Articles

Productivity and Habitat Modeling of Wood Storks Nesting in North and Central Florida

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Abstract

Rainfall, surface water levels, location within the state, and area and types of habitats ($n = 29$) surrounding wood stork *Mycteria americana* colonies in North and Central Florida were analyzed at 10-km, 20-km, and 30-km radii around each colony to examine their relationship with fledging rate and number of nests during 2003–2005. Seven variables within 10 km, 14 variables within 20 km, and 6 variables within 30 km of colonies were correlated with fledging rates. Fledging rate and number of nests were significantly associated with both wetland and nonwetland area and habitats. Among all the variables, fledging rate was most strongly associated with rainfall during the preceding 12–24 mo. Both larger colonies and colonies in North Florida had higher fledging rates. Although some variables had a positive association and other variables had a negative correlation with fledging rates, results were not consistent across all three radii, which suggests that the effects of hydrologic and habitat variables differs with increasing distance from a colony. The size of a wood stork colony was sensitive to a larger number of variables and varied by distances from the colony. Colonies were smaller in the northern part of Florida, and coastal colonies were larger than interior colonies. Because wood storks often use ephemeral foraging sites closer to a colony early in the season and those sites may not be available later in the season, wood storks may shift to alternate, more distant sites and habitats later in the season. A hypothesis is proposed whereby wood storks establish their colonies using proximate clues of prey availability based on the effects of past rainfall and certain preferred habitat types. These proximate cues to prey availability and foraging substrate surrounding a colony are detected by wood storks before the onset and during the initial nesting season. However, the long-term stability of a colony may ultimately be determined by yearly rainfall patterns and habitat variables at larger distances and by fledging rates that contribute to recruitment of nesting birds and an increase in number of nests.

Keywords: Florida; habitat modeling; landscape analysis; *Mycteria americana*; productivity; wood stork

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Introduction

Historically, the wood stork *Mycteria americana* (Figure 1) bred in numerous colonies throughout southeast Georgia and most of Florida (Coulter et al. 1999). However, precipitous declines in its range and population occurred during the mid-1900s (Kushlan and Frohring 1986; Ogden et al. 1987). Ultimately, the U.S. population was listed as endangered pursuant to the U.S. Endangered Species Act (ESA 1973, as amended) in 1984 (USFWS 1984). While the number of wood stork nests and colonies in Georgia and South Carolina appeared to increase during the 1980s and 1990s, wood storks have experienced nesting-related problems (e.g., whole colony abandonment, years of non-breeding activity, or low fledging success) in some regions of Florida, especially South Florida (Coulter et al. 1999). The most recent data indicate that there were about 7,200 nesting pairs in 22 colonies within Florida during 2001–2005 (Slay and Bryan 2001; Brooks and Dean 2008).

Wood stork fledging success varies among years and colonies (Kahl 1964; Ogden et al. 1978; Clark 1978; Ehrhart 1979; Hopkins and Humphries 1983; Coulter and Bryan 1995; Rodgers and Schwikert 1997; Rodgers et al. 2008). Food resources likely are the proximate factor responsible for fledging rates because predation and disease tend to be rare events and wood storks often fledge fewer birds than their clutch size due to brood reduction (Rodgers and Schwikert 1997). Wood storks use a variety of wetland habitats for foraging (Coulter et al. 1987; Hodgson et al. 1988; Bancroft et al. 1991; Coulter and Bryan 1993; Gaines et al. 1998, 2000; Coulter et al. 1999). Of the 43 habitat categories and communities identified in Florida by the Florida Fish and Wildlife Conservation Commission (2005), ≥15 are continuously or intermittently flooded wetlands. The status of most of these wetland communities (e.g., freshwater marsh and wet prairie, cypress swamp, marine–estuarine) is classified as poor and declining due to conversion to agriculture and development, withdrawal of ground water, incompatible forestry and land-use practices in adjacent areas, nutrient runoff, incompatible recreation activities (disturbance to and displacement of wildlife), and effects of sea-level rise on coastal wetlands. The challenge is to balance protection of our wetland communities for economic, public, and wildlife uses (Florida Fish and Wildlife Conservation Commission 2005). An objective in the Wood Stork Recovery Plan (1.1.2 Locate roosting and foraging habitat) is identifying foraging habitat critical to the recovery of the species (USFWS 1997, 2000). In addition, recovery task 1.2. (Prioritize habitat) recommends developing a prioritization scheme to identify colonies and which of their foraging habitats is under the greatest degree of threat. However, information is lacking on the amounts and types of wetlands around each colony available to foraging wood storks, especially in Florida. Furthermore, no published information exists on the relationship between wood stork nesting variables (fledging rate and number of nests) and the amount and types of wetland habitat surrounding each colony in Florida.

The basis for our study was an attempt to better understand the relationship of wood stork productivity with the landscape surrounding colonies in Florida. We believe both fledging success and number of nests should be a good metric for judging quantity and quality of habitat surrounding a colony. The U.S. Fish and Wildlife Service (USFWS) provided a grant to the Florida Fish and Wildlife Conservation Commission during 2003–2005 to determine the productivity of wood storks in Florida (Rodgers 2002; Rodgers et al. 2008). The USFWS is using these data to evaluate the status of the wood stork in the United States and to determine whether the species meets recovery criteria for reclassification from endangered to threatened (Brooks and Dean 2008, USFWS 2010a).

Here we test the hypothesis that colony productivity is associated with the hydrologic variables and amount and types of certain habitats within flight distances of each colony. Using the most recent satellite imagery data for the habitat surrounding individual wood stork colonies in North and Central Florida (Table S1, *Supplemental Material*), our objective was to model the relationship between productivity (mean fledging rate and number of nests per colony) and colony location within the state, hydrological data, area in hectares, and distance relationship of these habitat variables.

Study Population and Methods

Study area

The study area consisted of wood stork colonies monitored during a previous study (Rodgers et al. 2008; Figure 2; Table S2, *Supplemental Material*). Those colonies were distributed throughout North and Central Florida, including at interior and coastal sites. The latitude and longitude of all colonies were delimited with a WAAS-enabled GPS unit. The center point of the region occupied by nesting wood storks within each colony was averaged over the study period.

Study approach

Data on wood stork nesting variables (i.e., dependent variables: annual mean colony fledging rates and total number of nests) were collected as part of a previous study (Rodgers et al. 2008). Either all nests (colonies of fewer than 100 nests) or a sample of the nests (i.e., 25–50% of nests at larger colonies) were marked (details below) and monitored biweekly during the March–August breeding season for 22 colonies each year during 2003–2005 (Figure 3). Wood stork colonies were visited throughout the breeding season to avoid temporal biases that might occur during the nesting seasons (Rodgers and Schwikert 1997). Care was taken to reduce researcher effects on the breeding storks and other species of colonial waterbirds by 1) minimizing nest monitoring during pair formation and early egg-laying periods; 2) visiting colonies during the cooler morning and late-afternoon hours and not during inclement weather; 3) minimizing the time spent at each nest by using two people to observe and record data and map nest and tree distribution; 4) using binoculars to monitor nests from a distance within high-density, mixed-species subcolonies when the nestlings were visible and capable of leaving the nest; and 5) counting nests from a distance with binoculars to avoid causing premature fledging of

Figure 1. Wood storks *Mycteria Americana* **(a)** foraging and **(b)** in flight. Photographs by Ron Bielefeld.

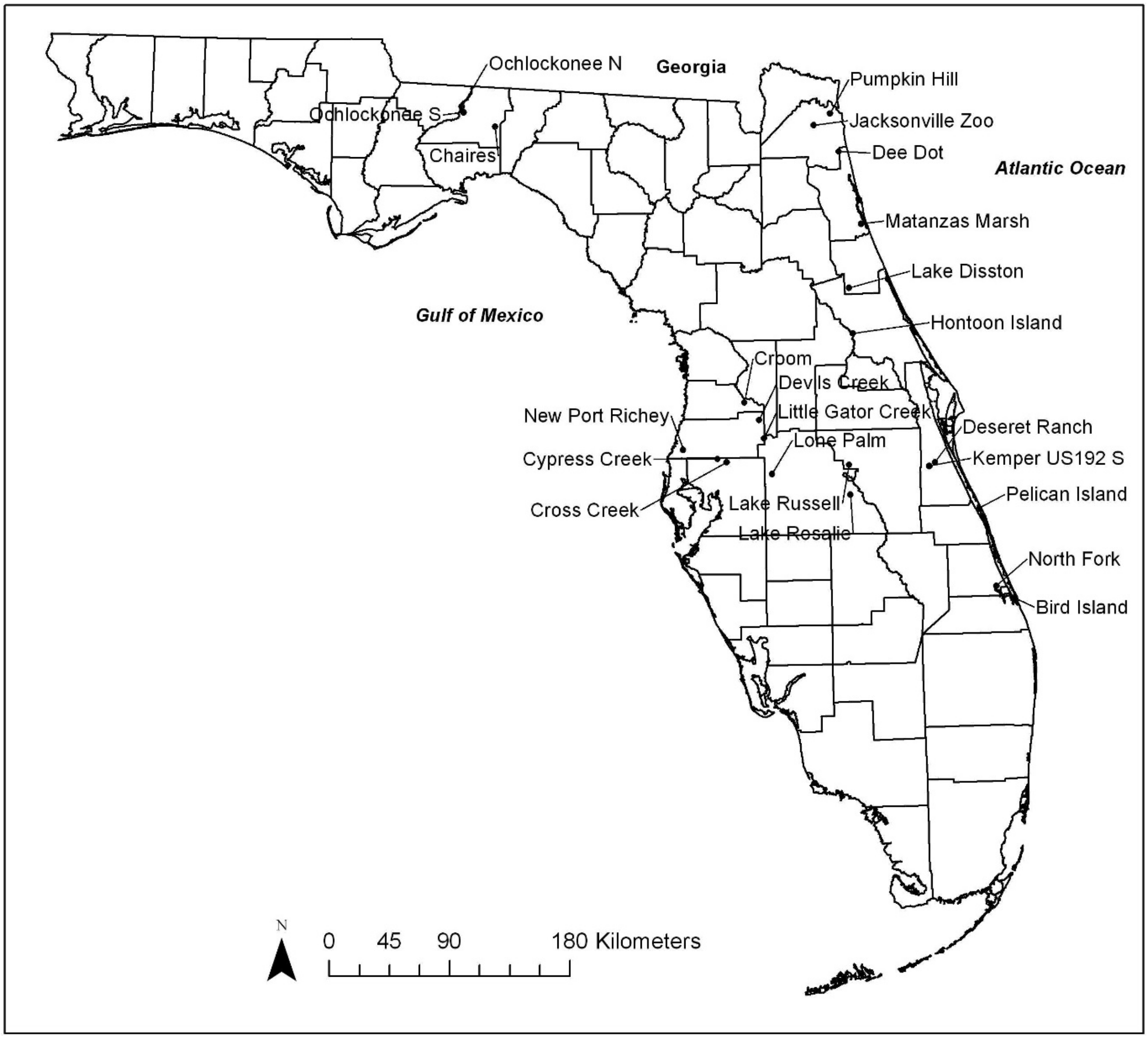

Figure 2. Wood stork *Mycteria americana* colonies monitored during 2003–2005 breeding seasons in North and Central Florida.

nestlings after they were 3–4 wk old. Nests and trees were individually marked with numbered, colored flagging tape or plastic tags, which facilitated distant viewing of each nest. Total number of wood stork nests in each colony was based on the maximum ground count from a minimum of two surveys of the entire colony during May–June. Associations between nesting variables and independent variables (i.e., hydrologic and types and area of habitat variables) were examined using GIS software (ESRI 2011) and statistical software (SAS Institute, Inc. 2003).

Hydrologic and habitat variables

Hydrologic conditions (rainfall, surface water levels) and area and types of habitats surrounding a wood stork colony are hypothesized as being important variables for determining fledging rates and number of nests in colonies via the availability of aquatic prey. Based on the feeding ecology and flight distances of foraging wood storks (Coulter et al. 1987; Bryan et al. 2005, 2008; Borkhataria et al. 2008) and the recommended zonal distances the USFWS used for management guidelines (USFWS 2008, 2010b), we used 10-km, 20-km, and 30-km radii around each colony to examine the relationships between wood stork nesting variables and available habitat surrounding each colony (Figure 4). By categorizing all habitats within the three distance radii, a large amount of open-water or ocean habitat was included around coastal colonies, which has the potential to affect the importance of different habitat variables. However, we also wanted to examine whether the amount of open-water habitat that is unsuitable for foraging (i.e., greater than the maximum 30–40-cm foraging depth) would have an effect on wood stork productivity.

Figure 3. Wood storks *Mycteria americana* nesting in bald cypress *Taxodium distichum* at the Hontoon colony in Volusia County, Florida.

For each radius, we extracted the area (ha) and types of habitat from the Florida 2003 Vegetation and Land Cover grid using GIS landscape information from the Closing the Gaps Program (Kautz et al. 2007). The 2003 land-cover data set has a pixel resolution of 30 m (900 m^2). Because the area of habitat within each 10-km distance from a colony increases as the square of the radius, there were about 314 km^2 within 10 km, 1,256 km^2 within 20 km, and 2,826 km^2 within 30 km of a colony (Figure 4). Thus, the models analyzed the associations of habitat classes from 0 to 10-km, 0 to 20-km, and 0 to 30-km distances surrounding each colony. The types of habitats follow Gilbert and Stys (2004) and are listed in Table 1.

Hydrological data from a recording station within 30 km of each wood stork colony were obtained from the Florida Climate Center (2005) and Hydrologic Data Collection (SJRWMD 2009) databases. If more than one recording station was within 30 km of a colony, we averaged these values for the variable. These variables included the following:

1. cumulative rainfall during the 12 mo before the onset of the nesting season (circa April),
2. cumulative rainfall during the 12–24 mo before the onset of the nesting season (termed previous year's rainfall), and
3. adjusted surface-water level (the difference between the current year's level and the average level over the preceding 10 y) at the onset of the nesting season for a recording station at a representative lake site.

Because unknown edaphic or geographical factors could influence the productivity of wood storks at the colony or regional level, we also identified each colony by latitude and longitude and arbitrarily characterized it as being either coastal (≤20 km from the Atlantic or Gulf coastline) or interior (>20 km from coastline) and coded this as a bivariate response ''Yes'' or ''No,'' respectively. Latitude, longitude, and coastal location were considered fixed variables in the full statistical model.

Statistical analyses

We analyzed data on fledging rate and number of nests as a colony-year unit. Thus, a colony monitored for 3 y is represented by 3 colony-years. We expressed

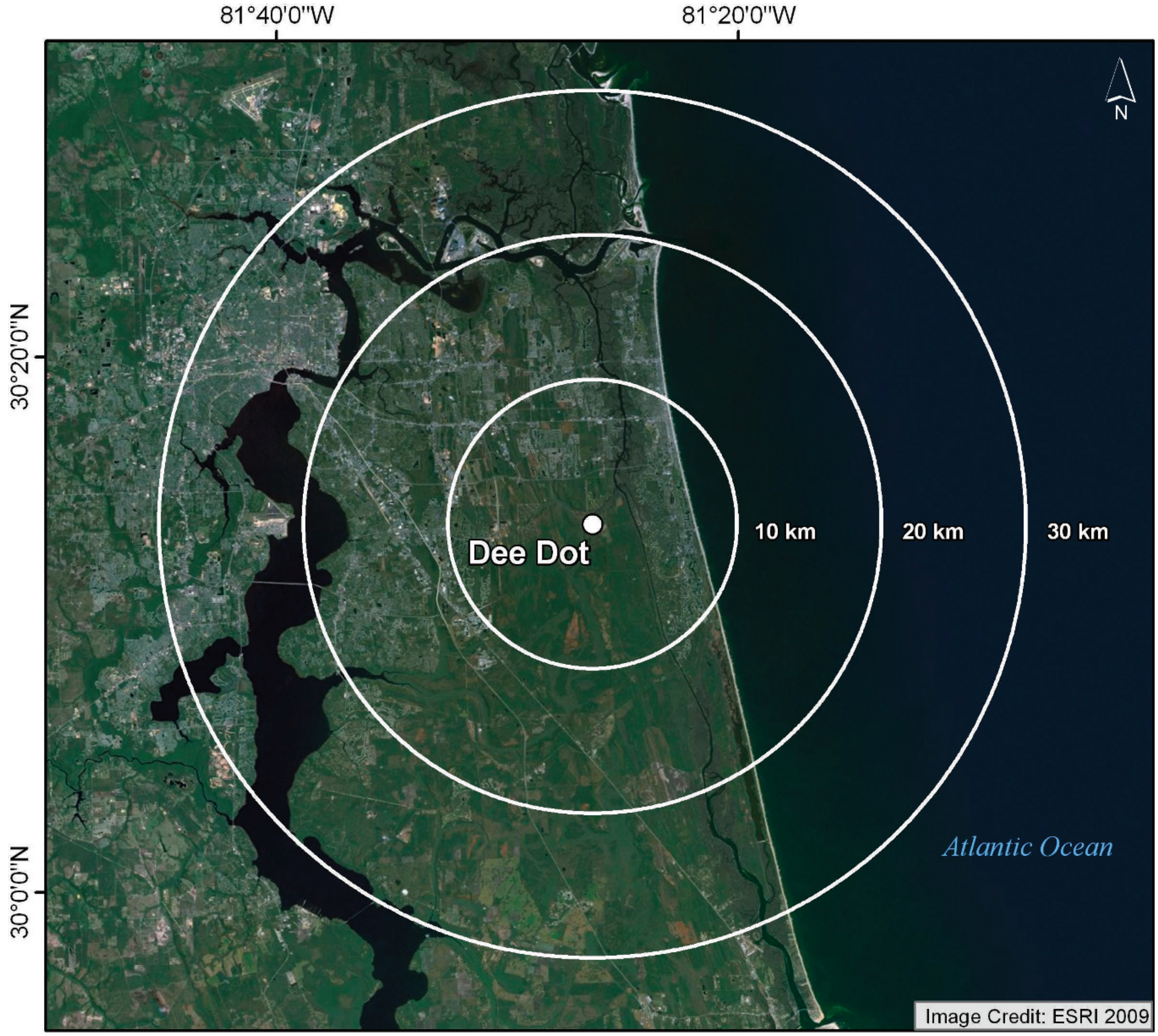

Figure 4. Satellite image of the region surrounding the Dee Dot wood stork *Mycteria americana* colony in Florida, with 10-km, 20-km, and 30-km regions delineated.

fledging rates as fledglings per nest and included nests that failed before young fledged.

Prior to the initiation of field work in 2003, we computed a power analysis to estimate the minimum sample size of wood stork nests that would allow detection of a difference of 0.25 fledgling/nest in mean colony fledging rate and attain a power = 80%, with α = 0.05 (Bond 2003; Friendly 2003). Using the mean of 1.29 fledglings/nest and a standard deviation of 1.16 (Rodgers and Schwikert 1997), we estimated that a minimum of 38–42 nests (range based on upper and lower CIs) should be monitored each year. We imposed a minimum of 2 y of data per colony for the modeling of wood stork productivity to preclude any biases that might be associated with 1 y of monitoring because we were interested in multiple-year associations as opposed to a single-year phenomenon.

We made statistical analyses with the Statistical Analysis System (SAS Institute, Inc. 2003). Unless stated otherwise, values are represented as the mean $\pm$ 1 standard deviation. Statistical analyses of reproductive variables were made only for colony-years with $\geq$38 nests. Prior to pairwise comparisons, we tested the data for normal distribution with the Shapiro–Wilk statistic using the UNIVARIATE procedure and for homogeneity of variances with Bartlett's likelihood ratio test using the DISCRIM procedure. The MEANS procedure was used to calculate standard descriptive statistics, including mean, standard deviation, and upper and lower 95th percentile confidence intervals. An inverse variance weighting option was used with the MEANS procedure to account for the uneven sample sizes among colonies. We assumed independence among years and a constant correlation within each colony.

The goal of the wood stork habitat modeling was to identify any associations between the nesting variables

Table 1. Results of modeling the relationship between wood stork *Mycteria americana* fledging rate with hydrologic, edaphic, and habitat types at 10-, 20-, and 30-km zones around 22 colonies in North and Central Florida. The productivity, rainfall, and water level data were collected during 2003–2005 and the area of each habitat type is from land cover data collected during 2003. The types of habitats follow Gilbert and Stys (2004). Values represent the Pr $> |t|$.[a]

	Distance from colony (km)		
Variable or habitat type	**10**	**20**	**30**
Annual rain	0.0422	ns	ns
Previous years rain	0.0425	0.0101	0.0027
Adjusted water level	ns	ns	ns
Number of nests	ns	0.0075	ns
Latitude	<0.0001	0.0021	ns
Longitude	ns	0.0014	ns
Coastal location	ns	0.0055	ns
Coastal strand	ns	ns	ns
Sand and/or beach	ns	ns	ns
Xeric oak scrub	ns	ns	ns
Sand pine scrub	ns	ns	ns
Sandhill	ns	ns	ns
Dry prairie	0.0002	0.0002	ns
Mixed pine–hardwood forest	ns	ns	0.0002
Pinelands	ns	ns	ns
Tropical hardwood hammock	ns	ns	ns
Freshwater marsh and wet prairie	ns	0.0132	<0.0001
Sawgrass	ns	ns	ns
Shrub swamp	ns	ns	ns
Bay swamp	ns	0.0072	ns
Cypress swamp	0.0003	0.0007	ns
Cypress and/or pine and/or cabbage palm	ns	0.0236	ns
Hardwood swamp	ns	ns	0.0039
Mixed wetland forest	0.0101	ns	ns
Salt marsh	ns	ns	ns
Mangrove swamp	ns	ns	0.0081
Tidal flat	0.0003	0.0011	ns
Open water	ns	<0.0001	<0.0001
Shrub and brushland	ns	ns	ns
Grassland	ns	ns	ns
Bare soil and/or clear cut	ns	ns	ns
Improved pasture	ns	0.0017	ns
Unimproved pasture	ns	0.0022	ns
Agriculture	ns	ns	ns
High impact urban	ns	ns	ns
Low impact urban	ns	ns	ns
AIC_c	116.1	212.1	158.4

[a] ns = nonsignificant correlation ($P < 0.05$).

(fledging rate and number of nests per colony) and the wetlands available as foraging habitat surrounding each colony. Hydrologic, habitat, and geographic predictors (x axis) were first displayed with each nesting variable (y axis) in scatter plots (continuous predictors) and box plots (ordinal and categorical predictors) for all colonies for visual analysis of simple bivariate patterns. We overlaid on each scatter plot a least-squares fitted simple linear regression trend line for possible linear relationships and a nonparametric Loess-smoothed trend line for possible nonlinear patterns of association to characterize the relationship between the dependent variables (fledging rate and number of nests) and independent variables (hydrologic variables, area of each habitat type, geographic location). We were especially looking for nonlinear relationships among the variables and predictors.

We assumed that the area of each type of habitat derived from the land-cover data in Kautz et al. (2007) was a constant property and represented the area of each type of habitat during 2003–2005. If the area of each habitat type varied somewhat by year (e.g., loss due to development), then these values would be similar to variables measured with Berkson errors (Berkson 1950) when the actual predictor values were more variable than the predictor values used in our study. Berkson errors have been shown not to cause much bias in parameter estimation, but they can inflate the apparent power beyond what is probably appropriate (i.e., precision and *P*-values appear more impressive than they really should be).

Because of the unbalanced design of this study due to no nesting activity at some colonies in certain years, we used the MIXED procedure to model associations between the two nesting variables and the hydrologic, habitat, and geographic variables. The MIXED procedure fits mixed linear models (generalizations of standard linear models) using both fixed (hydrologic variables, latitude, longitude, location in respect to coastline, and habitat variables) and random (year) effects. Neither productivity nor hydrologic variables were included for years with no colony activity. Colony and year were used as class variables; and latitude, longitude, and nest numbers were fixed covariates when colony-years were pooled.

Because so many hydrologic, habitat and geographic predictors initially were considered in the analysis, we used a 2-step approach to reduce the overparameterization of our modeling process. The FACTOR procedure was used to first calculate a correlation matrix among all the habitat variables in order to determine whether we could collapse or combine some of the habitat classification variables. This procedure resulted in the extraction of 36 habitat variables within the 30-km distances from all colonies from the original 43 habitat variables statewide. Further collapsing of these 36 variables resulted in 29 variables used in the modeling process. Next, we used a backward-stepping selection method to reduce the number of nonsignificant variables from the model (Harrell 2001). For each dependent variable, a full model containing all predictors was first fitted, and then the predictor with the highest Type III effect test *F*-statistic with a *P*-value >0.10 was removed from the list of included predictors and the regression model was refitted (Littell et al. 2006). We repeated this back-stepping procedure until all remaining predictor effect *P*-values were ≤ 0.05. Final Poisson and negative binomial models without random effects were compared using the small sample version of the Akaike Information Criterion (AIC_c). We summarized results for each dependent variable from the best nonrandom and random effects model by AIC_c. Standard errors also were computed for each effect estimate. We calculated fit statistics, overdispersion parameters, and characteristics of the relationship between observed and predicted values for the final models with and without the random effect.

Results

Surrounding habitat

The types and area of each habitat class varied among individual wood stork colonies in North and Central Florida (Table S1, *Supplemental Material*). Among all colonies within the 10-km distance, the most common habitat types were high urban (14.3%), pine lands (14.1%), open water (12.5%), improved pasture (8.8%), and hardwood swamp (6.8%); among all colonies within 0–20-km distance, the most common habitat types were open water (16.6%), pine lands (13.3%), high urban (12.4%), improved pasture (9.7%), and hardwood swamp (5.8%); and among all colonies within 0–30-km distance, the most common habitat types were open water (20.5%), pine lands (12.6%), high urban (10.5%), improved pasture (9.9%), and hardwood swamp (5.2%).

Fledging rates

The combined fledging rate for wood stork colonies during 2003–2005 was 1.19 $\pm$ 0.09 fledglings/nest (n = 4,855 nests). The mean fledging rate (0.61 fledglings/nest) for all colonies during 2005 was significantly less than the rate of 1.47 fledglings/nest in 2003 and 1.43 fledglings/nest in 2004. Seven variables within 10 km, 14 variables within 20 km, and 6 variables within 30 km of colonies exhibited significant correlations with wood stork fledging rate (Table 1).

The final model for the relationship between wood stork fledging rate and hydrologic and habitat variables within 10-km distance was

$$\begin{aligned}\text{Fledging rate} = & -12.8021 + 0.4458 \text{ total annual rainfall} \\ & + 0.6521 \text{ previous year's rainfall} \\ & + 0.4151 \text{ latitude} + 0.0004 \text{ dry prairie} \\ & - 0.0005 \text{ cypress swamp} \\ & + 0.0005 \text{ mixed wetland forest} \\ & + 0.5964 \text{ tidal flat.}\end{aligned}$$

The final model for the relationship between wood stork fledging rate and hydrologic and habitat variables within 20-km distance was

$$\begin{aligned}\text{Fledging rate} = & \ 109.2300 \\ & + 0.0036 \text{ number of nests} \\ & + 0.8836 \text{ previous year's rainfall} + 1.4475 \\ & \text{latitude} - 1.8502 \text{ longitude} \\ & - 2.79 \text{ coastal location} \\ & + 0.0002 \text{ dry prairie} - 0.0001 \text{ freshwater} \\ & \text{marsh and wet prairie} \\ & - 0.0027 \text{ bay swamp} \\ & - 0.0001 \text{ cypress swamp} + 0.0046 \\ & \text{cypress and/or pine and/or cabbage palm} \\ & + 0.0862 \text{ tidal flat} - 0.0001 \text{ open water} \\ & - 0.0001 \text{ improved pasture} \\ & + 0.0018 \text{ unimproved pasture.}\end{aligned}$$

The final model for the relationship between wood stork fledging rate and hydrologic and habitat variables within 30-km distance was

$$\begin{aligned}\text{Fledging rate} = 2.7056 &+ 0.9781 \text{ previous year's rainfall} \\ &- 0.0001 \text{ mixed pine hardwood forest} \\ &- 0.0001 \text{ freshwater marsh and wet prairie} \\ &- 0.0001 \text{ hardwood swamp} \\ &- 0.0002 \text{ mangrove} \\ &\text{swamp} - 0.0001 \text{ open water.}\end{aligned}$$

Only rainfall in the previous year (i.e., 12–24 mo before the beginning of the nesting season) had a significant positive association with fledging rates within all three distances, while rainfall in the current year (i.e., ≤12 mo before the current nesting season) exhibited a significant positive correlation only within 10 km. Except for improved and unimproved pasture within 20 km, there was no other significant negative association between human-altered habitats (e.g., bare soil and/or clear cut, agriculture, high and low urban) and fledging rate. In general, there were more negative correlations between fledging rate and variables at greater distances from a colony (i.e., 10 km with six positive correlations and one negative correlation, 20 km with seven positive correlations and six negative correlations, and 30 km with only one positive correlation but five negative correlations).

There was a negative correlation between fledging rate and coastal location (i.e., fledging rate increased with distance) up to 20 km, but no correlation was detected at 30 km. This is in contrast to the positive correlation between fledging rate and area of tidal flat within 20 km but consistent with a negative correlation between fledging rate and mangrove swamp within 30 km.

Surprising results included the positive association between dry prairie and fledging rate because this habitat does not appear to support aquatic prey or suitable foraging habitat for wood storks. The negative correlation between certain wetland habitats (e.g., cypress swamp, freshwater marsh and wet prairie, and mangrove swamp) and wood stork fledging rate also was unexpected.

Number of nests

The number of nests in wood stork colonies in North and Central Florida during 2003–2005 averaged 112.73 ± 81.79 nests. Nest numbers ranged from 8 to 335, with a median of 86 nests per colony. Unlike with the fledging rate, the number of habitat variables associated with number of nests increased with the distance from the colony.

The final model for the relationship between number of nests and hydrologic and habitat variables within 10-km distance was

$$\begin{aligned}\text{Number of nests} = -3{,}126.15 &+ 19.01 \text{ latitude} + 33.63 \text{ longitude} \\ &+ 63.71 \text{ coastal location} - 0.03 \\ &\text{shrub swamp} - 0.02 \text{ cypress swamp} \\ &+ 0.01 \text{ hardwood swamp} \\ &- 0.02 \text{ saltmarsh} + 0.03 \\ &\text{improved pasture} - 0.01 \text{ high urban.}\end{aligned}$$

The final model for the relationship between number of nests and hydrologic and habitat variables within 20-km distance was

$$\begin{aligned}\text{Number of nests} = 2{,}320.00 &+ 148.57 \text{ latitude} - 78.80 \text{ longitude} \\ &+ 199.74 \text{ coastal location} + 0.01 \text{ dry prairie} \\ &- 0.02 \text{ freshwater marsh and wet prairie} \\ &- 0.02 \text{ mixed wetland forest} \\ &- 0.01 \text{ hardwood swamp} - 0.02 \text{ saltmarsh} \\ &+ 4.18 \text{ tidal flat} + 0.01 \text{ improved pasture} \\ &+ 0.01 \text{ high urban.}\end{aligned}$$

The final model for the relationship between number of nests and hydrologic and habitat variables within 30-km distance was

$$\begin{aligned}\text{Number of nests} = -34{,}570.00 &- 453.58 \text{ latitude} \\ &+ 581.78 \text{ longitude} \\ &+ 620.46 \text{ coastal location} - 0.01 \text{ dry prairie} \\ &+ 0.66 \text{ freshwater marsh and wet prairie} \\ &+ 12.59 \text{ sawgrass} - 0.03 \text{ shrub swamp} \\ &- 0.01 \text{ cypress swamp} \\ &- 1.21 \text{ cypress and/or pine and/or cabbage palm} \\ &+ 0.03 \text{ mixed wetland forest} \\ &+ 0.02 \text{ hardwood swamp} \\ &+ 0.04 \text{ saltmarsh} + 0.18 \text{ mangrove swamp} \\ &- 10.90 \text{ tidal flat} - 0.01 \text{ improved pasture} \\ &- 0.01 \text{ high urban.}\end{aligned}$$

Colonies were smaller in the northern part of Florida. Coastal colonies also were larger than interior freshwater colonies. Several (e.g., improved pasture and high urban), but not all, human-related habitats had negative association with number of nests.

Discussion

Wood stork fledging rate and number of nests exhibited both positive and negative associations with hydrologic and habitat variables that varied by distance from a colony. Rainfall during the previous 12–24 mo had the most consistent correlation with fledging rates among all the variables, which suggests that nesting success is dependent upon rainfall during the previous 1–2 y. Rainfall in neither the previous nor the current year was associated with number of nests. However, rainfall may still be a factor in the initiation of nesting by wood storks (Ogden et al. 1980). Both larger colonies and colonies in North Florida had higher fledging rates. While some variables and wetland types (e.g., cypress swamp, tidal flat) had positive associations and other habitats (e.g., freshwater marsh and wet prairie, cypress swamp, hardwood swamp) had negative associations on fledging rates, these results were not consistent across all three zonal distances from colonies, which suggests that habitats may have differential effects with increasing distance from a colony. Bryan et al. (2012) found that forested wetlands were used as foraging sites at varying amounts (16–76%) by nesting wood storks throughout most of their U.S. breeding range. However, Herring and Gawlik (2011) did not find use of forested wetlands by wood storks nesting at three colonies in the Everglades region. Wood storks may not forage in wetland habitats if the vegetation is too dense to capture prey but readily forage in these habitats if there are openings and edges that allow for access to prey.

The negative correlation between open water (i.e., freshwater lakes and rivers, marine waters) and fledging rates in our study is probably due to wood storks not being able to forage in standing water deeper than 30–40 cm (see Bancroft et al. 1991; Gawlik 2002; Herring and Gawlik 2011). These large areas of unusable habitat also may have factored into the decrease in fledging rates at colonies within 20 km from the coastline. However, the positive correlation between fledging rates and tidal flat within 20 km suggests that tidal flats may be an important foraging habitat for wood storks at some colonies in North and Central Florida despite the absence or low occurrence of this habitat surrounding most colonies. Tidal flats have the potential to trap and concentrate prey in small pools during lower tides. Bryan and Robinette (2008) and Bryan et al. (2005) also found that wood storks used coastal tidal habitats during lower tidal periods and suggested that these habitats result in higher nesting success in Georgia. Wood storks nesting near the Atlantic coast potentially have less area of foraging habitat within 20 km (see Figure 4) but do have access to the unique tidal and coastal habitats not available to birds nesting at interior freshwater colonies.

Several anomalous associations were found between fledging rate and modeled variables. Certain forested wetland habitats (e.g., cypress swamp, hardwood swamp, bay swamp, and mangrove swamp) may support aquatic prey, but these habitats were not associated with greater fledging success, perhaps because wood storks cannot use their tactile foraging method effectively in such heavily vegetated habitats. We have no clear understanding of the negative correlation with freshwater marsh and wet prairie, which appear to be suitable foraging habitat, unless the emergent vegetation in those types of wetlands tends to be too dense to allow wood storks to feed. However, the positive correlation with unimproved pasture and dry prairie may be because this habitat often contains many small, ephemeral wetlands and ditches, which may not have been accurately detected with the 30-m pixel resolution used for the GIS land-cover analyses in this study. Wood storks and other wading birds frequently use these ephemeral wetlands as they draw down and concentrate prey (Kahl 1964; Coulter and Bryan 1993; Gaines et al. 1998, 2000; Bryan et al. 2001). These results could also be caused by errors in the land-cover data. Mapping dry prairie habitat was problematic: it can contain pockets of cypress domes, some pine flatwoods, and palmetto forest. Therefore, dry prairie could be misrepresented as habitat type and the area of dry prairie could be overestimated in each radius zone, creating a false importance for this habitat.

Both positive and negative correlations were evident between wood stork fledging rates and the 3 hydrologic, 4 edaphic, and 29 habitat variables considered in this analysis. The breeding response of wood storks to these 36 variables varied with their distance from the colonies; 6 of the 7 positive correlations were within 10-km distance and 7 of the 13 positive correlations were within 20-km distance. This differential response to use of habitats may allow wood storks to shift their use of foraging sites in response to the availability of prey (Bryan et al. 2005, 2012). Maintaining the integrity of these important foraging resources and lands surrounding a colony with varying distances or zones will present challenges for land managers.

Conservation Implications

This study did not examine the spatial distribution and interseasonal availability of the individual habitat types, which may actually be the determinants of when and what habitats wood storks use for foraging at various distances and times of the year. This information could be determined from temporal (both seasonal and interyear) location and habitat data used by foraging wood storks derived from radio-instrumented birds nesting at selected colonies in Florida. Quantitative prey sampling of the habitats and sites used by foraging wood storks is needed before specific recommendations for habitat preferences can be made. Ultimately, habitat use by wood storks and other waterbirds is dependent upon availability of prey interacting with water depth and area of habitat, all of which vary seasonably and yearly (Frederick and Collopy 1989; Bancroft et al. 1991; Gawlik 2002; Ishtiaq et al. 2010; Herring and Gawlik 2011). Another area of future investigation should be the differential effect of using the 10–30-km management zones of the USFWS (2008, 2010b) around colonies when a colony is near the coast (see Figure 4). These management zones may need to be increased for coastal colonies where a sizeable proportion of the area within a 20-km region is open water and unusable foraging habitat.

Wood storks are generalists in their selection of foraging habitats and should be expected to exhibit shifts in use of foraging habitats during the breeding season, as occurs in other avian species with variable prey and habitat preferences (Nummi and Poysa 1993; Nolet et al. 2002; Davis et al. 2009; Rioux et al. 2009; Mitchell et al. 2010). This habitat shifting is a strategy that involves use of the most profitable food resources and habitats (Madsen 1985). If wood storks preferentially use ephemeral habitats early in the season, these same habitats may not be available later in the season, which would force the wood storks to shift to alternate, more distant sites and different habitats later in the season. Both near and more distant sites with longer hydroperiods may be too deep early in the season, but may become suitable as foraging sites as they draw down later in the season or in the following year. Some of these habitats may not be accessible and only used during very dry years.

Based on known wood stork foraging ecology and results of this study, we propose a hypothesis for where wood storks locate their colonies. Wood storks may establish their colonies using proximate cues of prey availability based on the effects of past rainfall and the availability of preferred feeding habitat types within a set distance from a colony site. Wood storks may acquire these proximate cues to prey availability and suitable foraging sites surrounding potential colony locations before the onset of the first nesting season and during the early part of that first season. However, the long-term stability of a colony may be determined by yearly rainfall patterns and habitats $>$10 km from the site, fledging rates that contribute to future recruitment of nesting birds, and the resulting increase in number of nests. These ultimate factors are experienced by wood storks later in the breeding season and in subsequent years as they respond to rainfall and the distribution and current year status of foraging habitat surrounding a colony. Older wood stork colonies tend to have more nests and exhibit a greater probability of renesting than first-year colonies (Frederick and Meyer 2008); therefore, wood storks in younger and smaller colonies may be still assessing available resources and adjusting to the carrying capacity of the foraging habitat surrounding the colony. Number of nests may ultimately depend upon past nesting performance and the amount and quality of certain habitats within an energetically efficient flight distance from the colony. There are many potential negative habitat-related effects at large distances from a colony site, which suggests that a large amount of habitat is crucial for maintaining a colony of wood storks.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Table S1. Data set used for wood stork *Mycteria americana* habitat modeling for colonies during 2003–2005 in North and Central Florida.

Found at DOI: http://dx.doi.org/10.3996/022012-JFWM-016.S1 (64 KB XLSX).

Table S2. Wood stork *Mycteria americana* colonies monitored during 2003–2005 in North and Central Florida.

Found at DOI: http://dx.doi.org/10.3996/022012-JFWM-016.S2 (16 KB DOCX).

Reference S1. Ehrhart LM. 1979. Threatened and endangered species of the Kennedy Space Center: threatened and endangered birds and other threatened and endangered forms. Contract report 163122, KSC TR 51-2, volume IX, part 2. John F. Kennedy Space Center, Florida: National Aeronautics and Space Administration.

Reference S2. Ogden JC, Kushlan JA, Tilmant JT. 1978. The food habits and nesting success of wood storks in Everglades National Park 1974. Washington, DC: U.S. National Park Service report no. 16.

Reference S3. Slay C, Bryan AL Jr. 2001. Aerial surveys of wood stork nesting colonies in Florida May 2001. Final report submitted to the U.S. Fish and Wildlife Service, Jacksonville, Florida. Athens, Georgia: Coastwise Consulting.

Reference S4. [USFWS] U.S. Fish and Wildlife Service. 1984. U.S. breeding population of the wood stork determined to be endangered. Federal Register 49:7332–7335.

Reference S5. [USFWS] U.S. Fish and Wildlife Service. 1997. Revised recovery plan for the U.S. breeding population of the wood stork. Atlanta, Georgia: USFWS.

Reference S6. [USFWS] U.S. Fish and Wildlife Service. 2000. Wood stork (*Mycteria americana*). Pages 183–213 in Multi-species recovery plan for South Florida. Vero Beach, Florida: USFWS.

Reference S7. [USFWS] U.S. Fish and Wildlife Service. 2010a. Endangered and threatened wildlife and plants; 90-day finding on a petition to reclassify the U.S. breeding population of wood storks from endangered to threatened. Docket no. FWS-R4-ES-2010-0067. Also available: http://www.fws.gov/northflorida/WoodStorks/2009_Petition/90-Day_Finding/20100921_frn_Wood_Stork_90-day%20finding_as_submitted.htm (September 2011).

Reference S8. [USFWS] U.S. Fish and Wildlife Service. 2010b. Wood stork effect determination key for South Florida. Also available: http://www.fws.gov/verobeach/BirdsPDFs/20100518LetterServicetoCorpsFLProgrammaticStorkRevised1.pdf (September 2011).

All Supplemental References found at DOI: http://dx.doi.org/10.3996/022012-JFWM-016.S3 (10 MB PDF).

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References

Bancroft GT, Hoffman W, Sawicki RJ, Odgen, JC. 1991. The importance of the water conservation areas in the Everglades to the endangered wood stork (*Mycteria americana*). Conservation Biology 6:392–398.

Berkson J. 1950. Are there two regressions? Journal of the American Statistical Association 45:164–180.

Bond J. 2003. UCLA power calculator. Los Angeles: Department of Statistics, University of California at Los Angeles. Available: http://www.stat.ucla.edu/cgi-bin/textbook/powercalc/ (January 2003).

Borkhataria RR, Frederick PC, Hylton R, Bryan AL Jr, Rodgers JA Jr. 2008. A preliminary model of wood stork population dynamics in the southeastern United States. Waterbirds 31(special publication):42–49.

Brooks WB, Dean T. 2008. Measuring the biological status of the U.S. breeding population of wood storks. Waterbirds 31(special publication):50–59.

Bryan AL Jr, Brooks WB, Taylor JD, Richardson DM, Jeske CW, Brisbin IL Jr. 2008. Satellite tracking large-scale movements of wood storks captured in the Gulf Coast region. Waterbirds 31(special publication):35–41.

Bryan AL Jr, Meyer KD, Tomlinson BA, Lauritsen JA, Brooks WB. 2012. Foraging habitat use by breeding wood storks and the core foraging area concept. Waterbirds 35:292–300.

Bryan AL Jr, Robinette JR. 2008. Breeding success of wood storks nesting in Georgia and South Carolina. Waterbirds 31(special publication):19–24.

Bryan AL Jr, Snodgrass JW, Robinette JR, Daly JL, Brisbin IL Jr. 2001. Nocturnal activities of post-breeding wood storks. The Auk 118:508–513.

Bryan AL Jr, Snodgrass JW, Robinette JR, Hopkins LB. 2005. Parental activities of nesting wood storks relative to time-of-day, tide level, and breeding stage. Waterbirds 28:138–144.

Clark ES. 1978. Factors affecting the initiation and success of nesting in an east-central Florida wood stork colony. Proceedings of the Colonial Waterbird Group 2:178–188.

Coulter MC, Bryan AL Jr. 1993. Foraging ecology of wood storks (*Mycteria americana*) in east-central Georgia. I. Characteristics of foraging sites. Colonial Waterbirds 16:59–70.

Coulter MC, Bryan AL Jr. 1995. Factors affecting reproductive success of wood storks (*Mycteria americana*) in east-central Georgia. The Auk 112:237–243.

Coulter MC, Bryan AL Jr, Mackey HE Jr, Jensen JR, Hodgson ME. 1987. Mapping of wood stork foraging habitat with satellite data. Colonial Waterbirds 10:178–180.

Coulter MC, Rodgers JA Jr, Ogden JC, Depkin FC. 1999. Wood stork (*Mycteria americana*). Account 409 in Poole A, Gill F, editors. The birds of North America. Philadelphia: The Academy of Natural Sciences; and Washington, D.C.: The American Ornithologist Union.

Davis BE, Afton AD, Cox RR Jr. 2009. Habitat use by female mallards in the lower Mississippi alluvial valley. Journal of Wildlife Management 73:701–709.

Ehrhart LM. 1979. Threatened and endangered species of the Kennedy Space Center: threatened and endangered birds and other threatened and endangered forms. Contract report 163122, KSC TR 51-2, volume IX, part 2. John F. Kennedy Space Center, Florida: National Aeronautics and Space Administration (see *Supplemental Material*, Reference S1, http://dx.doi.org/10.3996/022012-JFWM-016.S3).

[ESA] U.S. Endangered Species Act of 1973, as amended, Pub. L. No. 93-205, 87 Stat. 884 (Dec. 28, 1973). Available at: http://www.fws.gov/endangered/esa-library/pdf/ESAall.pdf

[ESRI] Environmental Systems Research Institute. 2011. ArcGIS desktop: release 9.3. Redlands, California: ESRI.

Florida Climate Center. 2005. Center for Ocean–Atmospheric Prediction Studies, Florida State University, Tallahassee. Available: http://www.coaps.fsu.edu/climate_center/nav.php?a=go&s=data&p=various (June 2007).

[FWC] Florida Fish and Wildlife Conservation Commission. 2005. Florida's wildlife legacy initiative. Tallahassee, Florida: FWC. Available: http://www.MyFWC.com/wildlifelegacy (March 2006).

Frederick P, Collopy M. 1989. Nesting success of five species of wading birds (Ciconiiformes) in relation to water conditions in the Florida Everglades. The Auk 106:625–634.

Frederick PC, Meyer KD. 2008. Longevity and size of wood stork (*Mycteria americana*) colonies in Florida as guides for an effective monitoring strategy in the southeastern United States. Waterbirds 31(special publication):12–18.

Friendly M. 2003. Power analysis for ANOVA designs. Toronto: Psychology Department, York University. Available: http://www.math.yorku.ca/SCS/Online/power/ (January 2003).

Gaines KF, Bryan AL Jr, Dixon PH. 2000. The effects of drought on foraging habitat selection of breeding wood storks in coastal Georgia. Waterbirds 23:64–73.

Gaines KF, Bryan AL Jr, Dixon PH, Harris MJ. 1998. Foraging habitat use by wood storks nesting in the coastal zone of Georgia, USA. Colonial Waterbirds 21:43–52.

Gawlik DE. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329–346.

Gilbert T, Stys B. 2004. Descriptions of vegetation and land cover types mapped using Landsat imagery. Tallahassee, Florida: Florida Fish and Wildlife Conservation Commission. Available: http://199.250.30.194/GIS/Land Cover/fwcveg_descriptions03.pdf (May 2006).

Harrell FE. 2001. Regression modeling strategies. New York: Springer-Verlag.

Herring HK, Gawlik DE. 2011. Resource selection functions for wood stork foraging habitat in the southern Everglades. Waterbirds 34:133–260.

Hodgson ME, Jensen JR, Mackey HE Jr, Coulter MC. 1988. Monitoring wood stork foraging habitat using remote sensing and geographic information systems. Photogrammetric Engineering and Remote Sensing 54:1601–1607.

Hopkins ML Jr, Humphries RL. 1983. Observations on a Georgia wood stork colony. Oriole 48:36–39.

Ishtiaq F, Javed S, Coulter MC, Rahmini AR. 2010. Resource partitioning in three sympatric species of wood storks in Keoladeo National Park, India. Waterbirds 33:41–49.

Kahl MP Jr. 1964. Food ecology of the wood stork (*Mycteria americana*). Ecological Monographs 34:97–117.

Kautz R, Stys B, Kawula R. 2007. Florida vegetation 2003 and land use change between 1985–89 and 2003. Florida Scientist 70:12–23.

Kushlan JA, Frohring PC. 1986. The history of the southern Florida wood stork population. Wilson Bulletin 98:368–386.

Littell RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberger O. 2006. SAS for mixed models. 2nd edition. Cary, North Carolina: SAS Institute.

Madsen J. 1985. Relations between change in spring habitat selection and daily energetics of pink-fronted geese *Anser brachyrhynchus*. Ornis Scandinavica 16:222–228.

Mitchell GW, Taylor PD, Warkentin IG. 2010. Multiscale postfledging habitat associations of juvenile songbirds in a managed landscape. The Auk 127:354–363.

Nolet BA, Bevan RM, Klaassen M, Langevoord O, Van der Heijden YGJT. 2002. Habitat switching by Bewick's swans: maximization of average long-term energy gain? Journal of Animal Ecology 71:979–993.

Nummi P, Poysa H. 1993. Habitat associations of ducks during different phases of the breeding season. Ecography 16:319–328.

Ogden JC, Kale HW II, Nesbitt SA. 1980. The influence of annual variation in rainfall and water levels on nesting by Florida populations of wading birds. Transactions of the Linnaean Society of New York 9:115–126.

Ogden JC, Kushlan JA, Tilmant JT. 1978. The food habits and nesting success of wood storks in Everglades National Park 1974. Washington, D.C.: U.S. National Park Service report no. 16 (see *Supplemental Material*, Reference S2, http://dx.doi.org/10.3996/022012-JFWM-016.S3).

Ogden JC, McCrimmon DA Jr, Bancroft GT, Patty BW. 1987. Breeding populations of the wood stork in the southeastern United States. Condor 89:752–759.

Rioux S, Belisle M, Giroux J-F. 2009. Effects of landscape structure on male density and spacing patterns in wild turkeys (*Meleagris gallopavo*) depend on winter severity. The Auk 126:673–683.

Rodgers JA Jr. 2002. Productivity of wood storks *Mycteria americana* in North and Central Florida (PID 9292 100 1000). Grant agreement (no. 1448-40181-02-G-215) between the U.S. Department of Interior/U.S. Fish and Wildlife Service and the Florida Fish and Wildlife Conservation Commission, Atlanta, Georgia.

Rodgers JA Jr, Schwikert ST. 1997. Breeding success and chronology of wood storks *Mycteria americana* in northern and central Florida, U.S.A. Ibis 139:76–91.

Rodgers JA Jr, Schwikert ST, Griffin GA, Brooks WB, Bear-Hull D, Elliott PM, Ebersol KJ, Morris J. 2008. Productivity of wood storks (*Mycteria americana*) in North and Central Florida. Waterbirds 31(special publication):25–34.

[SAS] Statistical Analysis System Institute, Inc. 2003. The SAS system, release 8 for Windows. Cary, North Carolina: SAS Institute.

[SJRWMD] St. Johns River Water Management District. 2009. Hydrologic Data Collection. Palatka, Florida: St. Johns River Water Management District. Available: http://sjr.state.fl.us/hydrologicdata/index.html (November 2009).

Slay C, Bryan Jr AL. 2001. Aerial surveys of wood stork nesting colonies in Florida May 2001. Final report submitted to the U.S. Fish and Wildlife Service, Jacksonville, Florida. Athens, Georgia: Coastwise Consulting. (see *Supplemental Material,* Reference S3, http://dx.doi.org/10.3996/022012-JFWM-016.S3).

[USFWS] U.S. Fish and Wildlife Service. 1984. U.S. breeding population of the wood stork determined to be endangered. Federal Register 49:7332–7335 (see *Supplemental Material,* Reference S4, http://dx.doi.org/10.3996/022012-JFWM-016.S3).

[USFWS] U.S. Fish and Wildlife Service. 1997. Revised recovery plan for the U.S. breeding population of the wood stork. Atlanta, Georgia: USFWS (see *Supplemental Material,* Reference S5, http://dx.doi.org/10.3996/022012-JFWM-016.S3).

[USFWS] U.S. Fish and Wildlife Service. 2000. Wood stork (*Mycteria americana*). Pages 183–213 in Multi-species recovery plan for South Florida. Vero Beach, Florida: USFWS (see *Supplemental Material,* Reference S6, http://dx.doi.org/10.3996/022012-JFWM-016.S3).

[USFWS] U.S. Fish and Wildlife Service. 2008. Florida effect determination key for the wood stork in central and north peninsular Florida. Available: http://www.fws.gov/northflorida/WoodStorks/Documents/20080900_JAXESO_WOST_Key.pdf (September 2011).

[USFWS] U.S. Fish and Wildlife Service. 2010a. Endangered and threatened wildlife and plants; 90-day finding on a petition to reclassify the U.S. breeding population of wood storks from endangered to threatened. Docket no. FWS-R4-ES-2010-0067 (see *Supplemental Material,* Reference S7, http://dx.doi.org/10.3996/022012-JFWM-016.S3); also available: http://www.fws.gov/northflorida/WoodStorks/2009_Petition/90-Day_Finding/20100921_frn_Wood_Stork_90-day%20finding_as_submitted.htm (September 2011).

[USFWS] U.S. Fish and Wildlife Service. 2010b. Wood stork effect determination key for South Florida (see *Supplemental Material,* Reference S8, http://dx.doi.org/10.3996/022012-JFWM-016.S3); also available: http://www.fws.gov/verobeach/BirdsPDFs/20100518LetterServicetoCorpsFLProgrammaticStorkRevised1.pdf (September 2011).