

## **Resource Selection Functions for Wood Stork Foraging Habitat in the Southern Everglades**

Author(s) :Heidi K. Herring and Dale E. Gawlik

Source: Waterbirds, 34(2):133-142. 2011.

Published By: The Waterbird Society

DOI:

URL: <http://www.bioone.org/doi/full/10.1675/063.034.0201>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

# WATERBIRDS

JOURNAL OF THE WATERBIRD SOCIETY

VOL. 34, NO. 2

2011

PAGES 133-260

## Resource Selection Functions for Wood Stork Foraging Habitat in the Southern Everglades

HEIDI K. HERRING\* AND DALE E. GAWLIK

Department of Biological Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, FL 33431, USA

\*Corresponding author; E-mail: kirkheidi@hotmail.com

**Abstract.**—Modeling habitat selection of species with specific foraging requirements is an effective means to evaluate landscape quality for restoration and conservation purposes. Proportional hazards regression, a discrete choice model, was used to develop resource selection functions for breeding Wood Stork in the southern Everglades during the 2006 nesting season. Wood Storks showed the highest probability of habitat selection in a narrow range of shallow water depths. The quadratic form of water depth ( $\text{depth} + \text{depth}^2$ ) was an important indicator of habitat selection with mean water depths between -25 and 25 cm receiving the highest probability of use (a negative water depth is below average ground elevation). Foraging sites within 20 km of nesting colonies were selected over farther sites. Shrub swamp, mangrove swamp and saltwater marsh vegetation types were used in higher proportions than they occurred in the landscape. Results exemplify the importance of shallow water depths near established stork breeding colonies throughout the breeding season. *Received 14 July 2010, accepted 1 December 2010.*

**Key words.**—breeding, discrete-choice model, foraging, habitat selection, hydrology, *Mycteria americana*, wading bird, water management.

Waterbirds 34(2): 133-142, 2011

Quantifying the resources used by animal populations is important for endangered species, which often have very specific resource requirements (Minckley and Deacon 1968; Manly *et al.* 2004). Resource use can be measured in a biologically and statistically meaningful way by quantifying resource selection, which is when resources are used disproportionately to their availability (Manly *et al.* 2004). Selectivity is thought to be representative of choices made by either an individual or population and those choices may influence survival and fitness (Jones 2001). Food is a resource that can be limiting to birds (Lack 1954; Martin 1987; Weathers and Sullivan 1989) both during the breeding (Jones and Ward 1979; Wiens 1989) and non-breeding seasons (Gibb 1960; Wiens 1989).

In the Florida Everglades, food availability has emerged as the primary factor affecting wading bird reproductive success (Kushlan 1978; Frederick and Spalding 1994; Gaw-

lik 2002; Herring *et al.* 2010) with no evidence of density-dependent competition or substantial predation pressure. Although low winter temperatures, parasites and predators have been linked to nesting failures and poor health of wading birds in the Everglades, the prey availability hypothesis is the leading explanation for widespread and recurrent nesting failure (Frederick and Spalding 1994; Gawlik 2002). The prey availability hypothesis states that changes to the natural hydrologic system of the Everglades have reduced the availability of aquatic prey by altering the timing and location of seasonal prey concentrations, which has resulted in reduced wading bird reproductive success (Gawlik 2002). Everglades' Wood Storks (*Mycteria americana*) time their breeding season to coincide with increased prey availability brought on by receding water levels (Kahl 1964; Kushlan *et al.* 1975). In a seasonally fluctuating sub-tropical wetland such as the Everglades, aquatic prey availability may be

influenced by landscape-level environmental characteristics such as hydrography, topography and vegetation, each of which may promote or restrict wading bird foraging efficiency depending on conditions.

In a temporally and spatially dynamic landscape such as the Everglades, a statistical model that can account for daily fluctuations in water levels and other habitat conditions over the course of several months is needed in order to characterize the full range of habitat conditions needed for successful Wood Stork foraging. The proportional hazards regression model (PHRM) is a discrete-choice model that is becoming commonly used in the wildlife resource field because of its applicability to a range of habitat selection studies (Allison 1999; Manly *et al.* 2004; McDonald *et al.* 2006). Discrete choice models provide flexibility in that the composition of a choice set can vary with each time step (Manly *et al.* 2004; McDonald *et al.* 2006), thus allowing models to more accurately represent wildlife-habitat interactions in an environment where the location of resources change during the study period.

Documenting Wood Stork resource selection in the Everglades is critical because this region historically supported the majority of nesting by North American Wood Storks and habitat loss and degradation in the area is thought to be responsible for the population decline (Ogden 1994). Moreover, modifications to the ecosystem are scheduled as part of the restoration effort and successful Wood Stork breeding is being used as a performance measure for restoration efforts (RECOVER 2004; Frederick *et al.* 2009). Restoring sections of the Everglades to a more natural hydrologic state will likely alter the distribution of foraging habitat, thereby creating the need to better understand the resource requirements of Wood Storks and how the species will respond to restoration scenarios.

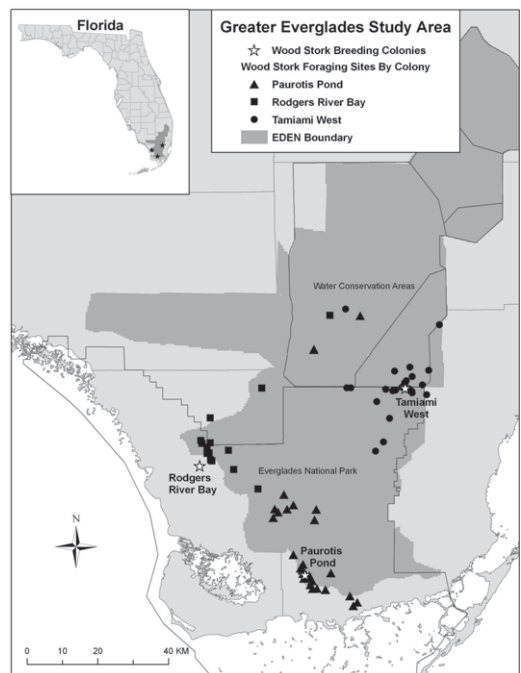
The goal of this study was to develop a resource selection model for breeding Wood Storks in the southern Everglades to 1) determine which landscape features and hydrological factors constitute suitable foraging habitat during the breeding season and

2) develop habitat suitability maps that identify areas that have the highest probability of use based on the foraging habitat selection model. Resource selection functions (RSF) using the PHRM were determined for a population of breeding Wood Storks that nested successfully during the year of study, and therefore, met their resource requirements for reproduction with the set of choices observed.

## METHODS

### Study Site

Wood Storks were followed to foraging sites from three separate Wood Stork colonies in the central and southern Everglades of Florida, USA [Everglades National Park (ENP), southern Water Conservation Area (WCA) 3A and WCA 3B; Fig. 1]. Paurotis Pond, Tamiami West, and Rodgers River Bay colonies are each surrounded by different hydrological and vegetative landscape features. Paurotis Pond is located in central southern ENP (25°16'N 80°48'W) approximately 20 km north of Florida Bay in freshwater marsh occupied by mangrove trees. Tamiami West is located in northeastern ENP (25°45'N 80°32'W) in freshwater marsh. The Rodgers River Bay colony is located in northwest ENP (25°33'N 81°04'W), between Lostmans River and Broad



**Figure 1.** Greater Everglades Study Area and spatial extent of the Everglades Depth Estimation Network (EDEN; water surface data were obtained in October 2006). Symbols indicate colony-specific foraging locations.

River on a small island surrounded by brackish open water bordered by mangrove swamp. These three colonies are between 40 km and 60 km away from each other and represent a coastal colony (Paurotis Pond) influenced by conditions in the freshwater marsh and Florida Bay, an inland colony influenced overwhelmingly by conditions in the freshwater marsh (Tamiami West), and a coastal colony influenced by the Gulf of Mexico (Rodgers River Bay).

#### Foraging Sites

To locate foraging sites of breeding storks, adult Wood Storks were followed from a distance of at least 70 m from altitudes of 150-800 m in a Cessna 182 aircraft from their nesting colony to a foraging site following Bryan and Coulter (1987) and Smith (1995). Flights were conducted 15 February-8 June 2006 and at least one set of following flights was conducted from each colony every week. Flights were initiated between 09:00 and 10:00 (EST), when the storks typically left their colony to forage (Herring 2007). In the Everglades, Wood Storks utilize thermals to gain altitude from which they glide to foraging sites and feed on fish in shallow wetlands (Coulter *et al.* 1999). Once a target stork landed, habitat characteristics of the foraging site were recorded, the foraging flock, if present, was photographed, and the exact location was logged using a GPS.

#### Model Variables

*Water depth*—Values for the hydrological variables water depth, water recession, and dry down were calculated using the Everglades Depth Estimation Network (EDEN; water surface data obtained in October 2006). The EDEN models water depth for the entire freshwater portion of the Greater Everglades (Fig. 1), using a network of real-time water level gauges, water surface modeling and ground elevation modeling (USGS 2006). Because water depths in the Everglades change daily, drying with evapo-transpiration and rewetting with rainfall events, EDEN is calculated at daily time steps using real time water level readings obtained from 253 gauging stations throughout the Greater Everglades (USGS 2006). The model provides estimated depths for a grid comprised of 52,785 cells 400 m by 400 m in size. EDEN values for Wood Stork foraging sites and random points were obtained by extracting the cell values from the EDEN raster layer that corresponded to the day the following flight was conducted. Negative depth values indicate that water levels were below mean ground elevation in a 400 m × 400 m cell and do not indicate the absence of surface water.

The locations of eleven storks (15% of total locations) that foraged in the saltwater marsh and mangrove swamp areas south of Paurotis Pond and in the vicinity of Rodgers River Bay were outside the boundary of EDEN. In these cases, foraging site depths were obtained by using the depth measurement of the EDEN cell nearest to the foraging site (located between 0.5 km and 2 km from the foraging site).

Due to the lack of model validation at the time of our study, we independently evaluated EDEN depth accuracy within the mangrove portion of our study site, an area we were concerned about because there is a lower density of EDEN water gauges within this habitat type

and because there are problems with this boundary area in another major hydrologic model. We compared depth readings from six Audubon of Florida-Tavernier Science Center hydrostations to the EDEN cell they occurred within over the course of the 2006 dry season. Out of the six sites that were compared, five sites were consistently between 8 cm and 28 cm of their paired EDEN cell, an acceptable difference because local topography within a 400 m × 400 m area could easily vary by 28 cm, whereas one hydrostation showed a consistently large discrepancy of 48 cm between measured depths and its paired EDEN cell. Therefore, water depths for points that fell within the mangrove habitat surrounding this site were adjusted by 20 cm to bring the mean difference between the marsh gauge and EDEN to 28 cm. Since the completion of our study, model validations have been performed in the freshwater portions of the EDEN spatial domain and they showed that over 95% of the predicted water levels matched observed water levels within 5 cm (Liu *et al.* 2009).

For each foraging location, 250 random locations were selected within 80 km of the colony of origin. Water depths were estimated for all Wood Stork foraging sites and random points by overlaying the EDEN raster that corresponded with the sampling day and extracting depth values using ArcGIS 9.2 (ESRI Inc. 1999-2003). The quadratic form of water depth ( $\text{depth} + \text{depth}^2$ ) was used as the depth model term because wading birds tend to forage within an optimal range of water depths, with use decreasing as water depth becomes extremely shallow or extremely deep (Bancroft *et al.* 2002; Russell *et al.* 2002).

*Recession rate*—Daily water recession rates were calculated from the mean change in water depth seven days prior to an observation of habitat use. One week prior to an observation of habitat use was chosen as a suitable time period for recession rate because averaging over longer time periods may obscure short-term reversals in receding water levels caused by rain events.

*Dry down*—To determine whether an EDEN cell had completely dried out prior to use, we first estimated the amount of water left in the deeper portions of an EDEN cell when the depth value for the cell was zero. Water depth measurements taken in the field as part of a study of wading bird prey (Harris 2007; Pierce and Gawlik 2010) during the same time as this study were on average 15 cm greater than EDEN depths. Therefore, we defined an EDEN cell as dry if the EDEN depth was -15 cm or less.

*Vegetation classification*—The fl\_veg03 vegetation and land cover map published by Florida Fish and Wildlife Conservation Commission (Florida Fish and Wildlife Conservation Commission 2004; FFWCC) was used to categorize dominant vegetation types at foraging sites used by Wood Storks. The vegetation map classified vegetation types at a 30 m × 30 m resolution. Five vegetation categories typify southern Everglades marshes including freshwater marsh/wet prairie, sawgrass marsh, shrub swamp, salt water marsh and mangrove swamp, and these habitats were expected to be used by foraging Wood Storks (see FFWCC 2004 for in-depth description of vegetation composition).

*Distance from colony*—Distances between foraging sites (used and random) and their respective breeding colonies were calculated in ArcGIS 9.2 (ESRI Inc. 1999-2003) using the distance between points tool provided by the Hawth's Tools extension (Beyer 2004).

### Resource Selection Modeling

To determine foraging habitat selection of Wood Storks, RSFs were developed for ten habitat variables using the PHRM (PROC PHREG, SAS Institute Inc. 2003) and comparing habitat characteristics of known foraging sites to a set of random points, which characterized the potentially available habitat in the landscape. PHRM is a discrete-choice model that allows available resource units to change over time (Manly *et al.* 2004; McDonald *et al.* 2006), thus allowing models to more accurately represent wildlife-habitat interactions in an environment where the location and condition of resources change during the study period.

Known Wood Stork foraging sites, represented "used" habitat, and random points were generated in ArcGIS 9.2, represented landscape wide "available" habitat. A unique set of 250 random points were generated within an 80-km radius of the target colony for each day a following flight was conducted to represent the available foraging habitat for Wood Storks. The repeated evaluation of available habitat allowed us to sample the available water depths in the landscape for each day of following flights and allowed a different choice set of vegetation types for each colony. An 80-km radius around each colony was used as a cut off for available habitat in terms of distance because the longest foraging flight observed in 2006 was 74 km and greater distances are rarely reported (e.g. Browder 1984). If following flights were conducted from two different colonies during the same day then a separate set of random points was generated for each colony. Potentially "available" habitat was restricted to the boundary of EDEN, and encompassed the majority of the interior Everglades. Using a GIS framework, we determined water depth, recession rate, dry down, distance from colony and vegetation type of all random and used points.

The PHREG procedure performs regression analysis based on the stratified Cox proportional hazards model, expressed as

$$\lambda_{ij}(t) = \lambda(t; Z_i) = \lambda_{i0}(t) \exp(Z'_{ij} \beta)$$

where  $\lambda_{i0}(t)$  is the baseline hazard function for the  $i$ th stratum,  $Z_{ij}$  is the vector of explanatory variables for the  $j$ th individual, and  $\beta$  is the vector of unknown regression parameters associated with the explanatory variables (Cox 1972; Andersen and Gill 1982; SAS Institute Inc. 2003).  $\beta$  is estimated by the partial likelihood function and partial likelihood functions are given for each model variable (SAS Institute Inc. 2003; Allison 2005). Hazard Ratios were used to determine the magnitude of effect for each variable. The BRESLOW option was used in PHREG to handle ties because tied data were rare (Allison 2005).

### Probability of Use Modeling

Maps were produced illustrating the probability of Wood Storks using foraging habitat based on the survivor function given by the proportional hazards model. The survivor function is expressed as

$$S(t; Z_i) = [S_0(t)]^{\exp(Z'_{ij} \beta)}$$

where  $S_0(t)$  is the baseline survivor function, which estimates the baseline hazard function, and  $Z'_{ij}$  is the vector of explanatory variables (SAS Institute Inc. 2003). The

probability of use is  $1-S(t; Z_i)$  and was calculated from the equation above for each foraging flight. The calculated probability of use was then incorporated into the original PHRM where  $1-S(t; Z_i)$  estimates  $\lambda_{i0}(t)$  in Equation 1. Maps were produced showing the probability of use for February, March, April and May 2006 by using the mean baseline survivor function for each time period.

## RESULTS

Following flights from three ENP colonies yielded foraging site locations for 73 Wood Storks between 15 February and 6 June 2006. Twenty seven foraging sites were located for storks from Tamiami West, 30 from Paurotis Pond, and 16 from Rodgers River Bay (Fig. 1).

### Foraging Habitat Selection

The global model for foraging habitat selection model contained ten habitat variables (including recession rate, dry down, water depth, distance and six vegetation classes), the interaction term distance  $\times$  depth and distance  $\times$  vegetation (each vegetation class). The terms for recession rate, dry cells and interactions were not significant and were removed from the model.

A reduced model was then tested using only the main effects that were significant in the global model (distance and water depth) and the six vegetation classes. RSFs were then determined for each variable. Wood Stork forage site selection was influenced by the distance from the colony, the water depth at the foraging site and selected for shrub swamp, saltwater marsh and mangrove swamp vegetation types (Table 1). The final form of the model was:

$$h(x) = \exp \{-0.146 (\text{distance}) - 0.0004 (\text{depth} + \text{depth}^2) + 2.611 (\text{shrubswamp}) + 2.999 (\text{saltmarsh}) + 2.953 (\text{mangswamp})\}$$

Sawgrass marsh, freshwater marsh and rarely used vegetation types were not significant in the model indicating that their presence or absence did not affect foraging site selection.

Distance to foraging site was an influential factor in forage site selection. Sites closer to the colony were more likely to be chosen.

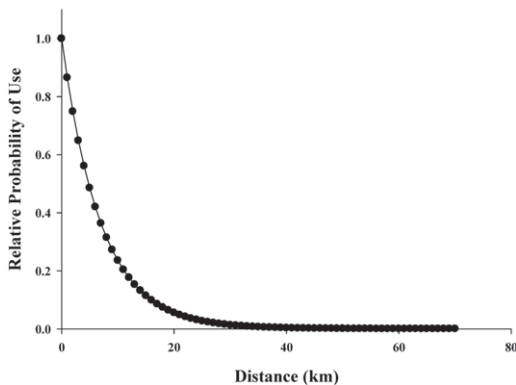
**Table 1. Parameter estimates and hazard ratios for all variables in main effects foraging site selection model for Wood Storks nesting in Everglades National Park.**

Variable	df	Parameter estimate	Error	Chi-square	P-value	Hazard ratio
Distance	1	-0.146	0.014	104.051	<0.001	0.864
Depth + depth <sup>2</sup>	1	-0.0004	0.0001	7.659	0.005	1.000
Freshwater marsh	1	1.207	0.737	2.679	0.101	3.344
Sawgrass marsh	1	0.550	0.795	0.477	0.489	1.733
Shrub swamp	1	2.611	0.806	10.472	0.001	13.616
Salt marsh	1	2.999	0.787	14.491	<0.001	20.066
Mangrove swamp	1	2.953	0.781	14.285	0.000	19.165
Rare vegetation types	0	0	—	—	—	—

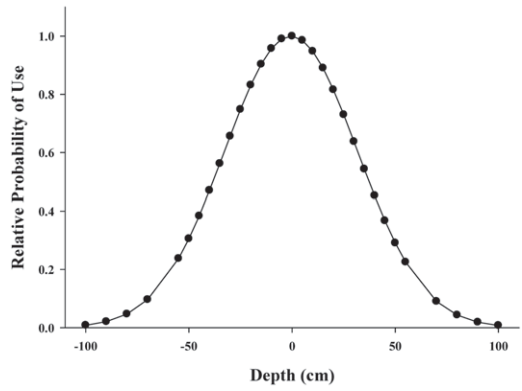
There was a 13.6% reduction in the chance of the site being used with every additional kilometer away from the colony (hazard ratio = 0.86; Table 1). The functional form of the distance effect showed a high probability of use close to colonies, declining steeply further from the colony (Fig. 2).

Wood Storks responded to water depth at foraging sites and the functional form of the depth+depth<sup>2</sup> variable showed that water depths between -25 and 25 cm had the highest likelihood of use (>50% relative probability of use), and that there was a rapid decrease in probability of use as depths increased or decreased (Table 1; Fig. 3).

Vegetation variables produced the largest parameter estimates, and therefore exhibited the strongest influence in the model. Large hazard ratios for shrub swamp, salt marsh and mangrove swamp indicated that there was very strong selection for these vegetation types. Freshwater marsh and sawgrass



**Figure 2. Relative probability of use function for distance. Probability of use declines sharply as distance from colony increases.**



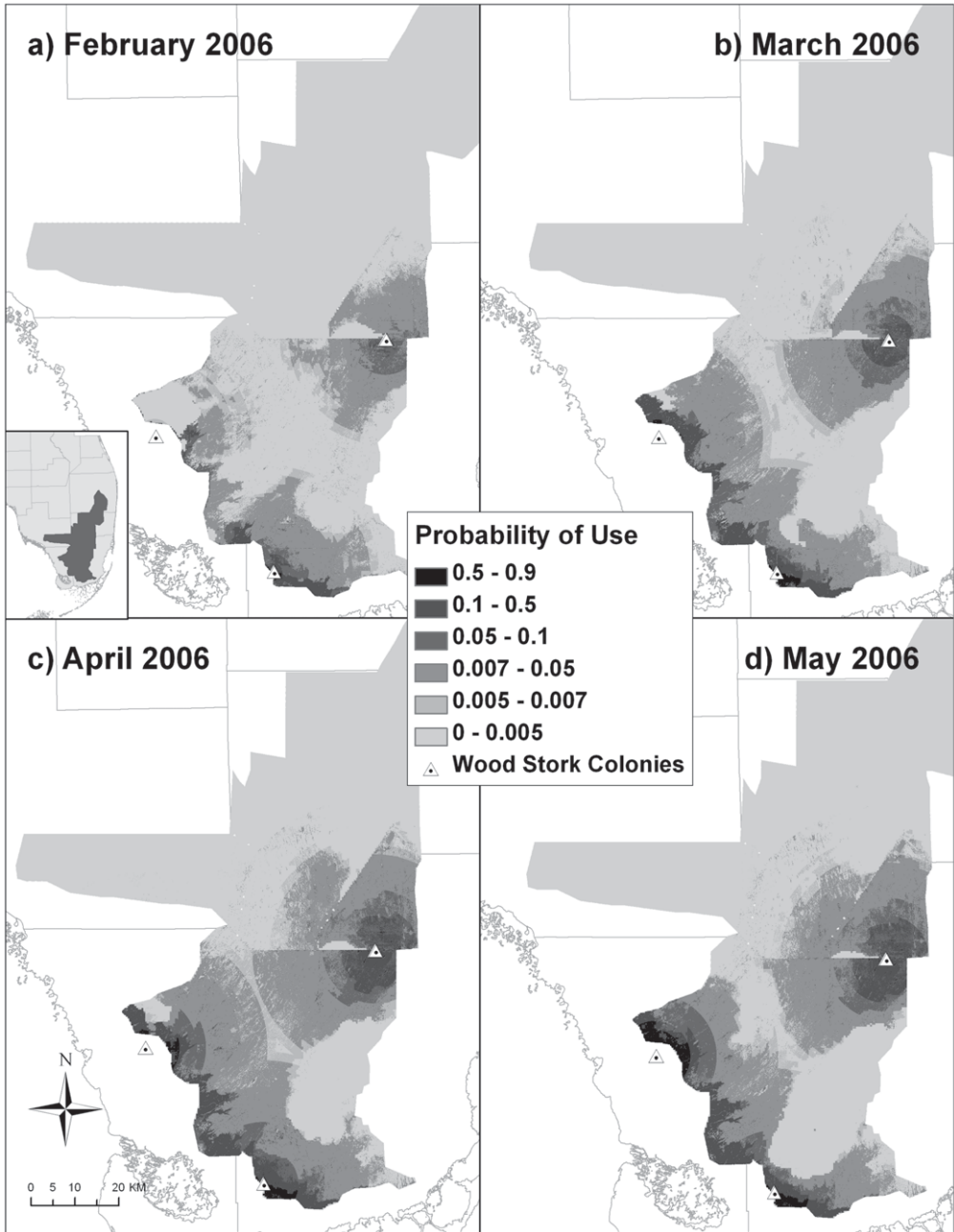
**Figure 3. Relative probability of use function for water depth (depth+depth<sup>2</sup>). Probability of use decreases as depths become very deep and very shallow.**

marsh were neither selected for nor avoided, but were used in the same proportion that they were available in the landscape.

#### Probability of Use

The mean monthly baseline hazard function  $S_0(t)$  decreased over the course of the season which resulted in an increase in the probability of use over the course of the season (Fig. 4). However, in late May, the mean baseline survivor function increased, causing an overall decrease in probability of use for that time period which coincided with a heavy rainfall event.

Maps show use probabilities based on distance from colony, depth+depth<sup>2</sup>, and the three vegetation classes that were significant in the foraging site selection model (Fig. 4). Because sawgrass marsh, freshwater marsh and rarely used vegetation types were neutral in the model, probability of use maps re-



**Figure 4.** The probability of use by Wood Storks from three colonies in Everglades National Park from 15 February-15 May 2006. In general, proximity to colony and vegetation type were strong and consistent factors in determining the probability of use. As water levels recede over the course of the breeding season, optimal water depths become more widespread and a larger proportion of the marsh has a higher probability of use. A) Highest probability of use is in southern ENP along the salt marsh and mangrove fringe. In the freshwater portion of ENP, the highest predicted use is in the shrub swamp and shallow water areas near the Tamiami West colony. B) Highest probability of use is again in mangrove and salt marsh habitats, especially in the marshes east of Rodgers River Bay. Suitable habitats are also becoming available north of Tamiami Trail in WCA 3B. C) Drying marshes have created favorable foraging conditions within 25 km of colonies except where extremely dry. Shrub swamp features and drying conditions near Tamiami West show highest probability of use in northeastern ENP. D) Highest probabilities of use persist along the southwestern edge of the study area and in the vicinity of Tamiami West. However, extremely dry conditions northeast of Pautotis Pond preclude foraging in this area of the marsh.

flect only the influence of distance and water depths in areas with these vegetation classes. Highest use was predicted to occur in mangrove and saltwater marsh habitats that are close to Rodgers River Bay and Paurotis Pond. Near Tamiami West, shrub swamp features indicated areas of higher potential use. Over time, changing baseline survivor functions and receding water depths yielded a higher probability of use along a gradient of optimal water depths and a lower probability of use in upland areas and persistently deep areas of the marsh.

### DISCUSSION

In south Florida, Wood Storks forage 10-50 km (usually 25-50 km) from their colony, although maximum foraging distances of 97-130 km have been recorded (Coulter *et al.* 1999). In this study, however, Wood Storks were highly selective for foraging sites that were within 20 km of their nesting colony. The use of nearby habitats may have been an artifact of the abundance of suitable habitat distributed evenly throughout the entire region in 2006. However, the abundance of nearby foraging habitat may also be indicative of why a colony was formed in that location. Wood Storks will nest at the same colony for decades (Ogden 1994), so alteration to the surrounding habitats may impair nest success if that colony was formed on the reliance that suitable forage conditions would be available in its vicinity.

The rainfall event that occurred in mid-May illustrated the importance of landscape heterogeneity and spatial extent (Fleming *et al.* 1994; Gawlik 2002). The abrupt water level increase in ENP appeared to disproportionately affect localized areas of the marsh. Because of the large heterogeneous extent of the Everglades and the ability of storks to forage effectively at great distances from their colonies, storks were able find foraging sites north of the heaviest rainfall in southern WCA 3A, 74 km from the Parotis Pond colony (Herring 2007). This area had not previously dried out and received less rainfall than ENP. We suggest that the presence of these alternate habitats could make the

difference between a successful and unsuccessful nesting season. The historic Everglades was roughly twice its current size and high quality foraging habitat would have been available over a wide range of hydrologic conditions; whereas in today's smaller Everglades, the range of hydrologic conditions that provide high quality foraging habitat has become narrower (Gawlik 2002).

The foraging site selection model revealed a relationship between water level and Wood Stork foraging habitat that was similar to the quadratic form found in other studies (Bancroft *et al.* 2002; Russell *et al.* 2002). Predicted foraging site use peaked at water depths near zero and then declined with increasing and decreasing water depths. Optimal water depths used by actively breeding individuals in our study indicate selection for a narrower range of water depths than reported by Bancroft *et al.* (2002), who used aerial transect data that does not distinguish breeding from non-breeding individuals. Results from this study suggest that selection for optimal water depths may be even more critical for nesting storks. However, the narrower range of depths used in this study might reflect the fact that in 2006, ideal hydrologic conditions (high water early in the dry season with a strong uninterrupted drying trend over the rest of the dry season; Gawlik 2002) occurred throughout much of the breeding season and resulted in a large nesting effort (Cook and Call 2006). We hypothesize that Wood Storks will respond to sub-optimal hydrological conditions by either utilizing sites with suboptimal water depths after a short search period, increasing their search time to locate a site with acceptable water depths or utilizing alternative vegetation types that contain optimal water depths. Observational data from our pilot study (Kirk and Gawlik, unpublished data), conducted in 2005 when water depths were consistently high and there was widespread Wood Stork nesting failure, indicate that Wood Storks likely increase their search time to locate shallow foraging sites at the cost of nesting success.

The narrow range of water depths selected by breeding Wood Storks highlights the



need for shallow water depths to be available during the entire length of the breeding season, and especially during the beginning of the nesting period when water levels throughout the Everglades are highest. The need for short hydroperiod wetlands to provide foraging habitat during the earliest stages of breeding (e.g. nest initiation and egg laying) is known to be critical to Wood Stork nest success (Kushlan 1986) and (modeled) water depths between -25 and 25 cm may be a good water depth goal for restoration of the shortest hydroperiod wetlands early in the breeding season.

Vegetation type also strongly influenced forage site selection in the model. Specifically, saltwater marsh and mangrove swamp had very large hazard ratios and thus were represented strongly on the probability of use maps. The value of mangrove swamp habitat may have been artificially inflated due to the location of the study area boundary (restricted by the EDEN boundary), which did not include the entire mangrove swamp habitat in ENP. The study area boundary bisected the mangrove swamp in southern and western ENP and resulted in only a fraction of the actual available mangrove habitat being included in the model thus resulting in the model treating mangrove habitat as an uncommon vegetation type. However, the mangrove swamp habitat that was included in the study area could be categorized as mangrove swamp fringe habitat because it incorporates a 3-5 km wide strip of mangrove swamp vegetation that borders the inland saltwater marsh habitat. The mangrove swamp-saltwater marsh ecotone is characterized by the meeting of the lower reaches of freshwater Everglades creeks and coastal estuaries, but does not include the dense mangrove forest which extends westward (from Rodgers River Bay) and southward (from Paurotis Pond) to the coast. When viewed in these terms, the model accurately reflects the importance of this mangrove-fringe habitat.

High use of shrub swamp habitat was observed relative to its abundance in the landscape. Shrub swamps, including willows and small wetland tree species, may attract storks due to higher nutrients in the soil which can

support larger sized fish (Rader and Richardson 1994). Bancroft *et al.* (2002) suggested that tree islands may be important features for Wood Storks due to the micro-topographic variation they provide. Our findings support the idea that vegetative features offer preferred foraging habitat. However, we also found that storks often foraged in freshwater marsh, similar to Bancroft *et al.* (2002) who found that area of slough (freshwater wetland type) had the greatest effect on bird abundance. Although not significant in our model because it was used in the same proportion in which it is found in the landscape, freshwater marsh was used in 36% of the foraging sites (Herring 2007).

Because the PHREG procedure cannot evaluate vegetation types that were not used by a Wood Stork but were detected in the random sites, avoidance of these vegetation types cannot be assessed. Wood Storks are known to use vegetation types that were not used during this study, such as cypress swamp (Coulter *et al.* 1999), and the absence of this vegetation type from our model does not imply avoidance.

Twenty one percent of the foraging sites were located at a saltwater marsh-mangrove swamp vegetation interface (Herring 2007), which supports the hypothesis that the mangrove fringe habitat is an important foraging area for Wood Storks from coastal colonies (Ogden 1994). Ogden *et al.* (1976) found that Wood Storks that foraged along creeks, streams and pools at the landward edge of mangrove swamps selected for larger sized fish and that larger sized fish were more abundant in this habitat. Additionally, the vegetation interface between mangrove swamp and saltwater marsh are likely a result of a change in ground elevation, soil type and/or salinity level, which may signal the presence of preferred prey types. At the meeting of two different vegetation types, prey fish specific to each type of habitat may coexist and increase the diversity and numbers of species present. Prey fish caught outside their preferred habitat type during a dry down may be especially vulnerable to foraging wading birds. In 2006, Wood Storks utilized the mangrove edges until hydrological

conditions (mid-May reversal in water recession) prevented successful foraging.

Important foraging habitat characteristics were identified for Wood Storks in the Everglades. The cues by which birds select foraging sites was not addressed here; however, because we observed the foraging sites that birds selected, we did note that Wood Storks landed at sites occupied by a flock of wading birds 99% of the time (Herring 2007) as compared to 76% in coastal Georgia (Bryan *et al.* 2002). Wading birds, including Wood Storks, are social foragers and are known to use white wading bird flocks to cue in to profitable foraging sites (Kushlan 1977; Green and Leberg 2005; Gawlik and Crozier 2007). Such behavior would be particularly beneficial in highly variable and unpredictable systems like the Everglades. In such ecosystems, a robust model of factors affecting habitat selection could benefit greatly by including information on the presence of other social wading birds.

#### ACKNOWLEDGMENTS

Funding was provided by Everglades National Park and U.S. Fish and Wildlife Service. We are grateful to S. Bass and T. Dean for facilitating support and sharing knowledge of wading bird ecology and thanks to J. Lorenz for the hydrologic data. R. Auringer flew all aerial following flights. E. Noonburg provided statistical and modeling advice. J. Beerens, N. Dorn, G. Herring and Z. Xie commented on the manuscript. Research techniques were approved by the Florida Atlantic University Institutional Animal Care and Use Committee (Protocol A05-31) and conducted under Everglades National Park Research Permit 2005-SCI-0004.

#### LITERATURE CITED

- Allison, P. D. 1999. Logistic Regression Using the SAS System: Theory and Application. SAS Institute, Inc., Cary, North Carolina.
- Allison, P. D. 2005. Survival Analysis Using SAS: A Practical Guide. SAS Institute, Inc., Cary, North Carolina.
- Andersen, P. K. and R. D. Gill. 1982. Cox's regression model counting process: A large sample study. *Annals of Statistics* 10: 1100-1120.
- Bancroft, T. G., D. E. Gawlik and K. Rutchey. 2002. Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA. *Waterbirds* 25: 265-277.
- Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatialecology.com/htools>.
- Browder, J. A. 1984. Wood Stork feeding areas in southwest Florida. *Florida Field Naturalist* 12: 81-96.
- Bryan, A. L., Jr. and M. C. Coulter. 1987. Foraging flight characteristics of Wood Storks in east-central Georgia, USA. *Waterbirds* 10: 157-161.
- Bryan, A. L., Jr., F. F. Gaines and C. S. Eldridge. 2002. Coastal habitat use by Wood Storks during the non-breeding season. *Waterbirds* 25: 429-435.
- Cook, M. I. and E. M. Call. 2006. System-wide summary. Pages 1-2 in South Florida Wading Bird Report Vol. 10 (M. I. Cook and E. M. Call, Eds.). South Florida Water Management District, West Palm Beach, Florida.
- Coulter, M. C., J. A. Rodgers, J. C. Ogden and F. C. Depkin. 1999. Wood Stork (*Mycteria americana*). In *The Birds of North America*, No. 409 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Cox, D. R. 1972. Regression models and life tables. *Journal of the Royal Statistical Society* 20: 187-220.
- ESRI Inc. 1999-2003. ESRI, ArcMap 9.2: ArcEditor. Redlands, California.
- Fleming, D. M., W. F. Wolff and D. L. DeAngelis. 1994. Importance of landscape heterogeneity to Wood Storks in Florida Everglades. *Environmental Management* 18: 743-757.
- Florida Fish and Wildlife Conservation Commission. 2004. Digital raster data: fl\_veg03. Florida Fish and Wildlife Commission, Florida.
- Frederick, P., D. E. Gawlik, J. C. Ogden, M. I. Cook and M. Lusk. 2009. The White Ibis and Wood Stork as indicators for restoration in the Everglades ecosystem. *Biological Indicators* 9: 83-95.
- Frederick, P. C. and M. G. Spalding. 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. Pages 659-692 in *Everglades: The Ecosystem and Its Restoration* (S. M. Davis and J. C. Ogden, Eds.). St. Lucie Press, Delray Beach, Florida.
- Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecological Monographs* 72: 329-346.
- Gawlik, D. E. and G. E. Crozier. 2007. A test of cues affecting habitat selection by wading birds. *Auk* 124: 1075-1082.
- Gibb, J. 1960. Populations of tits and goldcrests and their food supply in pine plantations. *Ibis* 102: 163-208.
- Green, M. C. and P. L. Leberg. 2005. Flock formation and the role of plumage colouration in Ardeidae. *Canadian Journal of Zoology* 83: 683-693.
- Harris, R. L. 2007. Characteristics affecting prey vulnerability and avian habitat selection in the Florida Everglades. Unpublished M.Sc. Thesis, Florida Atlantic University, Boca Raton, Florida.
- Herring, G., D. E. Gawlik, M. I. Cook and J. M. Beerens. 2010. Sensitivity of nesting Great Egrets and White Ibises to reduced prey availability. *Auk* 127: 660-670.
- Herring, H. K. 2007. Foraging habitat selection modeling and nesting ecology of Wood Storks in Everglades National Park. Unpublished M.Sc. Thesis, Florida Atlantic University, Boca Raton, Florida.
- Jones, J. 2001. Habitat selection studies in avian ecology: A critical review. *Auk* 118: 557-562.
- Jones, P. J. and P. Ward. 1979. A physiological basis for colony desertion by Red-billed Queleas (*Quelea quelea*). *Journal of Zoology* 189: 1-19.
- Kahl, M. P., Jr. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. *Ecological Monographs* 34: 97-117.
- Kushlan, J. A. 1977. The significance of plumage colour in the formation of feeding aggregations of Ciconiiformes. *Ibis* 119: 361-364.

- Kushlan, J. A. 1978. Feeding ecology of wading birds. Pages 249-296 in *Wading Birds* (A. Sprunt IV, J. C. Ogden and S. Winckler, Eds.). Research Report 7 of the National Audubon Society. National Audubon Society, New York, New York.
- Kushlan, J. A. 1986. Responses of wading birds to seasonally fluctuating water levels: Strategies and their limits. *Colonial Waterbirds* 9: 155-162.
- Kushlan, J. A., J. C. Ogden and A. L. Higer. 1975. Relation of water level and fish availability to Wood Stork reproduction in the southern Everglades, Florida. U.S. Geological Survey Open File Report 75-434, Tallahassee, Florida.
- Lack, D. 1954. The stability of the heron population. *British Birds* 47: 111-119.
- Liu, Z., J. C. Volin, V. D. Owen, L. G. Pearlstine, J. R. Allen, F. J. Mazzotti and A. L. Higer. 2009. Validation and ecosystem applications of the EDEN water-surface model for the Florida Everglades. *Ecohydrology* 2: 182-194.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald and W. P. Erickson. 2004. Resource selection by animals: Statistical design and analysis for field studies. Chapman and Hall, London, U.K.
- Martin, T. E. 1987. Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecology and Systematics* 18: 453-487.
- Minckley, W. L. and J. E. Deacon. 1968. Southwestern fishes and the enigma of "Endangered Species". *Science* 29: 1424-1432.
- McDonald, T. L., B. F. J. Manly, R. M. Nielson and L. V. Diller. 2006. Discrete-choice modeling in wildlife studies exemplified by Northern Spotted Owl nighttime habitat selection. *Journal of Wildlife Management* 70: 375-383.
- Ogden, J. C. 1994. A comparison of wading bird nesting colony dynamics (1931-1946 and 1974-1989) as an indication of ecosystem conditions in the southern Everglades. Pages 533-570 in *Everglades: The Ecosystem and its Restoration* (S. M. Davis and J. C. Ogden, Eds.). St. Lucie Press, Delray Beach, Florida.
- Ogden, J. C., J. A. Kushlan and J. T. Tilmant. 1976. Prey selectivity by the Wood Stork. *Condor* 78: 324-330.
- Pierce, R. L. and D. E. Gawlik. 2010. Wading Bird Foraging Habitat Selection in the Florida Everglades. *Waterbirds* 33: 494-503.
- Rader, R. B. and C. J. Richardson. 1994. Response of macroinvertebrates and small fish to nutrient enrichment in the northern Everglades. *Wetlands* 14: 134-146.
- RECOVER. 2004. Section 3.1 Greater Everglades Wetlands Module. Pages 3:3-3:58 in *Monitoring and Assessment Plan*; January 2004. Available at [http://www.evergladesplan.org/pm/recover/recover\\_map.cfm](http://www.evergladesplan.org/pm/recover/recover_map.cfm).
- Russell, G. J., O. L. Bass and S. L. Pimm. 2002. The effect of hydrological patterns and breeding-season flooding on the numbers and distribution of wading birds in Everglades National Park. *Animal Conservation* 5: 185-199.
- SAS Institute, Inc. 2003. SAS 9.1.3 SAS help and documentation. PHREG Procedure. SAS Institute, Inc., Cary, North Carolina.
- Smith, J. P. 1995. Foraging sociability of nesting wading birds (Ciconiiformes) at Lake Okeechobee, Florida. *Wilson Bulletin* 107: 437-451.
- U.S. Geological Survey. 2006. The Everglades Depth Estimation Network (EDEN) for Support of Ecological and Biological Assessments. U.S. Department of the Interior. Fact Sheet 2006-3087.
- Weathers, W. W. and K. A. Sullivan. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs* 59: 223-246.
- Wiens, J. A. 1989. *The Ecology of Bird Communities*. Volume 2. Processes and variations (R. S. K. Barnes, H. J. B. Birks, E. F. Connor and R. T. Paine, Eds.). Cambridge University Press. Cambridge, U.K.