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Parental Activities of Nesting Wood Storks Relative to Time of Day, Tide Level and Breeding Stage

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Abstract.—In 1995, parental activities of Wood Storks (*Mycteria americana*) were monitored in three coastal colonies during a series of 24-h long observation periods to document attendance, foraging, and other activities in relation to time of day, tide level, and breeding stage. During 5,400 nest-hours of observations, nest attendance declined and feeding rates increased with nestling developmental stage. Although some feeding arrivals occurred during darkness, the great majority of arrivals (including feeding) occurred during daylight periods. Mean times of return from feeding trips varied significantly among colonies and nestling developmental stages. Feeding arrivals were linked to tides, suggesting that most foraging occurred during the preceding low tide period. Inter-colony variation in foraging arrival times and interactions with tides were likely associated with differences in proximity to foraging sites and availability of both tidal and non-tidal (freshwater) foraging habitats. *Received 17 June 2004, accepted 20 October 2004.*

Key words.—attendance, coastal, feeding, foraging behavior, *Mycterica americana*, parental activities, tide, time of day, Wood Storks.

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Parent birds must make decisions concerning their activities on the basis of their energetics and those of their growing nestlings. The availability and abundance of prey and other parental duties (nest building and defense, incubation, brooding) must also be considered. Lack (1968) identified availability of food resources as one of the primary selective pressures shaping patterns of avian parental effort. Size of prey items, distance of food sources, food abundance and time of day all influence prey capture-rates of nesting birds and affect their activity patterns. Laying dates, clutch sizes, patterns of egg and nestling care, and composition of diet suggest an adjustment of parental effort to balance parental capacity (maximum effort) with environmental opportunity (Drent and Daan 1980).

Wading birds (Ciconiiformes) have diverse foraging behavior and utilize a multitude of aquatic and terrestrial foraging habitats (Kushlan 1978). Several wading bird species are known to be predominantly nocturnal in their foraging, especially in coastal environments (McNeil *et al.* 1993). Coastal wading bird species tend to synchronize their foraging activities according to prey availability, which is generally linked to low tide levels, regardless of time-of-day. The Wood Stork (*Mycteria americana*) has been reported to forage nocturnally in both coastal and inland environments in the non-breeding season (Bryan *et al.* 2001). In coastal regions, this species tends to forage almost exclusively in tidally influenced habitats during the non-breeding season (Bryan *et al.* 2002), but utilizes both freshwater wetlands and tidal salt marshes when breeding (Gaines *et al.* 1998, 2000). Temporal availability of these foraging habitat types is very different, with prey availability occurring seasonally in freshwater wetlands and daily (tidal) in estuarine wetlands (Odum *et al.* 1995). Parents must make decisions concerning their feeding efforts and activities based on the availability of prey in these foraging habitats.

Published accounts of the attentiveness and parental activities of nesting Wood

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Storks are few. Clark (1979) described the time budget of a single nesting pair of storks in eastern Florida, finding that attentiveness declined and time spent foraging (to feed young) increased as the nestlings became older. In east-central Georgia, parents met the increased demand for food of their growing young by foraging simultaneously, and by individual parents increasing the number, rather than duration, of foraging trips (Bryan *et al.* 1995). Neither of these studies occurred in a coastal setting or included analyses relative to tides. In 1995, we observed nesting storks in three coastal colonies during 24-h observation periods to (1) document and compare attendance and activity patterns of nesting storks among colonies, (2) examine the effect of time of day and breeding stage on activity patterns (and determine the prevalence of nocturnal activities by parent storks), and (3) examine the effect of the tidal cycle on activity patterns, particularly foraging.

METHODS

This study was conducted at three Wood Stork colonies in the coastal zone of Georgia. One colony was at Woody Pond (31°37.79'N, 81°16.50'W) on the Harris Neck National Wildlife Refuge, a large estuarine island between the South Newport River and Sapelo River. Storks in this colony foraged in a mixture of salt/brackish water and freshwater habitats, including freshwater impoundments managed by refuge personnel (Gaines *et al.* 1998). The second colony was at a freshwater impoundment on St. Simons Island (31°16.40'N, 81°21.20'W), a large barrier island approximately ten km east of Brunswick. Storks from this colony tended to forage more in freshwater wetlands than saltwater wetlands. The third colony was at a small wetland on Black Hammock (31°02.23 N, 81°30.82'W), a large estuarine island approximately 15 km south of Brunswick. Wood Storks from this colony forage more in saltwater wetlands than freshwater wetlands.

Activity patterns of parents attending a sample of nests in the three colonies were documented throughout the nestling season during 1995. Observations were initiated just prior to hatching at all sites. We monitored 19 nests at Harris Neck (six natural, 13 on artificial nest substrates), 15 nests at Black Hammock, and 13 nests at St. Simons Island. Nests were monitored from observation platforms on the edge of each colony with 10 ¥ 40 binoculars and 20-60× spotting scopes. Nocturnal observations were assisted by use of Star-Tron Mark 404 night vision systems. Attendance, arrivals and departures were recorded during five or six, 24-h observation periods (1200 h-1200 h) approximately evenly distributed throughout the developmental period in each colony. Observation periods of 24 h at Harris Neck were started on 25 April, 8 and 30 May, 13 and 27 June, and 11 July. St. Simon's Island observation periods were initiated on 2 and 22 May, and 7, 14, and 28 June. Observations at Black Hammock were initiated on 15 and 23 May, 8 and 20 June, and 5 July.

Parent Wood Storks were not studied during the courtship phase (during copulations) and not sexed. Therefore, data represent combined behavioral information for nesting pairs rather than individual storks. By noting what a parent did upon returning to the nest, an activity (foraging, watering, nest material or unknown) was assigned to each trip. For example, a trip that ended by an arriving stork regurgitating food to its nestlings after a 3-h absence was categorized as a foraging trip.

Activity budget variables analyzed included nest attendance (one parent, both or none present) and number of trips per 24-h period (feeding only), and were analyzed relative to colony, time of day, and developmental stage of the nestlings. Developmental stages were young nestling (hatching to 28 days), old nestling (28 to 50 days), and flying young (>50 days). The timing of nest arrivals was also examined relative to tide level. Tide levels used for Harris Neck were from a NOAA gauge on the South Newport River (31°37.98', 81°16.00') and levels for St. Simons and Black Hammock were from a gauge at the St. Simons Island lighthouse (31°07.90', 81°23.80').

Methods provided by Batschelet (1981) for circular variables were used to investigate the effects of time of day and stage of tide on arrival occurrence and type. Arrival times were converted to degrees by calculating a fraction of the day represented by the arrival time (i.e., time-of-arrival in minutes divided by the total minutes in a day) and multiplying by 360. For tide, times of high and low tides during all observation periods were obtained and the same procedure was followed as for time of day, except that the fraction of the total tidal cycle (from low tide to low tide measured in minutes) associated with each arrival was multiplied by 360. As measures of the mean location and degree of clustering of arrivals in relationship to time and tidal stages, the direction (ö) and length of the mean vector (r) for each nest was calculated (0 to 1, with an r value of 1 indicating complete clustering at one point), respectively. A second-order Hodges-Ajne test (Ajne 1968; Hodges 1955) was used to test the null hypotheses of random distribution of arrivals at nests in relationship to time of day and tidal stage. Second-order Hodges-Ajne tests were conducted for feeding and all other trip types combined for each colony-developmental stage combination, except when fewer than ten arrivals for the combination were recorded. Trip types other than feeding were combined into one category for statistical analyses to increase sample size. Mean vectors for individual nests at each colony were used to avoid pseudo-replication within colonies. Because tests for different trip types and different stages of development were not independent, a sequential Bonferroni correction across tests within each colony was conducted to maintain the overall $P < 0.05$ for significance.

A mixed models approach to repeated measures ANOVA was used to investigate relationships among nestling developmental stage, colony, nest attendance, feeding frequency and arrival timing (both in relationship to time of day and tidal stage). In all models, nestling developmental stage was used as a repeated measure. Feeding frequency was expressed as feeding arrivals per 24-h observation period at each nest; the frequencies of other arrival types were not analyzed because of small sample sizes for many stage-by-colony

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combinations. A variance/covariance structure with compound symmetry or unconstrained variance-covariance structure was included in the model as the error term when a null model log likelihood test indicated a significant ($P < 0.05$) increase in model fit when variance was modeled. To accommodate the circular nature of the time of day and tidal stage data, *x* and *y* coordinates of the end of the mean vector for each nest were analyzed separately. Overall, six analyses (nest attendance, feeding frequency, and *x* and *y* coordinates for time and tide stage) were conducted on measures from the same nest. To maintain the experimental wide error rate at $P < 0.05$, individual tests were considered significant at $P < 0.01$.

RESULTS

From the early stage of nestling development in early May through to the fledgling stage of development in late June, the percentage of time at least one parent attended the nest dropped significantly ($P < 0.001$) from ~90% to ~5% of the observation time (Table 1). The slightly lower nest attendance at the St. Simons colony during the early and late nestling stages was not significant. In general, the presence of both parents at the nest was rare during the nestling period. During the late nestling stage, when nests were unattended from 50% to 77% of the time, lack of attendance was concentrated between sunset and sunrise.

Accompanying the decrease in nest attendance with nestling stage was a significant ($P < 0.001$) increase in feeding arrival frequency (Fig. 1). This increase in feeding was similar among all colonies and involved a more than doubling of feeding arrivals from the early nestling stage to the fledgling stage.

In general, arrivals at nests were strongly concentrated during daylight hours (Table 2), with few arrivals at night (Fig. 2a). During all nestling developmental stages at all colonies, feeding arrivals were significantly clustered ($P < 0.02$ for all individual tests; $P < 0.05$ after Bonferroni correction for multiple comparisons) in relationship to time-of-day (daylight hours) (Fig. 2b). Additionally, when all other arrival types were considered, they were also significantly clustered in daylight hours ($P < 0.001$ for individual tests; $P < 0.05$ after Bonferroni correction for multiple comparisons) for most developmental stage by colony combinations with the exception of early nestling and fledgling stages at St. Simons. At St. Simons, arrivals other than feeding were not significantly clustered after a Bonferroni correction and testing was not conducted during the fledgling stage because of the low sample size.

Only peak feeding arrival times showed variation among colonies and developmental stages. There was a significant ($P < 0.001$) interaction between colony and developmental stage for *x*-coordinate of the mean vectors of individual nests. In general, each colony showed a different pattern of change in feeding arrival times with stage (Table 2). Mean time of return from feeding trips for Black Hammock shifted from mid-afternoon during the early nestling stage to near noon

Table 1. Nest attendance by parent Wood Storks during different nestling developmental stages at three colonies on the coast of Georgia, USA. Attendance was measured as the percentage of time out of a 24-h period that one, two or no parents were present at the nest.

		Mean ± SD	%time with number of adults at nest	
Colony	Nestling stage	0	1	2
Black Hammock	Early	5.6 ± 4.1	86.4 ± 5.5	8.0 ± 4.2
	Late	50.5 ± 5.7	49.1 ± 5.7	0.5 ± 0.2
	Fledgling	93.4 ± 3.0	6.5 + 3.0	0.1 ± 0.1
Harris Neck	Early	3.9 ± 2.3	92.1 ± 3.2	4.0 ± 2.5
	Late	59.9 ± 7.4	39.5 ± 7.3	0.6 ± 0.3
	Fledgling	91.9 ± 3.5	8.1 ± 3.5	<0.01 ± <0.01
St. Simons	Early	16.0 ± 5.2	83.6 ± 5.2	0.4 ± 0.1
	Late	77.0 ± 6.0	22.7 ± 6.0	0.3 ± 0.2
	Fledgling	93.2 ± 4.9	6.8 ± 4.9	<0.01 ± <0.01

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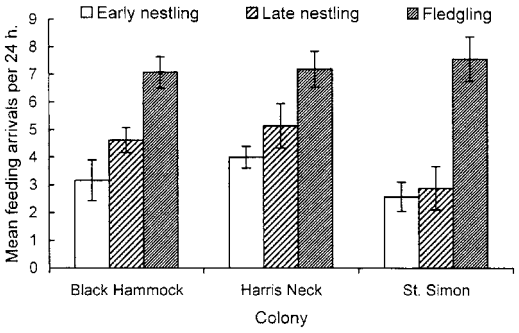


Figure 1. Change in mean number of feeding arrivals per 24 h period with nestling developmental stage at three Wood Stork colonies on Georgia's coast. Error bars are ±1 SE.

for later stages of development. In contrast, mean time of return from feeding trips for Harris Neck shifted from near noon to mid-afternoon with nestling development. St. Simons mean feeding times shifted from mid-afternoon to before noon, and then back to mid-afternoon as nestlings developed (Table 2). For other arrival types there were no significant differences in mean arrival times among colonies or developmental stages after correction for lack of independence.

In relation to tide, feeding arrivals were significantly clustered ($P < 0.01$ to 0.001 for individual tests; $P < 0.05$ after Bonferroni correction for multiple comparisons) during incoming tides for all developmental stages at all colonies except during early stages at Harris Neck and St. Simons (Fig. 3). A concern was that the observation period spacing (approx. every 2+ weeks) may not represent all combinations of time of day and tidal stage times and thus might bias analyses by tide. Although all combinations were not represented, Fig. 4 indicates the broad coverage of tidal stage times including nocturnal incoming tide stages and, in combination with Fig. 2B, provides further evidence of the association between incoming tide stages and feeding arrivals. Clustering of other arrival types in relation to tide was rare, with only arrival types other than feeding significantly clustering during the late nestling and fledgling stages at Harris Neck ($P < 0.02$ and $P < 0.001$, respectively). Because arrival types other than feeding generally did not cluster in relationship to tide, we did not test for differences among stages and colonies. There was a significant interaction ($P < 0.01$) between colony and developmental stage in tide conditions at the time of feeding arrivals. This interaction was due to a predominance of feeding arrivals during high tides throughout early development at the St. Simons colony while feeding arrivals occurred mainly during incoming tides for all other stages of development at all colonies (Fig. 3).

Table 2. Mean arrival time of day, with standard deviation (SD), and degree of clustering (*r*) in parentheses for Wood Storks in three colonies in coastal Georgia. Values are given for arrivals associated with feeding, delivery of nest material, watering and all arrivals other than feeding (all others). Only estimates for sample sizes > 10 are given. Second-order Hodges-Ajne tests were used to test the null hypothesis of random distribution of arrivals in relationship to time of day for feeding and all other arrivals combined; in all cases, except other arrivals during the fledging stage at St. Simons (when sample size prevented testing), arrival times were significantly clustered ($P < 0.05$) after sequential Bonferroni correction for multiple comparisons within the same colony).

		Trip type			
Colony	Stage	Feeding	Nest material	Watering	All others
Black Hammock	Early nestling	15:46 (4:11, 0.40)	08:41 (1:27, 0.93)	13:48 (2:06, 0.85)	11:20 (4:17, 0.50)
	Late nestling	12:32 (4:01, 0.45)	10:40 (2:15, 0.82)	13:33 (2:12, 0.83)	12:15 (3:13, 0.70)
	Fledgling	12:38 (2:52, 0.72)	11:21 (3:22, 0.61)		13:20 (1:40, 0.60)
Harris Neck	Early nestling	12:27 (3:30, 0.58)	10:12 (2:28, 0.79)	14:12 (1:22, 0.94)	11:50 (3:33, 0.71)
	Late nestling	13:53 (4:01, 0.44)	10:40 (2:16, 0.82)	14:11 (1:04, 0.96)	11:52 (4:03, 0.57)
	Fledgling	14:11 (3:32, 0.57)			09:51 (3:17, 0.66)
St. Simon	Early nestling	13:26 (4:17, 0.37)	11:13 (3:10, 0.66)		10:43 (3:55, 0.59)
	Late nestling	11:44 (3:53, 0.48)	09:15 (2:39, 0.76)		10:59 (3:19, 0.69)
	Fledgling	14:39 (3:36, 0.55)	09:46 (1:45, 0.89)		12:10 (3:50, 0.49)

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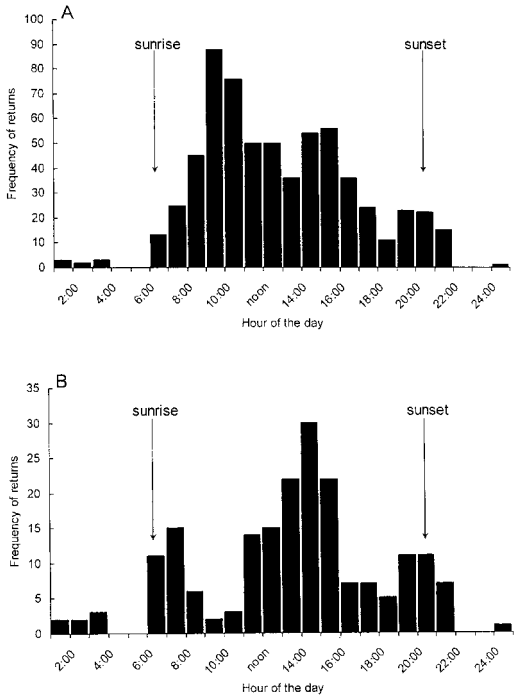


Figure 2. Distribution of arrival times at three coastal Wood Stork colonies on the Georgia coast, during the three nestling developmental stages combined in 1995: A.) All trips combined; B.) Feeding trips only. Sunrise and sunset (arrows) are means for the nesting period of 1995.

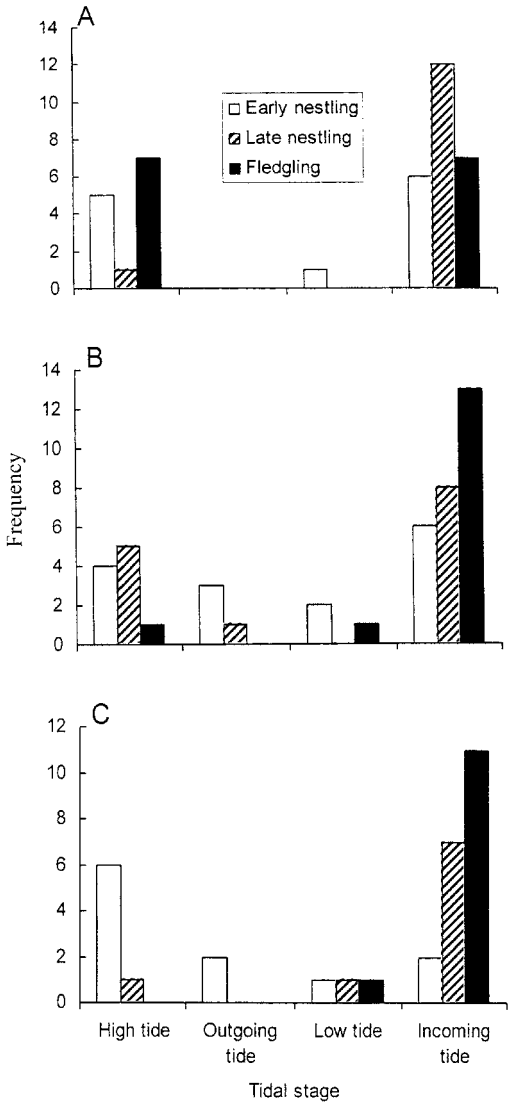


Figure 3. Frequency of feeding arrivals of parent Wood Storks in relationship to tidal stage and nestling stage at three breeding colonies along the Georgia coast (A—Black Hammock, B—Harris Neck, C—St. Simons).

DISCUSSION

Wood Storks have expanded their breeding range northward over the last 30+ years to include coastal habitats in Georgia and South Carolina (USFWS 1996) where they utilize both fresh- and saltwater foraging habitats. However, the temporal availability of these habitats differs considerably with freshwater sites having a seasonal drawdown and saltwater sites with a twice-daily (tidal) drawdown. Nesting storks must adapt their other parental duties (incubation, brooding, shading, nest defense) to the availability of prey resources.

Foraging habitat studies (diurnal) during the breeding season for these same three stork colonies indicated varied use of both fresh- and saltwater (tidal) systems (Gaines *et al.* 1998, 2000). Inter-colony differences in use of freshwater prey among coastal colonies within single breeding seasons have also been documented (Bryan and Gariboldi 1998; Romanek *et al.* 2000). Foraging in tidal systems was linked to low tide periods and freshwater systems were used during periods when water levels in the salt marshes were presumably too deep for effective stork foraging. Habitat diversity, habitat distribution in relation to the colony and tidal stage all interacted as important variables in stork foraging habitat use by individual colonies in the coastal environment. Also, the availability of freshwater systems can be affected by annual rainfall patterns and can re-

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sult in annual shifts between the two habitat types (Gaines *et al.* 2000).

Arrivals after foraging at all colonies were most common in daylight hours, but differences were observed in mean foraging arrival times among colonies and breeding stages. Overall, there tended to be concentrations of foraging arrivals in early morning, mid-day and late evening (see Fig. 2b). The observed differences among colonies may be associated with variation in foraging habitat proximity and availability and their effects on foraging travel. Unlike foraging strategies of coastal Wood Storks during the post-breeding season (Bryan *et al.* 2001), nesting storks from these three colonies did not appear to regularly depart for and/or arrive after foraging trips during the nocturnal period, although a few such arrivals were observed. Nocturnal low tides were available (Fig. 4), but their utilization did not result in nocturnal arrivals at and departures from the colonies. However, this does not imply that storks were not foraging nocturnally. Storks may have flown out of the colony during diurnal hours to roost and await better foraging conditions (low tide level) in the estuaries. Wood Storks from Black Hammock, where nocturnal activities of parents were more prevalent, typically foraged more in tide-influenced wetlands than non-tidal freshwater wetlands (Gaines *et al.* 1998, 2000). Clark's (1979) observations of one pair of nesting storks in eastern Florida did not suggest nocturnal activities were occurring.

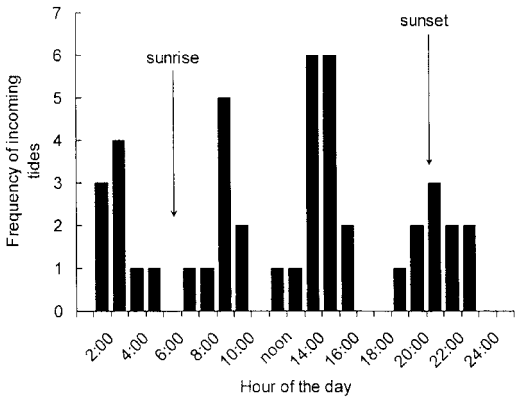


Figure 4. Frequency of incoming tides at all three stork colonies as a function of time of day during this study. Sunrise and sunset (arrows) are means for the nesting period of 1995.

Feeding arrivals were significantly clustered during incoming tide periods, suggesting that low tide events were extensively utilized for foraging. Since these were nest observations, it is not known which portion of the low tide events (late outgoing, low, early incoming) were being utilized by storks. Distances of these foraging trips from the colony, and their effects on foraging travel time, were not known. Breeding storks typically foraged at greater distances than roosting (non-breeding season) storks in the coastal environment (Bryan *et al.* 2002). Another confounding effect was the use of freshwater wetlands during periods of higher tide levels.

A significant interaction between tide and breeding stage was found, but this was largely an artifact of a trend at one colony (St. Simons) during one breeding stage (early). This interaction was linked to feeding arrivals associated with high tides at that colony and stage, as compared to the other study scenarios (Fig. 3). During that stage there was a cluster of arrivals at sunrise at that colony, which coincided with a high tide. Most of the parent storks had departed the previous evening, so they had either foraged during low tide and waited to return or foraged in freshwater wetlands prior to returning. Storks nesting in the St. Simons colony generally foraged more in freshwater habitats than the other two coastal colonies (Gaines *et al.* 1998; Romanek *et al.* 2000).

Overall attendance/activity patterns exhibited by parent storks from the three colonies were relatively similar. As expected, attendance rates declined as the nestlings developed and were better able to thermoregulate and defend themselves. Concurrently, prey deliveries increased from approximately three to over seven deliveries per day as the nestlings underwent the growth associated with the middle and older nestling stages (Kahl 1962). This increased number of prey deliveries is similar to that observed at the Birdsville colony in east-central Georgia (Bryan *et al.* 1995).

This study has demonstrated both similarities and contrasting foraging strategies by

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Wood Storks in the coastal environment during the non-breeding and breeding seasons. During the non-breeding season, activities of storks were predictable and appeared to be driven by the tide cycle, with extensive use of nocturnal low tides and resultant arrivals and departures from their roost. During the breeding season, requirements at the nest and of the eggs/nestlings likely added constraints to activity patterns of parents and may have limited nocturnal arrivals and departures. The tidal cycle still produced two periods of available foraging habitat daily, but demands of the nest and young probably did not allow the parents to use only tidal wetlands to successfully fledge their young. The young may require food during times other than the pulse of prey ability around each low tide. However, we still found an association between foraging arrivals of parents and tide levels, suggesting the utilization of low tide events. The use of freshwater foraging habitat provided parent storks with opportunities to forage without limits due to tidal fluctuations and likely weakened the association of foraging arrivals and tide.

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