MODELING POPULATION VIABILITY AND HABITAT SUITABILITY FOR THE ENDANGERED WOOD STORK (*MYCTERIA AMERICANA*) IN THE SOUTHEASTERN UNITED STATES

By

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To Colin
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I modeled population dynamics and habitat suitability for the endangered Wood Stork (*Mycteria americana*) in the Southeastern United States using count data from synoptic aerial surveys and survival and movement data obtained using satellite telemetry. Using a simple, count-based diffusion approximation approach I determined that while the population as a whole has been relatively stable since 1976, population dynamics varied regionally. Georgia and South Carolina were shown to support increasing subpopulations while subpopulations in Florida were either stable or decreasing. High inter-year variability resulted in very wide confidence intervals, however, and I could not eliminate the possibility of long-term population decline in spite of recently measured population increases. The South Florida subpopulation had the highest probability of quasi-extinction, with a 69% probability of declining by 90% over the next 30 years. Quasi-extinction probabilities over the same time period were 34% for North and Central FL, 38% for GA, 0.4% for SC, and 24% for the Southeastern population as a whole.

I compared these extinction probabilities to those obtained using a stage-based population matrix model to incorporate observed differences in survival rates among age classes. Data obtained via satellite telemetry was used to estimate age specific survival for endangered Wood
Storks in the Southeastern United States using a live-recovery, live-resight, and tag recovery model. These estimates were incorporated into a stage-based matrix model that was used to estimate the long-term population growth rate and the probability of a population decline of 50% or 90% over the next 50 years. I used an elasticity analysis to determine the stage with the largest influence on the population growth rate and a sensitivity analysis to determine the effects of a simultaneous increase in vital rates or the occurrence of sporadic “boom” years. Survival was lowest for birds in their first year (0.2772) and highest for adults (0.8612). The stage based model indicated that the population was decreasing ($\lambda = 0.94$), however, and the population declined by 50% in under 10 years. The model was most sensitive to changes in adult survival rates but a simultaneous increase in vital rates of 10% resulted in population growth ($\lambda = 1.03$). When survival estimates from the Barker model were used, boom years had to occur approximately 30% of the time for the population to grow.

I also examined the impact of environmental conditions in South Florida on Wood Stork population dynamics as a whole. Wood storks in South Florida have shown a marked change in phenology in response to hydrological changes in the Everglades and as a result of drainage and diversion of water from the Florida Everglades, Wood Storks have delayed nest initiation in the Everglades by 3-4 months. As a result, juvenile storks that fledge from these colonies do so at the beginning of the summer wet season, when water levels are high and rising. I used data from juvenile Wood Storks outfitted with satellite transmitters over 4 years to determine whether juvenile survival was influenced by the hydrological conditions into which the birds fledged. Survival rates were higher (0.3673) when storks fledged in low water levels (< 20 cm) than when they fledged into conditions with high and rising water (> 30 cm) and survival was low (0.1429). Storks also spent more time foraging in Everglades wetlands in drier years while in wetter years
they were more likely to disperse into agricultural settings. I used these results to parameterize a stochastic demographic model in which frequency of wet and dry years varied. I projected a hypothetical population containing 2500 adult females forward 30 years and calculated the end population size under a variety of wet/dry scenarios. I found that dry conditions would have to occur at least 58% of the time for the population to remain stable. Because of the late date at which birds currently fledge, they are unlikely to encounter these conditions and under current conditions the population in south Florida would decline based on juvenile survival alone. This study underscores the need to restore the Everglades so that Wood Storks initiate nesting sooner. Finally, I used location data obtained using satellite telemetry to create a range-wide habitat suitability for the Wood Stork in the Southeastern U.S. Due to their wide range, extreme vagility, and opportunistic use of rapidly changing hydrological conditions, Wood Storks lack a critical habitat determination under the Endangered Species Act. Nonetheless, it is important to identify regions and habitats that are important to the Wood Stork in order to evaluate their current levels of protection and to foster inter-agency management and agreements. I used logistic regression (LR) and Mahalanobis distances (MD) to create habitat suitability maps for the Wood Stork across the Southeastern U.S. using locations obtained from satellite telemetry to identify used habitats. The models were validated using an independent dataset of satellite telemetry locations obtained from Wood Storks captured as part of another study, and compared using Receiver Operating Characteristic (ROC) curves. I found that the LR model provided the best overall fit to the data, but that each model had strengths and weaknesses in different portions of their range. I then used a composite of the 2 models to characterize regions and habitats of importance to the Wood Stork. This represents the first range-wide habitat suitability model for the Wood Stork in the Southeastern U.S.
The Wood Stork (*Mycteria americana*, Ciconiiformes) is distinctive among wetland birds breeding in the United States as the largest wading bird and the only stork. Although the species also breeds in Central and South America, the subpopulation occurring in the Southeastern US is considered separate and distinct from the other subpopulations.

In contrast to egrets and herons, which locate prey primarily by sight, Wood Storks use a grope-foraging technique, or tactilocation, to locate their prey. This technique requires a high density of prey, which generally occur ephemerally as wetlands undergo seasonal changes in water levels. In South Florida, the seasonal drying cycle of the Everglades once provided abundant foraging opportunities over the course of the breeding season. Prior to the 1960’s, the majority of Wood Storks nested in the South Florida. In the 1960’s, however, extensive changes were made to the hydrology of the Everglades as these wetlands were impounded and contained within a series of Water Conservation Areas (WCA) (Light and Dineen 1994). The natural drying cycle has been disrupted as water is now accumulated and held within the WCAs, and although seasonal drying still occurs the timing, duration, and spatial extent of the drying front have been altered. These changes have resulted greatly decreased nesting in Everglades colonies.

The marked decrease in nesting by birds in South Florida led to the Wood Stork being declared endangered by the United States Fish and Wildlife Service in 1984 (U.S. Fish and Wildlife Service 1996, Coulter et al. 1999). While numbers prior to 1960 are subject to debate and may never have exceeded 10,000-15,000 breeding pairs (Kushlan and Frohring 1986, Ogden 1994, Coulter et al. 1999), there was a well-documented decrease from an estimated 10,060 pairs in 1960 to approximately 5,110 pairs in 1976 (Ogden and Nesbitt 1979) and then to a low of
2,520 pairs in 1978 (Coulter et al. 1999, U.S. Fish and Wildlife Service 2002). Since then, there has been evidence of an increasing trend in overall numbers of nesting storks (Ogden et al. 1987, Brooks and Dean 2008) and in the number of nonbreeding storks counted in Christmas Bird Counts (McCrimmon et al. 1997), suggesting an increase in population size. There has been a well documented increase in the breeding range of the Wood Stork as well (Ogden et al. 1987, Brooks and Dean 2008).

Prior to the 1970’s, the majority of Wood Storks nested in several large colonies in South Florida (SFL) (Ogden and Nesbitt 1979). Since the late 1970’s, however, storks have exhibited a considerable northward shift in their breeding range (Ogden et al. 1987) with birds now breeding reliably in Central and North Florida (CNFL) (Rodgers et al. 2008), Georgia (GA) (Bryan and Robinette 2008, Winn et al. 2008), and South Carolina (SC) (Murphy and Coker 2008). This range expansion, coupled with increasing nest counts and high productivity in northern colonies, has led to an optimistic assessment of Wood Stork recovery (Borkhataria et al. 2008, Brooks and Dean 2008) and raised the possibility of the reclassification of the species from endangered to threatened in the foreseeable future.

In order to make informed decisions regarding the future management of the species, it is important to understand Wood Stork population trends across their range, and how the species’ is likely to be affected by current and future land-use or climate changes. This requires knowledge of Wood Stork abundance, survival rates, and habitat use across the entire Southeastern US. Integrating knowledge across their range is especially important because, due to the ephemeral nature of prey concentrations, Wood Storks tend to range widely and can cover large distances over relatively short amounts of time, exploiting a variety of habitat types in different portions of their range. Until recently, however, such information was nearly impossible to obtain, but
advances in satellite telemetry now make it possible to follow the fates and movements of individual Wood Storks across their entire range and over a span of several years.

I used satellite telemetry to follow the fates of juvenile and adult Wood Storks across the Southeastern United States from 2004-2008. In 2004 and 2005, I deployed a total of 68 satellite transmitters on juvenile birds at colonies in South Florida and Georgia. I used data from these birds to quantify fledging success and subsequent survival, adding to an existing dataset of juvenile birds collected by Hylton (2004). I also deployed or collaborated in the deployment of 40 transmitters on adult Wood Storks in FL, GA, and SC. I used survival data from these birds to model population dynamics for the Southeastern U.S. Wood Stork population.

To quantify general Wood Stork population trends, I used existing data on Wood Stork nesting numbers across their range to determine whether Wood Storks were increasing or decreasing, and whether these trends varied by region. I then compared these results to population projections based on age-specific survival estimates I obtained for juvenile and adult birds. Because of the historical importance of South Florida colonies, I also examined the influence of Everglades water levels on the survival of chicks fledging from this region and how those effects influenced population dynamics as a whole. Finally, I used locations from both juvenile and adult Wood Storks to build the first range-wide habitat suitability model for this species.

This study represents the first complete demographic population viability analysis for the Wood Stork in the Southeast U.S., as it incorporates both juvenile and adult survival rates. It is also the first to link juvenile survival to the environmental conditions encountered by juvenile birds as they disperse from their natal colony. These advances in the understanding of Wood Stork population dynamics and their vulnerability to environmental conditions will be
instrumental in the management of this species across its range, as will the habitat suitability model for the entire Southeast U.S. These models may also provide guidance for future decisions regarding the status of the Wood Stork as endangered or threatened.
CHAPTER 2
WOOD STORK POPULATION TRENDS IN THE SOUTHEASTERN UNITED STATES: A COUNT-BASED ANALYSIS

Introduction

Population viability analyses (PVA) provide a formal and widely accepted means for predicting future population scenarios and likelihood of extinction under different management or environmental scenarios (Dennis et al. 1991, Beissinger and Westphal 1998, Holmes and Fagan 2002, Morris and Doak 2002, Staples et al. 2004). The simplest approach to PVA is the count-based, or diffusion approximation (DA), approach. When its assumptions are met, DA allows the use of simple count data to predict population growth rates and probabilities of decline when detailed information on demographic parameters is lacking (Morris and Doak 2002, Holmes 2004). The assumptions of DA are: 1) the population growth rate and its variance do not change over time, 2) there is no environmental autocorrelation, 3) there are no catastrophes or bonanzas, and 4) there is no observation error (Morris and Doak 2002). Modifications of the basic DA are available, however, in the event that these assumptions are violated.

Count data for the Wood Stork have been collected intermittently since 1975 by the U.S. Fish and Wildlife Service as part of their synoptic aerial survey monitoring program (Brooks and Dean 2008). Most surveys focused on known colonies, however, with new colonies added opportunistically when encountered along survey routes or reported by citizens or biologists, creating potential biases in population estimates (Frederick and Meyer 2008). Another independent source of count data for the Wood Stork is the National Audubon Society’s Christmas Bird Count, which has been used in previous analyses of Wood Stork population trends (McCrimmon et al. 1997).
Here I present a population viability analysis for the southeastern U.S. population of Wood Storks as a whole and in each of four sub-regions using a count based approach. I used this approach to address the following questions at both scales: 1) Is the Wood Stork population or sub-population increasing or decreasing? 2) Are population trends obtained from nest count data supported by independent counts of nonbreeding birds? 3) Are population dynamics density dependent, and if so, how does density dependence influence population growth rates and probabilities of declining over time? 4) Which subpopulation contributes the most or least to overall population growth? And 5) What are the longterm probabilities of the population or subpopulation declining by 50 or 90%?

**Methods**

**Diffusion Approximation**

I used Wood Stork nest count data (Brooks and Dean 2008) to perform a count-based population viability analysis. These data reflect peak nest counts from aerial surveys conducted from 1975-2006 in Florida (FL), Georgia (GA), and South Carolina (SC) as part of a range-wide monitoring program. In South Florida (SFL), GA, and SC these counts were conducted annually over this 31 year time frame, while in North and Central Florida (NCFL) counts were intermittent. Pooled data for the entire Southeast were therefore intermittent, owing to gaps in the NCFL data. I also considered nest counts of zero for any given region to be a gap in the dataset, since the absence of nesting did not imply population extinction but rather was likely to reflect an extreme response to stochastic environmental conditions. I conducted PVAs for each of the four regions or “subpopulations” (SC, GA, NCFL, and SFL) and for the Southeast U.S. population (SE) as a whole. For simplicity, I considered each subpopulation to be independent of the others and did not attempt to incorporate movement among subpopulations.
I calculated the density-independent population growth rate by regressing the natural log (hereafter referred to as “log”) of the change in number of nests over the interval between counts against the time elapsed. To meet the assumption of equal variances in the dependent variable over time, a square-root transformation on the time between counts was used, and the change in nest numbers between counts was log transformed, to obtain the regression equation:

\[
\log(\frac{N_{i+1}}{N_i}) / \sqrt{t_{i+1} - t_i} = \log(\frac{N_{i+1}}{N_i}) / x_i = \log \lambda_i
\]

where \(N_i\) is the nest count at time \(i\), \(N_{i+1}\) is the count at the next time interval, and \(t_{i+1} - t_i\) (or \(x_i\)) is the time elapsed between counts (Morris and Doak 2002) (see Table 2-1). I calculated the slope and the residual mean square of the regression, to obtain the geometric mean of the log population growth rate (\(\mu\)) and its variance (\(\sigma^2\)), respectively (Dennis et al. 1991, Morris and Doak 2002). I also calculated the 95% confidence intervals for each of these estimates using the equation

\[
(\mu +/ - t_{0.05, q-1})
\]

where \(t\) is the \(t\) statistic and \(q\) is the total number of transitions between counts. The confidence interval for \(\sigma^2\) was calculated as:

\[
((q - 1) \sigma^2 / \chi^2_{0.025, q-1}, (q - 1) \sigma^2 / \chi^2_{0.975, q-1}).
\]

I tested for first-order temporal autocorrelation using the Durbin-Watson test statistic in SAS 9.2. I also performed a preliminary test for density dependence by regressing the log of the population growth rate between successive counts [\(\log(N_{t+1}/N_t)\)] against the number of nests at time \(t\) (\(N_t\)) (Morris and Doak 2002). If the interval between counts was greater than 1 year (\(\Delta t > 1\)), I did not include data from that year (\(N_t\)) in the analysis of density dependence. A significant negative relationship between nest counts and the subsequent population growth rate was taken as evidence of density dependence, indicating that population growth slowed or decreased as the
number of nests increased. I identified outliers in each dataset using the studentized residuals from the regression of $\log\left(\frac{N_{t+1}}{N_t}\right)$ versus time elapsed and the Diffits Statistic. The Diffits Statistic measures the influence of each observation on the regression parameter estimates by calculating the change in the predicted value of each observation caused by deleting that observation from the dataset. If an observation had a studentized residual $> 2$ and a Diffits value $> 2 * \sqrt{1/N}$ it was considered to be an outlier (Morris and Doak 2002). I used my best judgment to decide whether to exclude outliers from further analyses. If the value represented extreme fluctuations in growth rates at low population sizes for subpopulations that were newly established (GA, SC), I did not exclude them from the dataset. If they seemed to represent a very extreme environmental event that resulted in no or severely reduced nesting, I excluded them from further analysis. This resulted in the exclusion of one outlying value in the South Florida data set (1978).

Because Wood Storks have been more actively managed since their listing as endangered, I tested for differences in their population growth rate before and after listing. I calculated $\mu$ and $\sigma^2$ for the Southeast count data for the two time periods separately (1975-1984, 1985-2006) and tested for differences in their variances by calculating the ratio of the two with the larger estimate in the numerator, and the probability of observing such a ratio using the appropriate F statistic (Morris and Doak 2002). Given equal variances, I compared estimates of $\mu$ from the two time periods using a two-sample t-test and decided a priori that if they differed significantly I would base further analysis on the latter dataset.

Comparison to Independent Data

I used Christmas Bird Count (CBC) data (NAS 2002) from 1975-2006 as an alternative data source with which to check consistency with the nest count data with respect to the general
trend in population growth for the Southeastern population as a whole. The National Audubon Society conducts CBCs each year, with volunteers counting all of the birds seen or heard within a 10.7 m radius count circle. I obtained counts ($N$), represented as number of storks observed per party hour, from the Southeastern U.S. (SC, GA, FL, AL) and used the count data from those 31 years to calculate the log population growth rate, calculating $\log(N_{t+1}/N_t)$ for each intercensus interval and regressing it against the time elapsed using the standard diffusion approximation approach to obtain $\mu$ and $\sigma^2$ for this dataset.

**Analysis of Density Dependence**

To gain insight into whether the observed relationship between nest counts and population growth rates was likely to be attributable to real density dependence, rather than occurring as an artifact of interannual variability or observation error, I used nonlinear regression to test whether a density dependent model would provide a better fit to the count data than a density independent model. I modeled population growth using the Ricker model, which assumes that population growth rates decrease linearly as the population size increases, as the density dependent model. The Ricker model is expressed as:

$$N_{t+1} = N_t \exp \left\{ r \left[ 1 - \left( \frac{N_t}{K} \right) \right] \right\} \quad \text{(2-4)}$$

where $r$ is the intrinsic or instantaneous growth rate and $K$ is equal to the carrying capacity of the population (Gotelli 2001, Morris and Doak 2002). The corresponding density independent model was simply $N_{t+1} = rN_t$.

Because $r$ and $K$ were unknown for both models, I used nonlinear regression to estimate $r$ for several values of $K$. The values I chose represent $K$ were 1) $K_{\text{average}}$—the average number of nests counted over the past 5 years, 2) $K_{\text{current}}$—current population size (nests counted in 2006), 3) $K_{\text{half}}$—half of the current population size, and 4) $K_{\text{double}}$—twice the current population size.
Because the nonlinear fitting of these population models required an uninterrupted dataset, I performed these analyses for the SFL, GA, and SC subpopulations only. For SFL, I did not use count data from years prior to 1979, in order to exclude the 1978 outlier from the analysis.

I compared the Ricker and density independent models by estimating each model’s maximum log likelihood using:

\[
\log L_{\text{max}} = -\frac{q}{2} \left[ \log(2\pi V_r) + 1 \right] \tag{2-5}
\]

where \( q \) = the number of data points, and \( V_r \) is the residual variance, obtained by dividing the error sums of squares of the regression by the number of data points used in the regression. I then calculated the corrected Akaike’s Information Criteria (AICc) for each model using:

\[
\text{AIC}_c = -2 \log L_{\text{max}} + 2pq / (q-p-1) \tag{2-6}
\]

where \( q \) again equals the number of data points and \( p \) equals the number of parameters in the model. The model with the lowest AICc was considered to provide the best fit for the data.

Akaike’s weights were also assigned to each model using:

\[
w_i = \frac{\exp[-0.5(AIC_{c,i} - AIC_{c,best})]}{\sum_{i=1}^{R} \exp[-0.5(AIC_{c,i} - AIC_{c,best})]} \tag{2-7}
\]

where \( AIC_{c,i} \) is the AICc for model \( i \), \( AIC_{c,best} \) is the AICc for the best model (the model with the lowest AIC) and \( R \) is equal to the number of models being compared. These weights sum to 1 and indicate the relative support for each model. The use of these techniques is described more fully in Morris and Doak (2002).

**Stochastic Population Viability Analysis**

I evaluated the long-term population trajectories for each of the subpopulations and the Southeastern population as a whole using \( \mu \) and \( \sigma^2 \) from the corresponding diffusion
approximation analysis. For the three subpopulations with complete time series, I also used the nonlinear regression estimates of \( r \) and \( \sigma^2 \) to compare population trajectories for the four different levels of \( K \) and for the density independent model.

For the analysis using estimates from the diffusion approximation models, I calculated the cumulative probability of the population reaching the decline threshold \( (x_0) \) during each yearly interval \( (G_t) \) as:

\[
G_t = \Phi\left(\frac{-d - \mu t}{\sqrt{\sigma^2 t}}\right) + \exp\left(-\frac{2\mu d}{\sigma^2}\right) \Phi\left(\frac{-d \mu t}{\sqrt{\sigma^2 t}}\right)
\]

where \( d \) is the natural log of the difference between the current population size and the decline threshold and \( \Phi \) is the standard normal cumulative distribution (Morris and Doak 2002). I used a boot-strap approach, randomly selecting values for \( \mu \) and \( \sigma^2 \) from the confidence intervals of the estimates obtained from the diffusion approximation analysis while using a normal probability distribution for \( \mu \) and a chi-square distribution for \( \sigma^2 \). I used the 2006 nest count estimates for my starting population size and then projected the population forward in time for 100 years using 50,000 replicates.

To evaluate the effects of incorporating density dependence into the population viability analysis, I used the estimates of \( r \) obtained by the nonlinear regression analysis to predict future population sizes under each carrying capacity scenario. I added an error term \( (\varepsilon) \) to the basic Ricker model (Equation 1-4), drawing a new value of \( \varepsilon \) for each year of the simulation from a normal distribution with a mean of 0 and the variance \( (\sigma^2) \) estimated by nonlinear regression (Morris and Doak 2002). Again, I projected the population forward in time for 100 years and used 50,000 replicates.
I evaluated the probability of a population declining by 90% (“quasi-extinction”) over the next 100 years for both the density independent and, when applicable, density dependent models. I also report the probability of the population declining by 90% over the next 30 years.

Results

Diffusion Approximation

The log of the population growth rate ($\mu$) for the entire Southeastern population from 1976-2006 was 0.0047, indicating a relatively stable population (Table 2-2). The variance of the estimate ($\sigma^2$) was 0.13627, indicating high variability in annual nest counts. The residuals were not significantly autocorrelated (DW = 2.339, $P = 0.21$) and there were no outliers. There was some evidence of density dependence, however, with the population growth rate declining as the total number of nests increased (Figure 2-1; $F_{1,15} = 5.79$, $P = 0.0469$).

Prior to listing, the population showed a declining trend ($\mu = -0.0495$, $\sigma^2 = 0.1709$, CI = -0.1491-0.6342), while since listing (1984-2006), the population has shown a positive trend in growth ($\mu = 0.0269$, $\sigma^2 = 0.1143$, CI = -0.0234, 0.6839). This difference was not significant, however, owing to the extremely large variance around the estimated population growth rates for the two periods ($t_{19} = 0.4606$, $P = 0.3252$) and I did not consider the periods separately in further analyses.

In SFL, Wood Stork nesting showed a declining trend since 1976 ($\mu = -0.02404$, $\sigma^2 = 0.8560$). There was no evidence of negative temporal autocorrelation in nest count numbers (DW = 2.523, $P = 0.0703$) but some evidence of density dependence (Figure 2-2; $F_{1,18} = 5.77$, $P = 0.0232$). The CNFL subpopulation was stable ($\mu = 0.0040$, $\sigma^2 = 0.2054$), and there was no evidence of temporal autocorrelation (the outlying nest count from 2001 was removed to obtain this estimate). There was strong evidence of density dependence (Figure 2-3; $F_{1,14} = 19.44$, $P = \ldots$
0.0006). The GA subpopulation showed an increasing trend ($\mu = 0.0841, \sigma^2 = 0.5500$), some evidence of temporal autocorrelation ($DW = 0.0563, P = 0.0563$) and no density dependence (Figure 2-4; $F_{1,29} = 0.0225, P = 0.4203$). There were 3 outliers (1975, 1976, and 1979) but I did not exclude them from analyses because they represented the early years of colony establishment in GA. South Carolina had the highest population growth rate ($\mu = 0.2083, \sigma^2 = 0.0331$), with no temporal autocorrelation ($DW = 2.491, P = 0.1033$) but some density dependence (Figure 2-5; $F_{1,23} = 7.6198, P = 0.0111$). There were 2 outliers (1984 and 1998). I did not remove these outliers from further analyses because 1984 simply reflected an increase from 22 to 74 nests between the 4th and 5th years of the establishment of nesting in SC and because although the number of nests counted in 1999 was much lower than those counted in 1998, declining from 1,093 to 520, the 1999 count was not an extreme value compared to other nest counts (median = 688 nests over 25 year time period).

Comparison to Independent Data

When I regressed the change in number of birds counted per count hour during Christmas Bird Counts against the time elapsed, I found that the log population growth rate of the Southeastern U.S. population of Wood Storks was 0.0313 (CI = -0.0159-0.0785). The variance of the estimate was 0.14311 (CI = 0.0908-0.2586).

Density Dependent Analysis

Density dependent models of population growth provided a better fit to the count data than did the density independent model for SFL and SC. For both subpopulations, the models in which carrying capacity was set equal to half of the current population size ($K_{\text{half}}$) or to the 5 year average ($K_{\text{average}}$) were indistinguishable from each other in terms of model fit (Table 2-3). For
GA, the 4 density dependent models and the density independent model had AIC values that differed by less than one.

Estimates of $r$ for SFL were 0.3839 ($\sigma^2 = 0.8176$) and 0.5127 ($\sigma^2 = 0.8267$) for the models in which $K$ was set equal to half of current or to the five year average respectively, while for the density independent model it was 0.0276 ($\sigma^2 = 0.9461$). For the same two density dependent models for SC, $r$ was equal to 0.4554 ($\sigma^2 = 0.1427$) and 0.4249 ($\sigma^2 = 0.1432$), while $r$ for the density independent model was 0.2083 ($\sigma^2 = 0.1830$). Values of $r$ from the density independent models for the GA subpopulation ranged from 0.1293-0.2170 with variances ranging from 0.5579- 0.5597. For the density independent model $r$ was estimated to be 0.0841 ($\sigma^2 = 0.5690$).

**Stochastic Population Viability Analysis**

**Density independent**

The density independent model indicated that the cumulative probability of the Southeastern Wood Stork population declining by 90% over the next 30 years was 0.23 (0.31-0.53) and 0.49 (0.08-0.85) over the next 100 years (Figure 2-6). The probabilities of the population declining by 50% over those same time intervals were 0.71 (0.37-0.88) and 0.83 (0.41-0.97) respectively.

Of the 4 subpopulations, the South Florida subpopulation had the highest cumulative probability of declining (Figure 8). The cumulative probability (CI) of a 90% decline was 0.69 (0.38-0.86) over the next 30 years and 0.85 (0.47-0.99) over the next 100 years. The cumulative probability of a 50% decline was 0.91 (0.78-0.97) and 0.96 (0.82-1.0) for the next 30 and 100 years respectively (Figure 2-7).
The Central and North Florida subpopulation was more stable than the SFL subpopulation, with a probability of declining by 90% of 0.34 (0.08-0.64) over the next 30 years and 0.58 (0.13-0.91) over the next 100 years (Figure 2-8). The Georgia subpopulation was also relatively stable, with a cumulative probability of 0.38 (0.11-0.67) of declining by 90% over the next 30 years, and 0.47 (0.12-0.82) over the next 100 years (Figure 2-9).

The South Carolina subpopulation had the largest population growth rate and had virtually 0 probability of declining by 90% over the next 100 years. Even the probability of a 50% decline over the next 100 years was low (0.19; CI = 0.04-0.48) (Figure 2-10).

**Comparison of density dependent and density independent analyses**

Using the nonlinear regression estimates of $r$ and $\sigma^2$, SFL had the highest probability of decline. The density independent model in this projection yielded probabilities of quasi-extinction of 0.5455 over the next 30 years and 0.7043 over the next 100. These estimates were lower than those obtained using the modeling approach in the previous section. They were also lower than the quasi-extinction probabilities obtained using parameter estimates from the two best models that incorporated density dependence. For the $K_{\text{half}}$ and the $K_{\text{average}}$ models, the probability of a 90% decline over the next 30 years was 0.9248 and 0.8080 respectively (Figure 2-11). The probability of quasi-extinction over the next 100 years for the same two models was 1.

The SC subpopulation had virtually no probability of quasi-extinction over the next 100 years using the independent model. For the $K_{\text{half}}$ model and the $K_{\text{average}}$ models the probability of quasi-extinction was 0.1139 and 0.0265 respectively (Figure 2-12).

For GA, the probability of decline was lowest for the density independent scenario and for the $K_{\text{average}}$ model than for the other density dependent models. For the density independent
model, the probability of quasi-extinction after 100 years was 0.4156 and for the \( K_{\text{average}} \) model it was 0.4120. Quasi-extinction probabilities after 100 years obtained using parameter estimates from the other density dependent models ranged from 0.8586-0.0062 (Figure 2-13).

**Discussion**

The Southeastern U.S. Wood Stork population appears to be generally increasing. Subpopulations in SC, GA, and northern and central FL were either stable or increasing, while for SFL, the population trend was dependent on the length of the time series used to estimate the population growth rate. When data from the 1975-1978 were included in the analysis, the best estimate of \( \mu \) was negative, while it was positive for the time series since 1979. Wide confidence intervals around the population growth rate estimates do not preclude the possibility of a negative population trend for any of the regions, but in general the trend appears to be toward an overall population increase. This conclusion is independently supported by the Christmas Bird Count data, which indicated an even higher rate of population growth than the nest count data.

Density dependence appeared to influence population dynamics in all regions except Georgia. This could reflect limitations in suitable nesting habitat or suitable foraging habitat, both of which are listed as possible factors in the Wood Stork’s steep decline in the latter half of the 20\(^{\text{th}}\) century (Ogden and Nesbitt 1979). Model fitting suggested that the SFL and SC populations are probably near or above their carrying capacity, and the relatively stable population growth rate for the NCFL subpopulation suggests the same for that region.

Due to the nature of the nest count data, these estimates of population growth rates and probabilities of decline should not be taken as absolute predictions. Rather, they indicate general trends in population growth or decline. These data violated several of the assumptions inherent to count-based PVA. Namely, the assumption that \( \mu \) and \( \sigma^2 \) do not change over time was
violated—there was evidence of density dependence in most of the subpopulations and in the population as a whole and catastrophes and bonanzas seem to have occurred, particularly in SFL. The occurrence of catastrophes would have had a negative effect on population growth rates, causing the estimates I have presented to be overoptimistic and possibly underestimating the probability of serious population declines. Conversely, the presence of bonanzas would cause my estimates to be overly pessimistic. The incorporation of catastrophes and bonanzas, however, requires information on their likelihood of occurrence that I did not possess. This was particularly true for GA and SC, where nesting began relatively recently.

Finally, observation error could not be excluded from this analysis. Potential biases in the nest counts could have been caused by the aerial survey method (Frederick and Meyer 2008) or if the proportion of the population that attempted to breed differed from year to year, as clearly occurred. This was reflected in the high variance around the estimated population growth rates. Observation error and the associated inflated variance generally results in a bias towards overly pessimistic assessments of population persistence (Morris and Doak 2002) and underscores the needs for count methods that enable the quantification of this source of error.

**Conclusion**

The endangered Wood Stork population in the Southeastern United States appears to be stable or increasing, as evidenced by nest count data and Christmas Bird Counts. This overall trend can be attributed to increases in numbers of birds nesting in Georgia and South Carolina. In Central and North Florida the number of nesting birds seems stable, while in South Florida it appears to be stable or declining. Restoration plans currently in place for South Florida, including the Comprehensive Everglades Restoration Plan (CERP), are expected to improve nesting conditions in SFL. Although declines in SFL have been offset by the population increase
to the north, a growing population in SFL would increase the population growth rate for the Southeast as a whole and the probability of reclassification from endangered to threatened.
Table 2-1. Annual log population growth rates for the inter-census interval for SFL, NCFL, GA, SC and the Southeastern U.S. Wood Stork population as a whole.

<table>
<thead>
<tr>
<th>Year</th>
<th>SFL</th>
<th>NCFL</th>
<th>GA</th>
<th>SC</th>
<th>SE</th>
</tr>
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<tbody>
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<td>1975</td>
<td>-0.8542</td>
<td>-0.3225</td>
<td>-2.1832</td>
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</tr>
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<td>0</td>
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<td>0.0855</td>
<td>0.0855</td>
</tr>
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<td>2001</td>
<td>0.1816</td>
<td>1.7204</td>
<td>0.0778</td>
<td>-0.0329</td>
<td>0.3416</td>
</tr>
<tr>
<td>2002</td>
<td>-0.6842</td>
<td>0.7073</td>
<td>0.2747</td>
<td>0.177</td>
<td>0.1151</td>
</tr>
<tr>
<td>2003</td>
<td>-0.1625</td>
<td>-0.2246</td>
<td>-0.0351</td>
<td>0.4167</td>
<td>-0.0505</td>
</tr>
<tr>
<td>2004</td>
<td>-0.9214</td>
<td>-0.6376</td>
<td>0.1297</td>
<td>-0.3798</td>
<td>-0.4101</td>
</tr>
<tr>
<td>2005</td>
<td>1.4997</td>
<td>0.9809</td>
<td>0.0593</td>
<td>0.3567</td>
<td>0.7073</td>
</tr>
</tbody>
</table>
Table 2-2. Log population growth rates ($\mu$), variance in growth rates ($\sigma^2$), and 95% confidence intervals from Wood Stork nest count data.

<table>
<thead>
<tr>
<th>Region</th>
<th>N</th>
<th>$\hat{\mu}$</th>
<th>Confidence Interval</th>
<th>$\hat{\sigma^2}$</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lower</td>
<td>Upper</td>
<td></td>
</tr>
<tr>
<td>Southeast</td>
<td>21</td>
<td>0.0047</td>
<td>-0.0409</td>
<td>0.0502</td>
<td>0.1363</td>
</tr>
<tr>
<td>South Florida</td>
<td>30</td>
<td>-0.0240</td>
<td>-0.1375</td>
<td>0.0895</td>
<td>0.8560</td>
</tr>
<tr>
<td>North &amp; Central</td>
<td>21</td>
<td>0.00404</td>
<td>-0.0802</td>
<td>0.0883</td>
<td>0.4661</td>
</tr>
<tr>
<td>Georgia</td>
<td>31</td>
<td>0.08414</td>
<td>-0.0068</td>
<td>0.1751</td>
<td>0.5500</td>
</tr>
<tr>
<td>South Carolina</td>
<td>25</td>
<td>0.0905</td>
<td>0.0155</td>
<td>0.1654</td>
<td>0.0331</td>
</tr>
<tr>
<td>Subpopulation</td>
<td>N</td>
<td>$\hat{r}$</td>
<td>$K$</td>
<td>$\hat{\sigma}^2$</td>
<td>Model Likelihood</td>
</tr>
<tr>
<td>---------------</td>
<td>----</td>
<td>--------</td>
<td>-----</td>
<td>---------------</td>
<td>----------------</td>
</tr>
<tr>
<td><strong>SFL</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$K_{\text{average}}$</td>
<td>26</td>
<td>0.5127</td>
<td>1987</td>
<td>0.8267</td>
<td>-33.9090</td>
</tr>
<tr>
<td>$K_{\text{current}}$</td>
<td>26</td>
<td>0.4262</td>
<td>2648</td>
<td>0.8688</td>
<td>-34.5542</td>
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<tr>
<td>$K_{\text{half}}$</td>
<td>26</td>
<td>0.3839</td>
<td>1324</td>
<td>0.8176</td>
<td>-33.7640</td>
</tr>
<tr>
<td>$K_{\text{double}}$</td>
<td>26</td>
<td>0.1725</td>
<td>5296</td>
<td>0.9286</td>
<td>-35.4195</td>
</tr>
<tr>
<td>Density Independent</td>
<td>26</td>
<td>0.0276</td>
<td>---</td>
<td>0.9462</td>
<td>-35.6631</td>
</tr>
<tr>
<td><strong>GA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$K_{\text{average}}$</td>
<td>30</td>
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<td>0.1952</td>
<td>1928</td>
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<td>964</td>
<td>0.5597</td>
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</tr>
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<td>$K_{\text{double}}$</td>
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<td>0.1293</td>
<td>3856</td>
<td>0.5652</td>
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<td>---</td>
<td>0.5690</td>
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</tr>
<tr>
<td><strong>SC</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$K_{\text{average}}$</td>
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<td>0.4249</td>
<td>1593</td>
<td>0.1432</td>
<td>-10.2227</td>
</tr>
<tr>
<td>$K_{\text{current}}$</td>
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<td>0.3768</td>
<td>2010</td>
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<td>-10.8871</td>
</tr>
<tr>
<td>$K_{\text{half}}$</td>
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<td>0.4554</td>
<td>1005</td>
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<td>$K_{\text{double}}$</td>
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<td>0.2824</td>
<td>4020</td>
<td>0.1686</td>
<td>-12.1817</td>
</tr>
<tr>
<td>Density Independent</td>
<td>24</td>
<td>0.2083</td>
<td>---</td>
<td>0.1830</td>
<td>-13.1674</td>
</tr>
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</table>
Figure 2-1. Relationship between the number of nests in year $t$ and the population growth rate over the next interval for the Southeastern Wood Stork population as a whole.
Figure 2-2. Relationship between the number of nests in year $t$ and the population growth rate over the next interval for the SFL Wood Stork subpopulation.
Figure 2-3. Relationship between the number of nests in year $t$ and the population growth rate over the next interval for the NCFL Wood Stork subpopulation.
Figure 2-4. Relationship between the number of nests in year t and the population growth rate over the next interval for the GA Wood Stork subpopulation.
Figure 2-5. Relationship between the number of nests in year $t$ and the population growth rate over the next interval for the SC Wood Stork subpopulation.
Figure 2-6. Cumulative probability of the Southeastern US Wood Stork population declining by 50% (gray) or 90% (black) over the next 100 years based on diffusion approximation results. The solid line represents best estimates and the dashed lines represent 95% confidence intervals.
Figure 2-7. Cumulative probability of the SFL subpopulation of Wood Storks declining by 50% (gray) or 90% (black) over the next 100 years based on diffusion approximation results.
Figure 2-8. Cumulative probability of the NCFL subpopulation of Wood Storks declining by 50% (gray) or 90% (black) over the next 100 years based on diffusion approximation results.
Figure 2-9. Cumulative probability of the GA subpopulation of Wood Storks declining by 50% (gray) or 90% (black) over the next 100 years based on diffusion approximation results.
Figure 2-10. Cumulative probability of the SC subpopulation of Wood Storks declining by 50% (gray) or 90% (black) over the next 100 years based on diffusion approximation results.
Figure 2-11. Cumulative probability of the SFL subpopulation of Wood Storks declining by 90% (black) over the next 100 years for the density dependent and density independent models.
Figure 2-12. Cumulative probability of the GA subpopulation of Wood Storks declining by 90% (black) over the next 100 years for the density dependent and density independent models.
Figure 2-13. Cumulative probability of the SC subpopulation of Wood Storks declining by 90% (black) over the next 100 years for the density dependent and density independent models.
CHAPTER 3
AGE-SPECIFIC SURVIVAL IN THE WOOD STORK: IMPLICATIONS FOR LONG-TERM VIABILITY OF THE SPECIES

Introduction

While count-based population viability analyses such as the ones in the previous chapter can be important conservation tools, particularly when estimates of vital rates for the species are lacking, the assumptions upon which such analyses are based can limit their applicability. This may be especially true for the Wood Stork. In particular, the assumption that observation error does not affect the measured variability in population growth rates (Morris and Doak 2002) is almost certainly violated in the case of the stork. The count-based analyses for the Wood Stork have been based on synoptic aerial surveys conducted by the Fish and Wildlife Service (see Brooks and Dean 2008). These counts are subject to 3 sources of observation or sampling error: errors in accuracy of the count itself, which may vary with observer, colony size, and species composition (Rodgers et al. 1995, Rodgers et al. 2005); differences between the number of breeding birds and the peak number of birds counted, which may be due to asynchronous nesting or renesting (Frederick et al. 2006); and differences in the proportion of the population counted in any given year, which might occur if birds do not attempt to nest when conditions are unfavorable, as is likely.

Age or stage specific population viability analyses (PVA) are preferable to count-based analyses when individuals vary in their contribution to the population growth rate (Morris and Doak 2002), as is true of the Wood Stork. PVAs are widely used in the conservation and management of endangered or declining species to provide quantitative estimates of extinction risk over a specified time frame and to identify life stages or vital rates that should be targeted for management (Beissinger and Westphal 1998, Heppell et al. 2000, Morris et al. 2002, Ellner and Fieberg 2003). Their use is not without controversy, and a major criticism is that parameter
estimates too often lack precision owing to deficiencies in the available data (Beissinger and Westphal 1998, Ellner et al. 2002, Morris et al. 2002).

The simplest demographic model is the deterministic single population model, which requires information on age or stage structure, age or stage at first reproduction, and estimates of survival and reproduction for each age class or stage (Beissinger and Westphal 1998). The deterministic model results in a single estimate of the population growth rate, which can be used to determine the population size at some future time. Stochastic population models provide probabilistic estimates of extinction risk based on the means and variances of vital rates and their distributions. Their accuracy is limited by the length of the time series used to estimate vital rates, however, and precise estimates of extinction risk over $t$ years requires $5t$-$10t$ years of data (Fieberg and Ellner 2000, Ellner et al. 2002). In a review on the use of PVAs in the management of endangered species, Beissinger and Westphal (1998) recommend that PVA be used to generate relative rather than absolute predictions of extinction risk, that predictions be made over short time periods, and that simple models that can be supported by data be used.

Until recently, however, not even the simplest demographic models were applicable to the management and recovery of the Wood Stork due to the paucity of knowledge of Wood Stork vital rates. In 2008, Borkhataria et al. published a preliminary model of Wood Stork population dynamics based on apparent survival of juvenile Wood Storks monitored via satellite telemetry. Information on adult survival rates were lacking at that time, and the model was used to estimate adult survival rates necessary to maintain a stable or growing population based on information about Wood Stork productivity across the Southeast and juvenile survival rates. Without adult survival rates, however, it was impossible to estimate the population growth rate or extinction probabilities.
Here I present age-specific estimates of juvenile and adult survival based on mark-resight analysis of Wood Storks outfitted with satellite transmitters between 2002 and 2007. I then use these estimates to update the model of Borkhataria et al. (2008) and to estimate the population growth rate for the Southeastern Wood Stork population for comparison to that obtained from the count-based analyses in Chapter 1. Due to the short time series of data available on productivity and survival rates, I maintained the use of a deterministic rather than a stochastic model, and because the predictions of deterministic population models are very sensitive to the vital rates used in their parameterization, I also use the model to compare the use of apparent survival estimates to those obtained by maximum-likelihood modeling in Program Mark.

**Methods**

**Satellite Telemetry**

The birds included in this study were captured throughout the Southeastern United States (see Figure 3-1 for a map of locations and Table 3-1 for coordinates). Juvenile storks were captured on the nest at 2 Florida and 2 Georgia colonies. In Florida, birds were caught at the Tamiami West colony in Everglades National Park, Dade County (Hylton 2004), and at the Palm Beach Solid Waste Authority rookery (SWA) in Palm Beach County. In Georgia, I captured young birds at the Harris Neck National Wildlife Refuge, McIntosh County, and at the Chew Mill colony in Jenkins County. In all cases, young birds were caught by climbing to the nest using tree branches or ladders, and simply removing young by hand from the nest. Birds were tagged at four to six weeks of age and the oldest sibling per nest was chosen based on visual comparisons of culmen length and overall size to avoid potential bias associated with hatch-order and non-independence of siblings. Prior to attaching transmitters, birds were also given a brief physical exam, measurements were taken, and we extracted <0.5 ml of blood from the brachial vein for sexing and health analysis.
Adult birds were caught in Florida, Georgia, South Carolina, and Mississippi by myself and collaborators at the University of Georgia and the Jacksonville Zoo. The vast majority of storks included in this analysis were caught by rocket-netting, with the exception of one stork caught by drop net at the SWA. Ten storks were also caught by drop-net or clap-trap at the Jacksonville Zoo in Florida by our collaborators. As with the juvenile birds, adults were given a brief physical exam, I measured culmen and tarsus lengths, and 3-4 drops of blood were extracted from the brachial vein for sexing.

In 2004 and 2005, I deployed 68 satellite transmitters on juvenile storks, adding to a previous dataset which included 73 juvenile storks tagged in 2002 and 2003 (Hylton 2004). From 2004-2007, I also directly engaged in or collaborated in the deployment of 34 transmitters on adults. Satellite transmitters weighed 35g (2002-2003) or 45g (2004-2008) and were solar-powered ARGOS-PTT satellite tags (Microwave Telemetry, Columbia, MD). We attached the transmitters to the birds using a 0.25 cm wide teflon ribbon backpack-style harness (see Hylton 2004 for a complete description of tagging protocol). In 2002-2005, a 10g VHF transmitter was affixed to the satellite tag on young, whereas satellite transmitters deployed on adults for the most part lacked VHF transmitters. I used the VHF signal and/or final satellite transmissions to independently confirm mortality and to attempt to recover tags when birds stopped transmitting satellite locations. If I was unable to confirm mortality by relocating a tag for any reason, I used final transmissions from the satellite tag’s built-in activity counters and final locations to categorize a bird’s fate as either “dead” or “unknown.” A bird was considered to be dead if the activity counter indicated no movement for several days or, for GPS/PTTs, a bird did not change locations for several days. If a bird simply stopped transmitting without displaying either of
these characteristics, I considered it possible that the tag had simply failed, and considered the bird’s fate to be unknown.

Locations for the juvenile birds and 15 adults were recorded hourly, from 0600-2100, while locations for 19 adults were recorded every two hours, 24 hours per day.

**Sexing**

I sent blood samples to Zoogen Services Inc. (Davis, CA) or Avian Biotech International (Tallahassee, FL) for DNA sexing. If blood was not drawn from a juvenile bird for any reason, I did not attempt to assign sex on the basis of morphometric characteristics, but rather excluded that individual from any sex-based analyses. For adult birds, if blood was not drawn from an individual I attempted to assign sex on the basis of culmen and tarsus length. I compared mean culmen and tarsus lengths between females and males using a $t$-test, and assigned sex on the basis of the 95% confidence intervals (CI) around the mean for both sexes. If a bird fell within the confidence intervals for the same sex for both measurements, I assigned it that sex. If a bird had only one of the two measurements taken (most often tarsus), I assigned sex on the basis of that measurement alone. If the measurement exceeded the upper CI for males, the bird was designated male, and if it was under the lower CI for females the bird was designated female. If the measurement fell between the CIs for males and females or within the range in which the CIs overlapped I did not assign sex.

**Juvenile Fledging Success and Survival**

I considered a satellite tagged juvenile to have fledged when it flew $>0.5$ km from the colony and did not return to within 0.5 km of the colony for at least seven days. Birds that died within the colony were not considered to have fledged even if they were capable of flight and had previously left the colony. Fledging success was calculated as the number of tagged birds that fledged divided by the number of birds tagged.
I used two approaches to describe the survival of birds after they had fledged: proportions surviving from one year to the next (apparent survival), and survival estimates based on the joint modeling of live-recapture, live-resight, and tag-recovery data (Barker’s model) in Program MARK (Barker 1997, Cooch and White 2008). For both approaches, I considered first year survival to represent the probability that a bird survived from the day it fledged to the 365-day anniversary of its fledge date. Subsequent annual survival was also based on this date. I chose to use the anniversary of each bird’s fledge date rather than hatch date because survival estimates were to be used in post-breeding matrix models.

I calculated apparent annual survival separately for each year and calculated the mean and variance for each age class across years. Because sample sizes were low, particularly for the later age classes, I also combined data from across years to obtain a single estimate of survival by age group. It was not always possible to determine whether birds that stopped transmitting had died, and while I reported the numbers of birds known to be dead (i.e., tag retrieved or death confirmed by activity counter) versus the number of birds with unknown fates), for the purposes of calculating apparent annual survival, I assumed that all birds that stopped transmitting had died. This assumption was unlikely to have been true and probably leads to an overly conservative estimate of survival.

To incorporate the uncertainty in survival estimates associated with birds with unknown fates, I also used Barker’s model to estimate survival rates and the associated uncertainty in the estimates. Whereas typical capture-recapture models use data from a single source, such as live-recaptures in the case of the Jolly-Seber model or band returns from dead animals in the Brownie models, Barker’s model is appropriate when survival data arise from multiple sources, with some sources coming from periods between the discrete sampling occasions. Barker’s model is
typically applied when live capture occurs at distinct times and animals are resighted at some
time in the interval between distinct capture occurrences, and tags from dead animals are
sometimes recovered (Barker 1997). This model is especially useful when sample sizes are low,
as it allows the incorporation of all available data on a bird’s fate and the use of these additional
data can improve the precision of survival estimates. I adapted this model to fit the satellite
telemetry data by using location histories as proxies for physical recapture and resighting.

Because a key assumption of capture-recapture analysis is that recaptures occur
instantaneously (Williams et al. 2001), I considered a bird to have been recaptured if a location
was recorded for it on the exact 365 day anniversary of its initial capture and the location data
indicated that the bird was alive. I considered the bird to have been resighted if live location data
were recorded on any days in the time period between annual “recaptures.”

Encounter histories were coded in the live-dead format, where each capture occasion and
the following interval are paired (LDLDLDLDL). In this format, the L’s represent capture
occasions and the bird is either alive on that day and coded with a 1, dead on that day and coded
with a 0, or alive but not “recaptured” (i.e., did not transmit a location for that day), also coded
with a 0. The D’s represent the interval between capture occasions, and are coded with a 1 if the
bird died at any time during the interval, or with a 2 if the bird was recorded alive on any day
during the interval. For example, a bird that was captured on the first sampling occasion,
transmitted at least one location during the first 365 day interval, transmitted a location on the
exact anniversary of its capture, transmitted a location during the second 365 day interval and
again at the next annual capture anniversary, then died during the next interval would be coded:
121211. Had this same bird stopped transmitting during the second interval without any
evidence of death, the capture history would have been coded 121200 for the same time frame.
The Barker model in Program MARK estimates the following parameters (Barker 1997):

\[ S_i = \] the probability that an animal alive at time \( i \) is alive at time \( i + 1 \).

\[ p_i = \] the probability that an animal is captured at time \( i \) given that it is at risk of capture

\[ r_i = \] the probability that an animal that dies in the interval between \( i \) and \( i+1 \) is found dead and reported

\[ R_i = \] the probability that an animal that survives the interval between \( i \) and \( i+1 \) is resighted alive during the interval

\[ R'_{i} = \] the probability that an animal that dies during the interval between \( i \) and \( i+1 \) without being found alive is resighted alive during the interval before it died

\[ F_i = \] the probability that an animal at risk of capture at \( i \) is at risk of capture at \( i+1 \)

\[ F'_{i} = \] the probability that an animal not at risk at \( i \) is at risk of capture at \( i+1 \).

Because there was no boundary to the area covered by the satellite tags, I considered a tagged stork with a functioning tag to be incapable of leaving the study and to always be at risk of capture (\( F_i = 1 \)) and because this study did not include marked animals that we considered not to be at risk of capture, I set \( F'_{i} \) equal to zero. I also constrained \( R'_{i} \), fixing it at one, because birds invariably transmitted at least once during the annual interval, regardless of their fate. Due to the small sample size of tagged animals and the loss of degrees of freedom associated with the estimation of multiple parameters, I made the a priori assumption that recapture, reporting and resighting probabilities were unlikely to vary over time or by sex, and constrained them to be constant.

In computing survival rates, I parameterized models that I considered to be biologically relevant, rather than computing results for every possible combination of parameters. For juveniles, I compared 10 models with varying parameters associated with survival probabilities
(see Table 3-4), testing for differences among age classes and between sexes. I compared models in which survival differed for birds in their first, second, third and fourth+ year; differed in their first, second, and third+ year; differed only in their first and second+ year, or were constant over the entire birds’ lives (with no cohort effect). When years are represented with a “+”, it indicates that survival was assumed to equal adult survival at that time and to be constant from that point on. I repeated the analyses with survival modeled differently for males and females over all of the years in the analyses and also included a model in which sex influenced survival for birds in their first year but not thereafter. I selected the model with the lowest corrected Akaike’s Information Criterion (AICc) (Burnham and Anderson 2002) as the one that best fit the data. If AICc values differed by less than two for two or more models, I chose the model with the lowest number of parameters.

**Adult Survival**

Because the sample size for adult birds of known sex was relatively small and uneven among years [2004 (1), 2005 (8), 2006 (23), and 2007 (2)], I decided a priori to compare only eight models of survival and recapture. I tested for higher mortality in the first year after tagging (tag effects) by assigning one parameter to that year and a different, constant parameter to all other years and compared the model to one in which survival rates were held constant over all sampling periods. I also compared models in which survival rates were allowed to vary by sex or were held constant, for a total of four survival scenarios. I only considered two possible recapture scenarios, one in which recapture probabilities were constant vs. one in which they varied by sex. The two recapture scenarios combined with the four survival scenarios resulted in a total of eight possible models. Again, I selected the model with the lowest corrected Akaike’s Information Criterion (AICc) as the one that best fit the data. Because birds tagged as juveniles
exhibited adult survival in their third year and older, I also combined data from birds tagged as juveniles with that of birds tagged as adults to obtain a combined estimate of adult survival.

Demographic PVA

I used a deterministic matrix model, which I adapted from Borkhataria et al. (2008) to include the revised estimates of juvenile and adult survival presented here. As in Borkhataria et al. (2008), the basic model used a birth-pulse, female-only, post-breeding census and was structured as follows:

\[
\begin{bmatrix}
0 & 0 & f_4 \cdot s_{3+} & f_5 \cdot s_{3+} \\
0 & s_1 & 0 & 0 \\
0 & s_2 & 0 & 0 \\
0 & 0 & s_{3+} & s_{3+}
\end{bmatrix}
\] (3-1)

where \(s_1\) = first year survival, \(s_2\) = second year survival, and \(s_{3+}\) = survival of birds in their third year and beyond. The parameter \(f_4\) corresponded to the fertility of first time breeders, which were assumed to breed for the first time at the end of their fourth year, and \(f_{5+}\) to the fertility of experienced breeders.

I adopted the same fertility values I reported previously (Borkhataria et al. 2008), based on a pooled analysis of nests of more than 6,000 nests from South Carolina, Georgia, and Florida for 2002-2005, with nest success of 0.6375 and 1.99 chicks per successful nest, and multiplied this value by fledging success (divided by 2) to obtain the number of female young produced. I assumed that birds bred for the first time at age four, and that first time breeders reproduced with half the success of experienced breeders based on differences in nest success and productivity by age in the White Stork (\textit{Ciconia ciconia}) (Vergara and Aguirre 2006).

I parameterized the matrix above (Eqn. 3-1) for 4 scenarios: 1) apparent juvenile survival; 2) juvenile survival estimates from the Barker model; 3) juvenile survival (first and second
years) equal to the upper confidence limit for those estimates from the Barker model; and 4) all survival rates equal to the upper confidence limit for each estimate from the Barker model.

For each survival scenario, I calculated the stable age distribution by taking the right eigenvector of the parameterized matrix (Beissinger and Westphal 1998, Morris and Doak 2002). I then used the stable age distribution to create a population vector with 10,000 breeding females for each scenario. I projected each vector forward in time to obtain the population trajectory for the Southeastern population and the time it would take for an initial population of 10,000 birds to decline by 50 and 90%. I compared the population trajectories for each of the four scenarios to that obtained using the population growth rate ($\mu$) obtained from the count based analysis in Chapter 1. To obtain future population sizes using the count-based population growth rate, I used the following equation:

$$N_i = \exp(\mu i)$$

where $N_i$ is the population size after $i$ years. I then ran the first three models with a range of adult survival values (used for birds three+ years old) and regressed adult survival against $\lambda$ to determine the level of adult survival necessary to maintain a stable population ($\lambda = 1$).

**Sensitivity Analysis**

The proportional sensitivity or elasticity ($e_{i,j}$) of the long-term population growth rate ($\lambda$) to small changes in each vital rate was analyzed by calculating the proportional contribution of each vital rate ($a_{i,j}$) to $\lambda$, using:

$$e_{i,j} = \frac{\partial (\log \lambda)}{\partial (\log a_{i,j})} = \frac{a_{i,j} \partial \lambda}{\lambda \partial a_{i,j}} \quad (3-2)$$

where all other elements of the transition matrix are held constant (de Kroon et al. 2000, Caswell 2001).
Because elasticity analyses focus on the contribution of a single parameter at a time (Caswell 2001), I also conducted a sensitivity analysis to examine how sensitive the model would be to simultaneous changes in vital rates. I increased the vital rates for all parameters simultaneously by 5% and 10% and calculated $\lambda$ for each scenario. Because Wood Storks tend to have “boom or bust” dynamics, I also analyzed the sensitivity of the model to the sporadic occurrence of boom years, varying the frequency of that occurrence from 0-100% of the time using a bootstrap analysis with 5000 repetitions over 50 years. I arbitrarily considered a boom year to have fecundity and first year survival double the average and a 10% increase in the survival of older birds.

**Results**

**Sexing**

Of 101 juveniles sexed using blood DNA, 40 were female and 61 were male ($\chi^2 = 0.3984$, d.f. = 1, $p = 0.0360$). Of the 26 adult birds for which we obtained blood samples, DNA sexing showed 13 to be females and 13 to be males.

Mean culmen length was significantly shorter for adult females (209mm, SE 4.86, CI = 198.84-219.16, $N = 11$) than for adult males 233.7 (SE 5.09, CI = 223.04-244.36, $N = 10$) ($t_{19} = 3.5108$, $P = 0.0023$). Mean tarsus length was also significantly shorter for females (194.45mm, SE 5.21, CI = 183.55-205.36, $N = 11$) than for males (216.10 mm, SE 5.46, 95% CI = 204.66-227.54, $N = 10$) ($t_{19} = 2.86$, $P = 0.0099$). On this basis, I assigned sex to an additional eight birds: four adult females and four adult males.

**Juvenile Fledging Success and Survival**

Fledging success was highly variable among years ranging from 0.50-0.958 (Table 3-2) with a mean of 0.7678 (SE 0.0962) from 2002-2005.
Apparent first year survival rates ranged from 0.0588-0.4444, with the highest and lowest values for birds fledging from a single colony (TW in 2002 and 2003 respectively, Table 3-3). When years were pooled (Table 3-4), the proportion of all chicks surviving their first year was 0.30, increasing to 0.58 for birds in their second year and to 0.69 for birds in their third year. Sample size decreased as age increased, with only nine birds surviving into their fourth year and only five into their fifth.

The survival model which best fit the data for juvenile storks was the one in which survival rates differed by age for birds one, two, and three years old and older. For this scenario, there was no clear distinction between the models in which there was an effect of sex on first year survival, survival over all years, or no sex effects (Table 3-5). Survival estimates were slightly higher for females than males, particularly in their first year, with first year survival of 0.3750 (SE 0.0765) for females and 0.2295 (SE 0.0538) for males (Table 3-6). Overlapping confidence intervals indicated that differences between the sexes were not significant, but the small sample of tagged birds may have precluded statistical certainty. When differences between the sexes were ignored, first year survival was estimated as 0.2871 (SE = 0.0450, CI = 0.2074-0.3826).

Survival increased with age for the first three years after fledging, then appeared to level out. Second year survival was estimated to be 0.5559 (SE = 0.0931, CI = 0.3742-0.7238) and survival of birds in their third and older was estimated to be 0.8671 (SE = 0.0706, CI = 0.6626-0.9559) using the Barker model.

**Adult Survival**

For birds tagged as adults, the best supported model was the one in which survival was different in the first year after tagging than in subsequent years, and recapture probability was constant. Models that included sex as a factor affecting survival or recapture received little support (Table 3-7). The estimated survival rates from the preferred model for the first year after
tagging was 0.5440 (SE = 0.0875, CI = 0.3741-0.7042). In subsequent years, survival was estimated to be 0.8612 (SE = 0.0949, CI = 0.5668-0.9671). The nearly 32% difference in survival indicates a probable deleterious effect of the capture and/or tagging process, or of the tag itself. When birds in their third+ year were combined with adults in their second year after tagging, the confidence intervals around adult survival narrowed considerably, to 0.7137-0.9423, with the best estimate of adult survival equal to 0.8645. I considered this value to reflect the unbiased adult survival rate in further analyses.

**Demographic PVA**

When I used apparent survival rates of birds in their first and second years, and 0.8645 for birds in their third+ year, the long term population growth rate was 0.9381. When estimates from the Barker model were used for first and second year survival, \( \lambda \) was equal to 0.9333. When the upper confidence limits from the Barker model for first year survival were used, \( \lambda \) was 0.9505. When the upper confidence limits for first and second year survival were used, \( \lambda \) was 0.9692 and when the upper confidence limit for adult survival was also used, \( \lambda \) was 1.043. When the best estimates from the Barker model were used for first and second year survival and the upper confidence limit for adult survival was used for birds in their third+ year, \( \lambda \) was 1.008. The stable age distributions are presented in Table 3-8. Adult survival values necessary for the population to remain stable ranged from 0.898 when the upper confidence limits from the Barker model were used, to 0.930 when apparent juvenile survival was used, and 0.935 when the estimates from the Barker model were used. Using juvenile and adult survival values estimated by the Barker model, fertility would have to increase by approximately 150% in order for the population to remain stable.
When I projected the hypothetical population vector based on the stable age distribution for each of the four models forward, the population decreased in all scenarios except the one in which adult survival was equal to the upper confidence limits from the Barker model (Figure 3-2). For the declining populations, when estimates for juvenile and adult survival from the Barker model or apparent survival estimates were used, the population declined by 50%, from 10,000 to 5,000 experienced female breeders, in less than 9 years, and by 90% in less than 27 years. When the upper confidence limit for juvenile survival from the Barker model was used, the population declined by 50% in under 21 years and declined by approximately 79% over the 50 years of the projection. The population increased exponentially when adult survival values were set equal to the upper confidence limit of the Barker estimate.

**Sensitivity Analysis**

The elasticity analysis indicated that adult survival had the largest contribution to the population growth rate with elasticity equal to:

\[
\begin{bmatrix}
0 & 0 & 0 & 0.0022 & 0.0564 \\
0.0586 & 0 & 0 & 0 & 0 \\
0 & 0.0586 & 0 & 0 & 0 \\
0 & 0 & 0.0586 & 0 & 0 \\
0 & 0 & 0 & 0.0564 & 0.7090 \\
\end{bmatrix}
\]

When vital rates were increased by 5%, the population growth rate increased from 0.9358 to 0.9828 and when they were increased by 10% the population experienced a positive growth rate \(\lambda = 1.0325\). The addition of boom years also had an effect on the population trajectory, but they had to occur approximately 32% of the time for the population to grow (Figure 3-3).

**Discussion**

Contrary to count-based analyses of Wood Stork population trends, the demographic analysis indicated a declining population. Even when the upper confidence limit of estimated
juvenile survival was used, the population still declined. Since there is no direct evidence that
the population is declining, this raises questions about the accuracy of the survival estimates or
about the predictions of the count-based analysis, including the assumption implicit in the count-
based analysis that the conditions that produced its predictions are persisting. In Chapter One, I
found that the long-term population growth rate (μ) for the Southeastern U.S. Wood Stork
population as a whole was approximately 0.0047 using count based approach, indicating a stable
population. The wide confidence intervals around the estimate did not preclude the possibility of
a long term population decline, and when the density independent model was used, there was a
nearly 60% chance of the population declining by 50% over the next 50 years. Nonetheless,
when I used survival estimates from the Barker model the demographic model predicts a much
closer decline of approximately 50% in under 9 years.

It is possible that fledging success and juvenile survival exhibited a negative bias. These
rates were based predominately on birds captured at two South Florida colonies over four years
(119 of 141 tagged birds). Furthermore, two of those years represented poor foraging conditions
for dispersing juveniles owing to high water levels in Everglades wetlands (see Chapter Three).
If fledging success and first year survival rates estimates are averaged across the two better years
(2002, 2004) they increase from 0.7678 and 0.2772 to 0.888 and 0.3589 respectively, and the
population growth rate increases to 0.9547. The short time series of data coupled with the
limited geographic range and sample size of the satellite tagging effort may have resulted in
survival estimates that are not representative of the population as a whole. Even estimates of
productivity were collected over a short time frame and were unlikely to represent the range of
conditions experienced by breeding birds.
The satellite transmitters themselves may have introduced a negative bias in survival rates. Adult survival was clearly impacted by the capture/tagging process, with survival in the first year after capture nearly 32% less than that in subsequent years. It is unclear whether the high mortality in the year following capture is a product of the capture process itself, or whether there is a deleterious effect associated with carrying the satellite transmitter. At 45-55 g, the satellite transmitters were < 3% of the average body weight of adult Wood Storks. Survival estimates for migratory White Storks in Switzerland of 0.850 (Schaub et al. 2004) were actually lower than those obtained in this study (0.8612), yet that population was deemed to be sustainable. In that model, however, juvenile survival was higher than in this one, birds began breeding one year earlier, and survival was assumed to be at adult rates after the first year of life.

Population models are sensitive to their underlying assumptions, and the deterministic model I used did not incorporate density dependence. The incorporation of density dependence can increase or decrease extinction probabilities, with the end result depending on the type and strength of density dependence, environmental variability, and the population growth rate (Henle et al. 2004). Despite evidence from the count-based analysis that the population growth rate for the Wood Stork is density dependent, the mechanism of density dependence is unclear and it is unknown which vital rates are directly affected. For this reason, I did not attempt its inclusion in the model.

This analysis illustrates the need to increase the geographic and temporal range of research on Wood Stork vital rates. The inclusion of frequent boom years in the model resulted in population growth, but the frequency with which such years occur cannot be inferred directly from the data due to the relatively short time frame over which information was collected. It may take years or even decades to detect population level effects in long-lived species (Arnold et
al. 2006), and this may account for the discrepancy between the demographic and count-based predictions. Predictions from the count-based model were influenced by both current environmental conditions and those that existed more than 20 years ago. In contrast, the vital rates used in the demographic models reflect Wood Storks’ responses to environmental conditions over the past five years and may take years to manifest themselves as population level effects. Wood Storks are dependent upon coastal watershed along the southern Atlantic and eastern Gulf Coasts, yet thousands of acres of these wetlands are lost to development every year. Taken together, the Atlantic and Gulf Coasts of the U.S. lost 361,100 acres between 1998 and 2004 alone (Stedman and Dahl 2008). The loss of these habitats may be forcing Wood Storks to use suboptimal habitats such as agricultural areas and aquaculture facilities that may result in higher levels of mortality for these birds.

Wood Stork population growth rates were clearly most sensitive to changes in adult survival. For this reason, it is important to identify the use of suboptimal habitats and specific threats they may pose to adult survival. For example, Wood Stork deaths have been known to occur at aquaculture facilities (Borkhataria, unpublished data; Bill Brooks, personal communication), but the extent to which aquaculture related deaths occur is unknown. Given the importance of adult survival to the population, identifying and eliminating this threat through education or other mitigation might have important population level consequences.

**Conclusion**

While the Wood Stork was declared endangered in 1984, recent increases in numbers of birds nesting across the Southeastern U.S. have led to cautious optimism that the population may be rebounding. The survival estimates presented in this study and the demographic model that incorporated them indicates, however, that Wood Stork vital rates would have to be higher than those we have observed in order for the population to remain stable or increase. Wood Stork
survival rates were lowest for birds in their first year after fledging and highest for birds in their third year or older (adults). The model was particularly sensitive to changes in adult survival, indicating that management actions that increase adult survival are crucial for the recovery of the species. The model was also sensitive to the occurrence of boom years, in which productivity and survival simultaneously increased. For this reason, future studies should focus on the identification of the primary sources of adult mortality and on understanding of variability in productivity and the frequency of extreme recruitment and survival events. This information can be easily incorporated into the models I have described and will allow us to shed further light on the status of the Wood Stork in the Southeastern U.S.
Table 3-1. Locations of tag deployment on juvenile and adult birds included in analyses. Tags were deployed from 2002-2008.

<table>
<thead>
<tr>
<th>Location</th>
<th>Year</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Description</th>
<th># Tags</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bear Island WMA, SC</td>
<td>2006</td>
<td>32.574</td>
<td>-80.48</td>
<td>Wildlife Management Area near several SC colonies</td>
<td>1</td>
</tr>
<tr>
<td>Noxubee NWR, MS</td>
<td>2005</td>
<td>33.282</td>
<td>-88.798</td>
<td>Summer staging area on National Wildlife Refuge</td>
<td>5</td>
</tr>
<tr>
<td>Corkscrew Swamp Sanctuary, FL</td>
<td>2006</td>
<td>26.31433</td>
<td>-81.635</td>
<td>Birds caught in flooded ditch &lt; 5 mi SW of Corkscrew colony</td>
<td>5</td>
</tr>
<tr>
<td>Welaka National Fish Hatchery, FL</td>
<td>2006</td>
<td>29.433</td>
<td>-81.648</td>
<td>Birds caught after breeding season at fish hatchery</td>
<td>6</td>
</tr>
<tr>
<td>White Hall, SC</td>
<td>2006</td>
<td>32.723</td>
<td>-80.697</td>
<td>Colony on private land in South Carolina</td>
<td>1</td>
</tr>
<tr>
<td>Palm Beach SWA, FL</td>
<td>2008</td>
<td>26.767</td>
<td>-80.145</td>
<td>Colony at Palm Beach Solid Waste Authority</td>
<td>4</td>
</tr>
<tr>
<td>Jacksonville Zoo, FL</td>
<td>2004-2008</td>
<td>30.405</td>
<td>-81.645</td>
<td>Free-living colony at the Jacksonville Zoo</td>
<td>6</td>
</tr>
<tr>
<td>Juveniles</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tamiami Trail West, FL</td>
<td>2002, 2003</td>
<td>25.76</td>
<td>-80.545</td>
<td>Colony in northwestern corner of Everglades National Park</td>
<td>72</td>
</tr>
<tr>
<td>Palm Beach SWA, FL</td>
<td>2004, 2005</td>
<td>26.767</td>
<td>-80.15</td>
<td>Colony at Palm Beach Solid Waste Authority</td>
<td>46</td>
</tr>
<tr>
<td>Chew Mill Rookery, GA</td>
<td>2005</td>
<td>32.83</td>
<td>-82.098</td>
<td>Colony in private mill pond in GA</td>
<td>11</td>
</tr>
<tr>
<td>Harris Neck NWR, GA</td>
<td>2005</td>
<td>31.63</td>
<td>-81.275</td>
<td>Colony on National Wildlife Refuge in coastal GA</td>
<td>11</td>
</tr>
</tbody>
</table>
Table 3-2. Fledging success rates for juvenile Wood Storks outfitted with satellite tags in 2002-2005, from approximately 27 d of age to departure from the colony.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number tagged</th>
<th>Number Fledged</th>
<th>Fledging success</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>33</td>
<td>27</td>
<td>0.818</td>
</tr>
<tr>
<td>2003</td>
<td>34</td>
<td>17</td>
<td>0.500</td>
</tr>
<tr>
<td>2004</td>
<td>24</td>
<td>23</td>
<td>0.958</td>
</tr>
<tr>
<td>2005</td>
<td>44</td>
<td>35</td>
<td>0.795</td>
</tr>
</tbody>
</table>

Table 3-3. Apparent annual survival by age and cohort.

<table>
<thead>
<tr>
<th>Age</th>
<th>Cohort</th>
<th># of birds at start</th>
<th>Fate at the end of a 1-yr interval</th>
<th>Apparent survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alive</td>
<td>Dead</td>
</tr>
<tr>
<td>1st Year</td>
<td>2002</td>
<td>27</td>
<td>12</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>17</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>23</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>35</td>
<td>9</td>
<td>20</td>
</tr>
<tr>
<td>2nd Year</td>
<td>2002</td>
<td>12</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>8</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>9</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>3rd Year</td>
<td>2002</td>
<td>8</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>5</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>4th Year</td>
<td>2002</td>
<td>5</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5th Year</td>
<td>2002</td>
<td>5</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 3-4. Apparent survival of Wood Storks in each age class from 2002-2007.

<table>
<thead>
<tr>
<th>Age class</th>
<th># of birds at start</th>
<th>Fate at the end of a 1-yr interval</th>
<th>Apparent survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Alive</td>
<td>Dead</td>
</tr>
<tr>
<td>1st Year</td>
<td>102</td>
<td>30</td>
<td>55</td>
</tr>
<tr>
<td>2nd Year</td>
<td>30</td>
<td>18</td>
<td>5</td>
</tr>
<tr>
<td>3rd Year</td>
<td>18</td>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>4th Year</td>
<td>9</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>5th Year</td>
<td>5</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>6th Year</td>
<td>4</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 3-5. Model structure, AICc values, delta AICc, and number of parameters for models of survival of juvenile Wood Storks outfitted with satellite tags in SFL (2002-2005) and GA (2005).

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>S_{sex-all years, age 1, 2, 3+}</td>
<td>412.80</td>
<td>0.00</td>
<td>7</td>
</tr>
<tr>
<td>S_{sex-1st year, age 1, 2, 3+}</td>
<td>412.86</td>
<td>0.06</td>
<td>7</td>
</tr>
<tr>
<td>S_{age 1, 2, 3+}</td>
<td>413.21</td>
<td>0.41</td>
<td>6</td>
</tr>
<tr>
<td>S_{sex-all years, age 1, 2, 3, 4+}</td>
<td>414.93</td>
<td>2.14</td>
<td>8</td>
</tr>
<tr>
<td>S_{sex-1st year, age 1, 2, 3, 4+}</td>
<td>415.00</td>
<td>2.20</td>
<td>8</td>
</tr>
<tr>
<td>S_{age 1, 2, 3, 4+}</td>
<td>415.33</td>
<td>2.53</td>
<td>7</td>
</tr>
<tr>
<td>S_{sex-1st year, age 1, 2+}</td>
<td>417.11</td>
<td>4.31</td>
<td>6</td>
</tr>
<tr>
<td>S_{sex-all years, age 1, 2+}</td>
<td>417.12</td>
<td>4.32</td>
<td>6</td>
</tr>
<tr>
<td>S_{age 1, 2+}</td>
<td>417.47</td>
<td>4.67</td>
<td>5</td>
</tr>
<tr>
<td>S_{constant}</td>
<td>439.13</td>
<td>26.34</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 3-6. Survival estimates and confidence intervals for Model S_{1st yr sex, no cohort, age 2, 3+}.

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Sex</th>
<th>Survival Estimate</th>
<th>SE</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lower</td>
</tr>
<tr>
<td>1st Year</td>
<td>Female</td>
<td>0.3750</td>
<td>0.0765</td>
<td>0.2403</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>0.2295</td>
<td>0.0538</td>
<td>0.1409</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>0.2871</td>
<td>0.0450</td>
<td>0.2074</td>
</tr>
<tr>
<td>2nd Year Survival</td>
<td>Combined</td>
<td>0.5559</td>
<td>0.0931</td>
<td>0.3742</td>
</tr>
<tr>
<td>3rd+ Year Survival</td>
<td>Combined</td>
<td>0.8671</td>
<td>0.0706</td>
<td>0.6626</td>
</tr>
</tbody>
</table>
Table 3-7. Model structure, AICc values, delta AICc, and number of parameters for Barker models of survival of juvenile Wood Storks outfitted with satellite tags in SFL (2002-2005) and GA (2005).

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th># Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_{\text{tag effects}} R_{\text{constant}}$</td>
<td>105.64</td>
<td>0.00</td>
<td>6</td>
</tr>
<tr>
<td>$S_{\text{constant}} R_{\text{constant}}$</td>
<td>107.53</td>
<td>1.90</td>
<td>5</td>
</tr>
<tr>
<td>$S_{\text{tag effects}} R_{\text{sex}}$</td>
<td>107.96</td>
<td>2.33</td>
<td>7</td>
</tr>
<tr>
<td>$S_{\text{sex}} R_{\text{constant}}$</td>
<td>109.72</td>
<td>3.44</td>
<td>6</td>
</tr>
<tr>
<td>$S_{\text{sex}}, R_{\text{constant}}$</td>
<td>109.57</td>
<td>3.94</td>
<td>8</td>
</tr>
<tr>
<td>$S_{\text{sex}} R_{\text{sex}}$</td>
<td>109.81</td>
<td>4.17</td>
<td>6</td>
</tr>
<tr>
<td>$S_{\text{sex}}, R_{\text{sex}}$</td>
<td>111.40</td>
<td>5.76</td>
<td>7</td>
</tr>
<tr>
<td>$S_{\text{sex}}, R_{\text{sex}}$</td>
<td>112.01</td>
<td>6.38</td>
<td>9</td>
</tr>
</tbody>
</table>
Table 3-8. Stable age distribution and number of female birds in each age class for a hypothetical population with 10,000 adult females for 4 models with different survival parameters. UCL stands for the upper 95% confidence limit for the age-specific survival rate as calculated using the Barker model.

<table>
<thead>
<tr>
<th>Age class</th>
<th>Apparent juvenile survival</th>
<th>Barker estimates, juvenile and adult survival</th>
<th>Barker 1&lt;sup&gt;st&lt;/sup&gt; and 2&lt;sup&gt;nd&lt;/sup&gt; year survival = UCL</th>
<th>Barker model UCL’s for all survival estimates</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st year</td>
<td>0.2605</td>
<td>4675</td>
<td>0.2636</td>
<td>4688</td>
</tr>
<tr>
<td>2nd year</td>
<td>0.0833</td>
<td>1495</td>
<td>0.0811</td>
<td>1442</td>
</tr>
<tr>
<td>3rd year</td>
<td>0.0515</td>
<td>924</td>
<td>0.0483</td>
<td>859</td>
</tr>
<tr>
<td>4th year</td>
<td>0.0475</td>
<td>852</td>
<td>0.0447</td>
<td>795</td>
</tr>
<tr>
<td>Adult females</td>
<td>0.5572</td>
<td>10000</td>
<td>0.5623</td>
<td>10000</td>
</tr>
</tbody>
</table>
Figure 3-1. Locations where satellite transmitters have been deployed on juvenile (triangles) and adult (circles) Wood Storks from 2002-2007.
Figure 3-2. Future population size over the next 50 years when deterministic matrix is parameterized using apparent or estimated survival rates.
Figure 3-3. Population size (adult females) after 50 years when the proportion of boom years varied from 0-1. The gray dashed line represents the starting population size of 10,000 adult females.
CHAPTER 4
SURVIVAL OF JUVENILE WOOD STORKS IN RELATION TO EVERGLADES WATER LEVELS AND TIMING OF NESTING

Introduction

Habitat alteration and climate change are among the greatest threats to global biodiversity and it is difficult to predict to what extent individual species may adapt to changing conditions via phenotypic plasticity and/or the rapid evolution of adaptive traits. Global climate change has changed the timing of favorable environmental conditions for many organisms and the response has been a change in range or advancement in phenology for many taxa and species (Both et al. 2004, Both and Visser 2005, Marra et al. 2005, Parmesan 2006). For birds, these changes often manifest as earlier arrival of migrants and earlier breeding in response to warmer spring weather (Walther et al. 2002, Parmesan and Yohe 2003, Both et al. 2004). The fitness consequences of such changes depend on whether crucial interactions between species (e.g., predators and prey, herbivores and plants, parasitoids and hosts, etc.) are disrupted by asynchronous shifts or mismatches in phenology (Visser and Both 2005, Parmesan 2006).

So far, few temperate avian species have shown a delay in the onset of breeding. A review of 677 species found that only 9% had delayed spring activities, whereas 62% showed spring advancement in response to earlier onset of warm spring conditions (Parmesan and Yohe 2003). Phenological changes can have causes other than climate change, however, and in the Florida Everglades changes in the phenology of waterbirds have been linked to anthropogenic changes in hydrology rather than climate. Retention of water in the Water Conservation Areas and decreased flows to the Florida Bay estuary (to the south) and Gulf of Mexico (to the west) have led to changes in the timing and location of prey availability for Wood Storks. As a result, rather than initiating nesting in November or December as they did prior to 1960’s, Wood Storks in the Everglades now typically begin nesting in February and March (Ogden 1994).
The Everglades ecosystem consists of a mix of higher elevation, short hydroporid wetlands interspersed with deeper water sloughs. Historically, this system flooded during the wet season, inundating the higher elevation marshes and moving via sheet flow through the sloughs before draining into Florida Bay and into estuaries along the Gulf of Mexico (Fleming et al. 1994). High concentrations of food were available throughout the breeding season as a result of a seasonal drying pattern (November – April) which concentrated fish and invertebrates into increasingly smaller and shallower pools (Kushlan 1976, Ogden 1994). The deeper sloughs remained flooded and freshwater flows continued throughout the dry season into the estuaries and Florida Bay (Fleming et al. 1994), supporting productive nurseries for fish and shrimp and good foraging areas for wading birds (McIvor et al. 1994, Lorenz 1999). The majority of Wood Stork colonies occurred in the mangrove-freshwater ecotone during this time period.

Drainage, impoundment, conversion to agriculture and housing, and inappropriate water management during the 20th century (Fennema et al. 1994, Light and Dineen 1994) resulted in the outright or functional loss of many of the short hydroporid marshes and coastal habitats that supported nesting by Wood Storks early in the dry season. Higher elevation marshes remain inundated for longer periods of time, decreasing prey availability for wading birds during the early dry season and salinities in the mangrove-freshwater ecotone and Florida Bay have increased due to the reduction in freshwater inflows, negatively affecting fish and shrimp communities as well as those taxa that prey up them (McIvor et al. 1994, Lorenz 1999). As a result, Wood Stork colonies in the Everglades are a small fraction of their historical size and number and colonies initiate much later they did historically (Ogden 1994). This sharp decline in Everglades colonies led to the listing of the Wood Stork as Federally endangered in 1984 (U.S. Fish and Wildlife Service 1996).
The initiation and success of Wood Stork breeding colonies are known to be closely tied to water levels and prey concentrations (Kahl 1964, Kushlan 1976, Ogden 1994, Coulter et al. 1999) and late nesting has had a negative impact on Wood Stork productivity in South Florida (SFL). Ogden (1994) found that colonies initiated after December were smaller and less successful than those that were started in November and December, and that both size and success rates decreased as the time before initiation lengthened. A major reason for the low success rates of these later colonies is that Wood Storks are unable to finish their nesting cycle prior to the start of the summer wet season that extends from May through October. The onset of the summer rains causes water levels to rise across the Everglades, which decreases prey availability as fish and other prey that had become increasingly concentrated over the course of the dry season disperse into the rising waters. As a result, adult Wood Storks often abandon their nests before their young have fledged and nestlings are left to starve en masse (Frederick et al. 2008).

The reproductive cycle of the Wood Stork takes approximately 105-130 days (Coulter et al. 1999). When nesting began in November or December (“early”) young Wood Storks would typically fledge during the height of seasonal drying in March and April, when prey may be super-available (Kahl 1964). Since 1970, however, Wood Storks have only initiated nesting as early as December twice (Ogden 1994), and most nesting events begin in February through March (“late”) (U.S. Fish and Wildlife Service 1999). Late initiated colonies that are successful will fledge young in late May, June, or July (Figure 4-1), during a time of rising water, dispersing prey, and poor food availability.

If young birds do survive to fledge, there may still be consequences of dispersing so late in the year into such poor conditions. If late nesting and the related rising water conditions
during and following fledging have a negative effect on juvenile survival, recruitment of juvenile birds into the population will, by extension, be affected as well. In metapopulation models, similar asymmetries have been shown to increase the probability of population extinction (Vuilleumier and Possingham 2006, Benard and McCauley 2008). Until now, however, the effect of late nesting and water levels on juvenile survival and Wood Stork population dynamics has not been addressed.

A major goal of Everglades restoration and Wood Stork recovery is an increase in numbers of Wood Storks nesting in south Florida. The Wood Stork Recovery Plan calls for reliable nesting in south Florida of at least 2500 pairs (U.S. Fish and Wildlife Service 1996), however it is not currently clear whether the Everglades contributes to the larger population or whether it constitutes a population sink for the species in North America. If South Florida acts as a net importer, or sink, for the population (sensu Pulliam 1988), increased nesting in SFL without earlier nest initiation may be detrimental to the overall population.

Here, I present an analysis of post-fledging dispersal and survival from 2 South Florida Wood Stork colonies in relation to early wet season water levels and water recession rates in Everglades wetlands. My objectives were to describe the survival rates, post-fledging movement patterns, and habitat use of juvenile Wood Storks in south Florida when fledging into optimal (dry, typical of historic conditions) vs. suboptimal (wet, typical of most recent 30 years) conditions. I also present an analysis of the potential population-level effects resulting from the interaction between juvenile mortality and the frequency with which birds fledge into suboptimal conditions. Specifically, I wanted to test the hypothesis that high and rising water levels at the time of post-natal dispersal may cause South Florida Wood Stork colonies to act as a sink for the larger population.
Study Area and Methods

Using satellite telemetry, I followed the fates of juvenile birds fledged from two South Florida (SFL) colonies in 2002-2005. In 2002 and 2003, work was conducted in the Tamiami West colony (TW) (N25°45’31, W80°32’4) in Everglades National Park, Miami-Dade County, with satellite tags deployed by master’s student Rebecca Hylton (see Hylton 2004). In 2004 and 2005, this colony failed completely, and I captured birds in the Palm Beach Solid Waste Authority Rookery (SWA) (N26°46’06, W80°08’45), Palm Beach County.

After birds fledged, they dispersed widely across the southeastern United States. For the purposes of this study, however, I was particularly interested in their activities in South Florida (SFL), which includes all areas south of Lake Okeechobee, and in the remaining Everglades wetlands, which are contained within a series of Water Conservation Areas (WCAs) and Everglades National Park (ENP) (Figure 4-1).

Satellite Telemetry

A total of 113 satellite transmitters were deployed on juvenile birds over four years in SFL. In 2002 and 2003, Hylton (2004) used 35g solar powered Argos/PTT satellite tags (Microwave Telemetry, Inc., Columbia MD, USA, 10h on/24 h off duty cycle) with a 10g VHF transmitter attached (Advanced Telemetry Systems, Isanti, MN, and American Wildlife Enterprises, Monticello, FL). These tags had an accuracy range of 100-1000 m. In 2004 and 2005, I used 45g solar powered GPS/PTT satellite transmitters (Microwave Telemetry, Inc., Columbia MD, USA, hourly locations, 16h on/8 h off duty cycle) with attached 10g VHF transmitters (Advanced Telemetry Systems, Isanti, MN) and an accuracy of approximately 18 m. In all cases, birds were caught by climbing to the nest using tree branches or ladders, and simply removing flightless or poorly flighted young by hand from the nest. The largest sibling from each nest (based on visual comparisons of culmen length and overall size) was tagged at four to
six weeks of age. Transmitters were permanently attached to the birds using a 0.25 cm wide teflon ribbon backpack-style harness sewn through with elastic thread which provided a snug fit to immature birds but expanded as the birds grew (see Hylton 2004 for a complete description of tagging protocol). Birds were also given a brief physical exam and blood was collected from the brachial vein. Blood samples were sent to Zoogen Services Inc. (Davis, CA) or Avian Biotech International (Tallahassee, FL) for DNA sexing.

**Water Levels and Recession Rates**

I used daily water level measurements from gauging stations in Water Conservation Area 3A (CA3AVG) and Everglades National Park (Station P-33) to estimate mean water depths and daily recession rates by month for Everglades wetlands since 1962 (South Florida Water Management District 2008). CA3AVG represents a 3 gauge average from WCA 3A and is used by the SFWMD to characterize water conditions within that WCA (Abtew et al. 2009). Station P-33 is frequently used as an indicator of water conditions in freshwater marshes of the main drainage in Everglades National Park (Ogden 1975, Abtew et al. 2008).

Daily recession rates were calculated by subtracting the water depth at time \( t+1 \) from water depth at time \( t \) and dividing by number of intervening days. Positive recession rates indicate receding water levels and drying conditions, while negative recession rates indicate rising water. I used mean daily water depth and recession rate estimates from 2002-2005 to characterize hydrological conditions (i.e., wet vs. dry, rising vs. receding) encountered by dispersing juvenile Wood Storks in the early wet season (May and June) during this study. Water depth and recession rate estimates are reported as means (SE), and comparisons among years were made using a nonparametric Kruskal-Wallis chi-square approximation.

The entire 30 year period of record for these gauges was used to estimate the frequency with which dispersing storks were likely to encounter rising vs. receding water levels and to
illustrate seasonal differences in water depths and recession rates. I also used mean monthly water depths in November-February from 1962-1973 and from 1997-2008 to illustrate differences between historical and modern water levels in WCA3A.

**Survival of Young**

I used data from the 113 juvenile Wood Storks that were outfitted with satellite transmitters in the two SFL colonies (Tamiami West and the Palm Beach SWA) to examine the effect of Everglades water levels on fledging success and post-fledging dispersal dynamics. I quantified the number of satellite tagged juveniles that dispersed from the colony and that survived an entire year after dispersing. A bird was considered to have started the dispersal process when it did not return to within two km of the natal colony for at least seven days. I again used joint modeling of live-recapture, live-resight, and tag-recovery data (Barker’s model) in Program MARK to estimate survival rates for this subset of SFL birds for their first year after dispersal.

To isolate the effects of cohort, water level, and sex on survival, I then compared a range of models that allowed for variation in survival rates as a function of these three variables. To test for the effects of cohort, I used a model in which first year survival was estimated separately for each of the four cohorts of birds that were tagged. The effects of water level were built into the model by estimating two first year survival rates, one for the two wetter years combined, and another for the two drier years combined. I considered the possibility that survival rates were constant over the years of the study, and could be estimated by a single parameter. I also considered the possibility that survival rates under all of the above scenarios varied by sex, for a total of six survival scenarios with no interaction effects. Recapture rates were modeled as constant, varying by cohort, varying by sex, or varying by water level. I did not consider interactions among factors relevant for recapture rates. The combination of six survival models
with the four recapture models resulted in a total of 24 models for comparison. I chose the best model as the one with the lowest AICc (Burnham and Andersen 1998).

**Movement Patterns and Habitat Use**

I analyzed movement patterns, water depths and land cover types at Wood Stork telemetry locations in ArcGIS 9.2 (ESRI 2007). To describe general movement patterns I used location data from all 4 years, but, due to the limited accuracy (100-1000m) of the Argos/PTTs, I confined our analyses of habitat use to locations < 50 m altitude obtained from GPS-enabled tags in 2004 and 2005. Given the average hourly step length I observed for the time period in question ($\bar{x} = 4.38$ km, SE = 187.84, n = 7033), and the ability of birds to move more than 100 km in an hour, I considered all locations to be independent for this analysis.

To determine the type of habitats in which locations occurred, I used the U.S. Fish and Wildlife Service National Wetland Inventory (NWI) (U.S. Fish and Wildlife Service 2008) to quantify wetland types used by satellite tagged juvenile storks during their dispersal from the SWA rookery in June and July of 2002 and 2003. For areas not classified as wetlands by the NWI, I used the National Land Cover Dataset (NLCD) (Multi-Resolution Land Characteristics Consortium 2008) to quantify land cover types. I collapsed little used categories and included seven categories in the final analysis: forested wetland, emergent wetland, “other freshwater” (ponds, riverine, open water), marine (deepwater and wetlands), developed, agriculture, and “other terrestrial” (upland forest, shrub/scrub, grassland, and barren). I calculated the proportion of locations recorded in each land cover type and compared use between years during the early wet season (June and July) using multi-response permutation procedures (MRPP). MRPP is a nonparametric method for evaluating differences between groups, which tests whether two or more sets of locations share the same probability distribution (White and Garrott 1990, McCune
and Grace 2002). The test does not assume that data is normally distributed or that the variances are homogeneous (Zimmerman et al. 1985), rendering it particularly useful for the analysis of ecological data.

Because birds in 2004 dispersed broadly across Florida and northward into Georgia and South Carolina, while birds from 2005 remained in central and south Florida during those months, I did two comparisons: one in which all locations from both years were used, and a second, restricted, analysis in which I only used points from 2004 which fell within the minimum convex polygon (Beyer 2004) created from 2005 locations (see Figure 4-4).

I used the Everglades Depth Estimation Network (U.S. Geological Service 2008) to estimate mean water depths used by dispersing juvenile Wood Storks in the Everglades (Figure 4-2). EDEN integrates water levels, ground elevation models, and water surface models to provide scientists with continuous daily spatial interpolations of water stage level and water depth for the freshwater Everglades from 2000 through the present on a 400 x 400 m grid (Pearlstine et al. 2007). All locations within the area modeled by EDEN were assigned the EDEN daily water depth of the grid cell within which they occurred for the day the location was recorded. I used these values to calculate the mean water depth used by juvenile Wood Storks in 2004 and 2005 from the time they dispersed from the colony through the end of July.

**Stochastic Simulation Modeling**

I used a stochastic simulation model to test the effect of the frequency of favorable years on Wood Stork population dynamics. Prior to choosing to incorporate dynamics associated with water levels stochastically, I tested the mean water depth in WCA3A for June since 1962 for autocorrelation and periodicity using spectral analysis in the JMP 7.2 statistical software package. Since there was no evidence of temporal autocorrelation or periodicity in water depths over this time period, I modeled the frequency of favorable water levels in the Everglades as
independently and ideally distributed (Morris and Doak 2002). I then used a structured population matrix model (Borkhataria et al. 2008, Chapter Two) to simulate the growth or decline of an idealized hypothetical South Florida population of 2500 nesting pairs of Wood Storks over 30 years and varied the first year survival values to simulate changes in the frequency with which birds encounter favorable conditions when fledging, as below.

Again, I used the basic female-only, post-breeding matrix structure of Borkhataria et al. (2008):

\[
\begin{bmatrix}
  n_{0t} \\
  n_{1yo} \\
  n_{2yo} \\
  n_{3yo} \\
  n_{4+y0}
\end{bmatrix} =
\begin{bmatrix}
  0 & 0 & 0 & f_3 & f_4 \\
  s_0 & 0 & 0 & 0 & 0 \\
  0 & s_1 & 0 & 0 & 0 \\
  0 & 0 & s_2 & 0 & 0 \\
  0 & 0 & 0 & s_3 & s_{4+}
\end{bmatrix}
\]

(4-1)

where the initial vector represents the number of individuals in each age class at time \( t \) as determined for a stable population of 2500 nesting pairs (represented by female birds only) and the interior matrix represents age specific vital rates.

To determine the age structure for the initial population vector, I initially parameterized the basic stage-structured matrix for this population described in the previous chapter, retaining the second year and adult survival rates from the basic matrix but substituting the first year survival estimate from just the Florida juveniles averaged across the four years of the study. I derived the value of adult survival necessary to sustain a stable population by varying the values for adult survival used in the matrix from 0.85-0.95 in increments of 0.02 and calculated the resulting population growth rate. I then used linear regression to interpolate the value of adult survival necessary to result in \( \lambda = 1 \). Using this value for adult survival, I calculated the stable age distribution by taking the right eigenvector of the matrix and used it to create a stage-specific vector of initial population size for a population with 2500 nesting pairs.
I projected this population over the next 30 years, using one of two matrices. In the first matrix, first-year survival was equal to the estimated survival rate observed for the two drier years while in the second it reflected the mean value for the two wetter years. Because I have shown that second year survival differs from that of birds in their third year or older, I set second year survival equal to the observed value of 0.5775 (Chapter 2). To isolate the effects of first year survival on the population as a whole, however, I used the value for adult survival necessary to maintain a stable population rather than the observed rate in both matrices.

For each year the population was projected forward, one of these two matrices was drawn at random. I varied the frequency with which each matrix was drawn in order to simulate the population level effects of the probability of birds fledging into favorable or unfavorable conditions. I varied the probability of encountering favorable conditions from 0-1 in 0.1 increments and used a bootstrap analysis with 5000 replications.

**Results**

**Water Levels**

Average daily water depths in the early wet season (May and June) varied significantly among years in both WCA3A and ENP ($\chi^2 = 140.41$, 3 df, $p < 0.0001$; $\chi^2 = 86.95$, 3 df, $p < 0.0001$). Conditions were considerably deeper in 2003 and 2005 than they were in 2002 and 2004 (Table 4-1, Figure 4-3). In WCA3A, the average depths across May and June in the 2 drier years were 10.68 (0.78) cm and 19.12 (0.72) cm (2002 and 2004 respectively), while in the two wetter years they averaged 34.45 (0.76) cm and 31.30 (0.72) cm (2003 and 2005 respectively). While the two wetter years were approximately twice as deep as the 30 year average (1975-2005) of 16.63 (3.34) cm, they were within 1 standard deviation of that mean (std. dev. = 26.30).

In ENP, average early wet season depths in the drier years were 15.10 (1.27) and 12.63 (0.26) (2002 and 2004 respectively), while in the two wetter years they were 29.21 (1.15) and
13.7 (1.54) (2003 and 2005). The 30 year average at this gauge was 11.73 cm (3.14) and in 2003 water levels were more than 1 standard deviation higher than the mean (std. dev. = 17.24) although in 2005 it did not. The low mean depth in 2005 was due to the relatively late start of the rainy season in mid-June, however, and water levels during the last half month of that month averaged 31.28 cm.

The conditions encountered by fledging juveniles depended upon the month in which the majority of birds fledged. In 2002 (dry) and 2003 (wet), the majority of birds fledged from the more southerly TW colony in May, encountering average water depths in WCA3A of 10.68 (0.45) and 34.46 (0.76) cm and average depths in ENP of 7.78 (0.35) and 22.05 (0.99) cm for 2002 and 2003 respectively. In 2004 (dry) and 2005 (wet), the majority of birds fledged from the more northerly SWA colony in June, encountering average water depths in WCA3A of 8.63 (0.37) and 53.68 (2.71) cm and average depths in ENP of 11.98 (0.31) and 22.84 (2.02) cm. The mean EDEN cell depth at used locations in 2004 was 19.23 cm +/- 15.65 (n = 934, CI = 3.58-34.88) while in 2005 it was 43.90 cm +/- 3.61 (CI = 40.29-47.51).

**Recession Rates**

In WCA3A, water levels were still receding (positive values) in May of 2002 and 2004, and in June 2004 (Table 4-1) but were rising (negative values) in both May and June of 2003 and 2005 and in June 2002. Daily recession rates encountered by storks dispersing into WCA3A in the 2 drier years averaged 0.106 (0.320) cm (May 2002) and 0.163 (0.253) cm (June 2004) and averaged -0.481 (0.345) cm (May 2003) and -1.687 (0.359) cm (June 2005) in the two wetter years. Average daily recession rates in WCA3A differed significantly among years ($\chi^2 = 12.27$, 3 df, $p = 0.0065$; and $\chi^2 = 32.49$, 3 df, $p < 0.0001$ for May and June respectively).
At ENP, water levels were generally increasing in May and June for the years of this study, with the exception being May 2004, when water levels were, on average, still receding (Table 4-1). While average daily recession rate in May did not differ significantly among the 4 years of this study ($\chi^2 = 0.26, 3$ df, $p = 0.97$), the rate at which water was rising tended to be higher in 2003 and 2005. In June water levels were rising in all years and differences among years were significant ($\chi^2 = 11.71, 3$ df, $p = 0.0084$) with water levels rising most quickly in 2002, 2003, and 2005. Wood Storks dispersing into ENP during the two drier years would have encountered mean daily recession rates of -0.049 (0.155) cm (May 2002) and -0.122 (0.129) cm (June 2004) while those dispersing in the two wetter years would have encountered mean daily recession rates of -0.482 (0.382) cm and -1.128 (0.311) cm in ENP for 2004 and 2005 respectively.

When taken in their historical context, daily recession rates in WCA3A averaged by month over the past 30 years, have been mostly positive (receding) in May (22 times or 73% of the time) and negative (rising) in June (24 times or 80% of the time) (Table 4-2). In ENP, mean daily recessions have been mostly negative (rising) in both May (18 times, 60%) and June (26 times, 87%) (Table 4-3).

**Survival**

Of the 113 birds that were tagged in 2002-2004, 86 fledged from their natal colony and the rest died in or around the colony. First year survival estimates by cohort were lowest in 2003 and 2005, and highest in 2002 and 2004 (Table 4-4). The survival model that best fit the data was the one in which survival varied with water level and recapture rates were constant. There was little support for sex-based differences in survival (Table 4-5). When I combined estimates for male and female birds, survival for years with lower water levels was 0.3673 (SE 0.0689, CI
= 0.2452-0.5093), while for the wetter years the annual survival rate was estimated to be 0.1429 (SE = 0.0591, CI = 0.0607-0.3005). When first year survival was constrained to be constant among cohorts, it was estimated at 0.2738 (SE 0.04865, CI = 0.1892-0.3785).

**Use of Everglades Wetlands**

Due to the location of the Tamiami West colony within Everglades National Park (ENP), all birds dispersing from the natal colony in 2002 and 2003 had a strong likelihood of passing through ENP or the WCAs. A total of 99 post-dispersal locations occurred within the WCAs and ENP in May-July, 2002, with 21 of the 27 birds that dispersed from the Tamiami West colony located within these areas at least once. The number of days individual birds used these wetlands ranged from 1-8 (x = 3.09 +/- 2.21, SE = 0.48), and spanned the period from 16 May-16 June. In 2003, however, only 10 post-dispersal locations occurred in the WCAs and ENP in May-July 2003, with only 3 of the 17 birds that dispersed from the TW colony located within these wetlands. The number of days individual birds used these wetlands ranged from 1-3 and occurred on 28 May-01 June.

In 2004, seven of the 23 birds that dispersed from the SWA Rookery traveled south and made use of the Water Conservation Areas and/or Everglades National Park. These areas were in use from 12 June through 23 July, with the number of days any one bird was present ranging from four to 41. After leaving the Everglades wetlands, one bird flew to South Carolina, one took up residence in northern Florida, and the rest remained in central or south Florida. In contrast, in 2005 only two birds used the Water Conservation Areas and Everglades National Park and only eight locations from only one bird occurred within the area modeled by EDEN (13-14 June).
Mortality

In 2002, four dispersing juveniles died before the end of July. Two of these birds used
Everglades wetlands and then died in central Florida, one moved directly into central Florida and
died, and the last moved northward and died around 06 July in South Carolina. Of the birds that
survived to the end of July, 10 ended the month in central Florida, two in northern Florida, six in
Georgia, three in Alabama, two in Louisiana, and three in South Carolina. In 2003, only six of
the 17 tagged birds survived to the end of July and of these birds, two ended the month in central
Florida, one in northern Florida, and three in Georgia. The rest of the birds died in central and
south Florida.

Of the other 16 birds that dispersed northward or westward from the SWA Rookery in
2004, two ended July in South Carolina, four in GA, seven remained in central and south Florida,
one took up residence near Daytona Beach in northern Florida, and one flew northward to the
Florida/Georgia border then returned to central Florida. Three birds died in Florida before the
end of July, in Brevard, Glades, and Lafayette counties.

Of the 19 birds that dispersed from the colony in 2005, 12 died before the end of July. Of
these, eight died in habitats that were classified as agricultural. Of the remaining three deaths,
locations at the time of death were classified as emergent wetland, forested wetland, and
developed. There was one possible tag failure. All deaths occurred in central and southern
Florida, with the majority of deaths occurring in Palm Beach (4), St. Lucie (3) and Indian River
(2) counties. The 2 remaining deaths occurred in Broward and Hendry counties. No birds ended
July further north than Brevard Co. in Central Florida.

Habitat Use

When I compared the types of habitats used, I found that habitat use was significantly
different between 2004 and 2005, for both the range-wide analysis and the restricted analysis (A
= 0.0626, $P = 0.0093$ and $A = 0.0828, P = 0.0084$ respectively). In 2004, the most commonly used habitats range-wide were emergent wetlands (38.8%), agricultural areas (26.2%), forested wetlands (18.2%), other freshwater habitats (5.4%), and other terrestrial habitats (5.2%). Developed areas and marine areas were used relatively little (3.1 and 3.0% respectively). When I restricted the 2004 locations to the areas within the minimum convex polygon of locations from 2005 (south and central Florida), the same order of use was evident, with emergent wetlands (49.1%), agricultural areas (36.5%), forested wetlands (9.0%), other freshwater habitats (3.4%) used most commonly. In contrast, in 2005 the majority of locations occurred in agricultural areas (47.4%), followed by emergent wetlands (30.7%), forested wetlands (11.6%), and developed areas (7.6%). Other terrestrial habitats, other freshwater habitats, and marine areas made up less than 3% of locations.

**Stochastic Modeling**

The adult survival rate necessary to support a stable population of Wood Storks in South Florida was 0.9385. The stable age distribution for a population with 2500 adult females (age 4+) was 1207, 326, 174, 163, and 2500 for fledglings and 1-4+ year old birds respectively. This resulted in a total population size of 4370 female birds. When I projected this population forward, I found that the mean population size at the end of 30 years increased exponentially with increasing probability that fledging birds encountered favorable conditions (Figure 4-5). In order for the population to remain stable, young birds would have to fledge into favorable conditions approximately 58% of the time. Based on the above analysis of historical recession rates, birds fledging in April would be likely to encounter favorable conditions (receding water levels) approximately 80% of the time (averaged across WCA3A and ENP), which would result in population growth over 30 years of approximately 28%. In contrast, birds that fledge in June are likely to encounter favorable conditions only 20% of the time. This would result in a
population decline over 30 years of nearly 40% (Table 4-6). Birds that fledge in May would encounter favorable conditions only 40% of the time in ENP, but the unavailability of those wetlands might be ameliorated by the probability of encountering favorable conditions in WCA3A nearly 73% of the time. If that is the case, and all birds fledged reliably before June, the South Florida population would increase by approximately 18% or more over 30 years.

**Discussion**

First year survival by juvenile Wood Storks in South Florida was strongly influenced by the wetland conditions they encountered on dispersal. When water conditions in the Everglades were optimal, with water levels still receding and depths average depths below 20 cm, survival rates were high, whereas when water was too deep for Wood Storks to forage and water levels were rising, survival rates were much lower. Although the exact mechanism of their deaths was unknown, I saw significant differences in habitat use in dry vs. wet years which may have impacted survival. Although I only compared habitat use in two years, it was clear that in the drier year emergent wetlands were the primary habitat used by dispersing Wood Storks while in the wetter year dispersing juveniles moved quickly out of SFL wetlands and were located primarily in agriculture.

The time spent foraging in Everglades wetlands during low water conditions may have influenced subsequent juvenile survival by providing juvenile storks with a relatively benign setting in which to hone their foraging skills. In contrast, the agricultural habitats used by juvenile birds in the wetter years were characterized by fields of row crops dissected regularly by irrigation and drainage ditches. Due to the active management of these ditches, during wetter years agricultural habitats would have provided Wood Storks with lower water levels than those available in SFL wetlands at the time that they were dispersing.
The use of agricultural areas in the absence of optimal foraging opportunities is not unique to storks. For example, juvenile oystercatchers (*Haematopus ostralegus*) were much more likely to visit fields during high tides than adults (Caldow et al. 1999). Caldow et al. (1999) surmised that these fields were riskier for juvenile birds due to increased exposure to cars, trains, and electrical lines on their way to the fields and a higher risk of predation from predators that can take cover in hedgerows and trees. I believe that exposure to toxic chemicals and starvation due to inadequate resources were the more likely causes of high mortality in agriculture for juvenile birds in this study.

Subsequent survival may also have been influenced by the early use of wetlands if the use of these areas shaped future preferences. Foraging abilities and preferences may be shaped by the types of habitats used during natal dispersal (Davis and Stamps 2004, Benard and McCauley 2008). Young birds that learn to forage in appropriate wetland environments may have long-term advantages over those birds that are forced almost immediately into less productive hunting areas. Diet type and foraging method can have a large impact on survival (Durell et al. 2001), thus fledging into optimal habitats may improve both body condition and the ability to find and exploit appropriate resources. For example, in oystercatchers increases in foraging efficiency are associated with improvements in body condition and survival (Durell et al. 2001, Daunt et al. 2007).

Mortality related to water levels in the Everglades affected population dynamics in South Florida on the basis of juvenile survival alone. The frequency with which juvenile birds fledged into dry or wet conditions determined whether a target population of 2500 birds would increase or decline. For example, if Wood Storks nested reliably in December or January and their young fledged in April the population would grow by approximately 28% over the next 30 years.
However, if birds continue to initiate nesting in mid- to late February or March, with young birds fledging in June, they will encounter rising water levels approximately 83% of the time and the breeding population will decline by approximately 38% over the next 30 years.

To maintain a population of 2500 birds in Everglades colonies under these conditions, SFL would have to be a net importer of birds. Given recent trends in the timing of colony initiation by Wood Storks in South Florida, these colonies appear to be acting as a sink for the southeastern U.S. Wood Stork population. In order for SFL colonies to export birds to the larger population, Wood Storks must initiate nesting earlier in the dry season. This will depend on the establishment of a more natural hydrological cycle that restores freshwater flows to the estuaries and Florida Bay and allows for a strong dry-down and shallower depths in the freshwater Everglades during November, December, and January.

Wood Storks generally forage in water that is between 15 and 50 cm deep (Kahl 1964). Historically, these depths were usually available from November-January. For example, in the 12 year period between 1962-1973, mean monthly water levels in WCA3A were less than or equal to 50 cm six times in November, eight times in December, and nine times in January. Over the past 10 years, however, average monthly water depths in WCA3A have never been below 50 cm in November and have been less than or equal to 50 cm only three times each in December and January. It is not until February that there is a reliable drop in water levels.

**Conclusion**

The survival and movements of Wood Storks fledging from South Florida colonies were strongly influenced by Everglades water levels and the timing of dispersal. Birds that fledged into conditions of high and rising water moved quickly out of the Everglades ecosystem and had lower survival rates than those that fledged when water levels were low and receding. When hydrological conditions in the Everglades were favorable, juvenile storks were able to spend
more time in this relatively benign environment, learning important foraging skills and building up energy reserves prior to moving out of the system.

Although Wood Stork population dynamics are most sensitive to adult survival (Chapter Two), this model showed that juvenile survival alone could influence population dynamics in South Florida and determine whether the region acts as a source or a sink for the overall population. While SFL currently appears to function as a population sink (Chapter One), the reliable dispersal of juvenile Wood Storks into favorable hydrological conditions could increase juvenile survival enough that SFL colonies could become self-sustaining.

The Everglades is the subject of a multi-billion dollar restoration project aimed at restoring “natural” hydrologic conditions and earlier nesting by Wood Storks is one of their recovery goals. If Everglades restoration proceeds as planned and restores a more natural hydrological cycle, Wood Storks may once again flourish in South Florida. If not, the continued late nesting of birds in SFL colonies is likely to act to the detriment of the species as a whole.
Table 4-1. Mean daily water depths and recession rates in May and June of 2002-2004 for Water Conservation Area 3A (CA3AVG) and Everglades National Park (NP-33). Positive recession rates indicate receding water levels and negative recession rates indicate rising water levels.

<table>
<thead>
<tr>
<th>Station</th>
<th>Year</th>
<th>Mean daily water depths (cm)</th>
<th>Mean daily recession rates (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>May</td>
<td>June</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\bar{x}$</td>
<td>SE</td>
</tr>
<tr>
<td>CA3AVG</td>
<td>2002</td>
<td>10.68</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>34.46</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>19.13</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>31.30</td>
<td>0.70</td>
</tr>
<tr>
<td>NP-33</td>
<td>2002</td>
<td>7.78</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>22.05</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>13.24</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>4.85</td>
<td>0.45</td>
</tr>
</tbody>
</table>
Table 4-2. Mean daily recession rate by month and frequency of receding vs. rising water levels over a 30 year time period (1978-2007) in Water Conservation Area 3.

<table>
<thead>
<tr>
<th>Month</th>
<th>N</th>
<th>Mean Daily Recession Rate (cm)</th>
<th>SE</th>
<th># of years receding</th>
<th># of years rising</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>30</td>
<td>0.20</td>
<td>0.0564</td>
<td>23</td>
<td>7</td>
</tr>
<tr>
<td>February</td>
<td>30</td>
<td>0.24</td>
<td>0.0495</td>
<td>26</td>
<td>4</td>
</tr>
<tr>
<td>March</td>
<td>30</td>
<td>0.29</td>
<td>0.0491</td>
<td>24</td>
<td>6</td>
</tr>
<tr>
<td>April</td>
<td>29</td>
<td>0.34</td>
<td>0.0527</td>
<td>26</td>
<td>3</td>
</tr>
<tr>
<td>May</td>
<td>30</td>
<td>0.22</td>
<td>0.0705</td>
<td>22</td>
<td>8</td>
</tr>
<tr>
<td>June</td>
<td>30</td>
<td>-0.62</td>
<td>0.1239</td>
<td>6</td>
<td>24</td>
</tr>
<tr>
<td>July</td>
<td>30</td>
<td>-0.44</td>
<td>0.0734</td>
<td>4</td>
<td>26</td>
</tr>
<tr>
<td>August</td>
<td>30</td>
<td>-0.30</td>
<td>0.0793</td>
<td>7</td>
<td>23</td>
</tr>
<tr>
<td>September</td>
<td>30</td>
<td>-0.37</td>
<td>0.0862</td>
<td>8</td>
<td>22</td>
</tr>
<tr>
<td>October</td>
<td>30</td>
<td>-0.02</td>
<td>0.0895</td>
<td>16</td>
<td>14</td>
</tr>
<tr>
<td>November</td>
<td>30</td>
<td>0.23</td>
<td>0.0635</td>
<td>24</td>
<td>6</td>
</tr>
<tr>
<td>December</td>
<td>30</td>
<td>0.27</td>
<td>0.0495</td>
<td>26</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 4-3. Mean daily recession rate by month and frequency of receding vs. rising water levels over a 30 year time period (1978-2007) in Everglades National Park.

<table>
<thead>
<tr>
<th>Month</th>
<th>N</th>
<th>Mean Daily Recession Rate (cm)</th>
<th>SE</th>
<th># of years receding</th>
<th># of years rising</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>30</td>
<td>0.18</td>
<td>0.0252</td>
<td>27</td>
<td>3</td>
</tr>
<tr>
<td>February</td>
<td>30</td>
<td>0.15</td>
<td>0.0400</td>
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<td>6</td>
</tr>
<tr>
<td>March</td>
<td>30</td>
<td>0.17</td>
<td>0.0418</td>
<td>23</td>
<td>6</td>
</tr>
<tr>
<td>April</td>
<td>30</td>
<td>0.13</td>
<td>0.0419</td>
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<td>6</td>
</tr>
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<td>30</td>
<td>0.01</td>
<td>0.0731</td>
<td>12</td>
<td>18</td>
</tr>
<tr>
<td>June</td>
<td>30</td>
<td>-0.37</td>
<td>0.0795</td>
<td>4</td>
<td>26</td>
</tr>
<tr>
<td>July</td>
<td>29</td>
<td>-0.22</td>
<td>0.0689</td>
<td>7</td>
<td>22</td>
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<td>August</td>
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<td>19</td>
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<tr>
<td>October</td>
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<td>0.02</td>
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<td>14</td>
<td>14</td>
</tr>
<tr>
<td>November</td>
<td>29</td>
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<td>0.0441</td>
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<td>7</td>
</tr>
<tr>
<td>December</td>
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<td>0.21</td>
<td>0.0294</td>
<td>26</td>
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</table>
Table 4-4. First year survival estimates by cohort for juvenile birds fledged in SFL in 2002-2005.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Survival</th>
<th>SE</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lower</td>
</tr>
<tr>
<td>2002</td>
<td>0.3846</td>
<td>0.0954</td>
<td>0.2210</td>
</tr>
<tr>
<td>2003</td>
<td>0.0625</td>
<td>0.0605</td>
<td>0.0087</td>
</tr>
<tr>
<td>2004</td>
<td>0.3333</td>
<td>0.0962</td>
<td>0.1763</td>
</tr>
<tr>
<td>2005</td>
<td>0.2105</td>
<td>0.0935</td>
<td>0.0813</td>
</tr>
</tbody>
</table>

Table 4-5. Model structure, AICc values, delta AICc, and number of parameters for models of first year survival for juvenile Wood Storks outfitted with satellite transmitters in 2002-2005 in SFL.

<table>
<thead>
<tr>
<th>Survival</th>
<th>Recapture</th>
<th>AICc</th>
<th>Delta AICc</th>
<th># Parameters</th>
</tr>
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<td>0.46</td>
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<tr>
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<td>$R_{\text{constant}}$</td>
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<td>1.39</td>
<td>8</td>
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<td>$S_{\text{water level}}$, $\text{sex}$</td>
<td>$R_{\text{cohort}}$</td>
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<td>2.05</td>
<td>11</td>
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<td>$R_{\text{constant}}$</td>
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<td>2.46</td>
<td>8</td>
</tr>
<tr>
<td>$S_{\text{cohort}}$</td>
<td>$R_{\text{cohort}}$</td>
<td>328.76</td>
<td>3.05</td>
<td>10</td>
</tr>
<tr>
<td>$S_{\text{constant}}$</td>
<td>$R_{\text{constant}}$</td>
<td>328.81</td>
<td>3.1</td>
<td>4</td>
</tr>
<tr>
<td>$S_{\text{water level}}$</td>
<td>$R_{\text{water level}}$</td>
<td>329.07</td>
<td>3.36</td>
<td>7</td>
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<tr>
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<td>$R_{\text{constant}}$</td>
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<td>3.62</td>
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<tr>
<td>$S_{\text{cohort}}$, $\text{sex}$</td>
<td>$R_{\text{cohort}}$</td>
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<td>4.5</td>
<td>14</td>
</tr>
<tr>
<td>$S_{\text{cohort}}$</td>
<td>$R_{\text{sex}}$</td>
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<td>4.62</td>
<td>8</td>
</tr>
<tr>
<td>$S_{\text{sex}}$</td>
<td>$R_{\text{constant}}$</td>
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<td>4.7</td>
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<td>5.19</td>
<td>5</td>
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<td>5.91</td>
<td>9</td>
</tr>
<tr>
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<td>6.41</td>
<td>6</td>
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<td>$R_{\text{sex}}$</td>
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<td>13</td>
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</table>
Table 4-6. Mean total population size and mean number of breeding females at the end of 30 years for an initial population of 4370 female birds (2500 breeding females) when the probability of juveniles fledging into favorable conditions varies from 0-1.

<table>
<thead>
<tr>
<th>Probability of Favorable Conditions</th>
<th>Total Population Size (Females)</th>
<th>Number of Breeding Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x</td>
<td>Std. Dev.</td>
</tr>
<tr>
<td>0</td>
<td>2007</td>
<td>--</td>
</tr>
<tr>
<td>0.1</td>
<td>2326</td>
<td>182.92</td>
</tr>
<tr>
<td>0.2</td>
<td>2665</td>
<td>268.19</td>
</tr>
<tr>
<td>0.3</td>
<td>3018</td>
<td>340.26</td>
</tr>
<tr>
<td>0.4</td>
<td>3472</td>
<td>393.81</td>
</tr>
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<td>0.5</td>
<td>3917</td>
<td>452.4</td>
</tr>
<tr>
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<td>382.97</td>
</tr>
<tr>
<td>1</td>
<td>7060</td>
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</tr>
</tbody>
</table>
Figure 4-1. Timing of the reproductive cycle of the Wood Stork. Bars show the approximate timing of fledging for nests initiated in the first week of each month of the breeding season. If storks began nesting in the first week of the month (shown in dark gray), juveniles would fledge approximately 105-130 days later (shown in black).
Figure 4-2. Map of Florida showing the locations of the 2 colonies where satellite transmitters were deployed on juvenile Wood Storks, Tamiami West (circle) and the Palm Beach Solid Waste Authority Rookery (square). The dark green area depicts the Water Conservation Areas and Everglades National Park, which contain the wetlands that comprise the remaining Florida Everglades.
Figure 4-3. Daily water depths during the year for Water Conservation Area 3A (a) and Everglades National Park (b) in 2002-2004. Arrows indicate the month that the majority of birds fledged in each year. Gaps in the time series indicate missing data.
Figure 4-4. Locations of Wood Storks in 2004 (black circles) and 2005 (white circles) during the months of June and July. The yellow area shows the minimum convex polygon of locations from 2005.
Figure 4-5. Estimated mean total population size after 30 years as a function of the probability that juveniles fledge into optimal hydrological conditions (low and/or receding water levels). The initial population consisted of 4370 individuals.
CHAPTER 5
A COMPARISON OF TWO RANGE-WIDE HABITAT SUITABILITY MODELS FOR THE WOOD STORK (MYCTERIA AMERICANA) IN THE SOUTHEASTERN UNITED STATES

Introduction

The protection of critical habitat is often the primary tool used by managers in the recovery of endangered species. Critical habitat is defined in the Endangered Species Act as “specific areas within the geographical area occupied by the species . . . on which are found those physical or biological features essential to the conservation of the species and which may require special management considerations or protection . . .” (Sidle 1987). Critical habitat has not been designated for the Wood Stork, although habitat management guidelines are in place (Ogden 1990, Brooks and Dean 2008). These guidelines are vague, however, identifying freshwater and estuarine wetlands as important foraging, nesting, and roosting sites without specifying specific wetlands or geographic areas. The Wood Stork Recovery Plan (U.S. Fish and Wildlife Service 1996) identified the need to locate and prioritize important habitats for the Wood Stork and to work with landowners or through existing regulatory mechanisms to protect and manage these lands. Identifying these areas is difficult, however, given the wide range of the Wood Stork across the Southeastern U.S.

In order to identify critical habitat needs of Wood Storks, it is necessary to first determine where they are and why they are there (Aarts et al. 2008). Most studies of Wood Stork habitat use have been local in scope, focusing on where they nest or forage within specific geographic regions. Studies have occurred primarily in the wetlands of South Florida (Kahl 1964, Ogden et al. 1976, Browder 1984, Herring 2007), central and northern FL (Ogden 1991, Rodgers et al. 1996) or coastal Georgia (Coulter et al. 1987, Gaines et al. 1998, Bryan et al. 2002, Depkin et al. 2005) and have been conducted primarily via direct field observations or by following the flights of foraging Wood Storks by airplane.
These studies have shown that in Florida Wood Storks nest in freshwater and marine-estuarine forests consisting of mangroves (Laguncularia racemosa, Rhizophora mangle), bald cypress (Taxodium dystichum), black gum (Nyssa biflora), southern willow (Salix carolinensis), and pond apple (Annona glabra), while in Georgia and South Carolina they generally nest in cypress (Rodgers et al. 1996, Coulter et al. 1999). Wood storks also increasingly make use of altered and artificial wetland sites in Florida, often nesting in non-native species such as Australian pine (Casuarina australiana) and Brazilian pepper (Schinus terebinthifolius) on spoil islands (Ogden 1991, Rodgers et al. 1996).

Feeding by Wood Storks was shown to occur in both natural and artificial wetlands, with use predicated on prey densities and appropriate water depths. In SFL, Wood Storks are known to feed throughout the Everglades and Big Cypress basins, and in flooded agricultural fields as well (Coulter et al. 1999) and the Everglades Water Conservation Areas in Palm Beach, Broward, and Dade counties have been shown to be particularly important foraging habitat, with as much as 55% of the population foraging there during dry years (Bancroft et al. 1992). In southwestern Florida, marshes and wetlands in Collier, Lee, and Hendry counties were shown to be of particular importance for Wood Storks nesting at the Corkscrew Swamp Sanctuary (Browder 1984). In central and northern Florida, little information exists on preferred foraging habitats or wetlands.

In the coastal region of Georgia and South Carolina, Wood Storks were shown to forage in freshwater wetlands and in tidal creeks and pools both during and outside of the breeding season (Gaines et al. 1998, Bryan et al. 2002, Depkin et al. 2005). Foraging success was higher in tidal habitats, but temporally constrained to periods of low tide (Depkin et al. 2005). Birds nesting inland in Georgia foraged primarily in swamps and ponds (Coulter et al. 1987) and in South
Carolina they foraged primarily in palustrine wetlands, intertidal creeks, isolated wetlands, and managed marsh (Murphy and Coker 2008).

On the basis of these and similar studies, broad scale habitat suitability models have been generated for the Wood Stork as part of the U.S. Geological Service’s National Gap Analysis Program (GAP). GAP seeks to identify important areas for conservation by modeling species distributions and diversity using species-habitat relationships and determining whether biological important areas are currently protected (Jennings 2000). Species distribution maps for the Wood Stork are based on land cover type and vary from state to state. For example, the South Carolina GAP used 5 broad categories to describe Wood Stork habitat (freshwater, marsh/emergent wetland, swamp, and aquatic vegetation), whereas in Florida, Wood Stork habitats were made up of 33 different land cover types.

More mechanistic models have been confined to the ecosystems of South Florida and have been applied primarily to breeding dynamics. In one of the earliest models, (Browder 1976) modeled the relationship between rainfall, water levels, fish production, and the breeding success of Wood Storks in Southwest Florida. (Wolff 1994) used an individual based model to relate Wood Stork breeding dynamics in Everglades wetlands to dynamic environmental variables, and Herring (2007) used a proportional hazards regression model to predict the use of Everglades wetlands by breeding Wood Storks from three SFL colonies in response to vegetation type and changing hydrology.

Advances in telemetry have allowed researchers to broaden the scale of investigations into Wood Storks’ movements and habitat use. Comer et al. (1987) used VHF telemetry to track 5 adult Wood Storks from their breeding colony in Georgia to their winter range in Florida. More recently, satellite telemetry has been used to document the post-breeding movements of 4 adult
Wood Storks from Georgia, and to investigate population affiliations of Wood Storks captured along the Gulf Coast (Bryan et al. 2008). Hylton (2004) used satellite transmitters to track the movements of juvenile Wood Storks from South Florida, documenting survival and seasonal movement patterns and using their locations to estimate home range size and habitat selection. Until now, however, habitat use information obtained through satellite telemetry has not been incorporated into predictive models of habitat use.

I used locations obtained by satellite telemetry to create predictive habitat models for the Wood Stork across its range in the southeastern U.S. My objectives were to 1) determine whether a temporally and spatially coarse-grained modeling approach could be used to predict Wood Stork occurrences in the Southeast and 2) to compare the accuracy of 2 different habitat suitability modeling approaches.

**Study Area and Methods**

Wood Storks from the Southeastern U.S. population breed in South Carolina, Georgia, and Florida, and their non-breeding range also includes Alabama and eastern Mississippi. Elevations in these states range from 0-730 m above sea level, and all 5 states include coastal zones as well as a diverse range of land cover types and land uses.

Wood Storks were captured across the southeastern United States (Figure 5-1) from 2004-2008. Juvenile and adult birds were outfitted with GPS-enabled satellite transmitters from 2004-2008. The initial dataset included 77 birds, of which 46 were juveniles and 31 were adults. The juvenile birds were captured at the Palm Beach Solid Waste Authority rookery (SWA) in Palm Beach County, FL (31), the Chew Mill colony in Jenkins County, GA (7), and the Harris Neck National Wildlife Refuge in McIntosh County, GA (8), (see Table 1 for coordinates of all capture locations). Adult birds were captured in FL, GA, SC, and LA.
Solar-powered ARGOS-PTT satellite tags (Microwave Telemetry, Columbia, MD) were attached to the birds with a backpack-style harness of teflon ribbon. Global Positioning System (GPS) locations for the juvenile birds were recorded hourly, from 0600-2100, with an accuracy of approximately 18 m. For the adult birds, 15 birds had locations recorded on the same schedule, and 16 had locations recorded every 2 hours, 24 hours per day. All tags transmitted locations every 3 days. There were a total of 384,655 locations in the dataset.

I removed all birds from the dataset that transmitted for 90 days or less, and selected one location per day at random for the 47 remaining birds. Birds in the remaining dataset transmitted between 116 and 1,732 days. Although Wood Storks are capable of moving long distances between days, I did not consider these points to be temporally or spatially independent, nor did I consider autocorrelation of locations to be a detriment to the analysis as the alternative of eliminating autocorrelation by removing locations from a dataset has been shown to reduce statistical power and to mask biologically relevant information (De Solla et al. 1999, Cushman et al. 2005). I did assume, however, that each bird acted independently of the others.

**Spatial Analysis**

I used four existing datasets to categorize land cover, elevation, and linear water features across the Southeastern US, and created 18 raster layers using two mile grid cells to represent proportions of land cover types, landscape diversity, elevation and variation in elevation, and the total length of linear water features.

I created a map of land cover types using a combination of the 2001 National Land Cover Dataset (NLCD) (Multi-Resolution Land Characteristic Consortium 2008) and the National Wetland Inventory Polygon dataset (NWIP) (U.S. Fish and Wildlife Service 2008). The NLCD is a continent-wide land cover database that categorizes land cover types into 16 categories using 30 m cells (Homer et al. 2007). I collapsed the land cover classification into 9 categories: open
water, developed (including low, medium and high intensity use), barren, upland forest (including deciduous, evergreen, and mixed forests), shrub/scrub, grassland/herbaceous, agriculture (including hay/pasture and row crops), woody wetlands, and emergent herbaceous wetlands.

The National Wetlands Inventory applies specifically to wetland and deepwater systems in the United States and uses a hierarchical approach to classify these areas into 5 broad systems with nested subsystems and classes. I used the NWI wetland polygon layer to create a raster layer of wetlands across the Southeastern US at the broadest classification scale: marine, estuarine, riverine, lacustrine, and palustrine. To integrate the two raster layers (NLCD and NWI), I first assigned values from the NWI dataset to a raster map of 30 m cells. I then filled in the non-wetland or other areas not classified by the NWI data with values from the reduced NLCD dataset. For ease of interpretation, I considered the lacustrine and palustrine categories to correspond with “emergent herbaceous wetlands” and “forested wetland” respectively, and classified both marine and estuarine as “marine.” I used this 12 category map to create 2mi grids characterizing the proportion of each habitat type in each 2 mi grid cell, the diversity (total number) of habitats within each 2 mi cell, and the mean diversity of cells within a five cell moving window (see Appendix A).

I used the U.S. Geological Service’s National Elevation Dataset (NED) (U.S. Geological Service 2003) to quantify elevation across the Southeast and their National Hydrography Dataset (NHD) (U.S. Geological Service 2007) to quantify linear water features. The NED provides a 1 arc second (approximately 30 m) resolution map of elevation (m) for the US. I used this dataset to create a 2 mi grid of mean elevation and its variability (as represented by the standard deviation within each 2 mi grid cell). I used the digital line graphs available within the NHD to
map linear water features across the Southeast and summed their lengths in each 2 mi grid cell, creating three raster maps corresponding to the three feature types: artificial paths, streams/rivers, and canals/ditches.

**Habitat Suitability Modeling**

The primary goal of habitat suitability modeling is to use environmental variables to predict the likelihood that species will inhabit a specific area (Guisan and Zimmermann 2000, Hirzel and Le Lay 2008). Resource selection functions (RSFs) use the spatial distribution of resources to estimate the distribution and abundance of animals by yielding probabilities that are proportional to use (Boyce and McDonald 1999, Manly et al. 2002). The goal of resource selection analysis is to determine whether resources are used disproportionately to their availability (Erickson et al. 2001). I used logistic regression (LR) and Mahalanobis distance (MD) models to create rangewide habitat suitability models for the Wood Stork across the Southeastern U.S.

Use and availability may be described at the individual or population level. (Erickson et al. 2001, Manly et al. 2002). I estimated both habitat use and availability at the population level and did not account for temporal variability in either. A grid cell was considered used if any of the daily Wood Stork locations occurred within its borders at least once. I did not incorporate intensity of use into the analysis, so a cell received the same value whether it contained one or 100 locations.

To define available habitats, I used the daily locations from the 47 birds in the dataset to create individual 90% kernel home ranges. I then combined the overlapping home ranges to create a map of available habitat (Figure 5-2). The home ranges were constructed using the Animal Movement extension in ArcView 3.2. (Hooge and Eichenlaub 1997). I generated
10,000 random points within the available habitat and considered all cells in which random points occurred to be “available”. I recorded the values for the suite of environmental characteristics at each used and available cell and used these values to calculate the coefficients for the regression equation for the LR model, while for the MD model I incorporated used sites only.

**Logistic regression**

Prior to the regression analysis, I transformed the independent variables to better approximate normality, using an arcsin-root transformation on the proportions of land cover types and a log_{10} + 1 transformation on the other variables. Because logistic regression requires the use of uncorrelated independent variables (Ott & Longnecker 2001), I used a correlation matrix to identify pairs of variables with a correlation coefficient \( r > 0.60 \). If a variable was correlated \( r > 0.60 \) with more than one other variable I dropped it from further consideration. If it was correlated with only one other variable, I removed each from the regression separately and compared the fit of the resulting regression using Akaike’s Information Criteria (AIC) values (Manly et al. 2002), retaining the variables that resulted in the lowest AIC. Because barren areas, ponds, and open water were poorly represented on the landscape, I did not include them in the regression analysis.

I used the coefficients of the best regression model to map habitat suitability for the Wood Stork across the Southeast, using the function:

\[
\text{Probability of Use} = \frac{\exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_p X_p)}{1 + \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_p X_p)} \quad (5-1)
\]

where \( \beta_0 \) to \( \beta_p \) were the coefficients estimated from the logistic regression and \( X_1 \) to \( X_p \) were the landscape variables that were significant in the regression (Manly et al. 2002).
Mahalanobis distances

The Mahalanobis distance statistic differs from regression analyses in that only used resources need be identified. Conclusions regarding non-used or available habitats are unnecessary, with the exception of the delineation of the study area boundary (Clark et al. 1993, Manly et al. 2002). The Mahalanobis distance measures the dissimilarity in habitat characteristics between “ideal” habitat (as determined by use), and available habitats (Cayuela 2004). Habitat suitability models are created by assigning values to each grid cell corresponding to a vector composed of the values at that cell of the raster maps of independent variables, and measuring the Mahalanobis distance of the available units to the mean for the used units (Manly et al. 2002). The Mahalanobis distance is determined from the equation:

\[
\text{distance} = (x - \hat{u}) \sum^{-1} (x - \hat{u})
\]

where \(x\) is the vector of environmental characteristics associated with each cell, \(\hat{u}\) is the mean vector of environmental characteristics at each telemetry location, and \(\sum\) is the estimated covariance matrix (Clark et al. 1993).

I used the ADEHABITAT package (Calenge 2006, 2007) in the R statistical program to generate the Mahalanobis distance surface grid based on the grids of environmental characteristics, and to recode the grid into \(P\)-values based on a Chi-Square distribution. Because the analysis is robust to correlated variables (Clark et al. 1993, Knick and Rotenberry 1998, Manly et al. 2002), I used 15 grids of environmental variables to generate the Mahalanobis distance surface (% cover for emergent wetlands, forested wetlands, upland forests, marine habitats, shrub/scrub, grasslands, developed areas, and agriculture; local and surrounding habitat
heterogeneity; elevation and variability in elevation, and total length for streams/rivers, canals/ditches, and artificial paths.

**Model Testing**

I tested each model against 2 datasets: the dataset used to build the model and an independent data set of Wood Storks tagged as juveniles in 2002-2003 (see (Hylton 2004) for details). There were a total of 51 birds in the independent data set and a total of 16,958 locations.

To evaluate how well each model performed, I used receiver operating characteristic (ROC) plots. ROC plots can be used to compare model fit by evaluating the proportion of cells that are correctly and incorrectly classified (Cumming 2000, Boyce et al. 2002). They are constructed by first calculating the sensitivity and specificity of each model, where sensitivity refers to the proportion of positive cells that are correctly classified as used, and specificity refers to the proportion of negative cells that are correctly classified as unused (Cumming 2000). Positive cells are those cells which fall at or above a probability threshold, represented by the $P$-value of the habitat suitability model, which varies from 0-1. Negative cells are those that fall below the threshold. Plotting sensitivity against 1 minus specificity at different thresholds yields the ROC curve, with a well-fitting model rising steeply and then leveling off and a random model following a 45° diagonal line from the origin. The sum of the area under the curve (AUC) provides a measure of model fit by indicating the probability that a cell selected at random from the initial set of used locations will receive a higher “probability of use” score than one selected at random from a set of unused or random locations (Cumming 2000).
Results

Habitat Suitability Modeling

Logistic regression

There were 4107 used cells across the Southeastern US for the training dataset, representing a total of 26,759 locations (Figure 5-3). The independent dataset used to validate the models had a total of 16,958 locations and 3200 used cells (Figure 5-4).

The correlation matrix indicated that elevation and its variability were strongly correlated ($r = 0.8145$). Upland forests were positively correlated with both mean elevation ($r = 0.6671$) and variability in elevation ($r = 0.7352$) and total length of streams/river were correlated with variability in elevation ($r = 0.6249$). I removed upland forests from the regression analysis outright, then removed streams and mean elevation based on the AICs of the regression model.

The variables I retained following stepwise regression and model selection procedures were % cover for agriculture, grasslands, forested wetlands, shrub/scrub, marine, and emergent wetlands; local and surrounding landscape heterogeneity, the total length of canals and ditches, and variability in elevation (see Table 4-2). The association with use was positive for agriculture, forested wetlands, marine habitats, emergent wetlands, length of canals/ditches, and both local and surrounding landscape heterogeneity. It was negative for grasslands, shrub/scrub, and variability in elevation.

The habitat suitability map generated from the LR contained 45,682 cells and covered 473,355 km$^2$. The probability of use for individual cells ranged from 0-0.7963 (Figure 5-5). There were 14,619 cells with probability of use ($P$) under 0.1 and 148 with $P > 0.7$. The percentage of cells classified as used increased as the probability of use value went up, for both the training ($R^2 = 0.7746$) and independent datasets ($R^2 = 0.6451$, Figure 5-6). For cells with the
highest probability of use \((P \geq 0.7)\), 54% and 45% were classified as occupied using the training and independent datasets respectively.

**Mahalanobis distances**

The habitat suitability map generated from the MD model had 45,947 cells and covered 476,101 km\(^2\), with probabilities of use ranging from 0-1 (Figure 5-7). There were 26,927 cells with \(P < 0.1\), and 414 cells with the \(P = 1\). There was no clear linear relationship between the probability of use classification and the percentage of cells classified as used for either the training dataset \((R^2 = 0.4202)\) or the independent dataset \((R^2 = 0.2589, \text{ Figure 5-8})\). The relationship was better described by a cubic function, with the percentage of cells classified as used rising rapidly as the probability of use increased from \(< 0.1\) to 0.2, then leveling off, and rising rapidly again between \(P = 0.9-1.0\) \((R^2\) for cubic fit = 0.6658 and 0.6070 for the training and independent datasets respectively). For cells with the highest probability of use \((P \geq 0.9)\), 25% and 19% were classified as occupied using the training and independent datasets.

**Model Comparison**

The logistic regression resulted in better overall model fit than the use of Mahalanobis distances for both the training dataset and the independent dataset (Figures 5-9 and 5-10). For the training dataset, the LR model had an AUC of 0.8371, while the AUC for the MD model was 0.7310. For the independent dataset, the LR model had an AUC of 0.8249 while the MD model had an AUC of 0.6837.

When I compared the proportion of used cells within each dataset to the \(P\)-value of the cell in which they occurred, I found that for the LR model, only 1% of used cells from the training dataset and only 2% of those from the independent dataset corresponded to cells with \(P\)-values \(< 0.1\), while for the MD model, 20% of the used cells from the training dataset and 25% of those from the independent dataset corresponded to cells with \(P\)-values \(< 0.1\).
The largest difference between the two models was their sensitivity to the $P$-value used to classify cells as suitable. The number of cells in both models decreased rapidly as the $P$-value increased from 0-0.1, but the magnitude of the decline was much greater for the MD model, which also decreased more slowly and in a linear fashion for $P$-values over 0.1 (Figure 5-11). The LR model had more cells with $P$-values $\geq 0.1$, but the number of cells in the model decreased exponentially as the probability of use increased from 0.1-0.8 and there were less than 10,000 cells with $P$-values $> 0.3$ (See Appendix B). The number of cells in both models was closest for $p \geq 0.23$, with the LR model having 15,604 cells at or above this value and the MD model containing 15,721 (Figure 5-12).

The two models combined covered approximately 209,471 km$^2$, with approximately 116,673 km$^2$ overlapping (55.6%) (Figure 5-13). In general, the MD model gave cells in central and northern Florida and in Georgia a higher probability of use than did the LR model, while the LR model classified cells in SFL as having a higher probability of use than did the MD model. I used the two combined maps, including both overlapping and non-overlapping cells to delineate total habitat availability (Figure 5-14). The combined LR and MD habitat suitability maps for cells with $P \geq 0.23$ included 91.5% of locations from the training dataset (Figure 5-15) and 92% of locations from the independent dataset (Figure 5-16), while the areas in which the retained cells ($P \geq 0.23$) from the two models actually overlapped included 72.0% and 58.1% of locations from the two datasets respectively (Figure 5-17).

**Discussion**

These models represent the first attempt to predict the habitat requirements of the Wood Stork across its entire range in the Southeastern U.S. Although they are based on very coarse-grained habitat characterizations, both models correctly identified regions that are known from independent work to be of high value to the Wood Stork. In particular, both models showed a
high probability of use for cells in Hendry County in southwest FL and along the Georgia coastline. The LR model also identified the Everglades Water Conservation Areas and Everglades National Park as areas with a high probability of use and generally attributed higher probabilities of use to cells in SFL than the MD model, while the MD model generally gave higher $P$-values to cells in central and northern FL and GA.

Overall, the habitat suitability map based on the LR model provided more accurate predictions of actual Wood Stork usage than the map based on Mahalanobis distances. While both provided a better fit to the data than would a random model, the probability that the LR model would correctly assign a positive value to a used location was 11% higher for the training dataset and 14% higher for the independent dataset when compared to the MD model.

Mahalanobis distance models have received increasing use as a method of calculating habitat suitability in wildlife studies. They have been used in studies of Black Bears (*Ursus americanus*) (Clark et al. 1993, Hellgren et al. 2007), Black-tailed Jackrabbits (*Lepus californicus*) (Knick and Dyer 1997), wolves (*Canis lupus*) (Corsi et al. 1999, Cayuela 2004), and Timber Rattlesnakes (*Crotalus horridus*) (Browning et al. 2005). Their advantages relative to regression techniques are that characterizations of available habitat are not necessary and collinearity among the independent variables do not strongly affect the results of the model because statistically, the MD is determined from a new set of uncorrelated variables (Clark et al. 1993, Knick and Rotenberry 1998). The model assumes, however, that “animals are distributed optimally among habitats in the landscape” (Knick and Rotenberry 1998), an assumption that may not have held true for this dataset.

Because I used a large dataset of randomly selected daily locations to characterize habitat use and considered use of cells to be equal regardless of the number of individuals or locations
that occurred within each cell, use of suboptimal habitats may have been overrepresented in the model. Furthermore, optimal habitats for Wood Storks are known to be stochastic, varying over time and seasonally. I calculated a mean vector of habitat characteristics using a dataset that was pooled over several years and that did not account for seasonal variability in Wood Stork movements and habitat availability, however, and habitats that were optimal at one point in time would likely be suboptimal at some later point in time. This is especially true given the frequent reliance of Wood Storks on ephemeral wetland resources. This may account for the relatively low probabilities of use assigned to Everglades wetlands. Although these wetlands are known to be of high value to Wood Storks, particularly during winters when the rest of the southeastern US is relatively dry (Bancroft et al. 1992), they represent a small fraction of the landscape when compared to the entire model, are used during a limited period of time, and are only used when hydrological conditions are favorable.

While the LR model performed somewhat better than the MD model, its predictions were very strongly influenced by the probability of use threshold used to define suitable habitats. When the probability of use was $\geq 0.1$, the model included nearly the entire state of FL and much of the GA coast. While this may reflect the transient nature of storks and the possibility that they might occasionally occur in any of these areas, its lack of specificity does not provide particularly meaningful guidelines with regard to regions or areas that may provide important Wood Stork habitat. The rapid loss of habitats included in the model as the probability assigned to use increased also limited its applicability. When the probability of use was $\geq 0.4$, northern FL, GA, and SC were poorly represented in the model and AL and MS were scarcely represented at all.
While the LR model may have been influenced by the lack of temporal specificity in my approach it may also have been influenced by the way in which I defined available habitats. While the use of home ranges is frequently used to delineate available habitats (Erickson et al. 1998, Manly et al. 2002), it can create problems in the analysis, particularly since some used points may fall outside of the “available” habitat. A better approach may have been to use a minimum convex polygon around all pooled locations to delineate the available habitat. That approach was problematic as well, however, since the eastern and western edges of the Wood Storks’ observed ranged contained the northernmost points, resulting in the inclusion of a broad swath of land across western SC and northern GA in which no Wood Stork locations occurred and which may have been “unavailable” due to lack of appropriate habitats.

While neither model showed a perfect ability to predict habitat use using the environmental variables I considered, both models did have some predictive value. Both the results of the ROC plots and visual inspection of the models indicated that their fit was better than would be expected at random and that they identified regions that are known to contain important foraging areas for Wood Storks. Particularly impressive was the ability of both models to correctly identify as habitat areas along the Tombigbee, Alabama, and Mobile rivers in MS and AL that contained relatively few Wood Stork locations relative to the larger dataset but are important post-breeding summering grounds (Coulter et al. 1999, Hylton 2004, Bryan et al. 2008).

While the determination of the $P$-value required for habitats to be considered suitable is fairly arbitrary, it is probably more instructive to look at the area with the most overlap between models. Both models included similar numbers of cells when their $P$-values were $\geq0.23$, with more than 50% of the cells retained in each model overlapping. For areas which did not overlap,
the MD model was better at predicting use by Wood Storks in the northern and western portions of their range, while the LR was better at predicting use in south FL. By combining the 2 models, I was able to improve model fit and to accurately predict more than 90% of locations from both datasets.

These models can provide rough guidelines for managers seeking to understand Wood Stork habitat needs in areas where they have not previously been well-defined. This is particularly true outside of south FL. Future refinements to the models should include the incorporation of a temporal component and a refinement of the spatial grain. Models created on a state by state basis and using a grid of smaller cells might have greater utility for identifying areas that are especially critical for the conservation and recovery of the species.

**Conclusion**

I found that it was possible to use environmental data and Wood Stork locations with a fairly coarse temporal and spatial grain to predict approximately 90% of the occurrence of suitable habitat for Wood Storks across their range in the Southeastern U.S. Both logistic regression and Mahalanobis distances produced habitat suitability maps with good predictive abilities in at least parts of their range, although each had strengths and weaknesses relative to the other. By combining the two approaches, however, I was able to generate a map with good predictive capabilities and enough specificity to be useful for scientists, managers and planners.
Table 5-1. Locations of tag deployment on juvenile and adult birds included in initial dataset. Tags were deployed from 2002-2008.

<table>
<thead>
<tr>
<th>Location</th>
<th>Year</th>
<th>Latitude</th>
<th>Longitude</th>
<th># Tags</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bear Island WMA, SC</td>
<td>2006</td>
<td>32.574</td>
<td>-80.480</td>
<td>1</td>
</tr>
<tr>
<td>Harris Neck NWR, GA</td>
<td>2005, 2006</td>
<td>31.630</td>
<td>-81.275</td>
<td>11</td>
</tr>
<tr>
<td>Noxubee NWR, MS</td>
<td>2005</td>
<td>33.280</td>
<td>-88.798</td>
<td>5</td>
</tr>
<tr>
<td>Corkscrew Swamp Sanctuary, FL</td>
<td>2006</td>
<td>26.310</td>
<td>-81.635</td>
<td>5</td>
</tr>
<tr>
<td>Welaka National Fish Hatchery, FL</td>
<td>2006</td>
<td>29.433</td>
<td>-81.648</td>
<td>6</td>
</tr>
<tr>
<td>White Hall, SC</td>
<td>2006</td>
<td>32.723</td>
<td>-80.697</td>
<td>1</td>
</tr>
<tr>
<td>Palm Beach SWA, FL</td>
<td>2008</td>
<td>26.767</td>
<td>-80.145</td>
<td>4</td>
</tr>
<tr>
<td>Juveniles</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palm Beach SWA, FL</td>
<td>2004, 2005</td>
<td>26.767</td>
<td>-80.150</td>
<td>46</td>
</tr>
<tr>
<td>Chew Mill Rookery, GA</td>
<td>2005</td>
<td>32.830</td>
<td>-82.098</td>
<td>11</td>
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<tr>
<td>Harris Neck NWR, GA</td>
<td>2005</td>
<td>31.630</td>
<td>-81.275</td>
<td>11</td>
</tr>
</tbody>
</table>
Table 5-2. Results and regression coefficients from logistic regression of used vs. available habitats in relationship to environmental variables. The land cover types represent proportions of each habitat type in 3.219 x 3.219 grid cells and were arcsin-root transformed. The remaining variables were log + 1 transformed.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>DF</th>
<th>Estimate</th>
<th>Standard Error</th>
<th>Wald Chi-Square</th>
<th>Pr &gt; ChiSq</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1</td>
<td>-2.8415</td>
<td>0.1784</td>
<td>253.84</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Agriculture</td>
<td>1</td>
<td>0.9038</td>
<td>0.0726</td>
<td>155.14</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Grasslands</td>
<td>1</td>
<td>-0.3909</td>
<td>0.1662</td>
<td>5.53</td>
<td>0.0187</td>
</tr>
<tr>
<td>Forested Wetlands</td>
<td>1</td>
<td>0.9071</td>
<td>0.0815</td>
<td>123.99</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Shrub/Scrub</td>
<td>1</td>
<td>-1.2265</td>
<td>0.1909</td>
<td>41.27</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Marine</td>
<td>1</td>
<td>1.1697</td>
<td>0.0969</td>
<td>145.66</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Emergent Wetlands</td>
<td>1</td>
<td>1.3896</td>
<td>0.0898</td>
<td>239.31</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Landscape Heterogeneity (Regional)</td>
<td>1</td>
<td>0.3987</td>
<td>0.0948</td>
<td>17.80</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Landscape Heterogeneity (Local)</td>
<td>1</td>
<td>0.4241</td>
<td>0.0625</td>
<td>46.09</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Variability in Elevation (Std. Dev.)</td>
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<td>-0.6272</td>
<td>0.0399</td>
<td>246.57</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Canals/Ditches (Total Length)</td>
<td>1</td>
<td>0.0927</td>
<td>0.0255</td>
<td>13.19</td>
<td>0.0003</td>
</tr>
</tbody>
</table>
Figure 5-1. Locations where Wood Storks were captured outfitted with GPS-enabled satellite transmitters.
Figure 5-2. Overlapping 90% kernel home ranges for 47 Wood Storks created from daily GPS locations obtained via satellite telemetry, used to represent available habitat.
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$P = 0.23$
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CHAPTER 6
CONCLUSIONS

The generally increasing trend in the number of Wood Storks nesting in the Southeastern U.S. have led to some optimism regarding the recovery of the species and have raised the possibility of downlisting the species from “endangered” to “threatened” (Brooks and Dean 2008). The population viability analyses I have conducted as part of this study paint a different picture, however, and suggest that the Wood Stork population could still be in danger of dramatic declines even over the next decade.

Any understanding of Wood Stork population dynamics is complicated by the occurrence of boom and bust reproductive dynamics. Population dynamics are strongly influenced by environmental stochasticity (Saether et al. 2004) and Wood Stork reproduction is strongly tied to the stochastic environmental factors such as rainfall and water levels that govern prey availability. Although interannual population growth rates for the Wood Stork did show the occurrence of infrequent boom years ($\log \frac{N_{t+1}}{N_t} > 1$), they were more likely to reflect relatively stable population dynamics ($-1 < \log \frac{N_{t+1}}{N_t} < 1$) or bust years ($\log \frac{N_{t+1}}{N_t} < -1$) (see Chapter 2). I have shown, however, that boom years would have to occur nearly 32% of the time in order for the population to remain stable (Chapter 3).

Long-lived species are known to have significant time lags before extinction occurs, and projections as long as 100 years into the future may still not be adequate to for the prediction of longterm extinction risk (Armbruster et al. 1999). Nonetheless, despite generally increasing nest numbers, both the count-based analysis and the demographic analysis indicated that the Wood Stork population in the Southeastern U.S. has a relatively high probability of decline. While the declining trends may have been associated to some degree with uncertainty in the estimates and with negative bias associated with sampling error, it is also possible that they reflect an accurate
picture of the longterm outlook for the species. Further studies to elucidate the error associated with counting techniques are crucial, as is the development of a method for enumerating the proportion of birds that do not nest in a given year.

Hydrological conditions in the Florida Everglades appear to be unfavorable for juvenile survival following fledging the majority of the time. Given current trends in the timing of Wood Stork nesting this could have a negative impact on the population as a whole. Juvenile survival rates were extremely variable and strongly tied to the environmental conditions into which the young birds fledged (Chapter 4). For this reason, it is especially important to understand the types of habitats and environmental conditions that are favorable for juvenile survival. The habitat suitability model I have constructed provides a first step toward this understanding (Chapter 5). This map can be used to identify high value habitats in relation to Wood Stork colony sites, so that these areas can be managed appropriately during the times that Wood Storks are dispersing from their natal colonies.

This study represents a major advancement in the knowledge of Wood Stork population dynamics and habitat use. This is the first time adult survival rates have been estimated and have been incorporated into a demographic population viability analysis. It is also the first time habitat suitability has been evaluated across the Wood Storks range in the Southeastern U.S. The results of this study can be used by managers to evaluate the current risks to long-term Wood Storks population viability and may be helpful in deciding whether the endangered status of the species should be maintained or downgraded.
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BIOGRAPHICAL SKETCH

Rena Borkhataria was born in Baltimore, Maryland. Her love of animals was nurtured by her mother, Carmen, who loved all creatures furred and feathered. After losing her mother at an early age, Rena was eventually fortunate to take up residence with the Richardson family on their horse farm. She took long rides through the fields and forests of the Maryland countryside and it was here that her love of wildlife was instilled.

Upon graduating from high school, Rena enrolled at St. John’s College, where she studied the classics for one semester. She then transferred to the University of Maryland—Baltimore County where she majored in classics and learned to read ancient Greek. A fateful visit to a friend in Arizona changed her course, however, and she left the university for life in the desert a short while after.

While working at a coffeehouse in Tucson, AZ, Rena made the acquaintance of a wildlife biologist. It was as though the proverbial light bulb turned on over her head. She enrolled in the wildlife ecology program at the University of Arizona, where she excelled. During this time she worked as a field technician for the Arizona Cooperative Fish and Wildlife Research Unit and as a research assistant at the Udall Center for Studies in Public Policy. She received several departmental scholarships as well as two prestigious national scholarships: the Harry S. Truman Scholarship and the Morris K. Udall Scholarship. She graduated Summa Cum Laude and was named “Outstanding Graduating Senior” by the wildlife department.

Having been awarded a National Science Foundation Graduate Fellowship, she went on to the master’s program in zoology at North Carolina State University, where she worked with Jaime Collazo. For her thesis, entitled “Ecological and Political Implications of Conversion from Shade to Sun Coffee in Puerto Rico,” she examined differences in biodiversity in sun and...
shade coffee plantations and the effect of birds and lizards as predators on coffee insects. She also examined the social incentives for conversion from shade to sun coffee.

After graduating from NCSU and a stint at Duke University, she enrolled in the Ph.D. program in wildlife ecology and conservation at the University of Florida under the direction of Peter Frederick. Here she received support from an Environmental Protection Agency Science to Achieve Results (STAR) fellowship and as a co-principal investigator on grants from the U.S. Fish and Wildlife Service and the National Park Service. She received her Ph.D. from the University of Arizona in summer of 2009. She is married to fellow scientist Colin Saunders and lives with him, their 4 dogs, 3 cats, and 2 horses in West Palm Beach, FL.