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SPATIAL AND TEMPORAL PATTERNS OF WOOD STORK *MYCTERIA AMERICANA* FECES AND NUTRIENT DEPOSITION IN AN ORINOCO WETLAND OF VENEZUELA

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Abstract. This study estimated, on a landscape scale, the contribution of the Wood Stork *(Mycteria americana Linnaeus)* to nutrient loading and recycling in the Camaguan wetland of the Orinoco lowlands. We tested whether nutrient loading by Wood Storks was a key component of the nutrient dynamic in the wetland with oligotrophic soils. Over the breeding season, the average daily Wood Stork deposition was 79 ± 18 g dry/m^2/d for a density of 0.18 ± 0.06 chick/m^2. The seasonal measured values of excretion production and nutrient loading by storks were linearly compared with the theoretical values as estimated by Hahn's model. Statistical analysis indicates that the model performed well overall. Thus the measured and estimated feces productions were 3777 and 3396 g/m^2/season respectively. The nutrient concentrations (i.e. total N, NH_4-N, NO_3-N, total P, Ca, and Mg) in the feces showed two different patterns over the breeding period. These patterns reflected stork age and diet changes over the season. The total N and P fluxes reached maximum values of 4 g/m^2/d and 84 g/m^2/d, respectively. During the season the observed and modeled N values were 11.5 and 9.0 g/m^2/season, and for P loading, 29.9 and 26.1 g/m^2/season respectively. The three habitat groups corresponding to breeding sites, non-occupied sites, and the herbaceous layer of non-occupied sites were sorted by a range of edaphic variables using Discriminant Analysis. Best predictor variables were soil pH, NH_4-N, exchangeable Ca, and electrical conductivity. Compared with other sources, the nutrient input from Wood Storks was higher than that from meteorological deposition and litterfall. These results were particular to the Camaguan wetland, though they could prove similar in wetlands in other regions where the Wood Stork is dominant. *Accepted 16 November 2010.*

Keywords: biodeposition, Mycteria americana, *Orinoco lowlands, seasonally flooded palm savannas.*

INTRODUCTION

In wetlands, the contribution of birds to nutrient input through feces, egestion, and body decomposition is a key process in biogeochemical cycling between terrestrial and aquatic ecosystems (Gillham 1960, Haven & Morales-Alamo 1966, Frankenburg *et al.* 1967), particularly where birds gather in roosting areas and nesting colonies (Hutchinson 1950, Onuf *et al.* 1977, Bildstein *et al.* 1992, Post *et al.* 1998). Long-term nutrients released from bird feces have been recorded in an abandoned bird rookery of Okeefenokee Swamp (Oliver 1987). Aquatic birds tend to form large aggregations during their breeding seasons, when abundant prey availability occurs in seasonal freshwater wetlands (González 1993, 1997; Gaines *et al.* 1998, Gaines *et al.* 2000). The role of aquatic birds in transporting nutrients to wetlands from other areas, or in recycling nutrients within an ecosystem, is determined to a large extent by their feeding and food locations (Hahn *et al.* 2007).

The effect of bird nutrient input has been studied and modeled throughout a wide range of aquatic systems (Gillham 1960, Sturges *et al.* 1974, Patten 1975, Bayley & Odum 1976, Mitsch 1976, 1983; Hicks 1979, Oliver 1987, Oliver & Legovic 1988, Anderson & Polis 1999, Wait *et al.* 2005, Wetzel *et al.* 2005). This has implications for plant community dynamics and species richness (McColl & Burger 1976, Smith 1978, Nelson 1979, Ryan & Watkis 1989, Mun 1997, Ellis 2005). The redistribution of nutrients in oligotrophic wetlands is a decisive factor in the preservation of vegetation patterns in the Everglades landscape (Wetzel *et al.* 2005). Bird

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feces can also modify the spatial pattern in soil properties. Seabird guano deposition resulted in soil chemical modification on desert islands in the Gulf of California (Wait *et al.* 2005), and during the bird breeding season, nutrient loading in ecosystems led to biomass increases at various trophic levels (Sánchez-Piñero & Polis 2000).

This paper focuses on the contribution of Wood Storks (*Mycteria americana Linnaeus*) to feces and nutrient input in wetlands. Wood Storks can be found in swamps, marshes, and ponds in the southern United States, the Brazilian Pantanal, and as far south as Argentina in South America (Kahl 1964, Black 1977, Bryan *et al.* 2002, Bouton *et al.* 2005). Specifically in Belize, Brazil, the United States, and Venezuela, the Wood Stork is an endangered species due to habitat loss (Custer & Osborn 1977, Luthin 1987, Morales 1990, USFWS 1996, Bouton *et al.* 2005). Bird feces production can be combined with measurement of nutrient concentrations to give an estimate of various nutrient inputs (Hicks 1979, Anderson & Polis 1999, Wetzel *et al.* 2005). Although an increasing number of studies of nutrient loading and transfer is being undertaken at the marine/terrestrial interface (Ellis 2005), or in the freshwater habitat of temperate regions (Hahn *et al.* 2007), the results produced for tropical regions are inconclusive because of diversity in the patterns of nutrient cycling (Begon & Harper 2006). Due to the low number of tropical studies on waterbirds and nutrient budget, the verification of Hahn's model (Hahn *et al.*, 2007) provides an opportunity to estimate the effects of waterbirds and to generalize the model for a wide range of species and environments which are difficult to measure directly. This study aims to close an information gap by contributing data on nutrient loading from Wood Stork colonies, the chemical composition of feces, and feces deposition patterns in the soils of a wetland.

This research was conducted in the Camaguan wetland (19 300 ha) located 35 km north of San Fernando de Apure (Apure State, Venezuela) (Fig. 1)

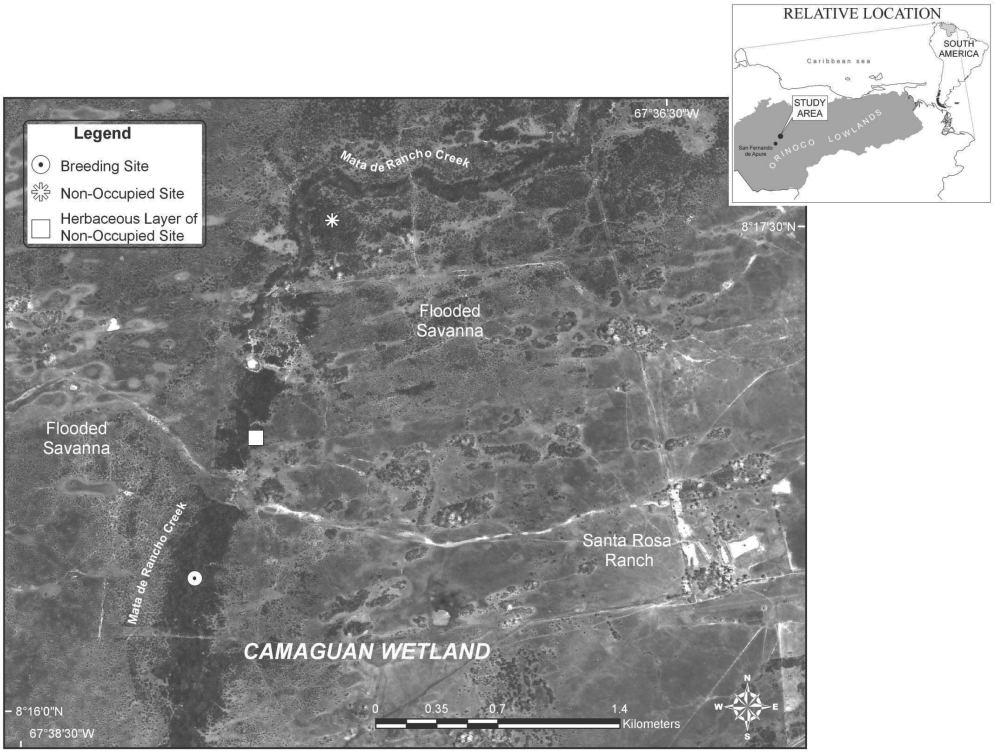

FIG. 1. Location of Wood Stork (*Mycteria americana*) breeding site, non-occupied site, and herbaceous layer of non-occupied site in the Camaguan wetland of the Orinoco lowlands. Image in 2007 from SPOT 5.

in the Orinoco lowlands. This wetland is a Wildlife Refuge (Briceño *et al.* 2005) designated in the year 2000 by the national government to preserve a unique wetland environment with wading and aquatic birds, representing a large portion of the total bird fauna (Pinowski & Morales 1981, Gómez-Dallmeier & Cringan 1989, González 1996a, 1997). It provides habitat conditions suitable for studying large foraging colonies of Wood Storks. However, elucidating the contribution of waterbirds to nutrient loading in wetlands still constitutes a major challenge in landscape ecology (Wetzel *et al.* 2005). Therefore, this study focuses on comparing nutrient loading from breeding Wood Storks with other nutrient sources entering wetland systems and predicting the implications regarding effects on the system. The objectives of this study were to (1) quantify feces and nutrient input from breeding Wood Storks in the Camaguan wetland of the Orinoco lowlands; (2) verify Hahn's model on nutrient loading by birds in a tropical environment in order to provide a sound basis for further application in regional studies; (3) describe the spatial pattern of soil chemistry in relation to breeding storks; and (4) compare the nutrient input of storks with other nutrient sources. We also related these results from the Orinoco lowlands to other wetlands subject to seasonal flooding. In the Camaguan wetlands, with oligotrophic soils, the role of Wood Storks in nutrient redistribution could be a key factor for nutrient hotspots. Such database enrichment will require baseline studies to compare with wetlands that may require restoration to re-establish nutrient redistribution mechanisms.

METHODS

General description of the Camaguan wetland. Research was conducted in the Camaguan wetland Wildlife Refuge, particularly at the Santa Rosa Ranch (8°16'N, 67°36'W) (Fig. 1). This area is located in southern Guarico State, Venezuela. The landscape is an alluvial plain formed during the Holocene. The climate is seasonal with a wet season from April to November, when 98% of the annual mean precipitation (1533 mm) occurs. Monthly mean temperature ranges from 29.0 (April) to 26.5 °C (December). Annual mean pan evaporation is 2280 mm, which reflects a proportion of 2:1 in comparison with rainfall data. The oligotrophic soils are heavily textured leading to poor drainage and an infiltration rate of 1.24×10^{-4} and 4.5×10^{-5} m/s at the surface and deep layers, respectively (Prieto & Lopez-Hernandez 1986). The predominant soils are Vertisols with pH ranging from 4.9 to 7.9; however, in certain areas Entisols (dunes) are found on the surface (Prieto & Lopez-Hernandez 1986). Across the study site, the fluvial dynamic has modulated an undulating relief of *medanos* (sandhills) (Ramia 1967). They are flooded annually by the Portuguesa River and precipitation. Thus the water level reaches 0.1 to 1.5 m from June through December, but the soil dries out from January to March. The vegetation is characterized by bush islands dominated by the palm *Copernicia tectorum* (Kunth) Martius, intermingled with some deciduous shrubs and trees. Woody vegetation density decreases with flooding. In the deepest flooded areas, floating and submerged macrophytes belong to the families Nymphaceae, Lentibulariaceae, and Cabombaceae. The herbaceous matrix is characterized by the families Poaceae and Cyperaceae.

Study sites. The work was conducted on the Santa Rosa Ranch. Three 10-ha sites were selected one km apart (Fig. 1). The first featured the Wood Stork breeding site (i.e., trees with nests). In the same locality, the second site had no storks at all (hereafter referred to as the *non-occupied site*). The third site corresponded to the herbaceous layer of non-occupied site. In each study site, four plots of 123 m x 56 m were selected randomly. The location of each of the four plots was determined using a Global Positioning System (Garmin 12). Distance between plots was at least 150 m. On each plot the tree cover was calculated by taking the elliptical axes from the horizontal projection of the tree canopy.

On the breeding site, nests were located on *menudito* trees (*Lonchocarpus* sp.), often making use of a platform of branches. These trees are a common element in small islands of woody vegetation clustered around the palm tree *Copernicia tectorum*, which were distributed in the herbaceous layer. During the breeding season from November to March, an exhaustive survey throughout the breeding site indicated that Wood Storks were living in a monospecific colony. All nests in and feces below Wood Stork colony trees were produced by that species. However, Wood Storks sometimes do breed among other colonial waterbirds (e.g. *Casmerodius albus*, *Ardea cocoi*, *Bulbucus ibis*, *Egretta thula*, and *Jaribu mycteria*) in the same tree species in other habitats (González 1996b, Perez-Aguilera 1997). Other possible important sources of nutrient input in the wetland, such as houses located around the site and surface runoff in agricultural areas, are precluded

because of the preserved status of the system as a Wildlife Refuge. Furthermore, visitors (i.e., feeding birds) in the stork breeding site were not observed during the period of measurements. The Wood Stork is highly dependent on shallow, declining surface water conditions, which concentrate prey (Ogden 1994, Gawlik 2002). A detailed description of the ecology of the Wood Stork is given by Kahl (1964) and Coulter *et al.* (1999). During the wet season the three sites were connected by seasonal flooded conditions. Structural characteristics of the tree vegetation (i.e., cover and diversity) at the breeding site, non-occupied site, and herbaceous layer of non-occupied site were not significant different (Mann-Whitney U-test in Sokal & Rohlf 1998).

Daily amount of feces input from Wood Storks during the breeding season. On the breeding site, Wood Stork abundance was measured using roadside counts twice per week from the middle of the dry season January 15 to the late dry season February 28. While driving a standard distance of 2 km, using binoculars ensured that the individuals were unaware of our presence. The number of birds observed was used as an index of abundance (Krebs 1972). During 1999, activity patterns of parents attending the colony were observed throughout the nesting season. At the beginning of the dry season, field observations indicated that both Wood Stork parents begin building and maintaining nests of about 1 m^2 on the tree canopy as a loose, bowl-shaped assortment of plant material. During the period November 15-21, each adult female lays from two to five eggs. Incubation duties by both parents take approximately 30 days. After hatching, the chicks are guarded by at least one parent for approximately 33 days. Then parents leave the nest at the same time to forage for young chicks. Fledging occurs in mid-March, and all Wood Storks leave the nest sites after approximately 134 days. Thereafter, the young continued to return to the colony for another 15 days to roost or to get food from their parents. Most of the bird feces were produced by adults during the first four weeks of the breeding season. From four weeks onwards, youngsters apparently produced more feces than adults. At the beginning of the breeding season, 500 nests were randomly selected and marked. At each nest, chicks were counted with a mirror on an extendable pole and their status monitored until fledglings made their first flights. The number of chicks per nest was determined by starting 61 days after hatching to avoid negative human impacts during the critical early stages of nesting and incubation (González 1997).

In each plot of the breeding site, one tree (*Lonchocarpus* sp.) with nests (i.e., breeding site) was chosen at random. At each selected tree, bird nests and chicks were counted and five high-grade plastic sheets (30 cm x 26 cm) were placed at random on the soil and fixed with plastic pins. From January 22 to March 3 1999, the feces (combined excretory products with feces) on each plastic sheet were collected daily during the morning hours (from 09:00 h). Once the feces were collected, the five plastic sheets were placed at random for the next collection time. The collected feces from the five plastic sheets were dried at room temperature for a week. Subsequently, they were dried at 30° C in a vented hood for 24 additional hours and weighed as outlined by Stewart (1973). The total number of samples was 800 (five plastic sheets x four trees x 40 days). During the chick rearing period, the amount of feces deposited was calculated on the basis of the information on number and age of chicks per nest.

Hahn's model (Hahn *et al.* 2007), which elaborated on an excretion production approach, was evaluated on the basis of the measurements conducted in this work. Thus daily and seasonal feces depositions were determined using allometric equations. The loading encompasses the amount of feces deposited by adults ($X_{adult\text{-}feces}$) (eq. 1) and offspring ($X_{offspring\text{-}feces}$) (eq. 3). For the feces deposition by adults, the equation takes the form:

$$X_{adult\text{-}feces} = (M_{feces})\ (T_{nest}) \quad (1),$$

where it is assumed that one adult is present at the nest; M_{feces} is the total daily excrement production from a breeding bird (g/day); and T_{nest} is the duration of the nesting period (days).

The total daily excrement production (M_{feces}) is calculated as:

$$M_{feces} = (\alpha)\ [(DER) / (E)(AM) \quad (2),$$

where α is a fixed ratio between food intake and feces; we took α = 0.38 for Wood Storks based on data reported for the carnivorous waterbird with the largest adult body mass (1195 ± 335 g) (Marion *et al.* 1994). DER is the daily energy requirement during the nestling phase, calculated as 2877 ± 496 KJ/day (Nagy *et al.* 1999). E is the gross energy content of food (KJ/g) and we assumed E = 23.9 ± 0.46 KJ/g for a carnivorous diet (Karasov 1990), and AM (apparent metabolizable energy coefficient) was taken as 0.76 ± 0.013 for a carnivorous diet (Karasov 1990)

For the offspring, the feces model takes the form:

$X_{offspring\text{-}feces} = (\beta)(CS)\ \{(\alpha)\ [(TER_{chick}) / (AM)(E)]\}$ (3),

where β is a correction factor set to 0.5 (Hahn *et al.* 2007); CS is the specific mean clutch size, and TER-*chick* is the total energy requirement over the chick-rearing period calculated as outlined in Weathers (1992).

Concentration of nutrients in the feces. From each dried sample, 10 g were taken and analyzed for total and available nitrogen (NH_4-N and NO_3-N), total calcium, total magnesium, and total phosphorus. Nitrate was determined colorimetrically with sulphanilamide and (1-naphtyl) ethylene-diamide di-HCl (Golterman 1969). Total nitrogen content was measured by the micro-Kjeldahl and colorimetric method (Bremner 1965), and NH_4-N concentration was determined colorimetrically (Technicon Auto-Analyzer 1978). Total phosphorous was determined after H_2SO_4 digestion of the samples and reaction with molybdate (Golterman 1969). Ca and Mg were determined in a modified acid digestion (Jackson 1958) using atomic absorption spectrophotometry with a Varian AA-6-Spectrophotometer. The total number of determinations was 4800 (800 samples x 6 variables).

Hahn's model (Hahn *et al.* 2007) was also assessed on the basis of the feces nutrient measurements carried out in this work. Thus nutrient loading includes the amount of nutrient input by adults ($NX_{dult\text{-}feces}$) (eq. 4) and offspring ($NX_{offpring\text{-}feces}$) (eq. 5). For adults, the equation was:

$NX_{adult\text{-}feces} = (NX_{nb\text{-}feces})\ (T_{nest})$ (4),

where $NX_{nb\text{-}feces}$ is the daily nutrients contribution from a breeding bird (g/day). The $NX_{nb\text{-}feces}$ was determined as:

$NX_{nb\text{-}feces} = (A)(\alpha)\ [(DER) / (E)(AM)]\ (NX_{feces})$ (5),

where A is the total portion of nutrients released that is deposited into the water. We assumed A = 1 for Wood Storks as carnivorous internal loaders that forage in aquatic habitats, and NX_{feces} the nutrient concentration of feces (mg/g).

For the offspring, the feces nutrient model takes the form:

$NX_{offspring\text{-}feces} = (\beta)(CS)\ \{(\alpha)\ [(TER_{chick}) / (AM)(E)]\ (NX_{feces}) - (NX_{syn})\}$ (6),

where NX_{syn} is the total amount of N and P fixed in a chick's body with an assumed 2.82 % N and 0.46 % P fresh body mass (Dierenfeld *et al.* 2002). The equations relating nutrient input to time were used to estimate the nutrient input of the missing period when field data wer not available (i.e., incubation and beginning of chick-rearing period).

Feces nutrient input compared with other sources. At each selected plot corresponding to the non-occupied sites, fifty 1 m x 1 m litter traps were randomly placed under the woody canopy and litter was collected monthly for one year. The litter nutrient concentration was determined by San José & Montes (1987). The nutrient content of meteorological input is given by Montes & San José (1989). These sources were compared by using 95 % confidence limits of means.

Interpretation of soil chemical differences between breeding site and non-breeding site. To assess the impact of Wood Storks on soil chemical differences, we chose four plots at breeding site, non-occupied site, and the herbaceous layer of non-occupied site. Differences were evaluated by Discriminant Analysis (Snedecor & Cochran 1967, Hair *et al.* 1984, Brown 1998). This analysis permits determination of the best predictor (i.e., linear combination of variables) of soil differences between sites. At each selected tree on the breeding site and non-breeding site, as well as the herbaceous layer of non-occupied site, ten composite soil samples were collected at random from 0.0 to 0.20-m depth. Organic residues on the soil surface were not included in soil samples. These samples were analyzed as follows: pH was determined using a glass electrode in a 2:5 water slurry; organic carbon percentage was measured by the Walkley and Black method (Jackson 1958); total nitrogen (N) was determined by the Micro-Kjeldahl method (Bremner 1965); ammonium concentration was determined colorimetrically (Technicon Auto-Analyzer 1978); and finally, available phosphorous (P) was extracted by the Olsen method and its concentration determined by the vanadate-molybdate colorimetric method (Olsen & Dean 1965). Exchangeable cations (K, Ca, and Mg) were extracted with a 1N-NH_4Cl solution and their concentrations determined by atomic absorption spectrophotometry using a Varian AA-6-Spectrophotometer. Electrical conductivity was measured using a Denver Instrument Conductiver (Denver Instrument Company, Arvada, CO, USA). In the soil samples, the texture was determined by the sedimentation (Bouyoucos method) (Day 1965). The total number of determinations was 1200 (i.e., 10 soil samples x 4 trees or herbs x 3 sites x 10 variables). In the landscapes of the breeding site and non-occupied site, the aerial input to soil chemical

features was obtained by summing the area-weighted surfaces which were estimated from the area covered by woody and herbaceous life forms.

At the breeding site, non-occupied site, and herbaceous layer of non-occupied site, soil bulk density under the woody canopy and herbaceous covers was determined from the volume occupied by 10 soil samples of 1 m x 1 m area to a depth of 0.20 m, as outlined in Pla Sentis (1977).

A variable analysis was performed to decrease the redundancy of the edaphic variates. Thus, the variables were subjected to a preliminary analysis by using the variance inflation factor (Montgomery & Peck 1982). Collinear variables were deleted from the variables and the eleven original variables were reduced to four. Subsequently, the responses of soil chemical features to the variation in the three selected sites were established using Discriminant Analysis. The function (*D*) for discriminating among sites was derived by the relationship

$$D = d_i z_i + \ldots + d_p z_p \quad (7),$$

where d_i is the standardized value of the original variable and z_i is the standardized classification function. Diagnostic and statistical tests of our assumptions were carried out using Statistica Version 6 (Statsoft, Tulsa, Oklahoma).

RESULTS

Feces input during the breeding season. For the Camaguan wetland, the estimated index of abundance of Wood Storks was 8.9 ± 6.6 birds/km^2 The nest density was 111 ± 91 nests/ha ranging from 50 to 180 nests/ha. After hatching, the Wood Storks' daily average dry mass of deposited feces on the breeding sites followed a parabolic trend (Fig. 2). Thus, the deposition increased with chick growth from 42 ± 17 g dry mass/m^2/d to a maximum plateau (93 ± 7 g dry mass/m^2/d). Thereafter, it decreased to a minimum value of 15 ± 11 g dry mass/m^2/d.

The performance of Hahn's model was evaluated by a linear regression of the observed data of feces deposition as a function of estimated data. The

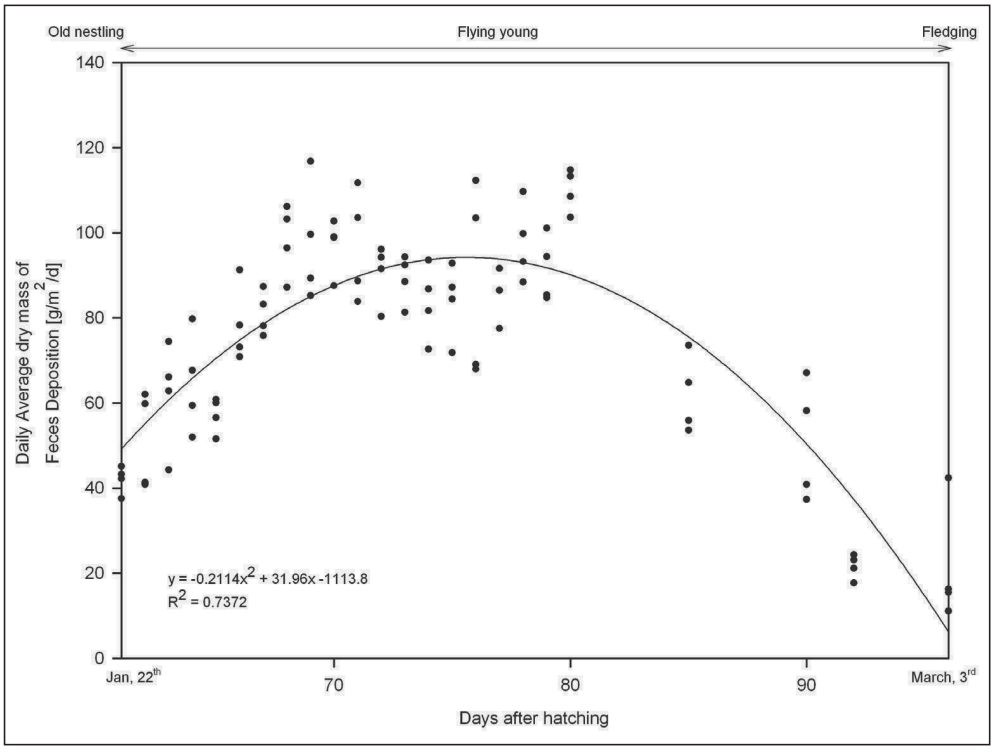

FIG. 2. Daily feces deposition by the Wood Stork during the breeding season in the Camaguan wetland of the Orinoco lowlands.

slope, intercept, and coefficient of determination were 1.135, 1.021 and 0.97, respectively. The root mean square error, the systematic root mean square error, and unsystematic root mean square error were 6.90, 4.41 and 5.32 g/m^2/d, respectively. The number of data points for the measurement period was 135. It is clear that the model performed well overall.

Daily nutrient concentration and fluxes from the feces. Over the breeding period, the daily trend of nutrient concentrations showed two different temporal patterns (Fig. 3). An exception was total P concentration, which did not show any trend. Total N, NH_4-N, and Mg decreased exponentially to 63, 60 and 89%, respectively. By contrast, the daily NO_3-N trend showed a 6.0-fold increase and total Ca an asymptotic increase of 1.7-fold over time.

Over the breeding period, the nutrient fluxes from feces showed two different patterns (Fig. 4). Total N, NH_4-N, and Mg followed an exponential pattern, with minimum values at 96 days after hatching. In the case of NO_3-N, total P and Ca, the parabolic pattern showed that a maximum value occurred when the juveniles began to fledge.

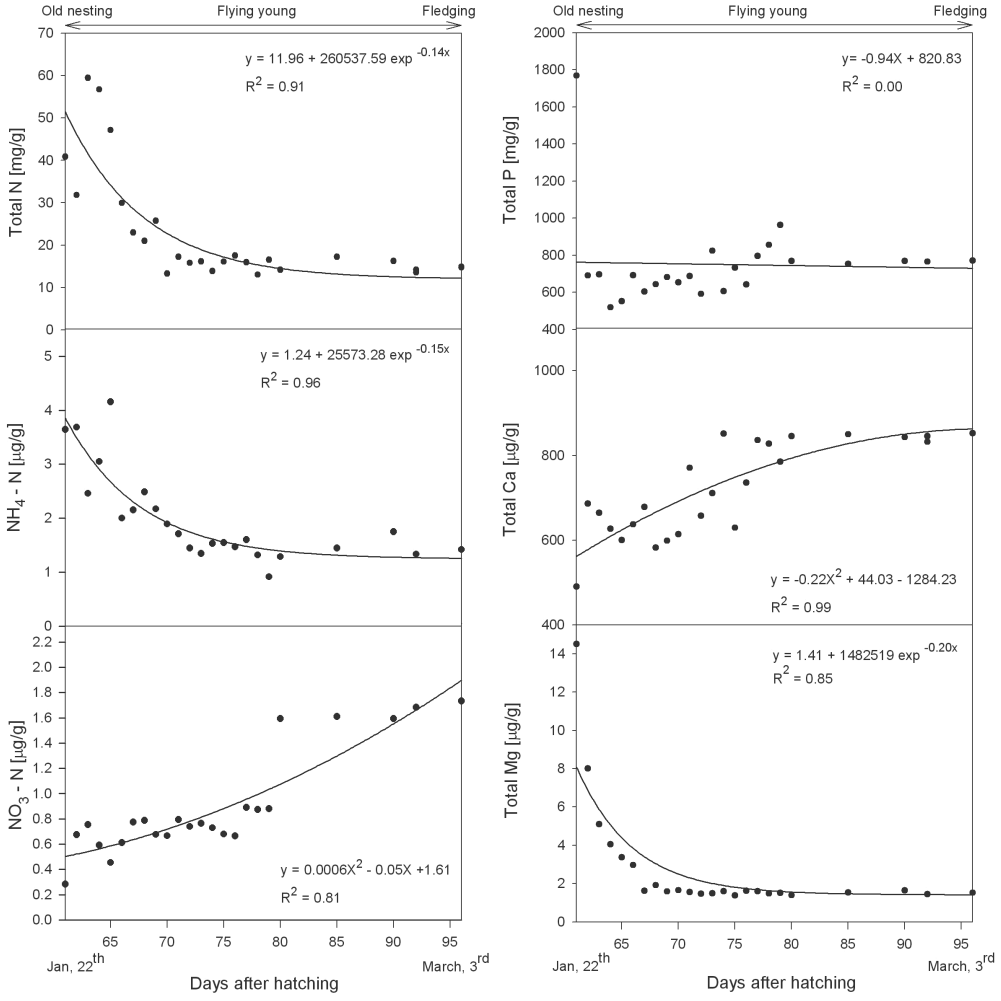

FIG. 3. Nutrient concentrations in Wood Stork feces deposited during the breeding season in the Camaguan wetland of the Orinoco lowlands. The curve fitted to data was the best fit estimate.

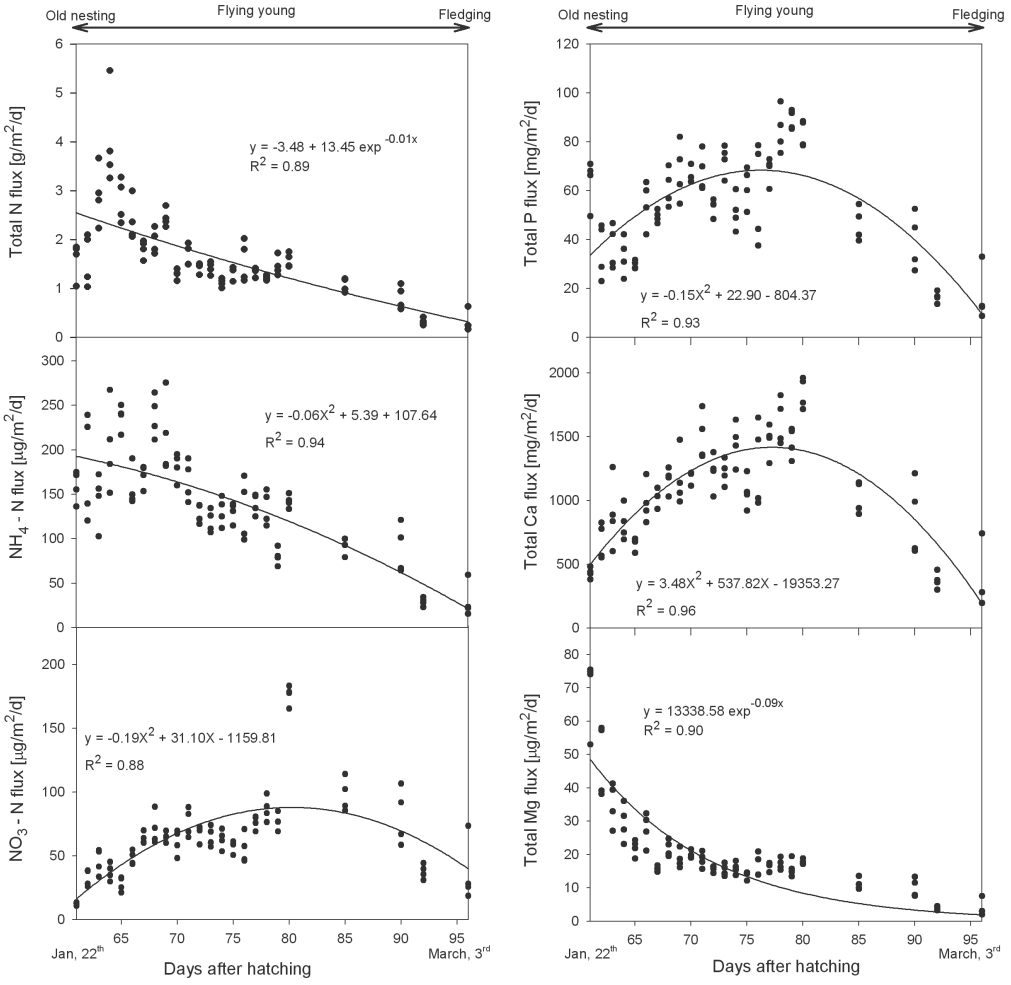

FIG. 4. Nutrient fluxes from Wood Stork feces deposited during the breeding season in the Camaguan wetland of the Orinoco lowlands. The curve fitted to data was the best fit estimate.

On the basis of the linear regression, the results indicate that Hahn's model adequately simulated the contribution of Wood Storks to nutrient loading into the freshwater habitats of the Camaguan wetland. It is clear that given the breeding site and wetland condition data, the model performs well overall.

Comparison of sites with storks and without storks. Discriminant function analysis indicates that the three groups of selected sites (breeding, non-occupied, and herbaceous layer of non-occupied site) were discriminated by a linear combination of variables as Wilks' lambda and Chi-square were 0.0019 and 65.4 with a significance level < 0.001, respectively. For discriminant functions 1 and 2 the eigenvalue was 81.5 and 5.1, respectively. Best predictor variables were soil pH, NH_4-N concentration, exchangeable Ca, and electrical conductivity (Table 1).

DISCUSSION

Contribution of Wood Stork feces and nutrient loading. During the Wood Stork fledging stage in the Camaguan wetland, the downward trend of excrement production was associated with the decreasing number of chicks per nest (Fig. 5), which reached 1.18

TABLE 1. Standardized coefficients for discriminant variables among breeding site, non-breeding site, and herbaceous layer of non-breeding site in the Camaguan wetland of the Orinoco lowlands. Values denote the contribution of each variable to the discriminant functions 1 and 2. Total number of samples per group was 160.

Variables	Standardized coefficient		Groups (mean ± standard deviation)		
	Discriminant function 1	Discriminant function 2	Breeding site	Non-occupied site	Herbaceous layer of non-occupied site
Soil pH	-0.69066	0.81344	5.32 ± 0.46	4.84 ± 0.43	5.22 ± 0.30
NH_4-N (µg gr^{-1})	1.04919	1.22461	6.24 ± 1.58	2.09 ± 0.58	0.87 ± 0.21
Exchangeable Ca (µg gr^{-1})	0.71642	1.58322	4.41 ± 1.22	2.11 ± 0.46	0.55 ± 0.30
Electrical conductivity (mmhos cm^{-1})	0.94771	-1.33065	1.43 ± 0.20	0.81 ± 0.05	0.04 ± 0.01

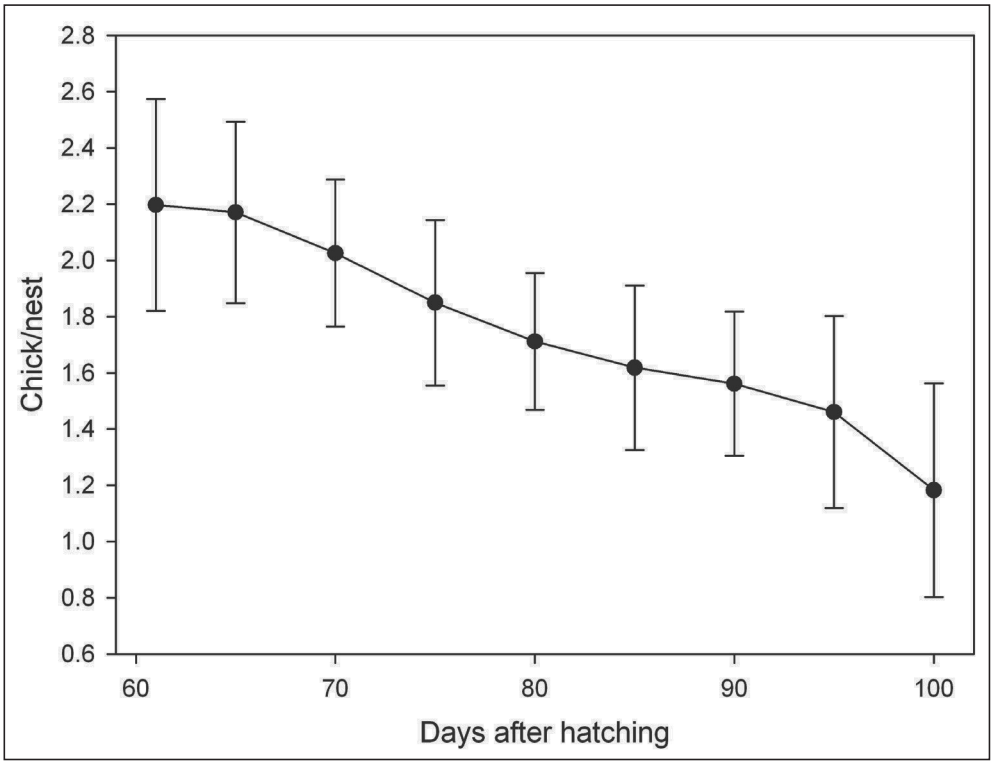

FIG. 5. Trend of wood stork chicks per nest during the breeding season in the Camaguan wetland of the Orinoco lowlands. Data was fitted using a β spline function. Bars correspond to 95% confidence limits.

± 0.23 chicks per nest at fledging. At this stage, 1.32 birds were fledging per nest (Perez-Aguilera 1997). A similar ratio (1.67 birds per nest) has been reported for the seasonally flooded savannas of Apure (Gónzalez 1993). Over the breeding period, average daily Wood Stork deposition was 79 ± 18 g dry mass/m^2/d for a density of 0.18 ± 0.06 chicks/m^2. Here, feces input to the system was lower than that of *Phalacrocorax* (*Leucocarbo*) *bougainvillii* Lesson (240 g dry mass/m^2/d) (Hutchinson 1950, Stewart, 1973), a carnivorous waterbird occurring in the Ballestas Islands, Peru. The difference between species in feces deposition could be related to bird density and biomass. Over the Wood Stork breeding period in the Camaguan wetland, the collected feces input was 2832 ± 566 g of dry mass/m^2. If 25% of the feces input was intercepted by tree branches (Hicks 1979), then the total feces input would be 3777 ± 755 g dry mass/m^2. The observed value of feces deposition in the Camaguan wetland can be compared with the theoretical contribution of carnivorous water birds to nutrient loading in freshwater habitat as estimated by the Hahn model (Hahn *et al.* 2007). This theoretical approach considers the changes in food requirements and feces with chick age by means of allometric equations and conceptualization. It is based on 1) directly measured body mass, clutch size, nesting period. and nutrient concentration of the excrement, and 2) parameterization of available references. Applying this model, the observed data and the theoretical estimates of excrement produced per season by Wood Stork parents and offspring were 3777 ± 755 and 3396 g/m^2/season, respectively. On the landscape scale, the reported dataset on excrement production by Wood Storks serves as a supplement to the wetland nutrient budget.

In Wood Storks, the temporal differences in feces nutrient concentration patterns were similar to those reported for Herring Gull chicks and adults (*Larus argentatus* Pontoppidan) along the northeastern Scottish coast (Sobey & Kenworthy 1979). In the Camaguan wetland, the temporal pattern of the feces nutrient concentration could be related to age and their period-dependent nutrient requirement. González (1997) found that stork stomach contents collected during the nesting period revealed variations in the prey taken, which regulated fecal nutrient concentration. Commonly, during periods of reproduction, birds' nutritional requirements may increase (Murphy 1996). As a consequence, the daily nutrient concentration in excretion might be lowered (Fox & Kahlert 1999).

The total N and P fluxes from Wood Stork feces reached a maximum value (4 g/m^2/d and 84 mg/m^2/d, respectively) higher than that measured in feces of carnivorous wintering waterfowl (*Anas* sp.) (14-31 mg N/m^2/d) and colonial omnivorous Red-winged Blackbirds (*Agelaius phoeniceus* Linnaeus) (6-12 mg P/m^2/d) living in man-made wastewater treatment wetlands in Southern California's San Jacinto Valley (Andersen *et al.* 2003). The observed and estimated N and P loading were compared with the theoretical contributions of carnivorous water birds estimated by Hahn's model (Hahn *et al.* 2007). Thus the observed and estimated N loading from Wood Stork parents and offspring were 11.5 and 9.0 g/m^2/season, respectively and for P loading 28.9 and 26.1 g/m^2 season, respectively. In oligotrophic Camaguan wetlands with N and P limitations, the nutrient enrichment by Wood Storks can drive the system's dynamic.

We measured how important the nutrient input in the Camaguan wetland is to this particular breeding colony in relation to other sources (e.g. meteorological input and litterfall) (Fig. 6). They were compared by using 95% confidence limits of the mean. Results indicate that total N (51 ± 20 kg/ha/yr), NH_4-N (16 ± 7 kg/ha/yr), NO_3-N (9 ± 7 kg/ha/yr), total P (145 ± 34 kg/ha/yr) and Ca (5 ± 2 kg/ha/yr) input from Wood Storks were higher than those reported via general meteorological input (4 ± 1, 2 ± 1, 0.2 ± 0.1, 0.5 ± 0.2, and 3 ± 1 kg/ha/yr, respectively) (n= 2723 samples) at the Biological Reserve of the Orinoco lowlands during three consecutive annual courses (Montes & San José 1989). This Reserve is located 50 km from the study site. Therefore, the ratios of measured feces deposition to meterological input for total N, NH_4-N, NO_3-N, total P and Ca would be 12, 8, 47, 181 and 1.4-fold, respectively. These results indicate that feces depositions were more important nutrient sources than those from meteorological input. This was not the case for Mg content; meteorological input was higher (4.2-fold) than that of feces deposition. Similarly, nutrient additions to cattail stands in central New York State from droppings of roosting Red-winged Blackbirds (*Agelaius phoeniceus*), Common Grackles (*Quiscalus quiscula*), Brown-headed Cowbirds (*Molothrus ater*), and European Starlings (*Sturnus vulgaris*) were also greater than that coming via precipitation (Hayes & Caslick 1984). In South Carolina, nutrient input from colonial-nesting White

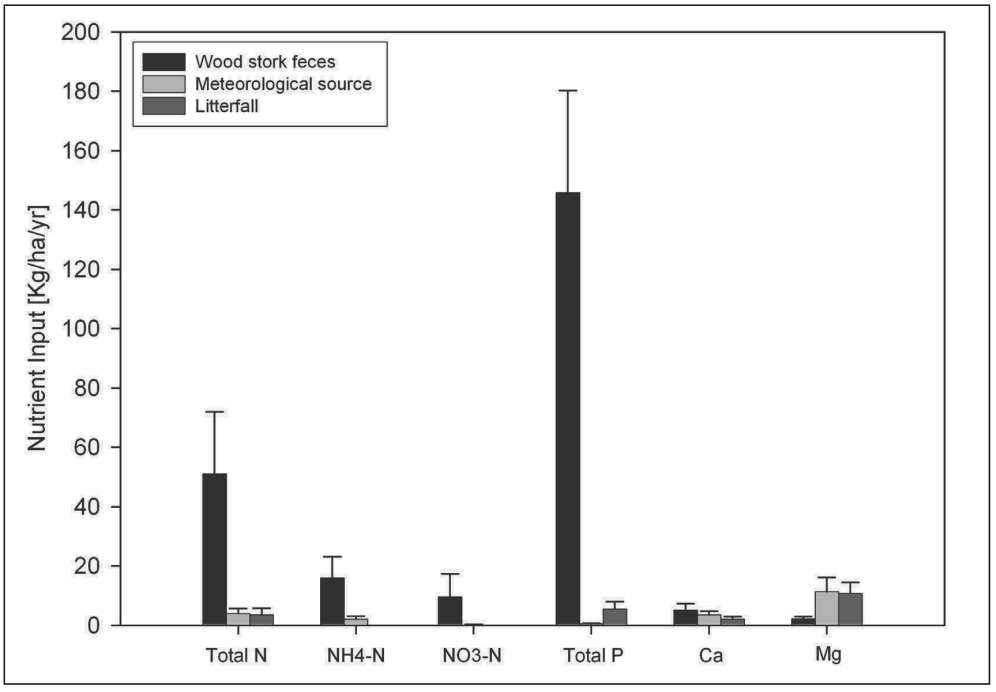

FIG. 6. Contribution of nutrient sources loading in the Camaguan wetland of the Orinoco. Bars correspond to 95% confidence limits.

Ibis (*Eudocimus albus*) to estuaries was substantial when compared with that from atmospheric sources (Bildstein *et al.* 1992). The total input of P by a colony of Franklin's Gulls (*Larus pipixcan*) nesting in cattails at the Agassiz National Wildlife Refuge was comparatively higher than that from atmospheric sources (McColl & Burger 1976). All these results show the relative importance of the biotic vector in nutrient transport. Comparatively, the contribution of Wood Storks to input of total N, total P and Ca input (Fig. 6) (51 ±20, 145 ± 34, and 5 ± 2 kg/ha/yr, respectively) was greater than from litter (3 ± 2, 5 ± 2, and 2 ± 0 kg/ha/yr, respectively). However, Mg was lower in the feces than in the litterfall (2 ± 0 vs. 10 ± 3 kg/ha/yr). In the Everglades, a high P input from wading birds was also reported by Frederick & Powell (1994). They found that the P input was 20 times above the annual input from other sources. In summary, comparisons of nutrient sources in the Orinoco lowlands indicate that the storks might be major players in total N, total P and Ca input.

Edaphic variables maximizing the differences between breeding site, non-occupied site, and the herbaceous layer of non-occupied site. The amounts of variance accounting for the Discriminant edaphic variables were significant as assessed by the Wilks' lambda test. Discriminant Analysis showed common underlying edaphic features between groups. The larger contribution to the prediction of the group characteristics (i.e., larger standardized coefficients) were NH_4-N concentration and electrical conductivity as function 1, and exchangeable Ca and electrical conductivity as function 2. Similar effects of nutrient loading by birds on soil features have been reported for different systems (Hutchinson 1950, McColl & Burger 1976, Sobey & Kenworthy 1979, Hogg & Morton 1983, Wainright *et al.* 1998, Anderson & Polis 1999, Wait *et al.* 2005). Consequently, the edaphic features discriminating between sites with storks and without storks across the Camaguan wetland were indeed reflecting nutrient loading by the Wood Storks. Therefore stork breeding sites and associated waste products have an impact on soil nutrient availability relative to the surrounding area.

Breeding sites and nutrient redistribution may play a key role in the preservation of the Camaguan

wetland and therefore the basis for human life (ecosystem service). Nutrient redistribution in the Florida Everglades has been proposed as a biotic agent in maintaining tree islands (Wetzel *et al.* 2005). In the Florida Everglades, nutrients are transferred by Wood Storks from sloughs where they feed to their rookeries (Kahl 1964). The link between aerial biota and aquatic components has been modeled by Oliver & Legovic (1988). Potentially, Wood Storks play an important role as a vector in the movement of the material. As a non-migratory bird, the Wood Stork contributes significantly to landscape nutrient circulation by foraging in specific areas and depositing wastes in others.

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