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Abstract.—We documented roosting and foraging habitat use by Wood Storks during the post-breeding season in the coastal zone of Georgia from 1994-1998. Larger, more persistent aggregations of roosting storks typically occurred in enclosed wetlands on large estuarine islands. Smaller, more ephemeral aggregations tended to occur on salt marsh/upland ecotones, where storks appeared to be waiting for local conditions (tide levels) to become suitable for foraging. Examination of habitat types within a 2-km radius of the larger (mean > 10 storks/survey) vs. smaller (mean <10 storks/survey) roosts showed that surrounding habitat structure, including those used for foraging, were similar. Foraging storks typically fed in close proximity (median = 0.5 km) to large roosts, much closer than storks using coastal wetlands during the breeding season. Tidal creeks were used almost exclusively as foraging habitat (92%). Storks and other wading birds were almost always present when the study bird arrived. The foraging patterns of study birds and four storks carrying radios suggested that storks often used the same foraging sites and/or marsh systems in the non-breeding season. Coastal Wood Storks apparently selected roosting sites based on the presence of conspecifics, abundant local prey, or possibly as shelter from adverse weather conditions. *Received 3 January 2001, accepted 20 April 2002.*

Key words.—Coastal, foraging, habitat use, *Mycteria americana*, non-breeding season, roosting, Wood Stork.

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Like many avian species that breed in colonies and forage in flocks, Wood Storks (*Mycteria americana*) roost communally, especially during the non-breeding season. Proposed advantages of communal roosting include functioning as "information centers" for location of ephemeral feeding sites (Ward and Zahavi 1973), attracting other foragers to good food "patches" to enhance foraging efficiency (Buckley 1996), reduction of predation risks (Lack 1968), and more energetically efficient thermoregulation in cooler climates (Stalmaster and Gessaman 1984). Major roosts can also form near ephemeral super-abundant food patches (Morrison and Caccamise 1985). Regardless of their function, locations of roosts are important features within a bird's overall habitat. Identifying the spatial and temporal characteristics of such roosts in relation to foraging habitats is important, particularly for an endangered species like the Wood Stork where habitat protection is essential to maintain sustainable populations.

Roosting and foraging sites use of Wood Storks during the non-breeding season has received little study. Bryan *et al.* (2001) found that daily stork attendance at a large coastal roost was linked to tide level, with stork departures, presumably to forage, typically occurring 2-3 h prior to low tide. Wood Storks foraged during both daytime and night time periods, but more storks were at the roost, and so not foraging, during the daylight hours. Ogden (1990) suggested that Woods Storks tend to roost in habitats similar to nesting habitats (trees over water or on islands), but might use a wider range of temporary sites during the non-breeding season. Wood Stork roosts observed during aerial surveys near Cumberland Island, Georgia, were found most frequently at upland/salt marsh interfaces (Walsh 1990; Pearson *et al.* 1992). Further, the use of a coastal roost varied both seasonally and annually (Bratton and Hendricks 1988). Roosts used year after year and/or used by more than 25 storks are considered important sites to be protected (Ogden 1990).

Wood Storks were classified as an endangered species in 1984, primarily due to a population decline resulting from foraging habitat loss (USFWS 1996). During this decline, the use of the coastal region of Georgia by storks increased in both breeding and non-breeding seasons (Harris 1995). Concurrently, the area of coastal wetlands in the southeastern United States has declined and

continues to be threatened by urban and recreational development (Hefner *et al.* 1994).

From 1994-1998, we examined roost use and foraging patterns outside of the breeding season of Wood Storks in the coastal region of Georgia and South Carolina. Specifically, we surveyed the coastal zone to document locations and habitats of roost sites and monitored a sample of roosts to evaluate their use and/or "importance." We also documented foraging and movement patterns of storks from roosts, and examined variation in habitat types around larger vs. smaller roosts. This research addresses five tasks in the recovery plan (USFWS 1996) for this species: tasks 1.1.2 (locate roosting and foraging habitat), 1.2 (prioritize habitats for protection), 3.6.2 (study coastal foraging ecology), 3.6.3 (determine foraging requirements in the non-breeding season) and 3.7 (determine importance of roosts).

STUDY AREA AND METHODS

Preliminary Roost Surveys

Coastal habitats were examined for Wood Stork roost sites during surveys from fixed-wing aircraft (Cessna 172 or Piper Supercub). In 1994 and 1995, the survey area consisted of different sections of the Sea Island coastal region (Sandifer *et al.* 1980) of Georgia and South Carolina. In 1994, the survey area was bounded to the north by the Broad River and Hilton Head Island, by Interstate Highway 95 to the west, by the Altamaha River/Wolf Island to the south, and by the Atlantic Ocean to the east. In 1995, the remaining (southern) portion of the Georgia coast was surveyed. This area was bounded to the north by the Altamaha River/Wolf Island, by Interstate 95 to the west, and by St. Mary's River to the south.

Surveys were flown at an altitude of 100-200 m at approximately 165 km·hr^{-1} (90 knots). All surveys were made during daylight within ±3 h of high tide, when water levels in tidal creeks would presumably be too high for efficient foraging by storks (Bryan *et al.* 2001). Habitats were surveyed systematically by examining islands, estuaries, river drainages, impoundments and other wetland habitats. Unlikely roost habitats for storks, such as extensive urban areas and unbroken tracts of pine forest, were not surveyed. Wood Storks and other wading birds were counted at all roosts, although only stork data are discussed here.

In 1994 and 1995, a sample of roosts was opportunistically re-visited during additional surveys to examine if certain roosts, and types of roosting habitat, were used more frequently than others. A sample of 38 of the 1994 roosts was surveyed twice in 1995 to observe if roost classifications varied among the two years.

Roost Monitoring

In 1998, 61 Georgia roost sites located in the 1994 and 1995 surveys were monitored for stork use at least weekly from mid-August through November (N = 19-21 surveys at each roost). These included all roosts that averaged at least 20 storks/survey and a sample of roosts that averaged less than 20 storks/survey. After these surveys, the roosts were classified in relation to the average number of storks utilizing them throughout the survey period, and numbers in early vs. late survey dates. Roosts were categorized into groups that averaged 0-10 storks/survey (inclusive), 10.1-20 storks/survey (inclusive), and over 20 storks/survey. Early (August/September) and late (October/November) stork-use averages were compared to examine seasonality of use of roosts that averaged >10 storks per survey.

Roost Site Habitat Classification

The habitats in which roosts occurred were classified by on both general and specific scales (see detailed description in Table 1). *General* site characteristics classified where sites were located in the coastal zone, ranging spatially from "barrier islands" to the "mainland." *Specific* habitat classifications described roost structure, listing whether the roost occurred on an ecotone, in a wetland surrounded by trees (enclosed wet-

Table 1. Description of general and specific habitat classifications of Wood Stork roost sites.

Habitat type/classifications	Description
General	Location within coastal zone
Barrier islands	Islands bordered on one side by active, ocean-formed beach and on the other by tidal marshes, creeks and/or rivers
Estuary/Salt marsh	Non-upland portions of the intertidal zone, semi-enclosed by land, but having at least some access to open ocean and freshwater run-off from land
Large estuarine islands	Upland islands > 100 ha in size, embedded within the intertidal zone
Small estuarine islands	Upland islands < 100 ha in size, embedded within the intertidal zone
Mainland	Continuous terrestrial habitat not included in the previous categories
Specific	Roost structure
Salt marsh/Upland ecotone	Boundary between upland vegetation (trees) and expansive saltmarsh
Enclosed wetlands	Wetland openings surrounded by trees and shrubs
Open wetlands	Wetland openings lacking a border of trees and shrubs

land) or an open wetland. The number of storks observed per survey for ecotone and enclosed wetlands were compared. Open wetlands were not included in the comparison because of a low sample size.

Additionally, we examined abundance of various wetland habitat types around the 1998 roosts to assess if these potential foraging habitats influenced roost use. The Georgia land use coverage (GDNR 1995; 1998-90 Landsat Thematic Mapper™ satellite imagery with wetland enhancement from 7.5 min. USGS quads in 1992; 60 m pixels) was employed within a geographic information system (GIS) to examine habitat types and abundances within a 2.0-km radius surrounding each roost. Radius length was based on the average foraging distance of storks on roosts (see below). We compared the abundance of these habitat types in 12.6 km^2 areas (2-km radii) around smaller (mean <10 storks/survey) and larger (mean >10 storks/survey) roosts.

Foraging Patterns

Foraging patterns of Wood Storks utilizing roosts were examined by two methods. First, storks were followed from several roosts to foraging sites by an observer in a fixed wing aircraft (see above). Following flights were made on 27 and 29 August and 2-4 September in 1997 within 2-3 h of low tide, using methods described in Bryan and Coulter (1987). When the followed bird landed, its location was plotted on a 1:100 000 scale USGS topographic map and logged. A general habitat classification for the site was recorded as well as the number of storks and other wading birds already present when the followed bird arrived. Direct distances between the roosts and their associated foraging sites were determined within a GIS and were compared to distances between three coastal colony sites and foraging sites in 1997 (Gaines *et al.* 2000).

The second method included the monitoring of coastal habitats used by radio-tagged storks (in 1998) to provide information on habitat use by individual birds. Four storks were fitted with 40g VHF radio transmitters. Each bird was located 13-22 times from 5 August to 30 October by an observer in a Cessna 172 with wing-mounted antennas. When the birds were located, we recorded data similar to that recorded for the followed birds (see above).

Data Analyses

Due to skewed data distribution, comparisons of roost use and foraging distances were made by Wilcoxon rank-sum tests. Medians and ranges were presented for most variables. Means were presented ±1 standard error (SE) for some variables to allow for comparisons with other studies.

RESULTS

1994 Roost Use Surveys

A total of 110 roost sites were located in the northern portion of the study area during seven survey-days from mid-August through early October 1994. Most of these roosts were located on large estuarine islands and occurred along the salt marsh/upland ecotone (Table 2).

Sixty-five (59%) of these roosts were also monitored during 2-7 repeated surveys in 1994. Thirteen roosts (20% of sample) averaged over 20 storks per survey. The majority of these roosts occurred on large estuarine islands in an enclosed wetland (Table 3). Approximately one-fourth (N = 16) of the roosts averaged 10-20 storks, with most located on either large estuarine or barrier islands throughout the range of specific habitat

Table 2. General and specific habitat types of Wood Stork roost sites located during aerial surveys of the coastal zone of Georgia and South Carolina in 1994 & 1995.

	1994 roosts		1995 roosts		Total	
Habitat type/classification	N[a]	Percent	N[a]	Percent	N[a]	Percent
General habitat						
Large estuarine islands	49	45%	5	11%	54	34%
Small estuarine islands	29	26%	17	36%	46	29%
Mainland	15	14%	5	11%	20	13%
Barrier islands	14	13%	18	38%	32	20%
Estuary/Salt marsh	3	3%	2	4%	5	3%
Totals	110		47		157	
Specific habitat						
Salt marsh/Upland ecotone	65	59%	34	72%	99	63%
Enclosed wetlands	32	29%	10	21%	42	27%
Open wetlands	13	12%	3	6%	16	10%
Totals	110		47		157	

[a]N = number of roosts.

Table 3. Habitat and Wood Stork use classifications of coastal roosts monitored during multiple aerial surveys[a].

	1994 (N = 65 roosts)				1995 (N = 23 roosts)				1998 (N = 61 roosts)			
	Average storks per survey				Average storks per survey				Average storks per survey			
Habitat	0-10	10-20	> 20	Total	0-10	10-20	>20	Total	0-10	10-20	>20	Total
General												
Mainland	5	2	1	8	2	0	0	2	3	1	0	4
Large estuarine islands	24	9	9	42	1	1	1	3	11	3	4	18
Small estuarine islands	6	1	2	9	3	1	4	8	17	2	6	25
Barrier islands	1	4	1	6	8	2	0	10	10	3	1	14
Specific												
Enclosed wetland	5	6	11	22	1	3	2	6	7	6	8	21
Open wetland	4	3	2	9	0	0	1	1	2	0	1	3
Marsh-Upland edge	27	7	0	34	13	1	2	16	32	3	2	37
Total	36	16	13	65	14	4	5	23	41	9	11	61
%	55	25	20		61	17	22		67	15	18	

[a]Number of repeated surveys and stork use classifications are described in detail in the Methods section.

types. Roosts averaging less than ten storks typically occurred on the marsh/upland ecotone of large estuarine islands (Table 3).

1995 Roost Use Surveys

Forty-seven roost sites were located in the southern portion of the study area during three survey-days in early- to mid-October of 1995. Most of these roosts were on barrier (38%) and small estuarine (36%) islands and occurred at a saltmarsh/upland ecotone (72%; see also Table 2).

Twenty-three roosts (49% of total) were monitored three times. Five roosts averaged over 20 storks, occurring on small and large estuarine islands and occurring in all three specific habitat types (Table 3). Four roosts (9% of total) averaged 10-20 storks per survey and typically occurred in enclosed wetlands in most general habitat types. Approximately 60% of the roosts averaged less than eleven storks/survey. Most were located on the marsh/upland ecotone of barrier islands.

Thirty-eight roosts from the 1994 surveys, including eleven roosts that had averaged over 20 storks/survey, were monitored twice in October of 1995. Only five of the eleven roosts (45%) averaged over 20 storks/survey in 1995. None of the remaining 27 roosts averaged over 20 storks/survey.

1998 Roost Monitoring

Over 96% (59 of 61) of the 1994-95 roosts was used by at least one stork during the 1998 surveys. Eleven roosts (18%) averaged over 20 storks (Table 3), including three roosts that had averaged less than 20 storks/survey in previous years. Storks were present in these roosts during most surveys (90 ± 3% of surveys). These more-utilized roosts were typically located on large or small estuarine islands and occurred in enclosed wetlands. Nine roosts (15%) averaged 10-20 storks/survey and were more equally distributed among the general habitat types. Storks were present in these sites during 66 ± 5% of the surveys. Six of these roosts were located in enclosed wetlands. Roosts averaging less than ten storks/survey were also distributed equally among the general habitat types, but 76% (32 of 41) occurred on an upland/salt marsh ecotone. Storks were present in these sites during only 28 ± 3% of the surveys. Roost use of specific habitat types was significantly different ($Z = 3.65$; $P < 0.003$) when comparing enclosed wetlands to ecotones (open wetlands were not included due to low sample size). Roost size within enclosed wetlands was higher (N = 18, median = 18.8 storks/survey, range: 0-46) than roosts associated with marsh/upland ecotones (N = 39, median = 2.3 storks/survey, range: 0-65).

There appeared to be a seasonal component to stork use of a few of the 20 roosts that averaged over ten storks per survey (Table 4). Two roosts received greater use in the early half of the study and two roosts received greater use in the latter half of the study.

Habitats Surrounding Roosts

Examination of habitats surrounding large and small roosts suggested no obvious differences (Table 5).

Foraging Habitat Use

Storks followed from coastal roost sites typically traveled to brackish/saltwater foraging sites within 2 km of the roost of origin, requiring short (<7 min) flight times (Table 6). Foraging site distances (direct line) of these non-breeding storks (median = 0.5 km, range: 0.3-11) were significantly shorter ($Z = 5.46$, $P < 0.001$) than 86 foraging distances of breeding storks from coastal colonies in 1997 (median = 4.2 km, range: 0.1-68), including both freshwater and saltwater wetlands. Non-breeding foraging distances remained significantly shorter ($Z = 5.54$, $P < 0.001$) than for breeding storks followed to saltwater foraging sites (N = 61, median = 4.2 km, range: 0.5-16).

The 24 storks which were followed resulted in the identification of only twelve foraging sites, indicating that many birds used the same foraging sites. Two of the twelve foraging sites were used by at least four followed storks (Table 6). Concurrently, most of the foraging sites (79%) already had storks and/or other wading birds present when the followed bird arrived at the site. Storks tended to be the most common wading bird present.

Eleven of 12 (92%) of the foraging sites located were saltwater habitats: ten tidal creeks and one tidal pool. The remaining site was a drying freshwater wetland adjacent one of the larger roosts.

Four storks tagged with transmitters were located (total N = 69 locations) in 48 foraging sites and at 17 roosting sites. Salt marshes/tidal creeks were used almost exclusively (90%) as foraging habitat. One tidal site was used on three occasions by one stork.

DISCUSSION

All roost sites located throughout this study were similar in that they were located on an edge of open wetland, such as a pond or marsh, which would allow easy access for these large birds. The roost sites receiving the greatest use (>20 storks per survey) had a similar structure to those used for colonies in that eight of eleven (73%) of these wetlands were enclosed (open or vegetated water surrounded by tall trees). However, two important roosts (18%) were located on the ecotones of small estuarine islands. These roosts were positioned on the leeward side of these islands, away from prevailing coastal winds.

Many roosts were used by large numbers of storks throughout the study, but numbers at some of the roosts varied among years. The initial small number of repeat surveys

Table 4. Seasonal use of Wood Stork roosts sites in coastal Georgia in 1998.

	Number of storks/survey				
	Early season[a]		Late season[a]		
Roost No.	N[b]	Median (range)	N[b]	Median (range)	P[c]
001	12	61 (10-115)	9	27 (0-64)	0.02
065	12	23 (0-50)	9	0 (0-21)	0.01
146	12	0 (0-29)	9	32 (0-53)	0.01
148	12	14 (0-45)	9	42 (0-53)	0.02

[a]Early season = August/September; Late season = October/November.
[b]N = number of surveys.
[c]Compared by Wilcoxon rank-sum tests.

Table 5. Percentages of different habitat types[a] surrounding large (mean >10 storks/survey) and small (mean <10 storks/survey) Wood Stork roosts, based on the 1998 aerial surveys.

	Roosts	
Habitat type	Large	Small
Salt & brackish marsh	41%	39%
Open water	25%	24%
Forest (dry)[b]	20%	23%
Freshwater wetland[c]	8%	10%
Pasture/Cropland/Clearcut	4%	3%
Tidal flats/Beaches	2%	1%

[a]Habitat types from GDNR 1995 land use coverage (see Methods).

[b]Dry forests are made up of coniferous, hardwood, and mixed forest classifications.

[c]Freshwater wetlands are made up of emergent, scrub/shrub, and forested wetland classifications.

probably affected the identification of important roosts in 1994 and 1995. Also, three roost sites designated "important" in 1994 were used by fewer storks in 1998, probably because the area had been modified structurally or hydrologically since 1994. Seasonal use of roosts was observed, but only to a limited degree. Two of the roosts exhibiting seasonal use (65, 146; see Table 4) would have been classified as important (over 20 storks/survey) if only the active portion of the season was considered. Generally, the roosts used more frequently in the autumn period were in the northern half of the Georgia coastal zone and roosts used later were in the southern portion of the coastal zone. Thus, there was possibly a southerly movement of storks through the coastal zone as the fall/winter temperatures dropped.

According to the habitat management guidelines for this endangered species (Ogden 1990), almost all of the roosts monitored in 1998 would be classified as "important", given in that all surveyed roosts, except two, have been used in several years. Also, 32 (52%) of these roosts had over 24 storks present at least once during the 1998 surveys. Our analytical approach in this study was hierarchical, using average numbers of storks to emphasize relative importance of roosts. During any of our aerial surveys, approximately 60% of the storks observed were found in less than 20% (N = 11) of the survey roosts. These sites should be targeted for protection because of their continuous use by large numbers of storks.

Many of the roosts receiving intermittent or occasional use by small numbers of storks were probably locations where storks waited for water levels in nearby tidal creeks to drop to allow foraging. It is likely that storks roosting near such feeding areas later returned to a larger, primary roost that may have offered

Table 6. Wood Stork foraging flight and site characteristics from three important coastal Georgia roosting sites in 1997.

	Roost Sites			
	Priest Landing (N[b] = 9)	Jekyll Island (N[c] = 12)	Harris Neck[a] (N = 3)	Total (N = 24)
	Median (range)	Median (range)	Median (range)	Median (range)
Direct distance (km)	0.6 (0.3-11.0)	0.5 (0.5-3.6)	2.4 (0.9-2.5)	0.5 (0.3-11.0)
Flight time (min)	3 (1-52)	1 (1-11)	6 (2-12)	1 (1-52)
Wading birds already present:				
Wood Storks	2 (0-29)	15 (1-23)	0 (0-0)	3 (0-29)
Great Egrets (*Ardea alba*)	0 (0-5)	10 (0-10)	1 (1-4)	3 (0-10)
White Ibis (*Eudocimus albus*)	0 (0-25)	0 (0-0)	0 (0-0)	0 (0-25)
Snowy Egrets (*Egretta thula*)	0 (0-20)	0 (0-0)		0 (0-0)
Total	25 (0-53)	25 (0-33)	1 (1-4)	25 (0-53)

[a]Storks were followed from two roost sites on Harris Neck NWR.

[b]Four flights were to the same foraging site.

[c]Ten flights were to the same foraging site.

more protection or shelter in cool or windy periods, and which would explain the prevalence of enclosed wetlands at important roosts. The reasons that these locations were utilized extensively while other portions of the coastal zone had no important roosts were not clear. It is possible that these types of enclosed wetlands were limited, or that these roosts were surrounded by higher quality foraging habitat. Our examination of habitat abundance surrounding larger vs. smaller roosts did not indicate a difference in available foraging habitats at the landscape level, but the quality of these foraging habitats were not assessed. All roosts surveyed were adjacent to or near (<100 m) salt marsh habitat.

Following storks from coastal roosts to foraging sites indicated that they typically flew to tidal creeks in salt marshes within two km of their roost. Average foraging distances during the non-breeding period, when individual storks are only meeting their own energetic demands, were much lower than foraging distances during the breeding season, when parents must supply food to growing nestlings.

Just as storks followed from the same roost frequently fed in the same foraging site, individual (radio-tagged) storks often returned to the same site to feed. Followed Wood Storks typically landed to forage in wetlands where storks and other wading birds were already present. Both suggest that storks utilize roost locations because they are in close proximity to good foraging habitat and/or as a "central place" from which they can use other storks/waders to locate good feeding areas.

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