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The Effects of Drought on Foraging Habitat Selection of Breeding Wood Storks in Coastal Georgia

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Abstract.—Foraging habitat use by Wood Storks (*Mycteria americana*) during the breeding season was studied for three coastal colonies during a drought year and compared to habitat use during normal rainfall years. Information on the distribution of wetland habitat types was derived using U.S. Fish and Wildlife Service National Wetland Inventory (NWI) data within a Geographic Information System (GIS). Foraging locations were obtained by following storks from their colonies in a fixed-winged aircraft. Differences in hydrologic condition and, the resulting prey availability in coastal zone freshwater wetlands greatly affected foraging habitat use and breeding success of the three stork colonies. In 1997 (dry), although the foraging range of each colony did not differ from wetter years, storks used estuarine foraging habitats much more extensively. Breeding success (fledged young/nest) in 1997 was less than half the success of the wetter years. Palustrine (freshwater) wetlands seem very important to storks breeding along the Georgia coast. During dry years, estuarine wetlands, by themselves, do not appear to be able to support the breeding population of storks in this region. Reasons why these productive wetlands do not provide sufficient resources for successful breeding are unclear, but could include limitations to only two foraging periods (low tides) in a 24-hr period. *Received 26 October 1999, accepted 21 December 1999.*

Key words.—Coastal, drought, endangered species management, foraging habitat, Georgia, GIS, *Mycteria americana*, rainfall, Wood Stork.

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Freshwater habitat diversity, wetland distribution in relation to the colony, and tidal stage interact as important variables in Wood Stork (*Mycteria americana*) foraging habitat use in the coastal environment. Storks use coastal foraging habitats that provide prey concentration pulses on two temporal scales—estuarine daily (tidal) drawdowns and palustrine—seasonal drawdowns (Odum *et al.* 1995; Gaines *et al.* 1998). Other studies have documented Wood Stork use of estuarine habitats (Clark 1980; Rodgers *et al.* 1987) and this resource may be favored due to its consistency and availability (Walsh 1990; Pearson *et al.* 1992). Hodgson *et al.* (1988) documented effects of annual weather patterns (primarily rainfall) on stork foraging habitat for an inland colony and estimated a 47% reduction in use during a dry year, which was thought to diminish available food supplies. In the coastal environment, the availability of estuarine habitat may minimize the negative impacts of such periods of drought (Gaines *et al.* 1998). Furthermore, use of palustrine habitats in a coastal environment by foraging storks may be a function of limited estuarine availability due to tidal fluxes, and may also meet a physiological need of the adult storks and their young during the breeding season. For example, nestling White Ibis (*Eudocimus albus*) fed saltwater prey items exhibited significantly slower growth compared with those fed freshwater prey (Johnston and Bildstein 1990).

Variation in rainfall patterns over a three-year period allowed us to compare foraging habitat use by Wood Storks during a "dry" breeding season (this study) with habitat use during "wetter" or "normal" breeding seasons (Gaines *et al.* 1998). Specifically, the objectives of this study were to (1) determine the potential foraging area of three Wood Stork colonies during this "dry" year, (2) determine what wetland types were used by foraging storks, (3) determine how wetland habitats were used in relation to their availability within the colony's foraging area, (4) determine how foraging site use was related to tidal stage, and (5) compare stork habitat use during this "dry" breeding season to habitat use during the two previous "wetter" breeding seasons. This study addresses several research "tasks" considered important by the U.S. Fish and Wildlife Service for the recovery of this species including location of foraging habitats (Task 1.1.2.), prioritization of habitat (Task 1.2.) and describing stork foraging ecology in the coastal environment (Task 3.6.2.; U.S. Fish and Wildlife Service 1996).

METHODS

Study Area

The study was conducted during the 1995-1997 Wood Stork breeding seasons in the Sea Island coastal region of Georgia, USA (Sandifer *et al.* 1980). Forested barrier islands bordered on their inland side by tidal marshes and creeks characterize this region, which contains maritime, estuarine, freshwater, and upland ecosystems. The mainland bordering the tidal marshes (estuarine) has riverine drainages, which support associated palustrine (non-tidal) wetlands such as swamps, and marshes. Three Wood Stork colonies were included in this study. The Harris Neck colony (31°37.79, 81°16.50) is on the Harris Neck National Wildlife Refuge (NWR) on a large estuarine island between the Sapelo and South Newport rivers in McIntosh County, Georgia. The colony on St. Simons Island is in a freshwater impoundment on that barrier island (31°16.40, 81°21.20) in Glynn County, Georgia. The Black Hammock colony (31°02.23, 81°30.82) is on a large estuarine island in Camden County, Georgia between the Satilla River and Dover Creek.

The colony on the Harris Neck NWR is in a manmade impoundment (Woody Pond) that is managed to enhance successful breeding of Wood Storks. This management includes the manipulation of water levels to ensure deep water during the nesting season, reducing the likelihood of predation by raccoons (*Procyon lotor*) and other opportunistic omnivores, and the addition of artificial nest structures to the wetland to increase the number of breeding pairs utilizing the site (Robinette *et al.* 1995). Snipe Pond, a 9.7-ha impoundment adjacent to the Harris Neck colony, was stocked with 2,000 black bullhead (*Ameiurus melas*) in 1989 to provide additional food for storks. Fish sampling in this impoundment in 1995 found this species to be present and reproducing. Approximately 330,000 bluegill sunfish (*Lepomis macrochirus*) were stocked as additional forage in this site in the fall of 1994 in preparation for the 1995-breeding season. This wetland has shallow areas of appropriate depth for foraging throughout the year and has also been modified to allow water level manipulations to make it more suitable (shallower depths) as a foraging habitat. The water level in Snipe Pond was not manipulated during the three breeding seasons included in this study.

Foraging Habitat

Adult Wood Storks (N = 86) were followed by an observer in a fixed-wing aircraft (Cessna 152 or 172) from the colonies to foraging sites in 1997, using methods described by Bryan and Coulter (1987). All storks followed were assumed to be breeding birds. The locations of the foraging sites were plotted on 1:100,000 scale United States Geological Survey (USGS) topographic maps and logged into a Global Positioning System (GPS). Since this method supplied only a general location of the wetland, the observer took detailed notes describing the relative position, and habitat type (impoundments, forested drainages, non-flowing forested wetlands, tidal creeks or pools) of each wetland in order to truth each foraging point for future analyses. The number of storks and other wading birds already present when the focal individual arrived was also noted. Wading birds already present could not be determined for some sites due to the degree of canopy closure.

Data Analyses

Foraging habitat use during the 1995 and 1996-breeding seasons was analyzed in relation to wetland availability as determined from National Wetland Inventory (NWI) data, foraging site distance in relation to the colony, and tidal stage. A detailed discussion of these analyses is presented in Gaines *et al.* (1998). The results of the current study (1997 breeding season) which we classified as a "dry" year, were compared to results obtained in 1995 and 1996 (see Gaines *et al.* 1998), which were normal rainfall years. The "dry" classification resulted not only from a six-mo rainfall period below normal to start the 1997 breeding season, but also from a lengthy (nine-month) below normal rainfall period at the end of the preceding (1996) breeding season (Table 1). Additionally, during the 1997 breeding season, the

Table 1. Rainfall patterns preceeding[a] and during the 1995-1997 Wood Stork Breeding seasons.

	Quarterly Rainfall[b] (cm) Departure from 30-year Normal			
Breeding Season[c]	Aug.-Oct.	Nov.-Jan.	Feb.-Apr.	May-July
1995	+ 7.1	+3.0	-9.1	+ 6.4
1996	+20.6	-8.1	-2.5	-16.0
1997	+14.2	-5.3	-9.9	+ 4.1

[a] Months prior to the actual breeding season (see below) can affect presence and abundance of prey populations in freshwater wetlands.

[b] Rainfall data from Brunswick, Glynn County, GA (NOAA Station 09-1340-9).

[c] The breeding season for storks in coastal GA typically ranges from nest initiation in February-April through chick fledging in May-July.

Black Hammock colony completely dried, and the St. Simons colony water level was low (ALB pers. obs.). The water level in the Harris Neck colony was artificially maintained and thus was not affected by rainfall.

Geographic Information System Analyses

Foraging sites were digitized from the topographic maps into a GIS and made into point coverages. Additional foraging locations logged using a GPS were added to this point coverage. National Wetland Inventory (NWI) 7.5 min. coverages were used as the base habitat data. These coverages were downloaded from the USFWS Internet site and imported into the GIS. Foraging locations were verified as the correct habitat type shown on the NWI coverage by comparisons with the detailed field notes taken while flying over the actual foraging site. Since tidal creek habitat is not a classified wetland type within the NWI classification system, for the purposes of this study it was classified as estuarine subtidal unconsolidated bottom/tidal marsh (E1UBL/E2EM1N; Cowardin *et al.* 1979).

Using all foraging locations for each colony for the 1997-breeding season, minimum convex polygons (MCP) were created within the GIS to represent the maximum boundary of stork foraging habitat. A few widely scattered foraging sites can bias a MCP and thus it may not represent the true point pattern of a colony's foraging area. To correct this possible skewing, each colony was buffered within the limits of its MCP by representing the zones in which (approximately) 75% of the closest foraging points to the colony occurred. That is, a circle around the colony was made within this zone using the maximum distance of the 75th percentile foraging site as the radius (Fig. 1).

Statistical Analyses

Two series of chi-square tests were used to determine whether storks foraged in habitats as expected by the distribution of wetland types throughout the landscape within each colonys MCP and 75% foraging zone. The first series of chi-square tests examined wetland types in two broad classifications: freshwater and estuarine. The second series of chi-square tests looked at each specific habitat type. Due to the extensive categorization of the classification system for wetlands and deep-water habitats (Cowardin *et al.* 1979) used in the NWI maps, wetland habitat type was reduced to the class level. However, we did distinguish between freshwater and tidally-influenced forested wetlands. Because many expected values were less than one for this analysis, a randomization test was used to determine the significance level of the observed chi-square statistic. Expected values for both chi-square test series were calculated by multiplying the percent occurrence of a habitat type by the total number of foraging sites. A chi-square test was also used to determine if habitat use was different during the drought season than during the normal rainfall seasons. Expected values were calculated by multiplying the proportion of habitat used during the normal rainfall season by the total number of foraging sites during the drought season. A two sample t-test was used to determine differences in the mean direct distance to foraging location between wet and dry seasons.

An analysis of spatial segregation using bivariate K-functions (Dixon 1996) was used to determine if foraging sites tended to be clustered with other sites of the same habitat type. We tested to determine if foraging points were more often found within a distance *t* of other foraging sites of the same habitat type than would be expected based on chance alone. Due to limited sample size, habitat type was classified as either estuarine or palustrine for this analysis. This analysis was also used to determine if sites tended to be clustered with other points of the same ecological condition (e.g. normal rainfall vs. dry conditions). Monte Carlo simulations (950th of 999 replicates used as the upper bound) were used for all K-function analyses to determine the upper 95% confidence bound of the test statistic. This provided a one-sided test for clustering of sites into similar habitats. A Mann-Whitney U test was used to determine if foraging distances were significantly different based on estuarine and palustrine habitat. Kruskal-Wallis tests were used to compare the number of birds originally located at a foraging site between the normal and dry breeding seasons. Finally, a log linear model (Chi-square statistic) was used to determine if foraging site selection was dependent upon tidal stage. For this model, all colony locations were combined and tidal stage was classified as low (4 h block surrounding low tide), or high (4 h block surrounding high tide).

RESULTS

1997 Breeding Season

Foraging habitat type was dependent upon tidal stage for all three colonies combined ($\chi^2 2 = 44.312$, n = 86, P = 0.000). Storks used estuarine habitat more during lower tide levels when prey were more concentrated in shallow pools and tidal creeks, and used palustrine habitat more during higher tide levels. Habitat use based on availability differed between colonies with both St. Simons and Harris Neck storks foraging in palustrine habitats more frequently than expected (Table 2). Foraging site distances did not differ significantly in relation to habitat type (estuarine vs. palustrine) for either the St. Simons (Mann-Whitney U test; $U_1 = 93$; P = 0.688) or Harris Neck (Mann-Whitney U test; $U_1 = 171$; P = 0.093) colony. However, direct distances to foraging habitat did differ significantly, based on habitat type for the Black Hammock colony (Mann-Whitney U test; $U_1 = 12.5$; P = 0.013); storks flew longer distances to palustrine habitats.

There were significant spatial clusterings of foraging locations for all three colonies based on habitat type (estuarine vs. palustrine; Fig. 2). There was the tendency for foraging sites to be surrounded by other foraging sites of the same habitat type more

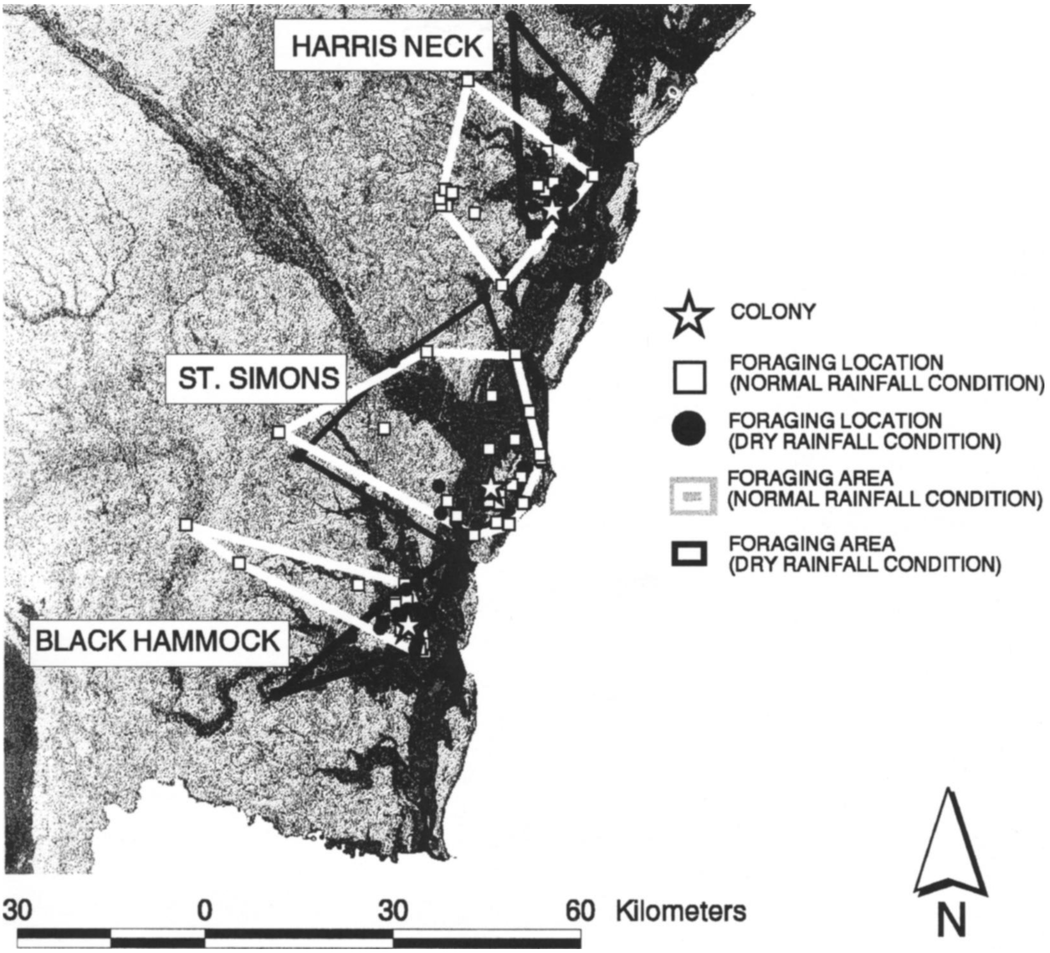


Figure 1. Atlantic coastal zone of southern United States. Stork foraging zones for each colony for the normal and dry breeding seasons are outlined. Black areas on the map represent wetlands and light grey areas represent open water.

often than expected by random chance. Estuarine sites were clustered at distances > one km apart for the Black Hammock colony, > eight km apart for the Harris Neck colony, and only at extreme distances for the St. Simons colony (probably due to edge effects within the analysis; see Dixon 1996); however, palustrine points were clustered at shorter distances for both the St. Simons and Harris Neck colonies.

Normal vs. Dry Years

The nesting success during the dry breeding season was lower than in the 1995 normal breeding season for all three colonies (Table 3). In fact, during the drought period, the Black Hammock colony had complete nesting failure. The total wetland area composing the 75% foraging range and 100% MCP varied by colony when comparing the normal and dry breeding seasons. However, when looking at total land area, the foraging ranges tended to be larger during the normal breeding seasons (Table 4).

The mean direct distances to foraging locations did not differ between wet and dry seasons for all three colonies (t-test: Two sample; P (two-tailed) > 0.40). There was significant spatial clustering of foraging sites based on rainfall condition (e.g. normal vs. dry) for the Harris Neck and Black Hammock colonies (Fig. 3). That is, there was the tendency for foraging sites to be surrounded by other foraging sites from the same rainfall condition more often than expected by random

Table 2. Chi-square tests to compare Wood Stork foraging habitats in 1997 with that expected as a function of wetland availability. Tests were performed using the total foraging area of the colony (100% of points) and the areas in which 75% (approximately) of the closest foraging points to the colony occurred.

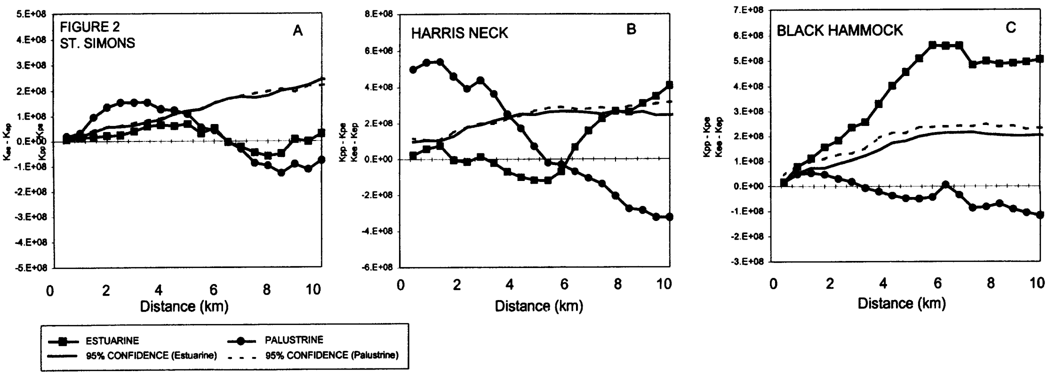
	Black Hammock				St. Simons				Harris Neck			
	75% of Foraging points		100% of Foraging points		75% of Foraging points		100% of Foraging points		75% of Foraging points		100% of Foraging points	
Wetland Classification Type	% Area	E[a]/O[b]	% Area	E/O	% Area	E/O	% Area	E/O	% Area	E/O	% Area	E/O
Tidal creek and associated saltmarsh	90%	16/16	88%	23/21	92%	20/14	51%	14/17	94%	25/20	85%	30/25
Palustrine Forested	6%	1/2	7%	2/4	5%	1/4	33%	9/6	4%	1/1	12%	4/2
Palustrine Emergent	1%	Tr[c]/0	1%	Tr/1	1%	Tr/0	9%	2/0	1%	Tr/6[d]	<1%	Tr/8[d]
Palustrine Unconsolidated Bottom	<1%	Tr/0	<1%	Tr/0	<1%	Tr/3	<1%	Tr/4	<1%	Tr/0	<1%	Tr/0
Other	3%	Tr/0	4%	1/0	1%	Tr/0	4%	1/0	4%	Tr/0	3%	Tr/0
	P = 0.788		P = 0.351		P = 0.004		P = 0.008		P = 0.000		P = 0.000	
Total Estuarine	91%	17/16	91%	23/22	93%	20/14	53%	14/17	95%	25/20	86%	30/25
Total Palustrine	9%	1/2	9%	3/4	7%	1/7	47%	13/10	5%	2/7	14%	5/10
	P = 0.616		P = 0.273		P = 0.000		P = 0.248		P = 0.000		P = 0.01	

[a] Expected number of foraging points based on the relative area of the corresponding wetland type.

[b] The observed number of foraging points for that wetland type.

[c] Tr = Less than 1 foraging point expected.

[d] All points associated with managed feeding pond next to colony.



Figures 2a-c. Ripley's K-function analysis of spatial clustering of foraging points for the St. Simons, Harris Neck, and Black Hammock colony (respectively) at distances of 0.5 to 10 km. Each figure indicates whether (or not) foraging points tend to occur in single habitat (either palustrine or estuarine) patches. Kii and Kij are bivariate K functions, where i represents the habitat type being tested for and j represents all other habitat types. Kii-Kij is positive when points of habitat type i are found near other type i points. This difference is statistically significant when the curve is above the 95% confidence bound, calculated by Monte-Carlo simulation. For example, in Figure 2a, palustrine foraging points are significantly clustered at distances between 2 km and approximately 4.5 km from other foraging points.

chance. Specifically, drought year foraging sites tended to cluster at distances between nine and ten km for the Harris Neck colony. For the Black Hammock colony, sites tended to cluster together at shorter distances (0.5-1.0 km) during normal rainfall conditions but did not cluster during drought conditions. Lastly, there tended to be more wading birds present at a stork foraging location during the normal breeding seasons than during the dry period (Kruskal Wallis $\chi^2 1 = 15.6$; P = 0.0001; Table 5). There also tended to be more wading birds present at stork foraging locations during the normal breeding season specifically for estuarine locations (Kruskal Wallis $\chi^2 1 = 9.02$; P = 0.0027), but there was no difference based on rainfall condition for palustrine locations (Kruskal Wallis $\chi^2 1 = 0.1535$; P = 0.6952; Table 5).

During drought periods, estuarine habitat was used more often than freshwater habitat than would be expected based on the frequency of habitat use during the normal rainfall periods for the St. Simons ($\chi^2 1 = 5.04$, P = 0.025) and Harris Neck ($\chi^2 1 = 20.67$, P = 0.000) colonies. However, use of foraging habitat type was not different than would be expected for the Black Hammock colony ($\chi^2 1 = 0.346$, P = 0.556).

DISCUSSION

Foraging habitats used by Wood Storks from three coastal colonies differed from one another by varying degrees. These differences may best be explained by colony position relative to coastal waters and their association with different-sized river drainage basins and subsequent associated wetland habitats. For instance, the majority of wetland habitat surrounding the Black Hammock colony is estuarine (Table 2; see also

Table 3. Mean and standard deviation of nesting success (fledged young / nest) for each colony during the 1995 normal and 1997 dry breeding season. Nesting data for 1996 are unavailable.

	Normal (1995)				Dry (1997)			
Colony	Visits/ observation	# nests observed	$\bar{x}$	SD	Visits/ observation	# nests observed	$\bar{x}$	SD
Black Hammock	5	15	2.5	0.9	5	44	0	0
Harris Neck	6	63	2.5	1.2	11	166	0.7	0.8
St. Simons	5	13	2.5	1.4	5	37	1.1	1.0

Table 4. Total area and wetland area for the 75% foraging zone and 100% Minimum Convex Polygon (MCP) for each colony during the "normal" breeding seasons[a] and the "dry" breeding season.

		Total Area (ha)		Total Wetland Area (ha)	
Colony	Foraging zone	Normal	Dry	Normal	Dry
Black Hammock	75% Foraging Zone	4,413	6,869	3,045	5,000
	100% MCP	21,845	16,229	10,728	12,364
Harris Neck	75% Foraging Zone	33,792	12,105	21,170	10,238
	100% MCP	40,575	32,326	24,595	23,873
St. Simons	75% Foraging Zone	21,856	19,770	16,300	14,943
	100% MCP	72,123	81,248	46,600	50,148

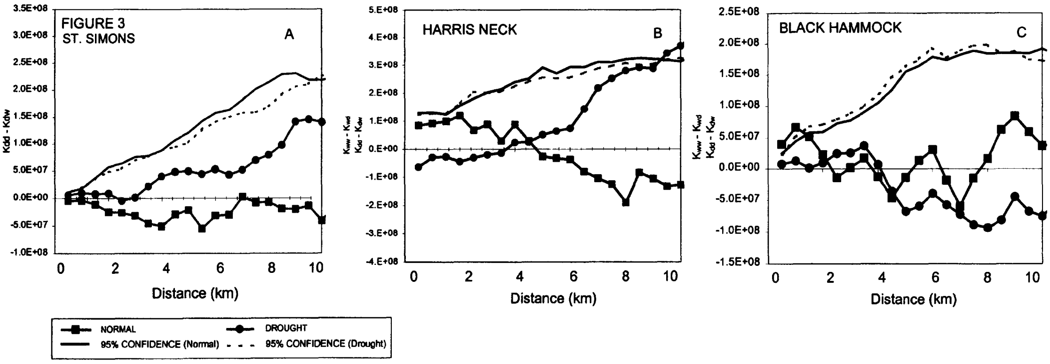
[a] From Gaines *et al.* 1998.

Gaines *et al.* 1998). A mixture of freshwater and saltwater habitats surrounds the St. Simons colony whereas the Harris Neck colony is surrounded by predominantly estuarine habitats. However, the presence and quality of resources within the managed freshwater feeding pond adjacent to Harris Neck also influences stork foraging (see Table 2).

Normal vs. Dry Rainfall Conditions

Foraging habitat use in relation to geographic availability was very similar between wet and dry breeding seasons when looking at the 100% Minimum Convex Polygon (MCP). For the Harris Neck colony, the 75% foraging range tended to be closer to the colony during the dry year (Fig. 1, Table 4). Storks from Black Hammock seemed to use wetlands based on their geographic availability while storks from the other two colonies did not, regardless of hydrologic condition (see also Gaines *et al.* 1998). Although it seems that the use of NWI coverages is helpful in understanding the habitat conditions around the colony, it alone cannot be used to predict stork foraging use.

Foraging flight distances and distance/habitat relationships were not different between the two previous "normal" breeding seasons and the 1997 drought breeding season (see Gaines *et al.* 1998, for results from the normal rainfall seasons). Since the MCPs and potential wetland areas within them were similar across years, storks did not appear to "expand" their foraging range or



Figures 3a-c. Ripley's K-function analysis of spatial clustering of foraging points for the St. Simons, Harris Neck, and Black Hammock colony (respectively) at distances of 0.5 to 10 km. Each figure indicates whether (or not) foraging points tend to occur in patches based on like rainfall conditions (either normal or drought). Kii and Kij are bivariate K functions, where i represents the rainfall condition being tested for and j represents the other rainfall condition. Kii-Kij is positive when points of rainfall condition i are found near other type i points. This difference is statistically significant when the curve is above the 95% confidence bound, calculated by Monte-Carlo simulation. For example, in Figure 3a, no foraging points are significantly clustered.

Table 5. Median, minimum (min.), and maximum (max.) number of wading birds[1] present at a stork foraging location during the "normal" and "dry" breeding seasons.

	Median	Min.	Max.
Normal			
Total	8.5	0	300
Estuarine	12	0	81
Palustrine	2	0	300
Dry			
Total	2	0	47
Estuarine	2	0	22
Palustrine	7	0	47

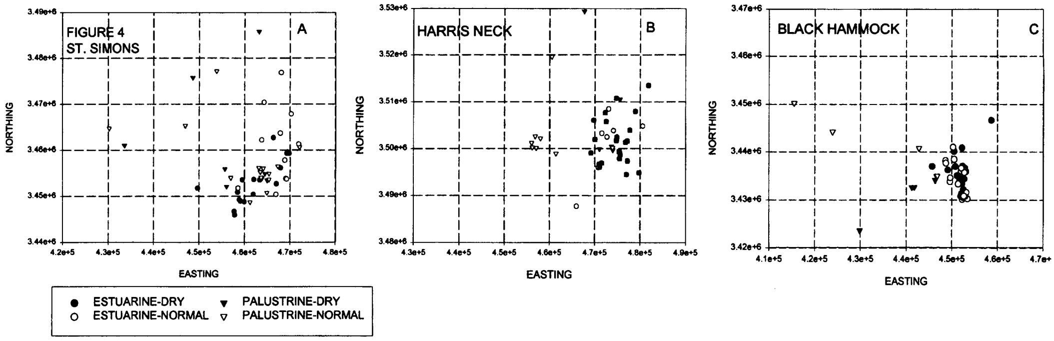
[1] Wading birds that were observed were: Wood Stork, Snowy Egret (*E. thula*), Little Blue Heron (*E. caerulea*), White Ibis (*Eudocimus albus*), Great Egret (*Casmerodius albus*), Great Blue Heron (*Ardea herodias*), and Tricolored Heron (*E. tricolor*).

shift foraging flight strategies to compensate for wetland unavailability due to the drought. However, many of the freshwater wetlands within the MCPs were likely unavailable to storks, which explains why estuarine sites were used significantly more as a whole than in previous years.

The grouping of foraging sites based on rainfall itself seemed to have little influence on the spatial distribution of foraging sites. Although there was some degree of clustering at short and long distances, the patterns were inconsistent between colonies (Fig. 3a-c), which suggests that rainfall may not be affecting the juxtaposition of foraging locations. This is supported by the fact that the degree of clustering of foraging sites based on habitat tended to be similar between the normal and dry breeding seasons (Fig. 2a-c; Gaines *et al.* 1998).

Since storks are social foragers, one would expect to see a greater utilization of sites with birds already present, regardless of rainfall condition (Kushlan 1977). However, there tended to be more wading birds present at estuarine stork foraging locations during the normal breeding seasons than during the dry period and no difference based on rainfall condition for palustrine locations. The utilization of palustrine sites may have been directed by availability, regardless of rainfall condition, due to typical seasonal drawdowns during the "normal" breeding seasons and reduced abundance during "dry" seasons. During the constrained conditions of drought, storks may not have the luxury of using a diversity of foraging sites, which would explain why storks used more estuarine sites regardless of the number of birds already present during the dry year.

While habitat use remained dependent upon tidal stage, with estuarine (tidal creek) use linked to lower tide levels and palustrine use linked with higher tide levels, storks used more estuarine sites during high-tide conditions in 1997. Although similar levels of effort were put forth to follow birds in both studies during the various tide levels, it was frequently difficult to obtain high tide level foraging sites in 1997. This was simply because fewer birds departed from the colony during those periods, possibly because prey (or appropriate freshwater habitat) was un-



Figures 4a-c. UTM x-y locations for all foraging locations for the St. Simons, Harris Neck, and Black Hammock colony (respectively).

available. This difference in habitat use or the inability of storks to locate suitable freshwater sites may explain the low breeding success during the 1997 drought season.

Wood Stork reproductive success in 1997 was much lower than that observed in the same three colonies in 1995 (Table 3). Complete failure (no young fledged) of observed nests in the three colonies ranged from 43%-100% during the drought year, as compared to only 6%-15% failure in the same colonies in 1995 (Bryan 1996). The greatest reproductive loss in 1997 occurred in the Black Hammock colony, when it completely dried underneath the nest trees. All of the monitored nests and almost all of the remaining nests were abandoned or suffered predation, presumably from raccoons. Raccoon predation has been a documented source of often "complete" mortality in Wood Stork colonies (Coulter and Bryan 1995; Rodgers 1987). However, Black Hammock nests were being abandoned prior to raccoon predation and the primary reason for nest loss at all three colonies in 1997 was thought to be reduced prey availability, which can be linked to low rainfall. Rainfall timing and quantities affect prey abundance and availability in freshwater wetland habitats and can have a considerable impact on stork and other wading bird breeding success (Frederick and Collopy 1989; Coulter and Bryan 1995).

Other avian species also require freshwater foraging habitats in the coastal environment. Negative impacts of the salt concentrations of estuarine prey (primarily crustaceans) have been documented for some young nestlings (Johnston and Bildstein 1990; Dosch 1997). Fish, which are osmoregulators, are the primary components of the diets of stork nestlings in coastal colonies (Bryan and Gariboldi 1998) which may suggest that salt concentrations in prey are not a problem for this species. However, effects on salt marsh fish of lower than normal freshwater inputs into the estuaries are also unknown and require thorough study concerning potential impacts on storks.

Differences in rainfall amounts and resulting prey availability in coastal zone freshwater wetlands greatly affected foraging habitat use and breeding success of the three Wood Stork colonies. During normal rainfall years, palustrine (freshwater) wetlands were found to be very important to Wood Storks breeding along the Georgia coast (Gaines *et al.*1998). This study strongly supports that conclusion, indicating that estuarine wetlands, by themselves, cannot support the breeding population of storks in this region, perhaps because the foraging parents are limited to only two foraging periods (low tides) in a 24-hr period. It is unknown what the estuarine productivity in this region was during the dry period and many factors such as predation also affect nesting success. Attendance requirements at the nest can constrain travel time and timing for breeding birds (Drent and Daan 1980), particularly when nestlings are young. Reduced foraging opportunities could negatively affect parental time budgets and their ability to provide food for their young.

CONSERVATION IMPLICATIONS

Breeding Wood Storks in the coastal environment during drought conditions seemed to simply shift to other habitats within their normal foraging range rather than expand their range to search for other palustrine sites. Wood Storks in east-central Georgia have flown as far as 63 km to foraging sites at relatively low energetic cost (Bryan *et al.* 1995). While it is not known if palustrine habitats at greater distances were available to the colonies studied, the shift to closer yet temporally less available estuarine habitat resulted in greatly reduced breeding success. Since palustrine wetlands in the coastal environment are obviously important to Wood Stork nesting success and also face considerable anthropogenic threats such as draining for agriculture and development (Hefner *et al.* 1994), their conservation must be considered of paramount importance for the recovery of this endangered species.

Further GIS applications that would be beneficial to stork conservation would be developing a predictive model of freshwater habitat availability near the coastal zone during different hydrological conditions. Using NWI coverages alone does not seem to predict stork foraging use consistently. However, combining the NWI coverages with hypsographic drainage models may help predict which freshwater wetlands storks may use and help managers prioritize the conservation of certain freshwater wetlands.

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LITERATURE CITED

Bryan, A. L., Jr. 1996. The foraging ecology of Wood Storks nesting in the coastal zone of Georgia and South Carolina in 1995. Report to the Georgia Department of Natural Resources, Nongame-Endangered Species Program, Brunswick, GA.

Bryan, A. L., Jr. and M. C. Coulter. 1987. Foraging flight characteristics of Wood Storks in east-central Georgia, U.S.A. Colonial Waterbirds 10: 157-161.

Bryan, A. L., Jr., M. C. Coulter and C. J. Pennycuick. 1995. Foraging strategies and energetic costs of foraging flights by breeding Wood Storks. Condor 97: 133-140.

Bryan, A. L., Jr. and J. C. Gariboldi. 1998. Food of nestling Wood Storks in coastal Georgia. Colonial Waterbirds 21: 152-158.

Clark, E. S. 1980. Attentiveness and time budget of a pair of nesting wood storks. MS Thesis, University of Central Florida, Orlando, FL.

Coulter, M.C. and A. L. Bryan, Jr. 1995. Factors affecting reproductive success of Wood Storks (*Mycteria americana*) in east-central Georgia. Auk 112: 237-243.

Cowardin, L. M., Golet, F. and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. Biological Services Program. FWS/OBS-79/31. U.S. Fish and Wildlife Service, Washington, DC.

Dixon, P. M. 1996. Second-order analysis of spatial segregation. Proceedings of Section on Statistics and the Environment, American Statistical Association, Alexandria, VA.

Dosch, J. J. 1997. Salt tolerance of nestling Laughing Gulls: An experimental field investigation. Colonial Waterbirds 20: 449-457.

Drent, R. H. and S. Daan. 1980. The prudent parent: energetic adjustment to avian breeding. Ardea 68: 223-252.

Frederick, P. C. and M. W. Collopy. 1989. Nesting success of five Ciconiiform species in relation to water conditions in the Florida Everglades. Auk 106: 625-634.

Gaines, K. F., Bryan, Jr., A. L., Harris, M. J. and P. M. Dixon. 1998. Foraging habitat use by Wood Storks nesting in the coastal zone of Georgia, USA. Colonial Waterbirds 21: 43-52.

Hefner, J. M., B. O. Wilen, T. E. Dahl and W. E. Frayer. 1994. Southeast wetlands: Status and trends, mid-1970's to mid-1980's. U.S. Department of the Interior, Fish and Wildlife Service, Atlanta, GA.

Hodgson, M.E., J. R. Jenson, H. E. Mackey, Jr. and M. C. Coulter. 1988. Monitoring Wood Stork foraging habitat using remote sensing and geographic information systems. Photogrammetric Engineering and Remote Sensing 54: 1601-1607.

Johnston, J. W. and K. L. Bildstein. 1990. Dietary salt as a physiological constraint in White Ibis breeding in an estuary. Physiological Zoology 63: 190-207.

Kushlan, J. A. 1977. The significance of plumage color in the formation of feeding aggregations of ciconiiforms. Ibis 119: 361-363.

Odum, W. E., E. P. and H. T. Odum. 1995. Nature's pulsing paradigm. Estuaries 18: 547-555.

Pearson, S. M., J. M. Walsh and J. Pickering. 1992. Wood Stork use of wetland habitats around Cumberland Island, Georgia. Colonial Waterbirds 15: 33-42.

Robinette, J. R., J. P. Davis and J. L. Hall. 1995. U.S. Fish and Wildlife Service Wood Stork enhancement and restoration projects in coastal Georgia. Pages 57-63 *in* The Wood Stork Symposium. The Georgia Conservancy, Savannah, GA.

Rodgers, J. A., Jr. 1987. On the antipredator advantages of coloniality: a word of caution. Wilson Bulletin 99: 269-270.

Rodgers, J. A., Jr., A. S. Wenner and S. T. Schwikert. 1987. Population dynamics of Wood Storks in north and central Florida. Colonial Waterbirds 10: 151-156.

Sandifer, P. A., J. V. Miglarese and D. R. Calder. 1980. Ecological characterization of the Sea Island coastal region of South Carolina and Georgia. Volume III. Biological features of the characterization area. FWS/OBS-79/42, U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC.

Strong, A. M., G. T. Bancroft and S. D. Jewell. 1997. Hydrological constraints o Tricolored Heron and Snowy Egret resource use. Condor 99: 894-905.

U.S. Fish and Wildlife Service. 1996. Revised recovery plan for the U.S. breeding population of the Wood Stork. U.S. Fish and Wildlife Service, Atlanta, GA.

Walsh, J. M. 1990. Estuarine habitat use and age specific foraging success of wood storks (*Mycteria americana*) MS Thesis, University of Georgia, Athens, GA.