# A Preliminary Model of Wood Stork Population Dynamics in the Southeastern United States

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**Abstract.**—We modeled population dynamics and extinction probabilities for the endangered Wood Stork (*Mycteria americana*) using count data from synoptic aerial surveys, annual measures of productivity from throughout the southeastern U.S., and survival data from satellite-tagged juveniles. Using a simple, count-based diffusion approximation approach we were able to quantify an increasing population trend since 1976. High inter-year variability resulted in wide confidence intervals and we could not eliminate the possibility of long-term population decline in spite of recently measured population increases. We also used a stage-based population matrix model to incorporate observed differences in survival rates among age classes. Fledging success, and survival of fledglings, one, and two-year-old birds were estimated using data from the satellite telemetry study. Because the survival rates of three-year-olds and adults are presently unknown, we analyzed population dynamics over a range of these values. Long-term population growth was most sensitive to changes in adult survivorship. This deterministic matrix model indicated that adult survival rates >0.94 were necessary to maintain a growing population, an estimate considerably higher than that observed in the European White Stork (*Ciconia ciconia*). This study underscores the need for reliable estimates of juvenile and adult survival in Wood Storks, and for a conservation focus on the factors that affect adult survival. It also provides a tool for understanding and projecting potential trajectories of the Wood Stork population in the Southeastern United States.

**Key words.**—Demography, *Mycteria americana*, population viability analysis, vital rates, Wood Stork.

The Wood Stork (*Mycteria americana*) population in the southeastern United States was declared endangered by the United States Fish and Wildlife Service (USFWS) in 1984 following a marked decrease in numbers of nesting birds (Coulter *et al.* 1999; USFWS 1996). 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; USFWS 2002). Since then, there has been evidence of an increasing trend in overall numbers of nesting storks (Ogden *et al.* 1987) and in the number of nonbreeding storks counted in Christmas Bird Counts (McCrimmon *et al.* 1997), suggesting an increase in

population size. Storks have also exhibited a considerable shift in their breeding range in the southeastern U.S. (Ogden *et al.* 1987; Rodgers *et al.* 1987). Until now, however, there have been no attempts to analyze the viability of the population, nor to project future population sizes and trends.

Population viability analyses provide a formal and widely accepted means for predicting future population scenarios and likelihood of extinction under different parameter scenarios (Dennis *et al.* 1991; Holmes and Fagan 2002; Morris and Doak 2002; Staples *et al.* 2005). Here we present a preliminary population viability analysis for the southeastern U.S. population of Wood Storks using two approaches. First, we used nest-count data from synoptic aerial surveys conducted intermittently since 1976 (USFWS 2002, 2003) to quantify the long-term population growth rate of the Wood Stork and to

estimate the risk that the population could become extinct or fall below 500 breeding pairs (quasi-extinction) over the next 50 or 100 years. Secondly, we parameterized a preliminary stage-based population matrix model using empirical data collected over four years on nest success, fecundity, and juvenile survival rates, in order to estimate population growth rates under a variety of survival and fecundity conditions. While a lack of data on adult survival rates precluded the full parameterization of the model, we were able to use elasticity and sensitivity analyses to identify life-stages of particular management concern.

## METHODS

### Count-based PVA

Aerial surveys to locate all wood stork nests in Florida, Georgia, and South Carolina have been conducted intermittently since 1976 as part of a range-wide monitoring program (USFWS 2002, 2003). Surveys were conducted using fixed-wing aircraft. While specific protocols have varied over time and by region, in general search protocols have focused on previously located colony sites (Rodgers *et al.* 2005; Meyer and Frederick 2008), with all known or suspected colony sites checked at least once per nesting season. New colonies were generally added to the database either by encounter during the surveys, or through citizen and birder reports. In Florida, aerial surveys consisting of transects or zig-zag search patterns have also been conducted intermittently over areas with no known colonies in order to identify new colony sites (Nesbitt *et al.* 1982; Meyer and Frederick 2008). Nest numbers from these surveys are presented in Annual Wood Stork Reports published by the U.S. Fish and Wildlife Service (2002, 2003).

The log of the change in number of nests over the interval between counts was regressed against the time elapsed between counts. 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:

$$\log(N_{i+1}/N_i)/(\sqrt{t_{i+1}-t_i}) =$$
$$\log(N_{i+1}/N_i)/x_i = \log\lambda_i \qquad \text{(Eq. 1)}$$

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).

A linear regression procedure in SAS (SAS 9.1, 2003) was used to calculate the slope and the residual mean square of the regression, which are equal to the geometric mean of the log population growth rate (μ) and its variance (σ²) (Dennis *et al.* 1991; Morris and Doak 2002). The strength of the autocorrelation of the regression residuals was measured. The regression re-

siduals are interpreted as representing the effects of environmental perturbations, using the Durbin-Watson d statistic and were tested for density dependence by regressing the log of the population growth rate between successive counts [$\ln(N_{t+1}/N_t)$] against the number of nests at time t ($N_t$) (Morris and Doak 2002). A standard two-tailed t-test was used to test for differences in population growth rates before and after listing (1984).

Matlab 7 (Mathworks, Release 14, 2004) was used to determine the cumulative absolute extinction and quasi-extinction probabilities over the next 50 or 100 years. The probability that an extinction threshold will be reached at any time between the present (t = 0) and a specified future time (t = T) can be calculated using the cumulative distribution function for the time to extinction:

$$G(T|d,\mu,\sigma^2) =$$
$$\phi\left(\frac{-d-\mu T}{\sqrt{\sigma^2 T}}\right) + \exp(-2\mu d/\sigma^2)\phi\left(\frac{-d-\mu T}{\sqrt{\sigma^2 T}}\right) \qquad \text{(Eq. 2)}$$

where $d = \log N_c - \log N_x$, the difference between the log of the current population size $N_c$ and the log of the extinction threshold $N_x$, and $\phi(z)$ is the standard normal cumulative distribution function (Morris and Doak 2002). A parametric bootstrapping approach was used to incorporate the uncertainty inherent in the estimates of μ and σ², drawing 500 values of μ and σ² from the appropriate probability distribution around the estimated values to calculate a range of values for G within a 95% confidence interval.

Absolute extinction was considered to be a population consisting of only one pair of birds. Given the potentially complex and unpredictable dynamics of populations at very low population sizes, however, predictions of time to absolute extinction are not considered reliable (Morris and Doak 2002). For this reason the same procedure was used a second time, with the extinction threshold ($N_x$) = 500, to determine the probability that a quasi-extinction threshold of 500 birds would be reached over the same time frames. Five hundred breeding pairs were arbitrarily chosen as the quasi-extinction threshold, a level deemed appropriate given the wide range and coloniality of the wood stork, which could result in problems finding mates at low densities.

### Estimation of Vital Rates

Pooled data on nest success and chicks per successful nest from colonies in Georgia, South Carolina, and Florida from 2002-2005 were used to estimate reproductive rates (Figure 1). The number of colonies followed varied from three in 2002 to 30 in 2005. Over the four year period, the fates of 6,451 nests were followed. In general, colonies were visited every one to two weeks and the fate of a subset of marked nests was followed (see Rodgers *et al.* 2008; Bryan and Robinette 2008, for basic protocols). Nests were considered successful if at least one chick survived to fledging, approximately six to eight weeks post-hatch.

Fledging success and survival rates of juvenile birds from 2002-2005 were estimated using satellite telemetry. As of July 2005, 35 g (2002-2003) and 45 g (2004-2005) solar-powered ARGOS-PTT satellite tags (Microwave Telemetry, Columbia, MD) were deployed on 135 juvenile wood
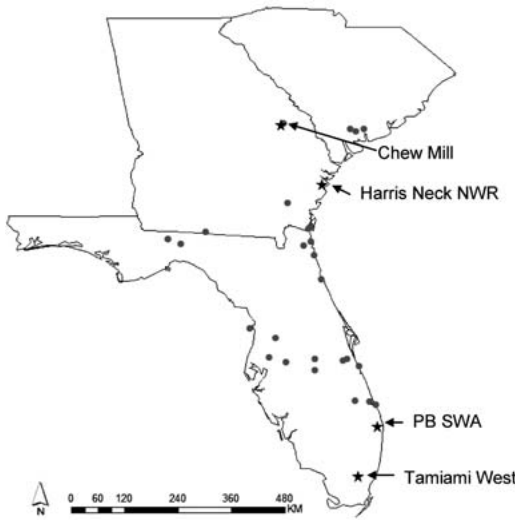
**Figure 1. Map of Wood Stork (*Mycteria americana*) colony locations. Gray dots indicate locations of colonies that were monitored in 2002-2005. Black stars indicate colonies where, in addition to monitoring nests, we deployed satellite tags on juvenile Wood Storks.**

storks in south Florida and Georgia (see Figure 1). Ten g VHF radios (Advanced Telemetry Systems, Isanti, MN, and American Wildlife Enterprises, Monticello, FL) equipped with a mortality sensor were attached to the satellite tags using epoxy and small bolts. 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. Transmitters were permanently attached to birds using a 0.25 cm 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).

Satellite tags allowed monitoring of the fates of tagged birds with relative certainty. Given the minimum expected three year lifespan of the solar batteries that power the tags, a bird was considered to have died when GPS locations from its tag stopped being received within a three year period. The last recorded coordinates and the VHF receiver were used to attempt to verify mortality and retrieve all tags through location of the tag and carcass.

Fledging success was based on a bird successfully leaving the colony. A bird was considered 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. Subsequent yearly survival rates were based on the number of birds surviving from 1 April to the following 31 March.

After fledging, birds were divided into stages corresponding to fledglings (post-dispersal), yearlings, two year-olds, three year-olds, and adults (four year-olds and older). A likelihood ratio test was used to determine whether stage had a significant influence on survival. Due to the low sample size of satellite-tagged birds, data from across years (April 2002-April 2006)

was pooled to obtain a single estimate of survival by age group for use in the deterministic demographic model that was developed.

Demographic PVA

The matrix model was based on a birth-pulse, post-breeding census. The basic deterministic population matrix was as follows:

$$\text{Matrix} = \begin{bmatrix} 0 & 0 & 0 & f_3 & f_{4+} \\ s_0 & 0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 \\ 0 & 0 & s_2 & 0 & 0 \\ 0 & 0 & 0 & s_3 & s_{4+} \end{bmatrix}$$

where $s_0$ = fledgling survival, $s_1$ = survival of one year-olds, $s_2$ = survival of two year-olds, $s_3$ = survival of three year-olds, and $s_{4+}$ = adult survival. The parameters $f_3$ and $f_{4+}$ corresponded to the fertility of birds at the end of their third year (i.e., four year-old birds) and to the fertility of adults. Each represented the number of female chicks fledged per adult female birds, and was the product of mean nest success, mean chicks/nest (divided by two, assuming an equal sex ratio), fledging success of juveniles, and adult survival. The parameter f3 represented the first breeding attempt; this was incorporated into the model in two ways: in the first scenario, the productivity of first-time breeders was assumed to be half that of adults, and in the second it was assumed to be equal to that of adults. The assumption of lowered productivity of first time breeders was justified based on differences in nest success and productivity by age in the White Stork (*Ciconia ciconia*). Vergara and Aguirre's (2006) nest success rates and chicks per successful nest for birds in the two- and three-year age classes vs. those in the older age classes were averaged. It was found that they were approximately 58% and 75% lower than those of older White Storks, resulting in total productivity of approximately 44% that of older birds.

As there are currently no good estimates of adult survival, population dynamics were modeled separately using values ranging from 0.85-0.95 for adult survival. These values were chosen based on Bancroft *et al.* (1992) in which the authors chose survival values ranging from 0.8-0.9 to calculate wood stork population size using a number of demographic assumptions. These values were increased by 0.05, however, to reflect changes in abundance and apparent population growth since that time. Specifically, the parameters for the deterministic model were:

$$\text{Matrix} = \begin{bmatrix} 0 & 0 & 0 & 0.4801/2*s_3 & 0.4801*s_4 \\ 0.31 & 0 & 0 & 0 & 0 \\ 0 & 0.59 & 0 & 0 & 0 \\ 0 & 0 & 0.79 & 0 & 0 \\ 0 & 0 & 0 & s_3 & s_4 \end{bmatrix}$$

for the scenario in which productivity of first time breeders was half that of adults, and $s_3$ was set equal to $s_4$, with $s_4$ varied from 0.85-0.95 in 0.025 increments. When productivity of adults and first-time breeder was assumed to be equal, the $f_3$ parameter was identical to that for $f_4$.

The long-term population growth rate ($\lambda$), the stable age distribution, and the reproductive value of each age class for the southeastern wood stork population were calculated in Matlab 7 using the deterministic model described above. Adult survival was plotted against $\lambda$ to determine the level of adult survival necessary to maintain a stable population ($\lambda = 1$) for populations under both productivity scenarios.

The proportional sensitivity or elasticity ($e_{ij}$) 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 ($a_{ij}$) to $\lambda$, using:

$$e_{ij} = \frac{\partial(\log\lambda)}{\partial(\log a_{ij})} = \frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial\partial_{ij}} \qquad \text{(Eq. 3)}$$

where all other elements of the transition matrix are held constant (de Kroon *et al.* 2000; Caswell 2001). A sensitivity analysis to examine how sensitive the model would be to a uniform underestimation of vital rates was conducted as elasticity analysis requires that only one parameter change at a time (Caswell 2001). Estimates of fecundity and survival of fledglings, one and two year old birds were increased simultaneously by either 10% or 25% and the population growth rate and the level of adult survival necessary to maintain a stable population recalculated.

## RESULTS

### Count-based PVA

Population growth rate since 1976 was calculated from the Wood Stork nest count data, and found to be 0.0197 (CI = -0.1131, 0.1525; $\sigma^2 = 0.1190$). The Durbin-Watson d statistic (d = 2.99) was inconclusive as to the significance of temporal autocorrelation in count numbers. While there was a weak negative relationship between the population growth rate and the numbers of nests counted (Figure 2), the relationship was nonsignificant ($R^2 = 0.1919$, t = -2.01, p = 0.0606). The regression remained non-significant when the outlier corresponding to the 1978 nest count was removed ($R^2 = 0.1812$, t = -1.88, p = 0.0782) indicating that density dependence had a negligible influence on population growth. There was no significant difference (p = 0.96) in estimated population growth rates between the period prior to listing (1976-1983) ($\mu = 0.0209$, $\sigma^2 = 0.1730$) and the period following listing (1984-2004) ($\mu = 0.0192$, $\sigma^2 = 0.0803$).

The best estimate of the cumulative extinction probability at the end of 50 years was very low (G = $1.872 \times 10^{-5}$) but the widening
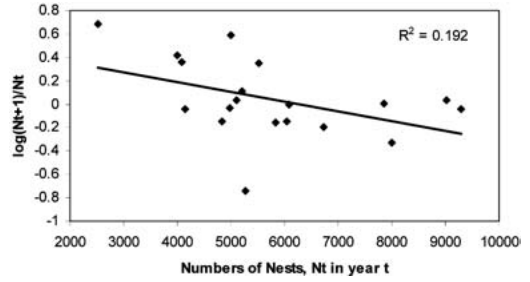


**Figure 2. The log of the change in Wood Stork population size between census intervals, log(Nt+1)/Nt, plotted against the number of nests counted in year t, Nt. The weak relationship indicates that density-dependence did not have a significant effect on population growth rates over this period.**

of the confidence intervals over the 50 year period (95% CI = $6.347 \times 10^{-20} - 0.105$) indicated that extinction within as little as 50 years cannot be ruled out (Figure 3). As one would expect, the probability that the population would reach the quasi-extinction threshold of 500 pairs over the same time frame was considerably higher (best estimate of G = 0.1150, 95% CI = $1.590 \times 10^{-5} - 0.909$), and the upper confidence limit did not rule out quasi-extinction even over the next decade (UCL = 0.112 at year ten) (Figure 4).

### Vital Rate Estimation

The mean proportion of successful nests for the southeastern population from 2002-2005 was 0.6370 (SE = 0.0285). The mean
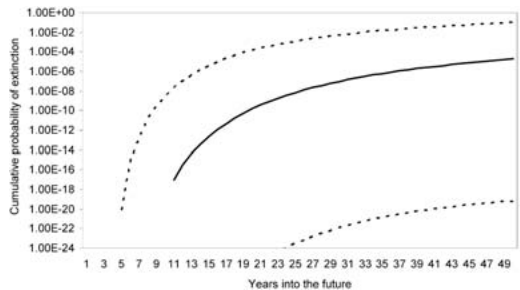


**Figure 3. Cumulative probability of extinction for the Southeastern US Wood Stork population based on aerial surveys of nests conducted intermittently since 1976. The solid line represents the best estimates of m and s² while the dashed lines show the approximate 95% confidence interval from bootstrapping. The x-axis represents the time required for a population with 10,000 pairs of birds to decline to a single pair.**
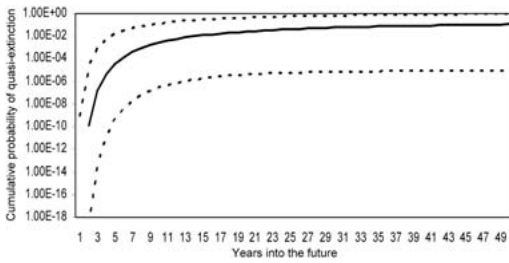
Figure 4. Cumulative probability of quasi-extinction for the Southeastern US Wood Stork population based on aerial surveys of nests conducted intermittently since 1976. The solid line represents the best estimates of m and $s^2$ while the dashed lines show the approximate 95% confidence interval from bootstrapping. The x-axis represents the time required for a population with 10,000 pairs of birds to decline to 500 pairs.

number of chicks per successful nest was 1.99 (0.047). Numbers of chicks per successful nest were similar among years while nest success rates showed more variability (Table 1). Fledging success was also highly variable among years (Table 2) with a mean of 0.7678 (0.0962) from 2002-2005. Average fecundity, estimated as the number of female chicks fledged was 0.4866.

Stage had a significant effect on juvenile survival (G = 10.45, 2 df, p = 0.0054), with survival increasing with age (Table 3). The proportion of all chicks surviving their first year was 0.31, increasing to 0.59 for birds in their second year and to 0.75 for birds in their third year.

Demographic PVA

The long-term population growth rate ($\lambda$) (Table 4), stable age distribution, and the reproductive value of each age class were calculated for the southeastern Wood Stork population using the deterministic model (Table 5). The value of adult survival necessary to maintain a stable population size ($\lambda$ = 1) was 0.9392 when productivity of first breeders was half that of adults, and 0.9374 when they were equal.

Across the range of values for adult survival analyzed, the population growth rate was most sensitive to adult survival, followed by the survival of juvenile birds. The population growth rate was least sensitive to variation in fertility rates. When fecundity and survival estimates were increased by 10% and 25% of their respective values, however, the survival rate of adults required to maintain a stable population decreased to 0.9213 (10%) and 0.8901 (25%) for the more likely scenario in which the productivity of first time breeders is less than that for adults.

DISCUSSION

While the count-based estimate of population growth reflected the generally increasing trend observed since 1976, the high variance in the population growth rate—spanning positive and negative values—indicates that we cannot dismiss the possibility of long-term population decline despite recent population growth. The analysis of cumulative extinction and quasi-extinction probabilities lent support to a cautious optimism regarding the long-term viability of the species.

While the best estimates of extinction probabilities were very low over the short-term, widening confidence intervals did not allow us to conclude with 95% certainty that absolute extinction will not occur within the next 50 years. Furthermore, when we looked

Table 1. Mean nest success rates and mean number of Wood Stork (*Mycteria americana*) chicks per successful nest based on pooled data from Florida, Georgia, and South Carolina from 2002-2005.

| Year | Nest success | No. of colonies | No. of nests | SE | Chicks/successful nest ($\bar{x}$) | SE |
|------|--------------|-----------------|--------------|--------|-------------------------------------|--------|
| All | 0.6370 | 85 | 6,451 | 0.0285 | 1.99 | 0.047 |
| 2002 | 0.6910 | 3 | 244 | 0.0513 | 1.94 | 0.010 |
| 2003 | 0.6536 | 20 | 2,186 | 0.0448 | 2.08 | 0.061 |
| 2004 | 0.7129 | 31 | 2,108 | 0.0457 | 2.11 | 0.096 |
| 2005 | 0.5395 | 30 | 1,913 | 0.0534 | 1.81 | 0.061 |

Table 2. Fledging success rates for juvenile Wood Storks outfitted with satellite tags in 2002-2005, from approximately 27 d to departure from the colony.

| Year | Number tagged | Number Fledged | Fledging success |
|------|---------------|----------------|------------------|
| 2002 | 33 | 27 | 0.818 |
| 2003 | 34 | 17 | 0.500 |
| 2004 | 24 | 23 | 0.958 |
| 2005 | 44 | 35 | 0.795 |

at the probability of the population falling below a threshold of 500 pairs, the wide confidence intervals indicated quasi-extinction was possible even in the short term (next decade).

Even the best estimates of quasi-extinction probabilities indicated that there was an 11% chance of quasi-extinction at the end of the 50 year period. Furthermore, it is possible that the number we chose to represent quasi-extinction—the level at which further population declines are likely to be unpredictable and potentially precipitous—is too low and that the true quasi-extinction threshold could be reached considerably sooner than we have projected.

The empirically-derived population matrix model indicated that very high levels of adult survival would be necessary to sustain a stable or growing population. If our estimates of fecundity and vital rates are accurate, nearly 94% of adult birds would need to survive annually. This estimate is much higher than the 86% annual adult survival observed in the European White Stork in Switzerland (Schaub *et al.* 2004), and may not be realistic. It is more likely that we have underestimated the true long-term survival rates and fecundity parameters. Because the data used in this analysis spanned a relatively short time period, the averaging of vital rates may not represent critical dynamics related

to the timing and frequency of extremely high or extremely low values. It is also possible that we induced a systematic negative bias through disturbance of colonies and application of satellite tags. When these parameters are adjusted to reflect a potential negative bias of ten or 25%, the levels of adult survival necessary for population size maintenance decrease considerably.

Conclusion

While these preliminary models provide new insights into wood stork population dynamics that have been unavailable in the past, there are still many population parameters that will need to be established or refined before a definitive demographic model can be developed. Adult survival is an obvious missing link, and we have recently begun deploying satellite transmitters on adult birds in an attempt to estimate this parameter. Another factor that must be addressed is the variance in vital rates and how sampling error and other observer- or research-induced biases factor into our estimates. Unless we can partition the variance in vital rates into that imposed by environmental stochasticity vs. that induced through sampling error, we will not be able to narrow our confidence intervals nor to make projections about future

Table 3. Number of Wood Storks in each life-stage that survived or died over one year intervals in the period 2002-2006.

| Stage | Total # of bird-years | Fate at the end of a one-year interval | | Proportion surviving one year |
|-------|------------------------|------|-------|--------------------------------|
| | | Dead | Alive | |
| First year | 102 | 70 | 32 | 0.31 |
| One-yr-old | 22 | 9 | 13 | 0.59 |
| Two-yr-old | 8 | 2 | 6 | 0.75 |
| Three-yr-old | 6 | 2 | 4 | 0.67 |

**Table 4. Long-term population growth rate (l) for different values of adult survival for the Southeastern US Wood Stork population from the deterministic matrix model.**

| | Long-term growth rate ($\lambda$) | |
|---|---|---|
| Adult survival | $f_3 = 0.5 * f_4$ | $f_3 = f_4$ |
| 0.850 | 0.9201 | 0.9233 |
| 0.875 | 0.9423 | 0.9444 |
| 0.900 | 0.9647 | 0.9665 |
| 0.925 | 0.9872 | 0.9889 |
| 0.950 | 1.0098 | 1.0113 |

**Table 5. Stable age distribution and reproductive values for the Southeastern US Wood Stork population from the deterministic matrix model when productivity of first-time breeders is half that of adults.**

| | Stable age distribution | | | Reproductive value | | |
|---|---|---|---|---|---|---|
| Adult survival | 0.85 | 0.90 | 0.95 | 0.85 | 0.90 | 0.95 |
| Fledglings | 0.2513 | 0.2583 | 0.2630 | 1.0000 | 1.0000 | 1.0000 |
| One-yr-old | 0.0855 | 0.0832 | 0.0809 | 2.9611 | 3.1061 | 3.2525 |
| Two-yr-old | 0.0549 | 0.0510 | 0.0473 | 4.6069 | 5.0693 | 5.5585 |
| Three-yr-old | 0.0449 | 0.0397 | 0.0352 | 5.6384 | 6.5083 | 7.4728 |
| Adults | 0.5616 | 0.5679 | 0.5736 | 6.0891 | 6.9632 | 7.9313 |

population sizes with any degree of assurance. Nonetheless, the count-based analysis of population dynamics indicates that the wood stork population is stable or increasing across the southeastern United States, lending support to a cautious optimism regarding the conservation status of the species.

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