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THE USE AND FUNCTION OF GREEN NEST MATERIAL BY WOOD STORKS

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ABSTRACT.—Wood Storks (*Mycteria americana*) add greenery to their nests prior to egg deposition, and new additions decrease as the nestlings mature and develop self-thermoregulation at 1–2 weeks of age. With time, the accumulated nest greenery becomes coated with guano and matted down to conform to and line the inner surface of the nest. Wood Storks use many plant species to line their nests. We demonstrate that the greenery functions to insulate nest contents in a rather porous, twig structure. Nest greenery probably does not function to repel nest ectoparasites of Wood Storks. *Received 5 Oct. 1987, accepted 25 Feb. 1988.*

Several avian species, including Wood Storks (*Mycteria americana*), place green plant material in their nests (Holt and Sutton 1926, Bent 1926, Howell 1932, Matray 1974, Wimberger 1984). Although green material probably serves a function similar to the rest of the nest twigs, its specific role in Wood Stork nests is uncertain. Proposed functions of greenery include: concealment of eggs and nestlings from predators (Welty 1962, Collias and Collias 1984); shade for eggs and nestlings (Bush and Gehlbach 1979); nest sanitation by covering debris (Orians and Kuhlman 1956, Newton 1979); advertisement of nest occupation (Newton 1979); and insulation of eggs and nestlings from environmental extremes (Mertens 1977, Newton 1979, Collias and Collias 1984). Recently, Wimberger (1984) hypothesized that nest greenery may repel ectoparasites from nestling raptors (also see Johnson and Hardy 1962, Clark and Mason 1985). We know of no studies of variation in use of green plant material in nests in different parts of a species' range, and only one experiment to determine the function of nest greenery (Clark and Mason 1985). Here we identify and compare intercolony variation in use of nest greenery in Florida Wood Stork nests, and we describe the results of two investigations of the possible function of such nest materials.

STUDY AREA AND METHODS

We studied six colonies in north and central Florida (Fig. 1). Location and species composition of the Dee Dot (No. 594004), Little Gator (No. 611024), Lake Yale (No. 612027), Moore Creek (No. 612007), Ochlockonee (No. 592003), and Pelican Island (No. 616007)

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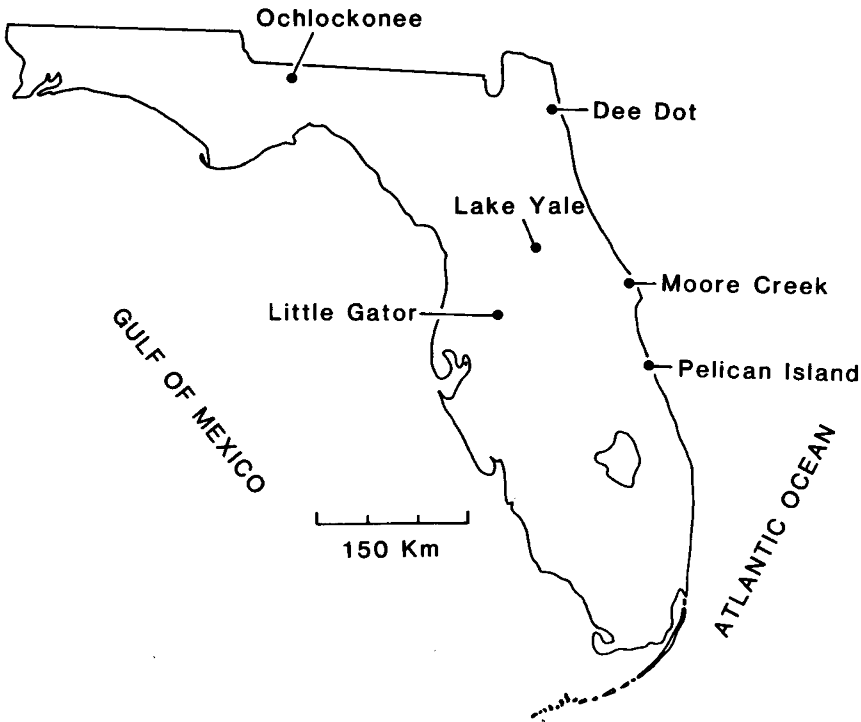

FIG. 1. Wood Stork colonies monitored in north and central Florida.

colonies may be found in Nesbitt et al. (1982) by colony number. Because Wood Storks pruned off leafy twigs, vines, and other herbaceous plants within and surrounding the colonies, it was impossible to quantify the surrounding habitats. However, qualitative descriptions of the habitat types are in Table 1. Colonies were visited every other week during May–June 1985 to identify plant species used in nests. For nest contents not readily visible, a mirror on a 7-m telescoping pole was used to identify nest greenery. Scientific and common plant names follow Kurtz and Godfrey (1962) and Lakela and Long (1970). Similarity in percent of plant species composition between and within colony habitats was calculated using Sørensen's Community Coefficient Index (Mueller-Dombois and Ellenberg 1974): Similarity = $2C/(A + B) \times 100$, where C is the number of species that the two sites share in common, and A + B is the total number of plant species in both colonies.

Common avian ectoparasites (e.g., mites and biting lice) are difficult to use in experiments because of their small size, susceptibility to desiccation away from their host, and the difficulties in counting and collecting them on live nestlings. Therefore, we used dermestid beetle larvae (*Dermestid nidum*) in an ectoparasite repellent experiment. Larval dermestid beetles are known ectoparasites of live Wood Stork nestlings (Snyder et al. 1984) that can cause severe external lesions. At the start of the experiment, 20 larvae (1.5–2.0 cm) were placed in the center of a 42 cm diameter pan (the approximate diameter of the greenery region of a stork nest). Equal amounts of dried carrion (approximately 30 g) were placed at

TABLE 1
VEGETATION OF WOOD STORK COLONIES AND SURROUNDING HABITATS. HABITAT TYPES FOLLOW DAVIS (1967)

Colony	Colony site	Surrounding habitat
Dee Dot	Cypress swamp	Longleaf–xerophytic oak woodlands
Little Gator	Cypress-hardwood swamp	Pine flatwoods–hardwood swamps
Lake Yale	Cypress swamp	Pine flatwoods
Moore Creek	Mangrove swamp	Coastal strand–mangrove swamp
Ochlockonee	Black gum swamp	Mixed hardwood–pine
Pelican Island	Mangrove swamp	Coastal strand–mangrove swamp

opposite sides: one sample was covered with moist paper towels (control), and the other side was covered with an equal amount (about 135 cm^2) of vegetation (experimental) of the plant species that we had earlier determined were most commonly used by storks. The side on which the vegetation was placed was randomly determined for each trial. At 24, 48, and 72-hour intervals, the number of larvae on the carrion at each side were counted. Occasionally, larvae would disappear during the experiment. However, if the total number per pan dropped below 15 larvae, the test run was voided and repeated. Because we could not be certain whether fresh or desiccated vegetation would be responsible for producing repellents, we added one fresh sprig of greenery at each 24-hour interval. Control versus experimental results were tested using the binomial test for small sample sizes (Siegel 1956).

For a nest insulation experiment, two Wood Stork nests (average 75 × 65 cm wide × 20 cm deep) were removed intact from the Dee Dot colony immediately after the nestlings had fledged. These "intact" nests contained both dried greenery and guano. After the experiment described below was run on the intact nests, each nest was then carefully cleaned of all guano and dried greenery to produce the "clean" nests. These clean nests were very porous, but they still contained most of the small finishing twigs similar to the natural pregreenery nests. To reconstruct the "fresh" greenery nests, three small sprigs each of cypress (*Taxodium distichum*), Virginia creeper (*Parthenocissus quinquefolia*), red maple (*Acer rubrum*), live oak (*Quercus virginiana*), wax myrtle (*Myrica cerifera*), poison ivy (*Toxicodendron radicans*), and Spanish moss (*Tillandsia usneoides*) were evenly arranged in the center of the clean nests and lightly pressed flat (approximately 3–4 cm deep). These fresh greenery nests were allowed to air dry for seven days after their part in the experiment to produce the "dried" greenery nests.

The following experiment was conducted on each of these four nest types (i.e., clean, fresh, dried, and intact greenery nests) in the same manner. The nests were suspended 1 m above the ground in an outdoor, shaded, windless site. Three Wood Stork eggs (modal clutch size), blown and filled with paraffin, were placed in the nest and covered with a small, adjustable heating pad such that the upper surface of the clutch reached and stabilized at 39.5°C. This temperature was about 1°C less than the core nesting body temperature of adult storks (Kahl 1963) and represents a reasonable approximation of the temperature of the egg/stork interface. Inside the nest, the temperature at the egg/nest interface was monitored beginning when the ambient temperature was 32°C (approximately 18:00–06:00 EST). The average values for the two nests were used in subsequent analyses. Differences in nest temperature curves were analyzed using the Kolmogorov-Smirnov two-sample test (Siegel 1956).

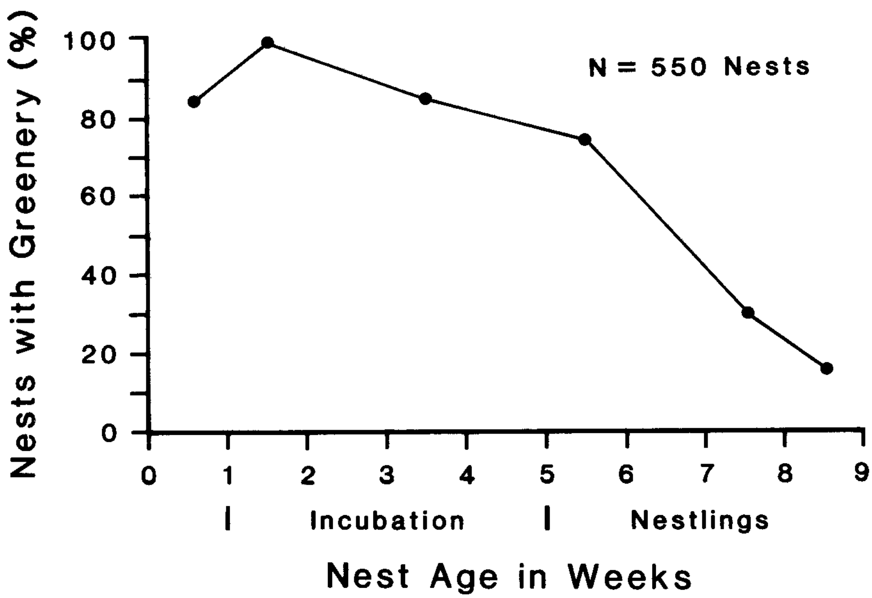

FIG. 2. Percent of Wood Stork nests with greenery material.

To investigate further the insulation properties of Wood Stork nests, the overall thermal conductance (*h*, expressed as W m^{-2} $°C^{-1}$) was determined for each of the above four nest types. The experimental apparatus and calculations are described by Skowron and Kern (1980).

RESULTS

Nest composition.—Wood Storks added green material to the upper surface of the nest after the main structure of dead twigs was completed, but in most cases before the eggs were laid (Fig. 2). Greenery continued to be placed in the nest through the incubation period, especially during nest relief ceremonies. Though greenery occasionally covered the eggs (1.2%; N = 1326 nest visits), we never saw nestlings hidden. By the time the nestlings were two weeks old and covered with thick downy plumage, the frequency of added greenery had decreased (Fig. 2).

Wood Storks used a variety of herbaceous and woody plant species for nest greenery that reflected vegetation both within the colony and surrounding habitat (Tables 1 and 2). In the coastal Moore Creek and Pelican Island nests, typical marine-estuarine vegetation of mangrove and cordgrass (*Spartina alterniflora*) was present. The introduced Brazilian pepperbush (*Shinus terebinthifolius*) and Australian pine (*Casuarina equisetifolia*), characteristic of upland, coastal areas in central and south Florida, were found in nests, even though they do not grow on these islands. In addition, Moore Creek nests might have had more white mangrove (*Laguncularia racemosa*), but a severe January 1985 freeze killed the trees to the high water mark (see Provancha et al. 1986). The use of pigweed (*Amaranthus hybridus*) in nests may reflect its now common status as an understory plant since the mangrove canopy was defoliated.

Of the freshwater swamp colonies, Wood Stork nests at Dee Dot exhibited the most species of plants used for all nests, but Lake Yale possessed the greatest mean number of species per nest (Table 2). Of the three cypress-dominated sites (Dee Dot, Little Gator, and Lake Yale), only Dee Dot nests did not contain a high frequency of cypress. The low use of cypress by storks at Dee Dot probably reflects the poor, stunted tree growth at the site because of impounding for nearly 40 years. The lack of vigorous cypress growth may have forced the storks to prune the surrounding longleaf–xerophytic oak woodland habitat more frequently than at other colonies, thus resulting in the higher number of species used as greenery. Of all the freshwater sites, only the Little Gator nests did not contain wax myrtle, despite its abundance in the surrounding pine flatwoods. At Ochlockonee, where no cypress was present, the storks relied upon black gum (*Nyssa biflora*) as their only nesting substrate and a frequent source of nest greenery. Ochlockonee nests also contained more northern Florida species of vegetation for nest greenery such as loblolly pine (*Pinus taeda*) and southern red oak (*Q. falcata*). All nests at freshwater sites regularly contained Spanish moss.

Greenery was similar in the nests at the marine-estuarine Moore Creek and Pelican Island sites ($S = 63.16\%$; Table 3), but differed from the other four colonies. However, both Moore Creek and Pelican Island possessed relatively low intracolony similarity of nest greenery with nesting substrate vegetation because Wood Storks use the surrounding coastal strand vegetation as a source of nest greenery. Likewise, nests at the four freshwater sites exhibited low to moderate use of within-colony vegetation ($S = 20.00–50.00\%$), whereas storks often used the surrounding upland vegetation as sources of nest greenery ($S = 23.53–63.76\%$).

Ectoparasite repellent experiment.—The results of the nest ectoparasite repellent experiment indicate that dermestid larvae are not repulsed by the most frequently used greenery species (black gum, cypress, red cedar [*Juniperus silicicola*], poison ivy, red maple, wax myrtle, water oak [*Q. nigra*], and Virginia creeper). For three species (black mangrove [*Avicennia germinans*], summer grape [*Vitis aetivalis*], and Spanish moss), there even appeared to be an attraction to the vegetation side of the experimental containers. Thus, these plant species probably do not function in repelling dermestid larvae from Wood Stork nestlings.

TABLE 2

PERCENT USE OF PLANT SPECIES AS GREEN MATERIAL IN WOOD STORK NESTS

Species	Colony					
	Dee Dot	Little Gator	Lake Yale	Moore Creek	Ochlockonee	Pelican Island
Longleaf pine (*Pinus palustris*)	8.8					
Loblolly pine (*P. taeda*)					12.9	
Bald cypress (*Taxodium distichum*)	14.7	88.2	57.4			
Red cedar (*Juniperus silicicola*)				4.3		
Saltmarsh cordgrass (*Spartina alterniflora*)				4.3		10.6
Grass sp. (*Paspalum* sp.)				37.2	2.0	6.4
Spanish moss (*Tillandsia usneoides*)	22.5	23.5	5.9		39.6	
Australian pine (*Casuarina equisetifolia*)				3.2		2.1
Southern willow (*Salix caroliniana*)	1.0	1.2				
Wax myrtle (*Myrica cerifera*)	70.6		38.2	22.3	2.0	
Turkey oak (*Quercus laevis*)					2.0	
Laurel oak (*Q. laurifolia*)		7.1				

TABLE 2
CONTINUED

Species	Colony					
	Dee Dot	Little Gator	Lake Yale	Moore Creek	Ochlockonee	Pelican Island
Water oak (*Q. nigra*)	20.6	1.2	8.8		2.0	
Live oak (*Q. virginiana*)	6.9		60.3		4.0	1.1
Southern red oak (*Q. falcata*)					1.0	
Glasswort (*Salicornia virginica*)				24.5		
Pigweed (*Amaranthus hybridus*)				6.4		
Sweet gum (*Liquidambar styraciflua*)	2.0					
Red maple (*Acer rubrum*)	7.8	64.7				
Brazilian pepperbush (*Shinus terebinthifolius*)						2.1
Poison ivy (*Toxicodendron radicans*)	12.7	2.4				
Dahoon holly (*Ilex cassine*)	2.0		1.5			
Virginia creeper (*Parthenocissus quinquefolia*)	1.0					1.0
Summer grape (*Vitis aetivalis*)	1.0					4.1

TABLE 2
CONTINUED

Species	Colony					
	Dee Dot	Little Gator	Lake Yale	Moore Creek	Ochlockonee	Pelican Island
Red mangrove (*Rhizophora mangle*)						43.6
White mangrove (*Laguncularia racemosa*)				7.4		4.3
Black gum (*Nyssa biflora*)			41.2		96.0	
Water ash (*Fraxinus caroliniana*)		5.3				
Black mangrove (*Avicennia germinans*)				96.8		42.6
Swamp primrose (*Aster dumosus*)	20.6	4.7				
Marsh elder (*Iva frutescens*)						3.2
Number of nests	105	94	68	95	108	80
Number of species of plants	14	9	7	7	9	9
Mean ± SD (species/nest)	1.91 ± 0.98	1.66 ± 0.88	2.15 ± 0.91	1.98 ± 0.77	1.64 ± 0.82	1.35 ± 0.61
Range (species/nest)	0–5	0–4	1–4	0–4	0–4	0–3

TABLE 3

SØRENSEN'S COMMUNITY COEFFICIENT INDEX OF SIMILARITY FOR WOOD STORK NEST GREENERY. INTRACOLONY VALUES COMPARE PERCENT USE OF NEST GREENERY (FROM TABLE 2) WITH FREQUENCY OF TREE SPECIES USED AS NESTING SUBSTRATE, WHILE INTERCOLONY VALUES COMPARE PERCENT USE OF NEST GREENERY BETWEEN COLONIES

	Colony					
Colony	Dee Dot	Little Gator	Lake Yale	Moore Creek	Ochlockonee	Pelican Island
Dee Dot	33.33%					
Little Gator	63.76%	50.00%				
Lake Yale	47.62%	40.00%	25.00%			
Moore Creek	8.34%	0.00%	11.76%	33.33%		
Ochlockonee	34.78%	23.53%	62.50%	10.53%	20.00%	
Pelican Island	8.70%	0.00%	12.50%	63.16%	11.11%	46.15%

Insulation experiment.—The experiment on the insulation properties of Wood Stork nests indicate that the clean nests barely functioned to maintain internal temperatures above ambient temperatures (Fig. 3). The clean nests were able to maintain the internal egg/nest surface temperature only 1.5–2.5°C above ambient temperature during the evening hours. In contrast, the three experimental nests with greenery exhibited higher insulation properties, especially the intact and dried greenery nests. No significant difference existed in the temperature curves between the intact and dried greenery nests ($K_D = 2.5$, $P > 0.05$) or between the dried greenery and fresh greenery nests ($K_D = 5.5$, $P > 0.05$), but the temperature curves for the intact nests were significantly higher than for the fresh greenery nests ($K_D = 7.5$, $P < 0.05$). The temperature curves of all three nests containing greenery (i.e., intact, dried, and fresh) were significantly higher than the clean nests ($K_D = 9.5, 8.0, 7.5$, respectively; $P < 0.05$). The fresh greenery nests had lower insulative value during the early hours of the experiment. This may be due to the initially higher water content of the fresh greenery and resultant greater heat transfer through evaporation. Nevertheless, after drying for more than two hours (initial temperature stabilizing period prior to 18:00 EST plus two hours of experiment), the moisture content and associated heat loss was reduced, and the insulative value was similar to the intact and dried greenery nests by the end of the experiment (Fig. 3).

In a further attempt to determine the insulating properties of the four nest types, they were held at 7.0°C in a refrigerated room. The internal egg/nest surface interface of the clean, fresh greenery, dried greenery, and intact nests stabilized at 11.1°C, 16.3°C, 16.6°C, and 17.5°C, respectively.

Thermal conductance.—The calculated thermal conductance (h) values for the clean, fresh greenery, dried greenery, and intact nests were 9.05

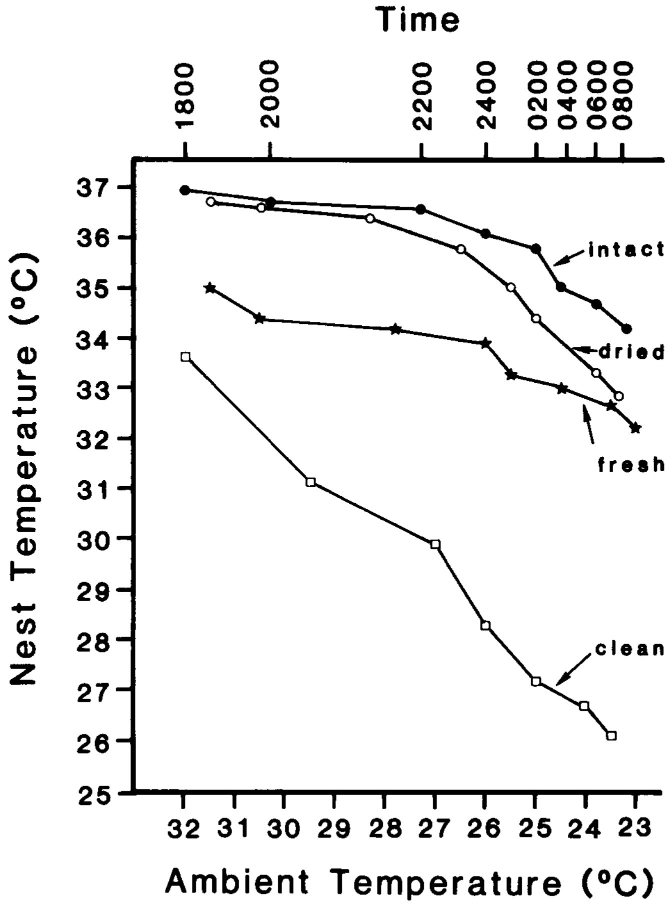

FIG. 3. Comparison of internal nest temperature versus outside ambient temperature for intact nests (solid circles), dried greenery nests (open circles), fresh greenery nests (stars), and clean nests (open squares). Values represent average of two nests, and time is EST.

W m^{-2} °C^{-1}, 6.44 W m^{-2} °C^{-1}, 6.09 W m^{-2} °C^{-1}, and 5.31 W m^{-2} °C^{-1}, respectively. Since the degree of insulation is inversely related to the value of *h*, the intact nest exhibited the greatest insulation properties, while the clean nest possessed the poorest insulation characteristics.

DISCUSSION

Although we observed some Wood Stork eggs that were concealed, few eggs and no nestlings were hidden by nest greenery in a way that would prevent predation. Storks are subject to raccoon (*Procyon lotor*) and Fish Crow (*Corvus ossifragus*) predation, but one adult stork is usually at the nest to defend its contents. Furthermore, as neither eggs nor nestlings usually are covered by greenery material, shading does not appear to be important as suggested for other avian species (Bush and Gehlbach 1979). Parent storks shade the nest contents with their bodies or outstretched wings during warm periods of the day. The development of thick downy plumage and self-thermoregulation by nestling storks at 1–2 weeks of age (see Kahl 1963:149) coincides with the noticeable decrease in the addition of greenery material (Fig. 2).

Adult Wood Storks regularly defecate over the edge of the nest; however, nestlings often defecate in the nest, suggesting the possible role of greenery material in nest sanitation during the nestling period (e.g., Orians and Kuhlman 1956, Newton 1979). Since greenery deposition is initiated prior to egg deposition and declines with increase in nestling age, its sanitation role is at best restricted to the early nestling period when the chicks can not stand off the nest. Nest greenery tends to prevent guano from passing through the nest twigs and thus the nest and nestlings become soiled. This fact reduces the plausibility of the nest sanitation hypothesis with regard to guano. One advantage of greenery may be associated with the feeding of young stork nestlings. Parent storks regurgitate food boluses on the floor of the nest near the young nestlings (Kahl 1964). The nestlings must find and consume the rather small food items. Thus, greenery material retains food on the nest surface for consumption by nestlings and improves nest sanitation by preventing the loss of small food down into the nest during the early nestling phase.

Wimberger (1984) hypothesized that nest greenery use by raptors aids in repelling ectoparasites via release of secondary compounds during drying or decay of the plant material. Clark and Mason (1985) found that European Starlings (*Sturnus vulgaris*) chose plants whose volatile compounds are likely to inhibit arthropod hatching (but not adult stage mites) and bacterial growth. The nature of some of the vegetation used by Wood Storks seems to support this hypothesis (e.g., the aromatic or resinous species in Table 1: cypress, red cedar, poison ivy, Brazilian pepperbush, pine sp., wax myrtle). However, the vegetation species we tested had little effect on dermestids. Wood Stork nestlings are subject to infestation by dermestid larvae (Snyder et al. 1984, pers. obs.), five species of biting lice (Emerson 1972), and numerous species of mites (pers. obs.) further discrediting the effect of nest greenery on ectoparasites. Effect of green vegetation on biting lice, mites, fleas, calliphorid or hippoboscid flies, ticks, fungi, and bacteria should be investigated to clarify this point. Inasmuch as intercolony similarity in use of plant species is low (Table 3), the other nonaromatic or nonresinous plants used for nest greenery probably reflect the most commonly available plants in the surrounding uplands, including the nesting tree.

Nest greenery may function in maintaining the Wood Stork pairbond and structural integrity of the nest. After completion of egg laying, the pairbond must be maintained for about 12–16 weeks in order to fledge the young. Use of ritualized nest-building behavior (Kahl 1972) in the form of returning to the nest and passing greenery probably functions in maintenance of the stork pairbond. Green twigs used to line the upper surface are more pliable than the basal, dead twig structure of the stork nest. After drying, the greenery becomes a rigid, entangled, and relatively smooth surface and may aid in stabilizing the nest structure. Finally, guano-coated twigs are noticeably more rigid and form an adobe-like structure in the upper surface of the nest, further suggesting a role in construction.

Though greenery may serve more than one function, we believe the results of the insulation experiment support a conclusion that the primary function of nest greenery is to enhance insulation of Wood Stork nests, or perhaps of any species with a twiggy, porous nest. Greenery may accomplish this by itself or in combination with guano to plug holes in the nest and prevent loss of heat from the eggs and incubating parent bird. Nest insulation depends on the materials used in its construction, and these materials, in turn, may depend on what is available to the bird (Whittow and Berger 1977, Skowron and Kern 1980, this study). Skowron and Kern (1980) found that the most important aspect of insulation was nest density, whereas Mertens (1977) concluded that dry material provided better insulation than fresh vegetation. Nest greenery, especially when dried and associated with guano, provides material of relatively high density and results in increased insulation of Wood Stork nests. Thus, greenery may be important in reducing the energetic cost of incubation and early brooding.

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