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Nocturnal Activities of Post-breeding Wood Storks

A. LARRY BRYAN, JR.,^{1,5} JOEL W. SNODGRASS,^{1,2} JOHN R. ROBINETTE,³ JAMES L. DALY,^{1,4} AND I. LEHR BRISBIN, JR.¹

¹Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, South Carolina 29802, USA;

²Department of Biological Sciences, Towson University, 8000 York Road, Towson, Maryland 21252-0001, USA; and

³U.S. Fish and Wildlife Service—Savannah Coastal Refuges, 1000 Business Center Drive, Suite 10, Savannah, Georgia 31405, USA

ABSTRACT.—Postbreeding season activities of Wood Storks (*Mycteria americana*) were examined during 24 h long observation periods at inland impoundments and a coastal roost site. Storks were

present at inland impoundments and foraged more at night there than at other times of the day. Wood Stork attendance at the coastal roost site was significantly reduced during nocturnal low tides than during daytime low tides or at either period of higher tide levels. Presumably, storks were leaving the roost to forage on fish concentrated in tidal creeks by dropping tides. Nocturnal foraging in freshwater

⁴ Present address: P.O. Box 374, Erie, Colorado 80516, USA.

⁵ E-mail: bryan@srel.edu

TABLE 1. Average number of Wood Storks present and foraging at the Kathwood impoundments in relation to time-of-day^a.

Date	Diurnal		Crepuscular		Nocturnal	
	Total present $\bar{X} \pm SD$	No. foraging storks $\bar{X} \pm SD$	Total present $\bar{X} \pm SD$	No. foraging storks $\bar{X} \pm SD$	Total present $\bar{X} \pm SD$	No. foraging storks $\bar{X} \pm SD$
7-8 Jul 94	56 ± 9	17 ± 19	73 ± 10	35 ± 29	76 ± 2	51 ± 25
14-15 Jul 94	22 ± 13	11 ± 14	29 ± 3	14 ± 13	30 ± 3	16 ± 12
18-19 Jul 94	63 ± 5	18 ± 24	112 ± 3	52 ± 35	107 ± 9	36 ± 32
28-29 Jul 94	59 ± 48	8 ± 19	101 ± 16	10 ± 10	108 ± 4	48 ± 34
1-2 Aug 94	7 ± 6	0 ± 1	43 ± 13	1 ± 2	55 ± 9	26 ± 12
3-4 Aug 94	0 ± 0	0 ± 0	22 ± 19	2 ± 3	33 ± 16	1 ± 4
13-14 Aug 95	20 ± 19	2 ± 3	40 ± 21	8 ± 6	55 ± 2	3 ± 8
27-28 Jul 95	46 ± 13	23 ± 22	58 ± 1	27 ± 16	58 ± 0	20 ± 20
10-11 Aug 95	22 ± 42	12 ± 27	122 ± 50	30 ± 48	156 ± 2	98 ± 44
19-20 Jul 96	8 ± 10	2 ± 3	37 ± 26	12 ± 12	66 ± 4	14 ± 3
Total	28 ± 36	9 ± 28	63 ± 41	19 ± 27	75 ± 38	31 ± 37

^a Time Periods (EST): Diurnal 0800 to 1800 h; Crepuscular 0500 to 0800 h, 1800 to 2100h; Nocturnal 2100 to 0500 h.

and estuarine systems may be an advantageous strategy for the tactile-feeding storks by reducing the likelihood of their being observed by their prey and possibly by reducing competition with other wading birds. Also, some prey species in both freshwater and saltwater environments are more active nocturnally than diurnally, this increasing their likelihood of capture by nocturnal-foraging Wood Storks. In the coastal setting, low tide events (two per ~24 h) typically provide at least one "pulse" of stork prey in draining tidal creeks during the nocturnal period.

Typically, wading birds (Ciconiiformes) forage most actively near dawn and dusk and rest at midday, although night foraging has been documented for several species (Kushlan 1978). Nocturnal activities have not been examined quantitatively for most species (McNeil et al. 1993). Nocturnality, including foraging, has been reported anecdotally for Wood Storks (*Mycteria americana*) (Bent 1926, Coulter et al. 1987, Kahl 1964). Nocturnal foraging is a likely strategy for Wood Storks due to their tactile feeding that does not require them to see their prey (Kahl 1964, Kushlan 1978). The Yellow-billed Stork (*M. ibis*), which also feeds tactilely, is considered "mostly nocturnal" in its foraging habits (Fasola and Canova 1993).

McNeil et al. (1993) suggested three hypotheses for why colonial waterbirds would forage nocturnally. First, nocturnal feeding provides supplemental food when daytime foraging is insufficient to meet energetic demands; second it provides the most preferential (or profitable) foraging opportunities; and third it reduces predation risk.

Here we quantify the prevalence of nocturnal activities of Wood Storks in two settings: inland (freshwater) impoundments and a coastal roost site. Storks used both locations in the late summer and early fall months, after the breeding season was completed. Activity pat-

terns of Wood Storks are assessed in relation to hypotheses proposed by McNeil et al. (1993).

Methods.—The Kathwood impoundments are located in Aiken County, South Carolina (Coulter et al. 1987). Three impoundments (11.3 ha) are stocked with bluegill sunfish (*Lepomis macrochirus*) and brown bullhead (*Ameiurus natalis*) and partially drained to an appropriate depth for stork foraging (15 to 30 cm) during the late summer months. Impoundment fish densities range from 10 to 30 fish/m² when water levels are lowered. The Priest Landing roost site is a 1.6 ha brackish water impoundment partially surrounded by trees on the northern tip of Skidaway Island, Chatham County, Georgia.

Stork presence at the Kathwood Ponds was determined by observations made every 15 min from 1200 h to 1200 h EST during 10 observation periods (Table 1). Total counts of Wood Storks and other wading birds present and numbers of each species actively foraging were recorded at each observation interval. At the Priest Landing roost, storks and other wading birds in the roost were counted every hour from 1200 h to 1200 h in 1994 (09 to 10 August, 29 to 30 August, 19 to 20 September) and 1997 (10 to 11 September, 16 to 17 September, 29 to 30 September, 14 to 15 October).

Observers monitored stork presence or activity from a blind on the edge of each study site. We used 10 × 40 binoculars and a 20–60× spotting scope during the day and a Star-Tron (MK-505) night-vision system at night.

Activity patterns of Wood Storks at the Kathwood impoundments were categorized for three light-related periods: diurnal 0800 to 1800 h EST, crepuscular 0500 to 0800 h and 1800 to 2100 h EST, and nocturnal 2100 to 0500 h EST. Stork presence and activity could not be compared statistically with regard to those periods because the number of storks present was not independent across those periods.

TABLE 2. Results of quadratic regression analyses of the relationships between centered number of storks at roosting and foraging sites, time-of-day, and tide levels.

Source	Coefficient	SE	T	P	R ²
Kathwood Foraging Site/Number of Storks Present					
Constant	-47.66385	2.55681	19.25	<0.0001	0.42
Time	0.11962	0.00486	25.31	<0.0001	
Time × Time	-0.00005	0.00001	26.29	<0.0001	
Kathwood Foraging Site/Number of Storks Foraging					
Constant	-21.37560	2.45211	-8.72	<0.0001	0.12
Time	0.05061	0.00472	10.86	<0.0001	
Time × Time	-0.00002	<0.00001	-10.82	<0.0001	
Priest Landing Roost Site/Number of Storks Present					
Constant	-59.62513	6.11273	-9.75	<0.0001	0.55
Time	0.09797	0.00936	10.47	<0.0001	
Time × Time	-0.00004	<0.00001	-10.47	<0.0001	
Tide	-0.53564	1.24537	-0.43	0.668	
Tide × Time	0.00336	0.00090	3.75	<0.0001	

We used quadratic models to investigate relationships between time-of-day and Wood Stork abundance at both observation sites. Because the mean number of storks at foraging and roost sites varied greatly among observation periods, we centered observations by subtracting the mean number of Wood Storks for an observation period from each observation in that period. For the Kathwood foraging site, we used a simple quadratic equation, with time as the independent variable and centered number of storks present and number of storks foraging as dependent variables. For analytical purposes, time was coded so that 0:00 h was 12:00 noon on the day an observation began and 24:00 h was 12:00 noon on the day the observation was completed. With that coding system, 12:00 midnight fell at the center of the observation period, and if Wood Stork foraging were greater at night, then a unimodal pattern would be expected across the coded time scale.

To assess the potential role of tide at the Priest Landing roost site, we added tide and its interaction with time to the quadratic model as follows:

$$y = \alpha + \beta_1(x_1) + \beta_2(x_1^2) + \beta_3(x_2) + \beta_4(x_1x_2).$$

In the expanded model, y is the number of storks at the roost, x_1 is time, and x_2 is tide level. The parameters β_3 and β_4 related to effects of tide; significance of β_3 indicates change in the y -intercept of the curve as a function of tide, and significance of β_4 indicates a change in shape of the curve as a function of tide. Hourly tide level data were obtained from the NOAA Romerly Creek Station ~1 km from the roost site. For analytical purposes, time was coded so that observation periods ran from 12:00 midnight (0:00 h) to 12:00 midnight (24:00 h) by placing observations from the second 12 h portion of the observation period in front of observations from the first 12 h portion of the observation period. That coding placed the time period of expected highest roost attendance

(and assumed lowest foraging activity) in the middle of the observation period. For both models, we used least-squares methods to estimated parameters values (α and β) and t -tests to test the null hypothesis of parameter estimates equal to zero for all parameters in the models.

Results.—Although Wood Storks were present and foraged during all observation periods at Kathwood, twice as many storks were present during crepuscular and nocturnal periods than during the diurnal periods (Tables 1 and 2, Fig. 1A). Nocturnal foraging also was observed during all 10 periods, but was very limited (averaged <5 storks) during two periods. Analyses of numbers of foraging storks relative to time of day also demonstrated a significant unimodal pattern with more storks foraging at night than other times, although that was a considerably weaker relationship than that for stork presence (Table 2, Fig. 1B).

Wood Storks consistently used the Priest Landing roost in both years of study, with the average number of storks present per hour for the 24 h periods ranging from approximately 30 to 60. Stork attendance was significantly linked to time of day and its interaction with tide, but not specifically to tide (Table 2, Fig. 2). More storks were present in the roost during daylight hours than nocturnal hours (Fig. 3A). During low tide levels (<1.0 m), storks were away from the roost more during the nocturnal hours than daylight hours ($R^2 = 0.42$, $P < 0.00001$; Fig. 3B). During very high tide levels (>2.0 m), storks remained in the roost more at night ($R^2 = 0.41$, $P < 0.0001$; Fig. 3C), although data for the early morning hours (midnight to sunrise) were scarce.

Discussion.—Wood Storks using the Kathwood impoundments were present in larger numbers and foraged as much at night as during other times of day, although the relationship between the number of storks foraging and time-of-day was very weak. Wood Storks appeared to be foraging in 1 to 4 h

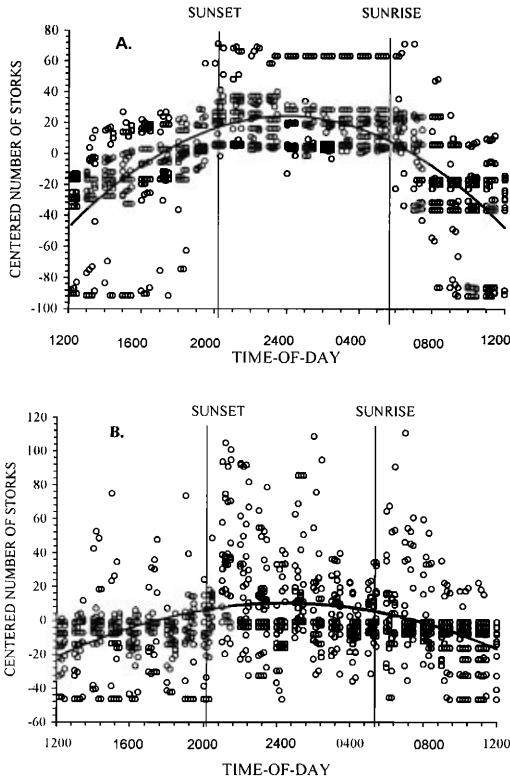


FIG. 1. Fit of a quadratic equation to describe Wood Stork use of the Kathwood impoundments (inland freshwater) relative to time of day: A. Total storks present. B. Number of foraging storks. Because the mean number of storks varied greatly among observation periods, we centered observations by subtracting the mean number of Wood Storks for an observation period from each observation in that period.

bouts interspersed with periods of little or no foraging activity (Fig. 4). Reasons for that periodicity in foraging are not known, although the pulse of foraging activity near sunrise could be linked to the arrival of other wading birds possibly stimulating the storks into activity. Stork attendance at the coastal Priest Landing roost was linked to time of day more so than to tide level, with higher attendance occurring during the day. Storks presumably departed that site to forage in tidal wetlands and tended to leave more when lower tides occurred during the nocturnal period than the diurnal period.

Of the three hypotheses proposed by McNeil et al. (1993) to explain nocturnal foraging in wading birds, predator avoidance is the least likely to contribute to stork nocturnality as free-ranging wading birds the size of storks have few documented predators (Kushlan 1978). Although storks undergo interregional movements (Kushlan 1981), the need for *supplemental*

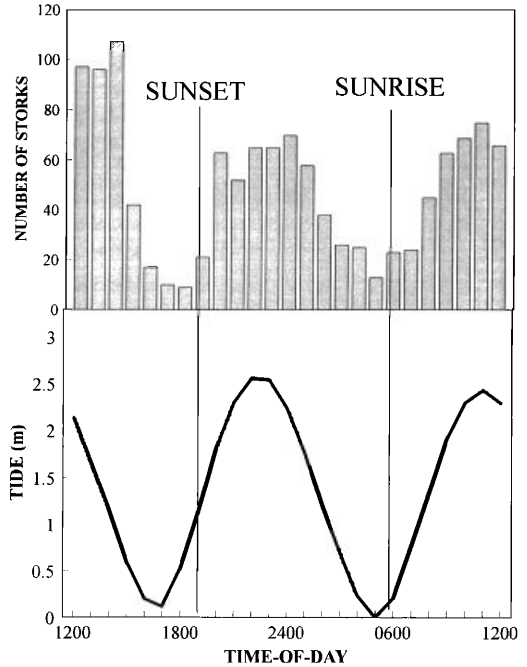


FIG. 2. Wood Stork attendance at the Priest Landing roost site in relation to tide level and time of day on 8 August 1994.

feeding is not thought to be the case here due to their relatively leisurely rate (several days including foraging stops) of travel to overwintering areas (Comer et al. 1987) and the fact that storks soar in thermals while doing so (Bryan et al. 1995). Moreover, the nocturnality observed in this study (August–October) occurred in a season when storks were not preparing for imminent long-distance travel.

Potential reasons for greater foraging success (preferential foraging) during the nocturnal periods are many. Wood Storks feed tactically more so than visually (Kushlan 1979) and should be as successful foraging during the nocturnal period as during daylight hours. Prey within the water column may have more difficulty seeing predatory storks in reduced light conditions. Also, freshwater prey species such as bullheads and catfish are more active nocturnally than diurnally (Darnell and Meierotto 1965) and thus should be more available as prey. Bluegill sunfish move into shallower waters after sunset in response to availability of their prey (Bauman and Kitchell 1974) and changes in dissolved oxygen concentrations, and may be more available as prey during these time periods.

Along the Georgia coast, tidal amplitude can be as great as 3.0 m. All surface water and potential prey in many marsh systems literally drain through one to multiple tidal creeks as water levels drop. Although Wood Storks typically do not forage in flowing fresh-

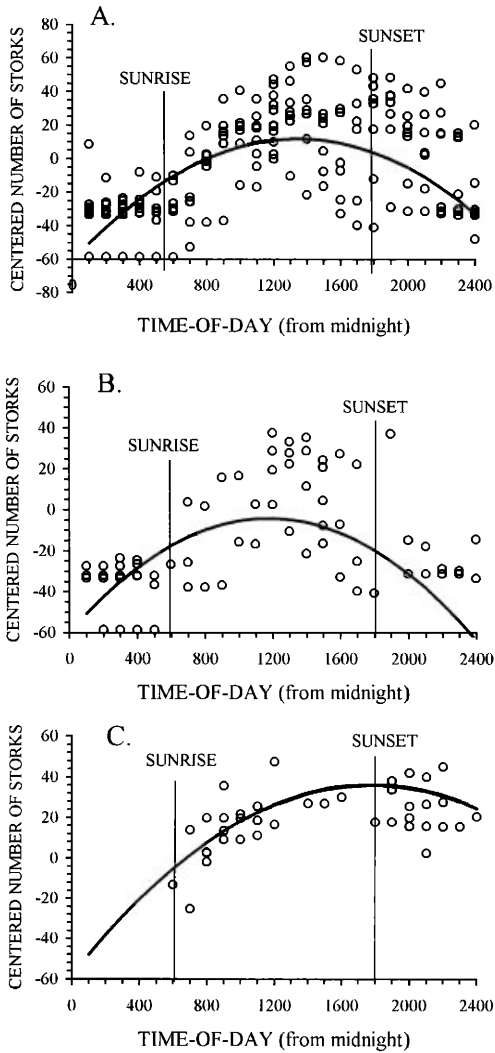


FIG. 3. Fit of a quadratic equation to describe Wood Stork attendance at the Priest Landing Roost relative to time of day: A. All observations ($n = 176$). B. Low tide observations (<1.0 m; $n = 68$). C. High tide observations (>2.0 m; $n = 39$). Because the mean number of storks varied greatly among observation periods, we centered observations by subtracting the mean number of Wood Storks for an observation period from each observation in that period.

water systems (Coulter and Bryan 1993), tidal creeks containing greatly concentrated prey should provide narrow bands of excellent foraging habitat for tactile predators approximately twice every 24 h. Also, prey species in estuarine systems, such as shrimp, are more active nocturnally (Shenker and Dean 1979).

Nocturnal foraging also may be important to storks due to reduced competition with diurnal wading bird

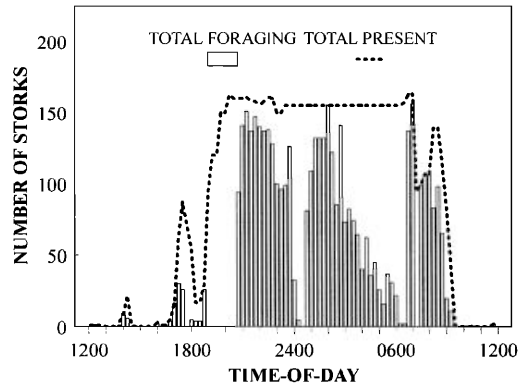


FIG. 4. Number of Wood Storks at the Kathwood impoundments on 17 to 18 July 1994. Foraging bouts (1 to 4 h long) were observed in all ten 24 h observation periods.

species. Great Egrets (*Ardea albus*) are the second most common wading bird using the Kathwood impoundments (after Wood Storks) and fed exclusively between sunrise and sunset on the impoundments. However, the interactions and competition between those two species require additional study. In the coastal roost, night herons (*Nycticorax* spp.) and Great Blue Herons (*Ardea herodias*) departure times typically approximated those of storks whereas Great Egrets and White Ibises (*Eudocimus albus*) tended to depart and return to the roost in the daylight hours.

Both sites were monitored for Wood Stork activity during the nonbreeding season and many of the study birds were prebreeding age (<3 years of age). Therefore those birds were fulfilling only their own energetic needs and were not constrained by attendance or energetic requirements associated with rearing young. The decision to forage actively was linked to the period when foraging conditions were probably optimal in regards to prey abundance, "catchability," and reduced competition. Maximizing foraging efficiency increases survival and the ability to reproduce successfully (Krebs 1978). Increased foraging efficiency through nocturnal foraging enhances the ability of adult storks to recover from the rigors of the breeding season and aides younger birds in their attempts to develop foraging skills for survival and eventually reach breeding age.

An appreciation of the high degree of nocturnality of those storks during the postbreeding season can help to insure efforts to define and protect critical foraging habitats used by storks. A reassessment of the degree to which certain proposed nighttime human disturbances or activities (e.g. dredging, fishing, and shrimp-ing) might negatively affect the foraging of Wood Storks in the area is needed, as well as the methods by which wetland systems are monitored for stork use.

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Timing of Breeding Range Occupancy Among High-latitude Passerine Migrants

ANNA-MARIE BENSON^{1,3} AND KEVIN WINKER²

¹Alaska Bird Observatory, P.O. Box 80505, Fairbanks Alaska, 99708, USA; and

²University of Alaska Museum, 907 Yukon Drive, Fairbanks Alaska, 99775, USA

ABSTRACT.—The brief subarctic summer limits the time available for birds to complete their reproductive activities, yet the temporal requirements of high-latitude passerine migrants are not well understood. Our analyses examined the timing of spring and au-

turn migration among 18 passerine species to obtain indirect estimates of the time they occupy their breeding ranges in northwestern North America. From 1992 to 1998, the Alaska Bird Observatory (64°50'N, 147°50'W) banded 31,698 individuals during the most intensive standardized mist-netting study ever conducted in subarctic North America. Among the migrants examined, the estimated num-

³ E-mail: ambenson@alaskabird.org