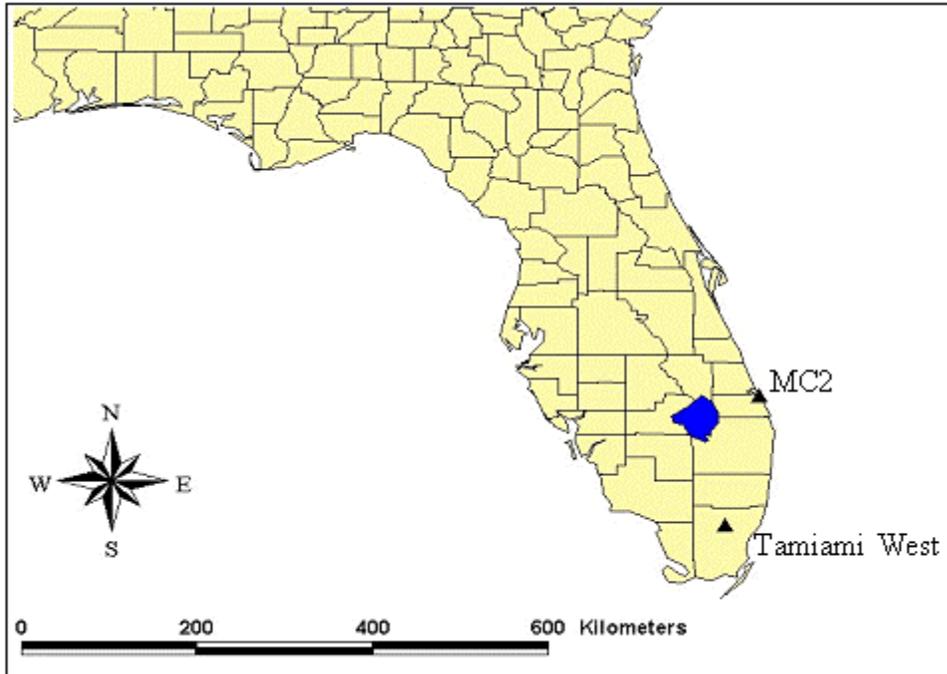


Figure 3-1. Map of Florida depicting colony locations (triangles) where juvenile Wood Storks were tagged in 2002 and 2003. The dark lines indicate county boundaries.

### Satellite Telemetry

After nestlings at TW reached 4-6 weeks of age, I randomly selected first-hatched nestlings for inclusion in telemetry studies. I placed transmitter harnesses on 33 juvenile Wood Storks between 4 and 6 weeks of age in TW between 26 April and 13 June 2002, and on 34 juveniles in TW between 23 April and 16 May 2003. Storks were considered to be at least 4 weeks of age when they had visible white contour feathers on the back and coverts and primaries 5-8cm in length (Kahl 1962). In 2003, an additional 5 birds of unknown hatch-order were tagged at MC2. Starting from the northern-most section of my transects in TW and moving southward on subsequent visits, I attached transmitters to the first chicks in marked nests (see Chapter 2) that were accessible and of an appropriate age. Earliest-hatched nestlings were preferred over later-hatched nestlings to avoid the problem of nonindependence of siblings and to control for biases related to hatching

order. In one case in 2002, the earlier-hatched chick was too mobile for capture, and the later-hatched nestling was chosen instead. All nestlings were caught by hand on the nest and were immediately hooded to reduce stress. Work in colonies took place only during morning hours (06:30–11:00 EST), when thermal stress was lowest, and when the possibility of interrupting feedings by adults was at a minimum.

Each captured bird was fitted with a backpack harness that carried a 10g VHF radio transmitter (2002: American Wildlife Enterprises, Monticello, FL, USA; 2003: Model A1120, Advanced Telemetry Systems, Isanti, MN, USA) and a 35g solar-powered Argos certified platform terminal transmitters (PTT) for satellite tracking (Microwave Telemetry, Inc., Columbia, MD, USA). A detailed description of the harnessing method can be found in Appendix A. The total weight of a Teflon (Bally Ribbon Mills, Bally, PA, USA) harness, VHF transmitter and PTT did not exceed 3% of the Wood Stork's fledging mass (2–2.8 kg) in accordance with recommendations from the Office of Migratory Bird Management, United States Geological Survey.

Grounded transmitters were those that showed evidence of the transmitter having become immobile (stationary signal from PTT, mortality signal from VHF). Transmitters collected from carcasses were either reused in the same year or refurbished by the manufacturer and reused in the subsequent year. Because I experienced problems with vultures separating the VHF transmitters from the PTTs on carcasses in 2002, I further secured each VHF to its PTT with 2 machine screws in 2003.

Location information for all PTTs was obtained daily by email from Service Argos, Inc. (Landover, MD, USA). The PTTs were programmed on a 10-hour on/24-hour off cycle. Argos assigned each fix to a location class (LC) based on their accuracy estimates.

Only locations with estimated accuracies of  $\leq 1000$  m (LC = 3, 2, or 1) were used in my study (Service Argos 1996, Keating et al. 1991). All location data were managed in Excel (Microsoft, Seattle, WA, USA) and analyzed in ArcView 3.3 or ArcGIS (ESRI, Redlands, CA, USA). Movement patterns and habitat use were analyzed using Hooge and Eichenlaub's (1997) Animal Movement Analysis extension for ArcView.

### **Statistical Analysis**

I tested for preferential habitat use of juvenile Wood Storks at two scales using compositional analysis (Aebischer et al. 1993). First, I compared habitat used by each bird (95% fixed kernel density utilization distributions, UD) to total available habitat within the entire range for all tagged storks. I defined the extent of the total habitat available to tagged storks as the area within a minimum convex polygon of all telemetry locations for all birds minus the areas covering the Atlantic Ocean and Gulf of Mexico. Second, utilized habitat (telemetry locations) for each tagged bird was compared to its available habitat within a 95% fixed kernel density utilization distribution, UD. The first analysis examined general habitat preferences for storks in the context of their entire range, while the second analysis examined habitat preferences within each stork's localized area of use (UD).

For each analysis, I tested the null hypothesis that habitat use was random with respect to the habitat categories chosen. For each bird hatched in 2002 that survived at least 3 weeks postfledging, the log-ratios of the utilized habitat composition were compared to the log-ratios of available habitat composition. If habitat use were found to be significantly nonrandom, I tested for specific preferences by comparing proportional use for all habitat types. To avoid using autocorrelated telemetry locations, a maximum of one location per 24 hours per animal was used in this analysis. As storks are capable

of traveling across broad landscapes quickly, I assumed that locations separated by at least 24 hours were biologically independent (Reynolds and Laundré 1990). When multiple locations were available in a 24-hour period, the earliest, best quality (LC 3>2>1) location was selected. Location data were collected from May 2002–October 2003.

Proportional habitat use within 1km buffers of all locations ( $\bar{x} = 147.73$  locations per bird, SE = 18.93, range = 31-332) was pooled and averaged for each stork. Only locations within the 95% fixed kernel UD were included in this analysis. I calculated 95% fixed kernel UDs using least squares cross validation to estimate the optimal smoothing parameter (Silverman 1986; Worton 1989, 1995; Seaman and Powell 1996). UDs were standardized across individuals by determining a median optimal smoothing parameter  $h$  at 95% fixed kernel UD levels during initial calculations (Worton 1995, Churchill et al. 2002). Each stork's UD was recalculated with the parameter set to the median value.

To achieve linear independence of proportions, log-ratios of each used and available habitat were created for each animal by dividing each habitat type proportion by the proportion of upland forest and then taking the  $\log_e$  (Aitchison 1986). The habitat type used as the divisor, upland forest, was randomly selected among all habitat types; the specific habitat chosen does not influence the results as all habitat types are proportional to one another in compositional analysis (Aebischer et al. 1993). To meet the assumption of multivariate normality, I used Wilks' lambda ( $\Lambda$ ) statistic to test for overall habitat selection. Matrices composed of the differences between the log-ratios for each animal were constructed for both used and available habitats. The  $\Lambda$  value, the difference

between the used and available matrices, was compared to a  $\chi^2$  distribution with  $D-1$  degrees of freedom, ( $D$  = number of habitats). A matrix ranking habitat types was created where ranks for each habitat type were assigned in order of use. If overall selection was found, t-tests were used to assess differences among habitat type ranks (Aebischer et al. 1993). Analyses were conducted using the statistical software R (R Foundation for Statistical Computing).

I used 1995 vegetation coverage maps from the National Land Cover Data set (United States Geological Survey). The National Land Cover Data were chosen because they provide 30m<sup>2</sup> resolution within a uniform habitat classification scheme across the range of the focal storks (Florida, Georgia, Alabama, South Carolina, and Mississippi). Similar habitat types were pooled to avoid statistical bias resulting from comparing large numbers of unused habitat types (Aebischer et al. 1993). Twenty habitat types were reduced to eight, with pooled categories listed in parentheses: 1) *developed* (low intensity residential, high-intensity residential and commercial/industrial/ transportation), 2) *barren* (bare rock/sand/clay, quarries/strip mines/gravel pits and transitional), 3) *shrubland*, 4) *herbaceous upland* (grasslands/herbaceous), 5) *cultivated* (orchards/vineyards, pasture/ hay, row crops, small grains, fallow, and urban/recreational grasslands), 6) *wetlands* (woody wetlands and emergent herbaceous wetlands), 7) *open water*, and 8) *forest* (deciduous forest, evergreen forest, and mixed forest).

Mann-Whitney  $U$ -tests were used with a  $Z$ -approximation for bivariate analysis of movement data. Values are reported as mean  $\pm$  SE, and a significance level of  $P \leq 0.05$  was set *a priori* for all statistical tests.

## Results

### Movement Patterns

In 2002, tagged birds were observed foraging with a few kilometers of TW individually and in large mixed-age groups (50–150 individuals) composed of adult and juvenile storks during and following fledging. Similar flocks were not noted in 2003, perhaps due to higher water levels around the colony and fewer numbers of fledged birds.

After juveniles left the natal area, I received no indication that any of the tagged storks traveled together. My ability to detect social relationships among tagged birds was high since their movements were monitored daily, but individuals were rarely within even 50 km of one another. This evidence is consistent with the idea that each tagged bird's behavior was independent of other tagged birds, an important statistical consideration. Many of these birds have frequently visited the same general areas throughout the southeastern United States, though never simultaneously.

The mean known age of tagged storks to fledge from the colony was 81 days in both 2002 ( $n = 14$ ) and in 2003 ( $n = 5$ ). In general, the birds hatched in 2002 (2002 cohort, 29 fledglings, mean fledge date = 9 June 2002) moved north through the large local wetlands within the WCAs, Big Cypress National Preserve (Big Cypress), and A.R.M. Loxahatchee National Wildlife Refuge (Loxahatchee, also known as WCA 1). Within the first 3 weeks of fledging, 2 individuals (7%) visited ENP, 3 (10%) birds visited Big Cypress, 17 birds (59%) visited WCAs 2 or 3, and 4 birds (14%) visited Loxahatchee (Figure 3-2). Mean distance moved within the first 48 hours of fledging was  $60 \pm 1.6$  km ( $n = 15$ ). Within the first week, fifteen (52%) of the fledglings moved into the extensive agricultural lands (Everglades Agricultural Area) surrounding Lake Okeechobee.

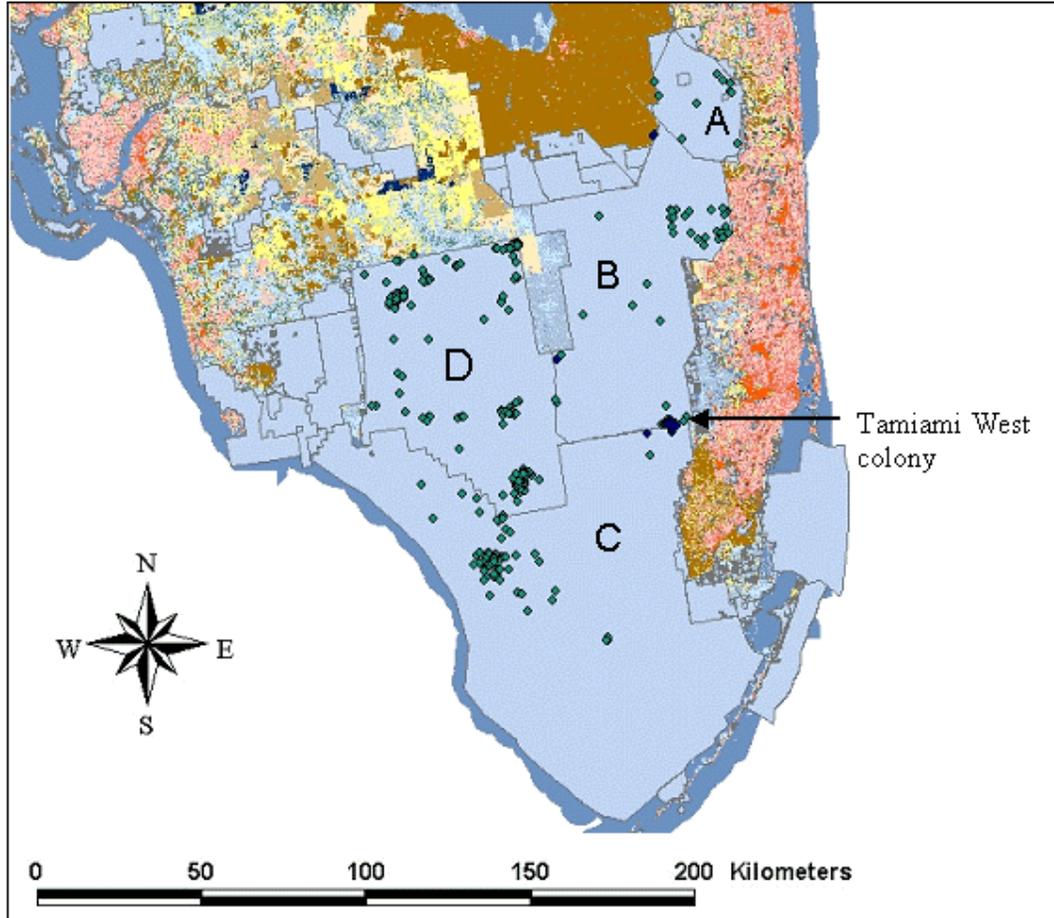


Figure 3-2. Map with all locations of tagged birds from May 2002 – October 2003 within A) Loxahatchee National Wildlife Refuge, B) Water Conservation Areas 2 and 3, C) Everglades National Park, and D) Big Cypress National Preserve.

The initial movements of birds hatched in 2003 (2003 cohort, 16 fledglings, mean fledge date 1 June) were quite different from those of the 2002 cohort. Very few birds used the large local wetlands of the Everglades near the colony. Only two birds had locations within WCA 3A, and both were immediately after fledging. No other locations were identified within the other WCAs, ENP, Big Cypress, or Loxahatchee. Instead, all birds in the 2003 cohort initially flew to the agricultural areas surrounding Lake Okeechobee. Mean distance moved within the first 48 hours of fledging for the 2003

cohort was  $109.5 \pm 3.6$  km ( $n = 10$ ) (Table 3-1). The initial flights by the 2003 cohort were significantly longer than those of the 2002 cohort ( $z = 3.25$ ,  $P = 0.0006$ ).

Following these initial movements, birds from both years quickly moved into the areas in which they then spent the remainder of the summer. I will refer to these areas used during the period June to September as the storks' summer ranges. Of the 27 birds that fledged in 2002, 11 (42%) remained in Florida for the summer of 2002. Although mortality during the first three weeks following fledging was high for the 2003 cohort, (47% of 17 birds died), a similar 44% of the 9 survivors remained in Florida for the summer of 2003. In both years most of these birds summered around the edges of Lake Okeechobee or further west along the Gulf Coast. These "western" birds were located between Tampa and Fort Myers, with a concentration in the C.M. Webb Wildlife Management Area southwest of Port Charlotte. The birds that did not remain in central Florida for the summer continued moving north, spreading across peninsular Florida and the coastal plains of Georgia, South Carolina, Alabama, and Mississippi (Figure 3-3). Although individual movements were highly variable, 79% ( $n = 33$ ) exhibited strong seasonally-dependent movement patterns, which I will henceforth refer to as migrations. In this paper, the term migration means "a regular round-trip movement of individuals between two or more ... seasonal ranges" (White and Garrott 1990). Two birds from the 2002 cohort (8%) and 5 birds from the 2003 cohort (50%) did not demonstrate migratory behavior, but instead remained in south-central Florida in the same area they moved to immediately postfledging.

In 2002, the tagged birds that left Florida did so in a roughly simultaneous way during the second week of June. The rate of movement on the summer ranges was

significantly lower than the rate of movement during travel to the summer range ( $z = 5.22, P < 0.0001, n = 23$ ). The average rate of movement during the northward migration for the birds in the 2002 cohort that exhibited migratory behavior (92%) was  $43.4 \pm 4.0$  km/d ( $n = 22$ ), while their average rate of movement within the summer ranges was  $6.0 \pm 1.1$  km/d ( $n = 24$ ). The rate of movement during the northward migrations for the birds in the 2003 cohort that exhibited migratory behavior (50%) was  $53.0 \pm 4.2$  km/d ( $n = 5$ ), while the average rate of movement within the summer range was  $6.50 \pm 1.15$  km/d ( $n = 9$ ) (Table 3-1).

The northern migrations took an average of 12 days to complete ( $n = 22$ ). On these northern migrations, the birds moved an average of  $388 \pm 42$  km ( $n = 21$ , Table 3-1) from their initial, local dispersal locations. In 2002, the number of days birds exhibited

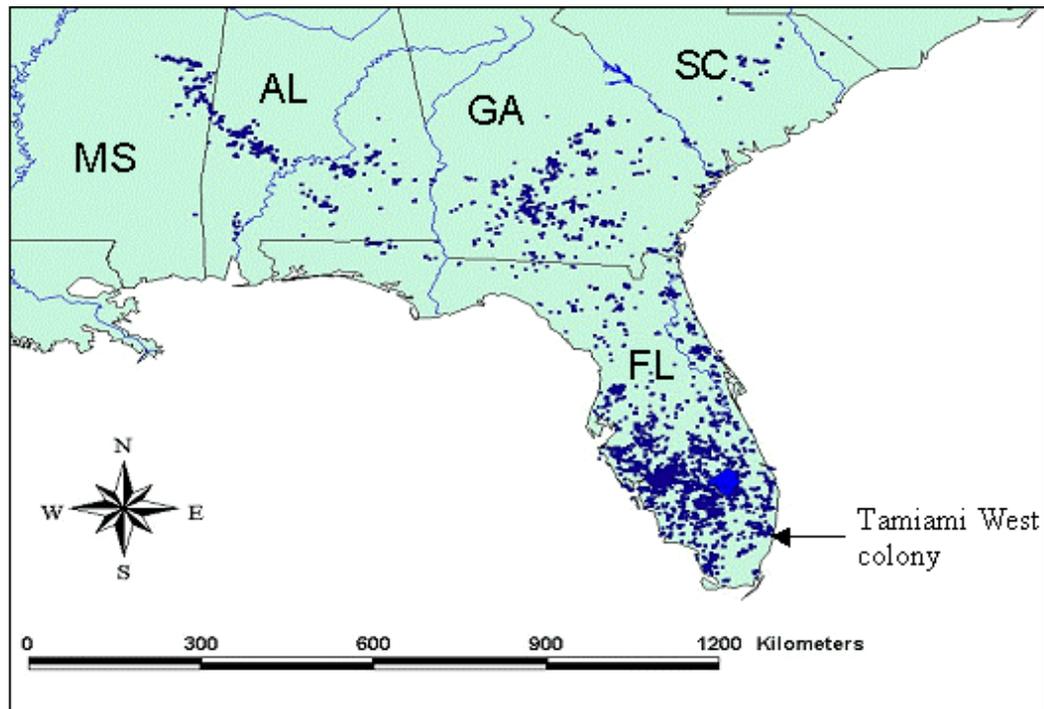


Figure 3-3. Map of all location points for tagged juvenile Wood Storks ( $n = 46$ ) from the Tamiami West colony (N25°45.31, W80°31.90) in Everglades National Park between May 2002 and January 2004.

Table 3-1. First-year movement rates of tagged juvenile Wood Storks between fledging dispersal areas, summer ranges and winter ranges in 2002 and 2003

Cohort	Mean Initial Flight Distance (km)	Initial Average Northward Migration Rate (km/d)	Average Southward Migration Rate (km/d)	Average Movement Rate in Summer Range (km/d)	Average Movement Rate in Winter Range (km/d)	Average Maximum Migration Rate (km/d)	Average Distance from Fledging Dispersal Area to Summer Range (km)	Average Distance from Summer Range to Winter Range (km)
2002	60 ± 1.6 (n = 15)	43.4 ± 4.0 (n = 22)	54.8 ± 6.5 (n = 16)	6.0 ± 1.1 (n = 24)	5.2 ± 0.7 (n = 16)	156 (n = 21)	388 ± 42 (n = 21)	336 ± 39 (n = 16)
2003	109.5 ± 3.6 (n = 10)	53.0 ± 4.2 (n = 5)	—	6.5 ± 1.2 (n = 9)	—	106 (n = 5)	387 ± 64 (n = 5)	—

migratory behavior was not significantly different between birds that summered in FL and those that left Florida ( $z = 0.668, P = 0.252, n = 22$ ). The average rate of travel during the northward migrations was greater for birds that established summer ranges outside Florida compared to the rate of travel for the birds that summered in Florida in 2002, although this difference was not quite significant ( $z = 1.537, P = 0.062, n = 22$ ).

During the migration period before birds established summer ranges, 11 birds moved through Georgia, 8 through Alabama, 3 through South Carolina, and 1 briefly crossed the border into North Carolina. A total of five birds eventually moved from

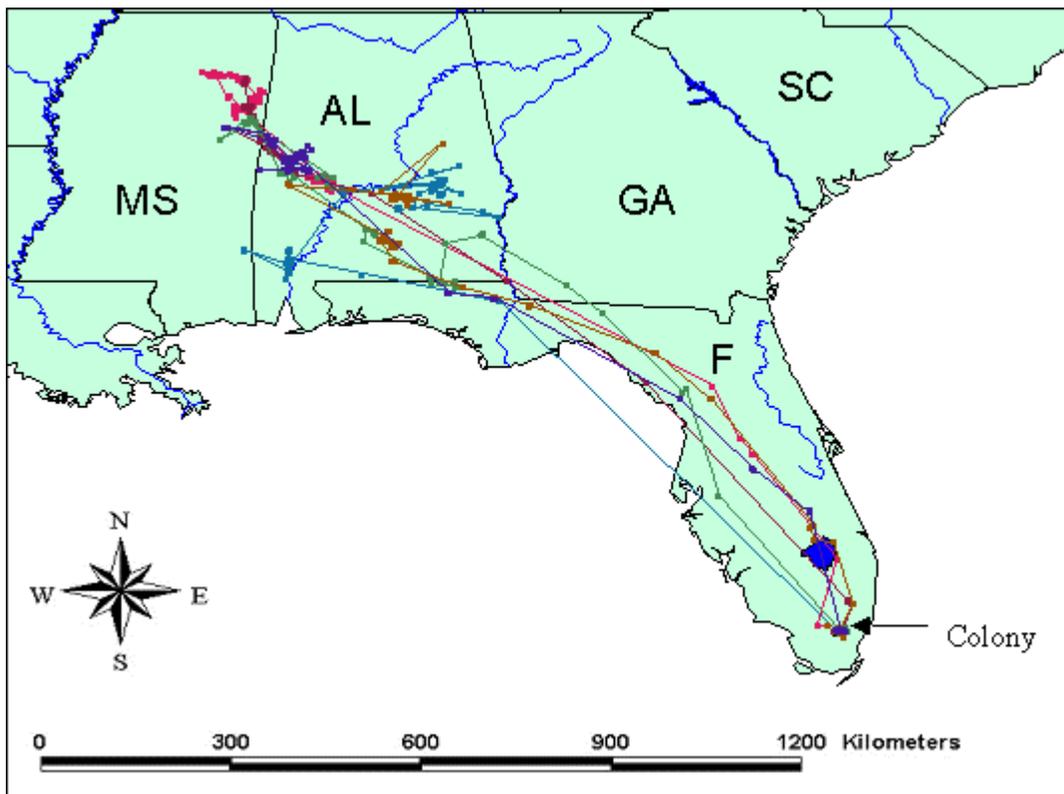


Figure 3-4. Migratory path and movements of satellite tagged juvenile Everglades Wood Storks that summered in Alabama (AL) and Mississippi (MS) in 2002. Each color represents a different individual ( $n = 6$ ). The lines connect consecutive location points obtained from satellite data.

Alabama into Mississippi, with the first bird arriving in Alabama the last week of June 2002. Fifteen of the 16 birds in the 2002 cohort that traveled outside Florida established summer ranges outside of Florida: 2 (13%) in South Carolina, 7 (47%) in Georgia, and 6 (40%) in western Alabama/eastern Mississippi. The remaining bird established a summer range in northeast Florida around Jacksonville. Unlike the 2002 cohort, which spread across six southeastern states, the 5 birds that left Florida from the 2003 cohort all established summer ranges in Georgia. These birds initially moved into Georgia between 12 June and 6 July 2003.

The tagged birds apparently did not travel together on their migrations, nor did all of them follow the same route. In 2002, three birds left southern Florida and migrated north through the west-central portion of peninsular Florida, turning northwest into Alabama once they reached the Florida panhandle. Two other birds from the same colony-year cohort arrived at the same destination, but followed a coastal path through Florida along the Gulf of Mexico before making their way north into Alabama. All five birds remained in Alabama or moved into northeastern Mississippi for the remainder of the summer (Figure 3-4). These birds then established summer home ranges along the Tennessee-Tombigbee Waterway (Tenn-Tom) in Alabama and Mississippi. An additional six birds spent most of their summer (June–September) in Georgia in 2002 (Figure 3-6). Of these, two migrated north along the Gulf Coast of Florida, two along the Atlantic Coast, and two directly through the center of peninsular Florida after leaving the colony.

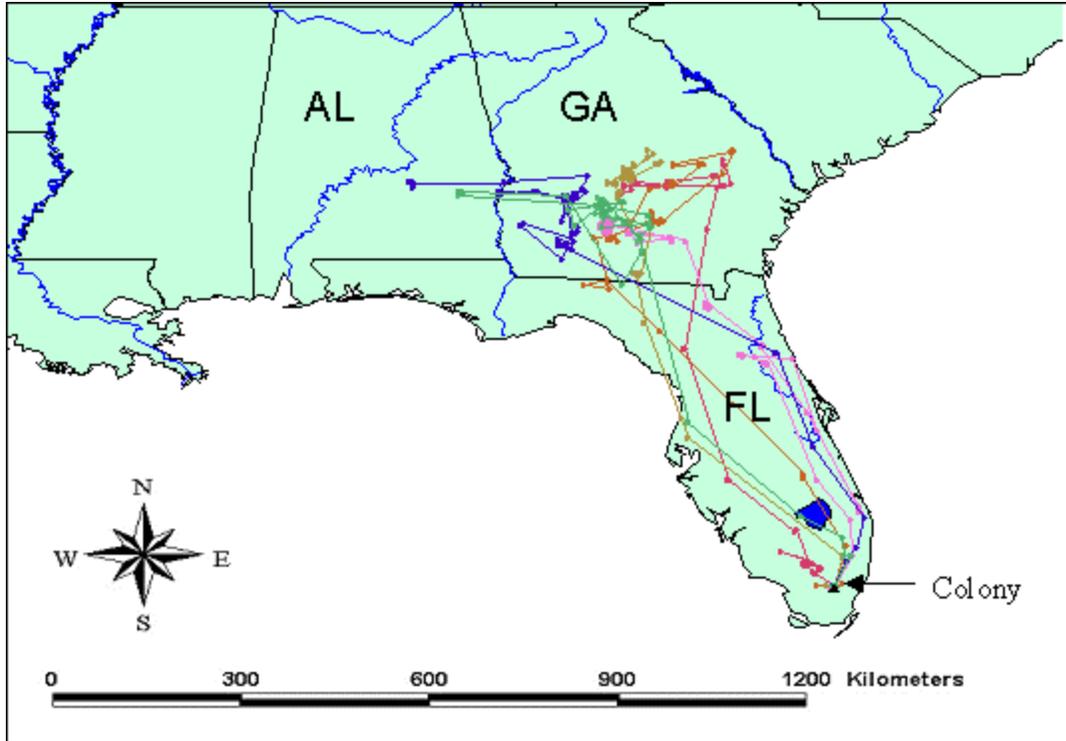


Figure 3-5. Migratory pathway of satellite juvenile Wood Storks tagged in Florida (FL) that summered in Georgia (GA) in 2002. Each color represents a different individual ( $n = 7$ ). The lines connect consecutive location points obtained from satellite data.

By the beginning of November 2002, all birds located outside of Florida had moved back south into central and southern Florida (Figure 3-6), where they remained through mid-May 2003. Three of the five birds from the 2003 cohort that established summer ranges in Georgia died before returning south for the winter, while another died in Florida immediately following the southward migration. Following relatively rapid movements of the 2002 cohort during the southward migration ( $\bar{x} = 54.8 \pm 6.5$  km/d,  $n = 16$ ), daily movement distances decreased markedly in winter ( $\bar{x} = 5.2 \pm 0.7$  km/d,  $n = 16$ , Table 3-1). I will refer to these areas of use from approximately November 2002 to May 2003 as the birds' winter ranges. Southwest Florida around Lake Okeechobee and

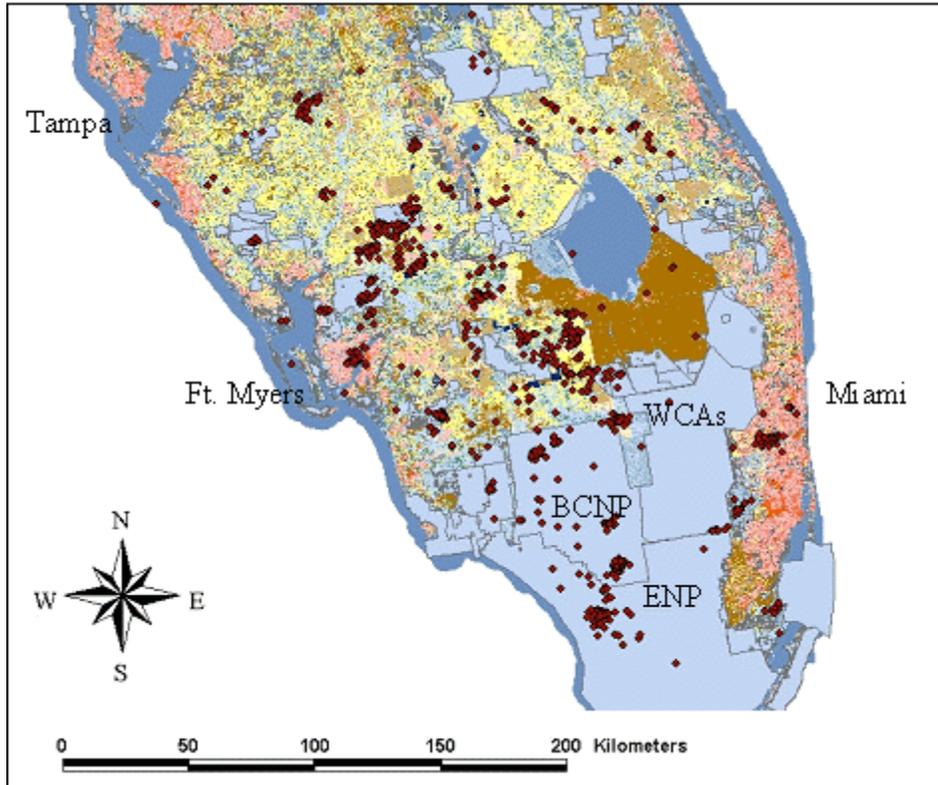


Figure 3-6. Locations of 17 juvenile Wood Storks from Nov 2002 – April 2003. Stork locations were concentrated in southwestern Florida. ENP = Everglades National Park and WCAs = Everglades Water Conservation Areas, and BCNP = Big Cypress National Park. The pink areas are highly urbanized zones. The light blue patches with gray borders indicate conservation areas.

along the Gulf Coast between Tampa and Ft. Myers was the most heavily used wintering areas for these juvenile birds.

The 2002 cohort remained in south and central Florida for most of the spring and summer of 2003. Although the 2002 cohort did begin moving north again by late May 2003, only 3 of the remaining 14 live birds (12%) left Florida during the summer of 2003. All three birds returned to the same summer range (successive summer ranges visually overlapped by at least 75%) they had used in 2002: one to Georgia, and two to the Tenn-Tom region of Alabama and Mississippi. All of the birds that summered in Florida

returned to those same areas in 2003 where they had been in 2002. In total, 82% ( $n = 11$ ) of the birds demonstrated fidelity in their 2<sup>nd</sup> year by returning to the same summer range established in their first year.

The average total distance moved during the second year (summer 2003) northern migrations by the 2002 cohort was  $241 \pm 38$  km ( $n = 8$ ). Total distances moved during migrations were calculated from the last location prior to accelerated travel rates to the location where movement once again returned to a lower travel rate. The distance traveled to the summer locations did not differ significantly for the 2002 cohort between their first and second years ( $z = 0.70$ ,  $P = 0.23$ ,  $n = 7$ ). The entire 2002 cohort returned to south/central Florida by mid October in both 2002 and 2003.

The rate of movement for the 2002 cohort during the 2<sup>nd</sup> summer was similar to that during the first summer, at  $5.4 \pm 0.71$  km/d ( $n = 11$ ). The average maximum rate for each individual during either the summer or winter migratory period was 156 km/d for the 2002 cohort ( $n = 21$ ) and 106 km/d for the 2003 cohort ( $n = 5$ ) (Table 3-1). The maximum rate of travel for any individual was 184 km/d, recorded for a bird during its first-year summer migration from southern Florida to Alabama. Although 79% ( $n = 33$ ) of all birds that survived at least 3 weeks of age exhibited migratory behavior, 2 birds from the 2002 cohort and 5 birds from the 2003 cohort did not (i.e., they stayed in south-central Florida in the same region they moved to initially upon fledging). At no time during the 18 months following fledging did any of the 2002 cohort spend more than 1 day within 20 km of its natal colony.

Table 3-2. Simplified ranking matrix of habitat preferences for juvenile Wood Storks of the 2002 cohort based on comparing proportional habitat used with proportional habitat availability across the entire area used by all tagged storks

	Open Water	Developed	Barren	Shrubland	Herbaceous Uplands	Crops	Wetlands	Upland Forest	Rank
Open Water		+++	+++	+++	-	---	---	---	3
Developed	-		+	+++	-	---	---	---	2
Barren	---	-		+++	---	---	---	---	1
Shrubland	---	---	---		---	---	---	---	0
Upland Forest	+++	+++	+++	+++	+++	-	-		5
Wetlands Combined	+++	+++	+++	+++	+++	+		+	7
Herbaceous Upland	+	+	+++	+++		---	---	---	4
Cultivated/Planted	+++	+++	+++	+++	+++		-	+	6

Signs indicate if a row habitat was used more (+) or less (-) than a column habitat relative to availability. A triple sign indicates a significant deviation from random at  $P < 0.05$ . Ranks are based on the number of significant differences.

### **Habitat Use versus Availability**

Habitat use (area within 95% UDs) differed significantly from habitat availability (MCP of all telemetry locations) across the entire range of tagged storks ( $\Lambda = 0.50$ ,  $\chi^2_7 = 14.07$ ,  $P = 0.027$ ). The ranking matrix for habitat use indicated use of Wetlands > Cultivated Lands > Upland Forest >>> Herbaceous Upland > Open Water > Developed > Barren >>> Shrubland. Wetlands, Cultivated, and Upland Forest habitats were preferentially selected over all other habitat types while Shrubland was used significantly less than all other habitat types in relation to availability (Table 3-2).

Habitat use (telemetry locations) did not differ significantly from habitat availability within the 95% UDs ( $\Lambda = 0.57$ ,  $\chi^2_7 = 12.67$ ,  $P = 0.081$ ), although the marginally significant result suggest that habitat use was not random. The ranking matrix for habitat use within the 95% fixed kernels indicated use of Cultivated Lands > Herbaceous Uplands > Wetlands >>> Upland Forests >>> Shrubland > Barren > Developed > Open Water. Cultivated Lands, Herbaceous Uplands, and Wetlands were all used significantly more than all other habitat types (Table 3-3).

## **Discussion**

### **Movement Patterns**

This was the first study to monitor the movement patterns and habitat use of a robust sample of juvenile Wood Storks at the landscape scale over multiple seasons, and the only study to date to focus on juvenile movement behavior. Although I had predicted that storks would heavily use the local wetlands in southern Florida following fledging, this was only partially true in 2002 and not evidenced at all in 2003. In 2003, the above

Table 3-3. Simplified ranking matrix of habitat preferences for juvenile Wood Storks of the 2002 cohort based on comparing localized proportional habitat use with proportional habitat composition within 95% fixed kernel utilization distributions

	Open Water	Developed	Barren	Shrubland	Herbaceous Uplands	Crops	Wetlands	Upland Forest	Rank
Open Water		-	-	-	---	---	---	-	0
Developed	+		-	---	---	---	---	---	1
Barren	+	+		-	---	---	---	-	2
Shrubland	+	+++	+		---	---	-	-	3
Upland Forest	+	+++	+	+++	---	---	---		4
Wetlands	+++	+++	+++	+	-	-		+++	5
Herbaceous Upland	+++	+++	+++	+++		-	+	+++	6
Cultivated Lands	+++	+++	+++	+	+		+	+++	7

Signs indicate if a row habitat was used more (+) or less (-) than a column habitat relative to availability. A triple sign indicates a significant deviation from random at  $P < 0.05$ . Ranks are based on the number of significant differences.

average water levels in WCA 3A, WCA 3B, and ENP (Sklar 2003) probably precluded the development of suitable foraging habitats near the colony throughout much of the nesting season. The lengthy first-flights were likely to have been energetically costly to the young, inexperienced birds and may have dramatically impacted the survival of the 2003 cohort (Bryan et al. 1995).

Following the initial movements, two periods of high mobility were identified for the storks in both years: 1) rapid dispersal north from southern Florida in June, followed by 2) a return to central and southern Florida in September/October. These patterns, observed in both 1<sup>st</sup> and 2<sup>nd</sup> year birds, matched my predictions and confirmed the previous findings described in Coulter et al. (1999).

In both years, the movement of tagged storks out of southern Florida coincided with the advent of the rainy season (May–June). The only exception was a second-year bird that remained in the metropolitan area near Fort Lauderdale from December 2002 through January 2004, and probably used a unique niche among urban ponds and canals. The overwhelming evidence from my study and from previous work implies that habitat conditions during the rainy season in southern Florida are highly inappropriate for storks. Storks in the Llanos of Venezuela and the Usumacinta wetlands of southern Mexico also leave the nesting grounds during the raining season (Coulter et al. 1999).

In general, rising water triggers abandonment of nesting by storks, and tends to disperse foraging birds (Kahl 1964, Kushlan 1987, Frederick and Collopy 1989, Frederick and Spalding 1994, Ramo and Busto 1992, Ogden 1994, Hoffman et al. 1994), because rising water disperses prey. This mechanism suggests strongly that storks are moving from the Everglades ecosystem of southern Florida northward during summer

months in search of better food availability. The pattern also suggests that young are fledging at a time when their local foraging environment is largely hostile, which may have ramifications for their survival.

Florida is obviously capable of supporting some storks during the summer months, as approximately 43% of the tagged juveniles stayed in central Florida or northeastern Florida in both years. Over half of the tagged storks moved to other states, flying with elevated rates of travel past areas in central and northern Florida where other tagged conspecifics established summer ranges. The results suggest that the availability of adequate foraging habitats in summer may be limited in Florida, at least in some years, and that the quality of foraging conditions in areas outside of Florida is worth the cost of the lengthy flight over unfamiliar landscapes. The southern coastal plain is typically experiencing a drying pattern during summer months, the opposite of conditions in southern Florida.

In my study, 82% of juvenile storks exhibited circannual movement patterns, returning seasonally to specific areas within Florida, Georgia, Alabama, and Mississippi in summer after wintering in southern Florida. This demonstrates evidence of migratory behavior, with rapid, predictable, biannual movement patterns, and philopatry to defined areas within a given season. The European White Stork (*Ciconia ciconia*) is migratory (Liechti et al. 1996, Berthold et al. 2002, Chernetsov et al. 2004), and the Wood Stork's congeners, the Yellow-billed Stork (*Mycteria ibis*), Painted Stork (*Mycteria leucocephala*), and Milky Stork (*Mycteria cinerea*), all display either migratory or nomadic behavior (Hancock et al. 1992).

None of the tagged storks traveled together. This result was interesting considering that many of the young birds fledged from adjacent nests and had plenty of opportunity to develop social relationships while in the colony. Storks are known to exhibit social foraging, nesting, roosting and strongly flocking (Kahl 1972, Comer 1985, Coulter and Bryan 1993), and the birds I tracked almost certainly socialized with other storks. It is possible that some juvenile Wood Storks followed adult storks during migrations, which would explain the rapid, direct movements to the summer ranges. In a recent displacement experiment, Chernetsov et al. (2004) found that naïve juvenile White Storks that were separated from adults did not exhibit expected autumnal migratory behavior. Chernetsov et al. (2004) suggested that White Storks, and perhaps other soaring migrants, rely on social interactions with experienced conspecifics during their first migration.

Dispersing juvenile storks demonstrated high fidelity to their summer ranges, with 82% of the tagged storks returning to the same areas in the 2<sup>nd</sup> summer. The summer ranges did not overlap completely between years, however, indicating that their specific movements within a given season varied. Given what is known about the ephemeral nature of foraging conditions for this species, it seems likely that the birds locally shifted locations as resources were depleted and new foraging areas became available.

Despite the large percentage of birds from the 2002 cohort returning to the same summer ranges in their second year, the spatial distribution of tagged birds was not consistent between the two cohorts. In 2002, tagged storks spread across five states, while in 2003 the 5 birds that left Florida only established summer ranges in Georgia. This apparent shift in distribution to only 2 states suggests that first-year summer ranges may be established based on a number of factors. I hypothesize that juvenile storks may

initially establish their first-year summer range based on environmental cues and/or adult behavior, while in subsequent years prior experience may play a greater role.

Similar seasonal movement patterns have been noted in other Wood Stork populations. In the United States, thousands of storks in the United States annually converge into Texas, Arkansas, Louisiana and the lower Mississippi floodplain in the summer months. Large numbers of storks have been observed flying north along the Gulf Coast of Mexico in June (Coulter et al. 1999), and are consistently seen soaring south through Veracruz, Mexico (up to 4,000–5,000 per day) during peak periods of fall raptor migration (Weidensaul 1999).

Of 1589 nestlings banded in southern Florida, J. Ogden (unpubl. data, study cited in Coulter et al. 1999) could calculate crude movement rates for only six birds from southern Florida. Movement rates for 5 of the birds ranged from 10.0–20.8 km/d, while 1 stork averaged 50.0 km/d. For juvenile birds followed directly by aircraft, estimates ranged between 35 and 48 km/h ( $n = 5$ ). With a minimum of six hours of flying time per day, Ogden estimated that the juveniles could travel 210–288 km/d (Coulter 1999). Adults are known to commonly travel 50 km one-way from a colony during foraging flights, although a maximum of 130 km one-way has been recorded (Browder 1978; Clark 1978; Kushlan 1986; Bryan and Coulter 1987; J. Ogden, unpublished data).

By comparison, the maximum rate of travel recorded for any stork in the current study was 184 km/d, with the average maximum rates during migration at 156 km/d (2002 cohort) and 106 km/d (2003 cohort). Although these values are accurate, they must be considered minimum travel rates since it is not clear how many hours of actual travel were involved. Based on minimum travel rates estimated from this and Ogden's

study, it is likely that storks may spend at least 6 hours a day in flight during peak migration periods (Coulter et al 1999).

### **Habitat Use**

Across the entire range of tagged storks, habitat use differed significantly from habitat availability ( $P = 0.027$ ). The range of tagged storks was consistent with the known range of the U.S. breeding population of storks (Coulter et al. 1999). From the eight habitat types I used for analysis, storks showed the strongest selection for landscape mosaics dominated by wetlands, cultivated lands and/or upland forest in relation to their availability. The lack of significant differences in use among the top three habitat types may indicate (1) the high degree of heterogeneity within the landscape, (2) the lack of resolution of the telemetry data, and/or (3) that the fairly broad habitat classifications may have obscured biologically important habitat differences.

These findings partially match my prediction of greater use of periodically inundated habitats (wetlands and cultivated lands), except for the finding that upland forests were preferred. Storks commonly use hydric forested habitats like bottomland hardwood forests for roosting (Pearson et al. 1992, Bryan et al. 1995) and nesting (Coulter et al. 1987, Coulter and Bryan 1993, Pearson et al. 1993, Rodgers et al. 1996, Coulter et al. 1999). The storks in my study may have spent relatively more time roosting compared to foraging, which might explain the heavy use of forested habitats. Storks may also have been using small isolated streams or wetlands within a denser mosaic of upland forest. If this were true, the scale of 1km buffering radius around each telemetry location may have overstated the importance of forests to these birds. Without more precise location information, it is difficult to determine the actual role of upland forests in stork habitat needs. It is clear, however, that storks do prefer habitats that occur

in matrices dominated by upland forests; for management purposes this is an important finding.

I also looked at habitat use relative to availability within the 95% UDs specific for each of the tagged birds. I found strong, though not significant, evidence for habitat selection ( $P = 0.081$ ) at this localized level. At this scale, storks showed significant preference for landscapes dominated by cultivated lands, herbaceous uplands and wetlands as compared to the other habitats. In addition, landscapes dominated by upland forest were selected significantly more often than landscapes dominated by shrubland, barren, developed, or open water habitats. Although storks showed preferences for wetlands at both the general and local scales, there was no evidence to validate my prediction that wetlands are preferred over other inundated habitats such as agricultural and cultivated lands. Again, there is the potential problem that the scale at which I identified use (1 km buffers around telemetry locations) was inappropriate if storks were choosing habitats at a smaller scale.

In general the tagged birds avoided urban areas at both the regional and local levels, except for one bird from the 2002 cohort that settled in the metropolitan area near Ft. Lauderdale from December 2002 – present. Although the birds were often located just beyond the periphery of a town or city, they were infrequently found within high intensity residential or commercial areas.

Storks are quite capable of moving large distances through the air, and the concept of physical or man-made barriers to their movement (such as roads) does not apply in the traditional sense (Meffe et al. 1997). One potential restriction to their range was seen in that they did not move farther west than eastern MS, despite the fact that western states

hosted large numbers of storks in summer months (Hancock et al. 1992, Coulter et al. 1999). This pattern is consistent with the findings for juvenile storks from southern Florida in the 1970s (Coulter et al. 1999). The tagged birds also generally avoided coastal wetlands, traveling inland instead. This was unexpected, as storks commonly use estuarine marshes for both foraging and colony sites in Georgia (Pearson et al. 1992, Rodgers et al. 1996, Gaines et al. 1998). I saw no indications that the storks migrated over the Atlantic or Gulf of Mexico.

### **Conservation Implications**

It is known that the Wood Stork breeding range increased across the southeast in the 1980s and 1990s (Ogden 1994, Rodgers and Schwikert 1997), though the historic breeding range will probably never be known. The general range of movements of juvenile storks reported here were consistent with the results of J. Ogden's tag study (unpubl. data, cited in Coulter et al. 1999). A true comparison of Ogden's study with this one is problematic as tag-resighting rates were generally low, and resighting rates in Alabama and Mississippi may have differed from those in Florida and Georgia. Nevertheless, there is evidence to indicate an overall increase in stork use in Mississippi and Alabama.

Only 2 of 66 (3.0%) storks banded in southern Florida in Ogden's study were resighted in Alabama or Mississippi, contrasted with 8 of 29 (27.6%) fledged birds in 2002 that traveled to and established summer ranges in these two states (Ogden unpubl. data). Since the 1960s, there has been a large increase in the number of storks reported at both the Noxubee National Wildlife Refuge, Mississippi and along the Tenn-Tom in Alabama and Mississippi, many of which likely originated from southern Florida populations (Richardson 2003).

In both this and Ogden's study, the Tenn-Tom region of west-central Alabama and east-central Mississippi was the most heavily used area in these states. Twenty-one percent of tagged, fledged birds used this waterway in 2002. Construction and filling of lakes along the Tenn-Tom during the 1970s and 1980s destroyed almost 14,000 ha of bottomland hardwood forests (McClure and Connell 2001), which may explain the relatively low use of this area by juvenile storks in Ogden's study. The first large concentrations of storks noticed by Tenn-Tom biologists in this area were during the late 1980s, after major construction on the waterway was completed (G. Houston unpubl. data). The US Army Corps of Engineers undertook additional wildlife habitat mitigation and replanting efforts in the mid 1990s however, including the acquisition of 35,000 ha within and surrounding the Tenn-Tom. Many of these habitats are now being exclusively managed for wildlife. It is very likely that stork movements in Alabama and Mississippi, and particularly along the Tenn-Tom, have increased dramatically in recent years in response to the land-use changes (Richardson 2003).

Until recently, storks sighted in Mississippi in summer months were assumed to have originated from the Mexican population (Coulter et al. 1999). My study documents heavy use of the area by the population breeding in the southeastern U.S. This area in eastern Mississippi appears to be an important summering location for Wood Storks, where birds spent up to  $\frac{1}{4}$  of their year. I recommend modifying the United States Fish and Wildlife Recovery Plan for the Wood Stork to include Mississippi in its list of southeastern states where storks are protected under Federal Law.

The longevity and easy detectability of stork colony locations make preservation of nesting sites a good conservation strategy for the species (Frederick and Ogden 1997).

However, based on their extensive use of a wide variety of landscapes across the southeastern United States during much of the year, concentrating recovery efforts solely on colony locations may not offer adequate protection to the species. Additional strategies for identifying and protecting important stork habitats outside the breeding season have proven more difficult to determine. The heavy-use areas, movement patterns, and migratory behavior of juvenile storks have now been partially identified in my study, although the inaccuracies involved in the type of satellite telemetry used here have made it difficult to identify which specific wetlands should be targeted for protection.

Additional satellite transmitters equipped with GPS location capabilities were deployed on juvenile storks in the spring of 2004 by the University of Florida. These 45 gram solar-powered GPS satellite transmitters (Microwave Telemetry, Inc., Columbia, MD, USA.) are accurate within 18 m of the true location, which will offer significantly better quality location information than the transmitters used in my study (1 km accuracy). This is a necessary next step for determining stork movement patterns and habitats needs. Identifying specific parcels of land used by tagged storks will allow for the development of a predictive habitat model for the species.

The storks' heavy use of landscapes dominated by cultivated lands offers a challenging conservation problem. Foraging within flooded agricultural lands or along drainage ditches may pose serious health risks to the birds (Parsons et al. 2000). Most of these agricultural lands are privately owned, making it more difficult to implement and enforce broad conservation initiatives. Once exact foraging locations within agricultural

landscapes are identified via improved telemetry data, potential health hazards should be investigated further.

Additional comparisons of juvenile and adult stork movement patterns should be conducted to identify whether the patterns observed in my study were unique to juveniles, or if adult storks also undergo predictable seasonal migrations. By June 2004, 10 storks from the 2002 cohort and 1 from the 2003 cohort remained alive. The transmitters used in my study are guaranteed to last at least three years and possibly more, so there is good potential to obtain information on adult movement behavior within the next few years using these same individuals.

Further analyses of movement patterns of storks hatched outside the Everglades system are necessary for establishing better conservation and management plans for the entire U.S. population. The broad differences between movement behaviors by the 2002 and 2003 cohorts demonstrated the necessity of monitoring stork movements over multiple years. Continued monitoring of these animals will allow managers to assess the full range of stork movements and allow for further hypothesis testing.

## CHAPTER 4 CONCLUSIONS

Occasional favorable years of high productivity are assumed to compensate for species, like Wood Storks, which may face many years of poor nesting success (Saether et al. 1996). The numbers of nesting attempts by storks have risen in the past decade, indicating some level of recovery for the U.S. population (Ogden 2002). Although the species' long lifespan may offset the lengthy investment (four months) of raising young and the infrequency of successful nesting, it may also hinder our abilities to identify gradual perturbations to the overall population. My study indicated that in a fairly successful year (2003, Gawlik and Crozier 2003), in which the storks faced high abandonment rates but a portion of young did fledge, none of those birds are likely to survive to reproduce. Even in what is generally considered a highly successful breeding year (2002, Oberhofer and Bass 2002), where most nests survived to fledge young, I estimated that only 17% may make it to breeding age. Relying solely on nesting attempt records or numbers of fledged young, factors that will be used for delisting this federally endangered species (U. S. Fish and Wildlife Service 1997), may grossly overestimate the success of the species. A greater understanding of postfledging survival rates and their role in population regulation is therefore needed.

In both years of the study, mortality rates were highest in the first months following fledging. Young storks in the 2003 cohort were largely unable to practice important foraging skills prior to fledging due to high water levels. This inexperience probably contributed significantly to the 60% mortality rates observed during the first month after

fledging. Good management for storks in the Everglades should include maintaining adequate foraging conditions (e.g., shallow and declining depths, open sparsely vegetated habitat) within 60km of colony sites throughout the nesting season, especially leading up to and including the time of fledging.

The ability of storks to move across large tracts of largely unsuitable habitat is probably an adaptation to living in a highly variable environment where resources are patchily distributed and unpredictable. Storks may spend up to four years away from colony sites prior to breeding, and half of the year away once they reach reproductive age. Based on their extensive use of a wide variety of landscapes across the southeastern United States during much of the year, concentrating recovery efforts solely on colony locations may not offer adequate protection to the species. Additional comparisons of juveniles and adult stork movement patterns should be conducted to identify whether the movement patterns observed in my study were unique to juveniles, or if adult storks also undergo predictable seasonal migrations. Further analyses of movement patterns of storks born outside the Everglades system are also necessary for establishing better conservation and management plans for the entire SE population.

The storks' heavy use of landscapes dominated by cultivated lands offers a challenging conservation problem, as foraging within flooded agricultural lands or along drainage ditches may pose serious health risks to the birds (Parsons et al. 2000). The private ownership of most agricultural lands may also make implementation and enforcement of broad conservation initiatives difficult.

The large variation in survival rates, effects of health on survival, and movement patterns between years demonstrated the necessity of monitoring this species over

multiple years. Continuing similar research with juvenile storks will enable us to fully understand the interannual variability in survival rates and the factors affecting survival. Conducting similar studies with adult storks would also provide much needed information on longevity, age at first breeding, and variability in survival rates. Long term monitoring and a functional demographic model will allow managers and biologists to understand the population dynamics of Wood Storks, enabling the development of better conservation strategies.

APPENDIX A  
HARNESS DESIGN AND EFFICACY OF USING SATELLITE TRANSMITTERS

**Harness Design**

Larry Bryan of Savannah River Ecology Lab developed a backpack harness for satellite transmitter placement on adult Wood Storks in which he attached four pieces of Teflon ribbon to a satellite transmitter, fitted each harness to the exact dimensions of the bird in hand, and secured the ribbon pieces on the bird's chest with a metal grommet (L. Bryan, unpubl. data). I modified Bryan's design by sewing two pieces of Teflon ribbon to the transmitter prior to having the bird in hand. Each satellite transmitter had three points of attachment: one centrally located on the anterior end of the transmitter away from the antenna, and two located posteriorly on either side of the transmitter (Figure A-1). Each end of a 43 x 1 cm piece of ribbon was looped through the anterior hook, overlapping 3 cm on itself, and sewn using 2-gauge Nylon thread. A second ribbon, 45 x 1 cm, was looped through a side attachment hook and secured by doubling and sewing (as above). All ends of ribbon and stitchings were further strengthened with a drop of Dritz Fray Check (Prym-Dritz Corporation, Spartanburg, SC, USA), a liquid anti-raveling agent. The harness dimensions were obtained from maximum body measurements of adult male and female captive Wood Storks at Homosassa Spring Wildlife State Park, Homosassa, Florida.

The storks being tagged were not fully grown, presenting the problem of creating a harness that would fit firmly on both adults and juveniles. Although juveniles approach adult size by 4-6 weeks, they are noticeably smaller than adults, with culmen length at

fledging 50 mm shorter than those of adults (Clark 1978), and their pectoralis mass has not developed fully due to relatively little opportunity for flight. To accommodate growth of juveniles, I designed an adjustable backpack harness that would fit adults and juveniles. The flexible harness concept was developed for White Ibises by J. Semones (2003). For storks, I stitched a single ¼ inch knit polyester elastic thread (56% polyester, 44% rubber) along the length of each Teflon ribbon. When stretched taut, the ribbon easily expanded to its full length, however when relaxed, the elastic resulted in a mild bunching along the length of the ribbon that held the transmitter in place more firmly on the bird.

With the hooded bird in hand, the anterior Teflon neck loop was slipped over the bird's head and neck so that the transmitter rested centrally on the bird's mid-back (Figure A-1). The unattached end of the side ribbon was then drawn under one wing, looped once through the neck loop on the chest, and brought across the chest and under the opposite wing. After ensuring flight feathers were not obstructed, I smoothed body feathers around the harness, checked that the ribbon was lying flat on the bird's body, looped the free end of the ribbon through the remaining unused side attachment point on the transmitter, and stitched the free end closed in the manner previously described. After minor adjustments for central placement of the transmitter on the back of the bird, the point at which the two ribbons overlapped on the chest of the bird was also stitched to ensure a better fit and prevent unnecessary sliding of the transmitter along the back until the bird reached full size. New stitchings were further strengthened using a drop of liquid anti-raveling agent. Each harness was double checked to ensure proper fit for the bird,

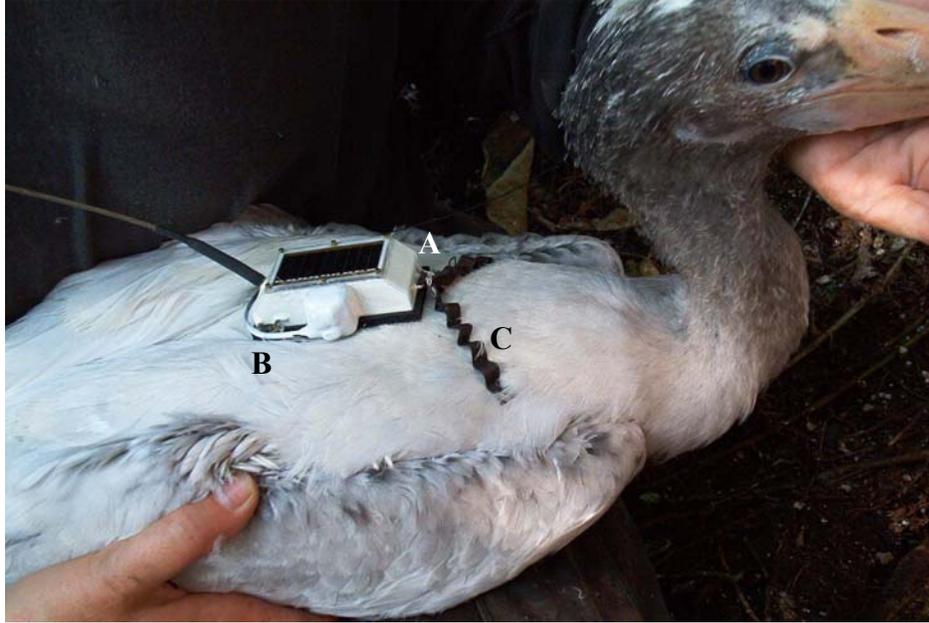


Figure A-1. A satellite (30g PTT) and radio (10g VHF) transmitter attached to a juvenile Wood Stork using a Teflon harness. The neck loop was attached to the anterior end of the transmitter away from the antenna (A), while the posterior loop attached to the sides of the transmitter passed under one wing, through the neck loop, and under the opposite wing (B). Elastic thread sewn in the Teflon ribbons (C) allowed for an expandable yet snug fit to the bird until it attained adult size.

after which I removed the hood from the bird and returned it to its nest. Each bird was handled for approximately 45 minutes. Upon replacement in the nest, birds were visually monitored to ensure they had adequately recovered to sit or stand in the nest.

### **Efficacy of Teflon Harnesses**

Prior to fledging, storks were visually monitored on subsequent visits to ensure that harness fit was not hampering movements or agility of the birds. There were no indications that the harnesses altered behavior or movements or caused chafing, and approximately 25 tagged individuals were observed flying in an apparently normal fashion when disturbed from their nest or roost. There were no signs of wear on any retrieved carcasses, although most were reduced to bones and feathers by the time of retrieval due to high decomposition rates.

The Teflon harness functioned very well for affixing transmitters to sub-adult storks. The mild elasticity of the harness allowed for additional growth of the juvenile, provided a closer fit, and prevented the transmitter from sliding. Although the color of recovered harnesses appeared moderately faded, the Teflon ribbons did not appear to be damaged or to have lost their resilience in any way. Although several transmitters recovered in the colony had torn or missing harnesses, I assumed these had been ripped apart by vultures, not by the storks themselves. All transmitters recovered on carcasses appeared fully intact and had caused no noticeable harm to the wearer (i.e., no body limbs or foreign materials caught or abrasions on the body).

#### **Efficacy of Satellite Transmitters**

In 2002, three grounded VHF transmitters were detached from the PTT when vultures scavenged the carcass, and these PTTs were not recovered. Despite taking additional precautions to secure each VHF to its PTT with two machine screws in 2003, in two known cases the VHF transmitters were detached from the PTT by scavengers. In another case, a VHF transmitter was detached in the colony while the PTT remained on the bird (unknown cause); I continued to receive PTT data for this bird for 14 months after fledging.

As of 15 January 2004, I had relocated 7 PTT and 9 VHF grounded transmitters deployed in 2002 and 15 PTTs and 18 VHF grounded transmitters deployed in 2003. Three sets of transmitters in 2002 and nine sets of transmitters in 2003 were taken off birds that died in sufficient time to be refitted with new harnesses and placed on additional birds. The success rate of relocating grounded transmitters within the colony was much higher in both years (2002: 67%,  $n = 6$ ; 2003: 57%,  $n = 21$ ) than relocating a transmitter from a fledged bird (2002: 20%,  $n = 15$ ; 2003: 38%,  $n = 16$ ). Mortalities of

prefledged birds were verified much more quickly while under daily monitoring in the colony via VHF signals than those of fledged birds, where lengthy gaps between transmissions of satellite data increased the uncertainty of mortality events. Overall for both years, I recovered 25 of 55 grounded transmitters (45%).

I received location information on each bird an average of 7.0 times per week (range 2.1 – 19.2, SE = 1.4,  $n = 32$ ) for 2002 birds and 9.1 times per week (range 2.3 – 17.5, SE = 1.2,  $n = 28$ ) for 2003 birds. I received fewer locations early in the season prior to fledging, presumably due to poorer transmitting and battery recharging conditions at nest sites beneath the tree canopy. These periods were also coincident with the onset of the rainy season, which is particularly cloudy. I also received fewer good quality fixes when birds remained in landscapes dominated by cypress forests for extended periods.

In summary, the solar-powered 35g satellite transmitters used on all 72 birds were ideally suited for this large, wetland species that spends much of its time foraging in open waters or roosting in treetops. The additional attachment of a 10g VHF transmitter was invaluable for retrieving the expensive PTTs from stork carcasses. Although I retrieved only 45% of all transmitters from suspected mortalities, reusing recovered transmitters increased my sample sizes by 10% in 2002 and 30% in 2003. Retrieving and refurbishing 22 satellite and 27 VHF transmitters dramatically reduced overall costs.

APPENDIX B  
REFERENCE MEASUREMENTS, MASS, MERCURY LEVELS, AND  
HEMATOLOGY OF JUVENILE WOOD STORKS

Table B-1. Reference body measurements, mercury levels, and hematology of juvenile Wood Storks.

	2002 Cohort					2003 Cohort				
	Mean	SD	Median	Range	<i>n</i>	Mean	SD	Median	Range	<i>n</i>
Culmen (mm)	157.5	15.3	157.0	122-189	33	135.4	13.7	136.0	111-163	39
Tarsus (mm)	199.0	14.5	196.0	161-230	33	186.9	15.0	187.0	147-220	39
Mass (g)	2351.3	297.3	2330.0	1810-3000	31	1975.0	334.4	1984.5	1276-2608	33
Mercury (mg/kg)	7.9	4.7	5.9	3.4-27.0	33	1.9	0.9	1.7	0.49-4.3	37
Hematocrit (%)	32.2	5.9	33.6	15.9-44.8	33	32.6	4.8	33.1	18.7-41.9	37
White Blood Cells (cells/mm <sup>3</sup> x 10 <sup>3</sup> )	25.6	12.9	23.6	7.2-67.3	24	24.1	9.9	23.0	9.7-47.9	36
Heterophils (cells/mm <sup>3</sup> x 10 <sup>3</sup> )	10.3	6.2	8.7	3.8-26.3	24	10.8	6.2	9.8	2.0-36.4	36
Eosinophils (cells/mm <sup>3</sup> x 10 <sup>3</sup> )	3.0	1.7	2.7	0.7-7.1	24	3.7	2.0	3.3	1.3-8.4	36
Basophils (cells/mm <sup>3</sup> x 10 <sup>3</sup> )	0.1	0.5	0.0	0.0-2.7	24	0.0	0.0	0.0	0.0	36
Lymphocytes (cells/mm <sup>3</sup> x 10 <sup>3</sup> )	11.2	6.2	11.1	2.3-33.0	24	8.7	4.2	7.9	2.6-19.1	36
Monocytes (cells/mm <sup>3</sup> x 10 <sup>3</sup> )	1.0	1.1	0.6	0.1-4.7	24	0.9	0.9	0.7	0.0-3.5	36
Heterophil/Lymphocyte ratio (H/L)	1.0	0.6	0.8	0.3-2.3	24	1.4	0.9	1.2	0.4-4.2	36

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## BIOGRAPHICAL SKETCH

Rebecca (Becky) Hylton developed her love of the outdoors while growing up in rural Virginia, with her home nestled deep in the Blue Ridge Mountains. Her interest in biology was encouraged and fostered by her unconventional high school biology teacher, Barbara Kolb, who was the first to expect her to think, explore, and question as a scientist. With the help and advice of her high school teachers, Becky achieved her dream of attending college by receiving a 4-year scholarship to Hollins College in Roanoke, Virginia, where she received a Bachelor of Arts degree in 1997. Her charismatic undergraduate advisor, Dr. Renee Godard, was responsible for placing binoculars in her hands, and introducing her to the wonders of avian ecology. Becky's undergraduate internship at the University of Texas Marine Biomedical Lab in Texas and her undergraduate honors thesis working with Indigo Buntings were instrumental in guiding her future career choices. Upon graduation, Becky dove head first into the life of field biology, working for nonprofit avian research organizations and universities across the country, with her resume reading like a roadmap across the United States. Becky joined the Everglades wading bird project in 2000, and began working on her Master of Science degree with the University of Florida in the fall of 2001. Her love of birds and dedication to avian conservation have only increased over time, and she is looking forward to the new adventures awaiting her upon graduation.