January 2000

Foraging ecology of the endangered wood stork recorded in the stable isotope signature of feathers

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Oecologia (2000) 125:584–594
DOI 10.1007/s004420000471

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Received: 23 February 2000 / Accepted: 15 June 2000 / Published online: 17 August 2000

Abstract Down feathers and regurgitant were collected from nestling wood storks (*Mycteria americana*) from two inland and two coastal breeding colonies in Georgia. The stable isotopic ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in these materials were analyzed to gain insights into the natal origins of juvenile storks and the foraging activities of adults. Down feathers differed in $\delta^{13}C$ between inland and coastal colonies, having average isotopic values that reflected the sources of carbon fixed in biomass at the base of the food web. Feathers from the inland colonies differed between colonies in $\delta^{15}N$, while those from the coastal colonies did not. These patterns primarily reflected the foraging activities of parent storks, with individuals capturing differing percentages of prey of distinct trophic status at each colony. Collectively, the carbon and nitrogen isotopic signatures of feather keratin were used to distinguish nestlings from each colony, except for instances where storks from different colonies foraged in common wetlands. The stable isotopic composition of food items in regurgitant was used to reconstruct the trophic structure of the ecosystems in which wood storks foraged. Predicted foraging activities based on the isotopic composition of keratin were generally consistent with the percentage of prey types (freshwater vs. saltwater and lower trophic level vs. upper trophic level consumer) observed in regurgitant, except for the coastal colony at St. Simons Island, where the $\delta^{13}C$ of feathers strongly suggested that freshwater prey were a significant component of the diet. This inconsistency was resolved by aerial tracking of adults during foraging excursions using a fixed-wing aircraft. Observed foraging activities supported interpretations based on the stable isotope content of feathers, suggesting that the latter provided a better record of overall foraging activity than regurgitant analysis alone. Observed foraging patterns were compared to the predictions of a statistical model that determined habitat utilization based on habitat availability using a geographic information system (GIS) database. Observed foraging activities and those predicted from feathers both suggested that some adult storks preferred to feed their young freshwater prey, even when saltwater resources were more accessible in the local environment. This conclusion supports the contention that wood stork populations are sensitive to changes in the distribution of freshwater habitats along the southeastern coastal plain of the United States.

Keywords Wood stork · Feather · Stable isotopes · Geographic information system · Conservation

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Introduction

Wood storks (*Mycteria americana*) are large wading birds that nest and forage in wetland habitats from the southeastern United States to South America (American Ornithologists' Union 1983). The largest breeding colonies in the United States have historically been found in southern Florida (Ogden and Nesbitt 1979), although over the last 15 years breeding colonies have expanded north into east-central Georgia and southern South Carolina (Ogden et al. 1987; Harris 1994; Murphy 1994). This expansion has occurred mainly along the coastlines of both states.

While wood storks were once prevalent in all coastal states between Texas and South Carolina, the species has declined in number from an estimated 20,000 breeding pairs in the 1930s to a low of 2,800 pairs in 1978 (Ogden et al. 1987). Because of this long-term population decline, the wood stork was declared an endangered species in 1984. The population decline is thought to have resulted from the degradation and destruction of wetland environments (USFWS 1986). In many areas, it is believed that man has impacted local drainage patterns to the extent that wetlands cannot support the food resourc-

es required by wood storks. In an effort to re-establish the species, some wetlands have been managed or artificial wetlands have been created to support nesting colonies (Ogden 1991).

Food resources and foraging strategies

Wood storks feed primarily on fish between 2 and 25 cm in length (Kahl 1964; Coulter 1987; Depkin et al. 1992), although other known food resources include crustaceans, amphibians, reptiles, mammals, birds and arthropods (USFWS 1996). Storks capture prey by tactilocation, wading through shallow water (<40 cm) with their beaks immersed and partially open, sensing prey by physical touch (Kahl 1964; Coulter and Bryan 1993). Prey densities must be relatively high and prey must be of sufficient size and/or shape for this foraging strategy to be effective (Kushlan 1981).

Wood storks forage within a wide variety of freshwater and saltwater wetlands, including marshes, shallow lakes, ponds, tidal creeks and mud flats. They prefer to forage in tidal flats and estuarine (saltwater to brackish) wetlands at times when prey are concentrated (e.g., low tide: Gaines et al. 1998) or in palustrine (freshwater) wetlands when water levels are low (e.g., due to seasonal rainfall patterns: Odum et al. 1995). The choice of foraging site is dependent on many factors including foraging range, energetic cost and habitat availability. Some studies suggest that estuarine habitats are favored because of the relatively constant supply of food from diurnal or daily tidal drawdowns (e.g., Walsh 1990) while other studies suggest a preference for palustrine settings, even when estuarine wetlands dominate the local landscape (e.g., Gaines et al. 1998).

This study uses several diverse lines of evidence to test the hypothesis that stable isotope ratios (C and N) from wood stork feathers provide a historical record of dietary information that can be deciphered in the context of habitat availability and utilization. This was accomplished by comparing the isotopic signatures of down feathers and regurgitant from pre-flight nestlings of coastal and inland breeding colonies of Georgia. Stable isotopic records were compared to the observed foraging activities of adult storks in coastal settings using aerial tracking methods. The results were incorporated in a geographic information system (GIS) model that compared observed and predicted habitat utilization to the actual distribution of wetland types within the foraging area of a colony.

If estuarine and palustrine wetland resources are isotopically distinct, then non-lethal tissue samples may provide insights into life history strategies that are intractable or exceedingly difficult to acquire by other methods. Such data are useful for the successful conservation of endangered species, such as the wood stork, that forage in diverse wetland habitats.

Stable isotopes as tracers of life history information

The stable isotope composition of avian tissues provides insight into the dietary history of individual birds. Most studies have focused on measuring carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotope ratios in blood, liver, muscle, and/or bone collagen (Hobson 1987, 1993; Hobson and Clark 1992a, 1992b, 1993; Alisauskas and Hobson 1993; Hobson et al. 1994; Alexander et al. 1996; Sydeman et al. 1997). Of these, blood has a relatively short turnover time (hours to days), while muscle records information on a time scale of up to a month depending on the tissue and metabolic activity of the host (Tieszen et al. 1983), and skeletal collagen has a turnover time that approaches a year (Hobson and Sealy 1991; Hobson and Clark 1992a).

Feathers provide an alternative tissue for the study of avian diets. The stable isotope signature of feather keratin has been used to document the feeding behavior and migratory patterns of various species of birds (Mizutani and Wada 1988; Mizutani et al. 1990, 1992; Hobson and Clark 1992a, 1992b; Chamberlain et al. 1997; Hobson and Wassenaar 1997; Marra et al. 1998). Feathers provide an optimal tissue for the study of endangered species because they represent a non-lethal source tissue that may be collected without invasive handling. Furthermore, feathers can preserve a high-resolution record of life history experiences because they grow over a relatively short time interval (usually 2–4 weeks), and record events that occur during or shortly after yearly molts (Hancock et al. 1992).

Stable isotopes and tissue-diet enrichment factors

The difference in isotopic composition between any tissue compartment of an animal (e.g., muscle, blood, feathers) and diet is represented by a tissue-diet enrichment factor $\varepsilon_{\text{tissue-diet}}$, where $\varepsilon_{\text{tissue-diet}} \cong \delta_{\text{tissue}} - \delta_{\text{diet}}$, and δ is the delta value for the isotope of interest (for definition of δ, see Craig 1957). Mizutani et al. (1990, 1991) reported a $\varepsilon_{\text{feather-diet}}$ of 4‰ for stable carbon isotopes in free-ranging and captive cormorants and attributed the difference to the fractionation of ^{13}C as it is incorporated in the keratin of feathers. Mizutani et al. (1992) extended this work to include other bird species and showed that $\varepsilon_{\text{feather-diet}}$ varied from 2.5 to 3.8‰, depending on species. Mizutani and Wada (1988), Mizutani et al. (1990, 1992) and Hobson and Clark (1992b) also observed significant differences in $\varepsilon^{13}C$ for regurgitant and feathers from free ranging and captive birds. Variability was attributed to a variety of factors including the relationship between the timing of feather growth and seasonality in the composition of potential prey and/or the lipid content of prey items (Bender et al. 1981; Sullivan and Krueger 1981; Hobson and Clark 1992a).

DeNiro and Epstein (1981) were the first to demonstrate that animal tissues are enriched in ^{15}N compared with their diets. Subsequently, Minagawa and Wada (1984) proposed a $\varepsilon_{\text{tissue-diet}}$ of ~3‰, stating that the par-

titioning of nitrogen isotopes in animals can be viewed as a steady state mass balance where excretory products (e.g., ammonia, uric acid, and urea) are depleted in ^{15}N, and tissues are enriched in ^{15}N compared with the diet. This enrichment is expressed for every step up in trophic level throughout an ecosystem, resulting in high-trophic-level consumers that are significantly enriched in ^{15}N compared with primary producers. Researchers have observed little intra-individual differences in the $\delta^{15}N$ of various avian tissues, including feathers (Mizutani and Wada 1988; Mizutani et al. 1991, 1992; Hobson and Clark 1992b). Thus, nitrogen isotope signatures in feather keratin may be used to distinguish birds that utilize differing food resources, provided that ecosystem resources are isotopically distinct and/or foraging strategies differ among colonies.

Materials and methods

Field sites

Nestling wood storks from two coastal and two inland breeding colonies of Georgia, United States, were studied (Fig. 1). The coastal colonies are located on the Harris Neck National Wildlife Refuge and St. Simons Island. The coastline in this region is characterized by forested barrier islands bordered by the ocean and expansive tidal marshes and creeks. The Harris Neck colony is situated on a large estuarine island while the St. Simons Island colony is located on a smaller barrier island. Both colonies reside above freshwater impoundments, and the wetland at Harris Neck is intermittently managed to enhance successful breeding practices (USFWS 1996).

The two inland breeding colonies at Chew Mill and Blackwater were chosen because they were both sufficiently far from the coast to preclude foraging activities in saltwater wetlands. The colony at Chew Mill is located above an old mill pond while the colony at Blackwater is located over a natural freshwater wetland.

Feathers and regurgitant

Down feathers and regurgitant were collected from nestling wood storks of 3–7 weeks of age in the spring of 1997. At this age, nestlings are unable to fly and must receive all of their food from parents who forage in and around the breeding colony (<50 km; Bryan et al. 1995). Juvenile storks were removed from the nest by hand and a single down feather was plucked from the breast area of each individual. In three instances, feathers were taken from siblings of a single nest to test for isotopic variability among individuals of the same nest. In the laboratory, feathers were washed in a mild detergent to remove natural oils, freeze-dried and finely chopped for stable isotope analysis.

Using the procedures outlined in Depkin et al. (1992), regurgitant was collected from the nestlings to determine prey composition and the isotopic content of food resources. Water off-loading was not required to extract food items as nestling birds usually regurgitated as a defense mechanism when they were approached in the nest. Upon collection, regurgitant was assigned to an individual and material was immediately put in plastic bags and placed on ice. Prey items were identified to species or genus when possible, and were subsequently frozen, freeze-dried and ground for stable isotopic analysis. No attempt was made to void the gut or extract lipids from prey items; crustacean carapaces were ground with soft tissue.

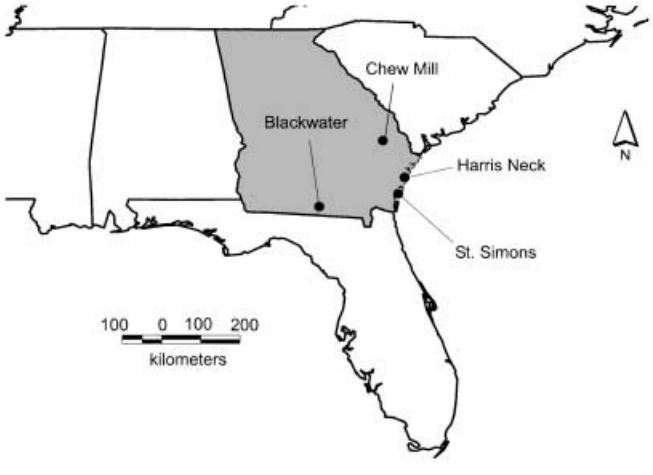

Fig. 1 Locations of the four breeding colonies in Georgia where wood stork feathers and regurgitant were collected for stable isotope analysis

Foraging flight surveys

An observer followed adult wood storks in a fixed-wing aircraft (Cessna 152 or 172) from coastal breeding colonies to foraging sites (for details, see Bryan and Coulter 1987). Foraging excursions were monitored from each colony approximately once every other week for a full day over the months of April and May in 1997. Monitoring foraging activity in this way ensured that excursions were observed over time intervals that included both low and high tidal periods in the local estuarine environment.

The locations of foraging sites were acquired using a global positioning system (GPS) and/or plotted on topographic maps. Observers recorded the habitat type of each foraging locality for cross-reference with a GIS database of wetland types provided by the National Wetland Inventory (NWI) of the United States Fish and Wildlife Service.

A total foraging area for each colony was estimated using the pooled data on individual forays and a minimum convex polygon protocol (Gaines et al. 1998). The actual ratio of estuarine to palustrine wetlands was determined within each area using a GIS database of wetland types (NWI; Cowardin et al. 1979). This ratio was compared to the ratio of foray-types that storks completed. Chi-square tests were performed to determine whether storks foraged in wetland types according to their proportions based on GIS analysis.

Isotopic analyses

Elemental analysis isotope-ratio mass spectrometry (EA-IRMS) was employed to measure the total carbon and nitrogen content, and the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios of individual samples (Barrie and Prosser 1996). All measurements were performed at the Analytical Chemistry Laboratory at the Institute of Ecology, University of Georgia.

Prior to isotopic analyses, chopped or ground material was further homogenized by grinding with an agate mortar and pestle. Approximately 1 mg of ground feather or 2 mg of prey material was loaded into a pre-cleaned and -weighed tin capsule for weighing to ±1 µg using an ultra-microbalance. Capsules were then sealed and placed in the autosampler of a Carlo Erba Elemental Analyzer (NA1500) attached to a continuous flow isotope ratio mass spectrometer (Finnigan Delta C). Samples were combusted to N_2 and CO_2 in oxidation/reduction furnaces, separated by gas chromatography and then measured for $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios on the mass spectrometer. An internal $N_{2(g)}$ working standard was admitted prior to the introduction of each sample and a $CO_{2(g)}$ standard was admitted at the conclusion of each combustion for calibration to the AIR (nitrogen) and V-PDB (carbon) international standards (Mariotti 1983; Coplen 1996). Stable isotope ratios

are reported in per mil units (‰) using standard delta (δ) notation (Craig 1957). External working standards of bovine liver and acetanilide were analyzed to determine external precision; these standards were reproducible to better than ±0.15‰ (1σ SD) for both $\delta^{13}C$ and $\delta^{15}N$.

Statistical analysis

Two methods were used for the statistical comparison of stable isotopic compositions. The appropriate two-tailed Student's *t*-test was used for the comparison of mean delta values from various groupings after sample variances were evaluated using an *F*-statistic. Statistical comparisons of related data (the $\delta^{13}C$ *and* $\delta^{15}N$ of individual feathers, compared between colonies) were made using the *K* nearest-neighbor statistic (Schilling 1986; Henze 1988; Rosing et al. 1998). A value of 4 was used for *K* for all pairwise comparisons and appropriate adjustments were made using the Bonferroni inequality method (Johnson and Wichern 1992). Chi-square tests were used to determine the significance of relationships between observed foraging excursions and those predicted based on the distribution of wetland types within the foraging area of a colony (Gaines et al. 1998, 2000). All comparisons were considered statistically significant at $P \leq 0.05$.

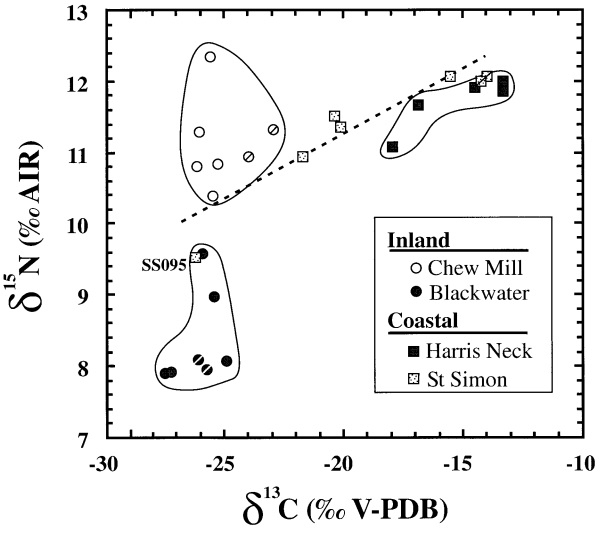

Fig. 2 Cross plot of $\delta^{13}C$ versus $\delta^{15}N$ for nestling down from inland and coastal wood stork colonies. Data for three of the colonies are circumscribed for clarity. Dashed line shows a least-squares linear fit of the data from the St. Simons Island colony ($\delta^{15}N=14.85-0.18\cdot\delta^{13}C$). Slashes through symbols represent siblings from the same nest. SS095 identifies a single down feather from a St. Simons Island nestling referred to in the text

Results

Feeding trial

The most direct way of determining a reliable $\varepsilon_{feather\text{-}diet}$ value for the wood stork would be to determine the $\delta^{13}C$ and $\delta^{15}N$ for feathers from captive birds fed a constant diet of known prey items over an extended period of time. This was done for four adult wood storks in an exhibit at Sea World of Orlando, Florida. During the period of $\varepsilon_{feather\text{-}diet}$ determination, these storks were maintained on a diet that consisted almost exclusively of small marine fish – principally capelin (*Mallotis villosus*), sardines (*Sardinops caerulea*), whitebait smelt (*Allosmerus elongatus*), and silversides (*Menidia menidia*), all obtained from a commercial supplier. This diet was fed to these birds for a year or more before body contour and down feathers were collected.

Isotopic analyses were performed on feather samples collected along with a representative sample of the fish fed to the storks. Weighting these food resources equally, the analyses indicated that the stork diet had an integrated $\delta^{13}C$ of –19.0±2.2‰ and $\delta^{15}N$ of 12.3±1.1‰ (n=4), while feathers averaged –15.7±0.2‰ and 15.1±0.4‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively (n=4). This resulted in calculated values for $\varepsilon_{feather\text{-}diet}$ of 3.3 and 2.8‰ for carbon and nitrogen, respectively.

Stable isotope content of nestling feathers

The carbon and nitrogen stable isotopic composition of nestling down feathers are plotted in Fig. 2. Feathers fell into three isotopically distinct populations that corresponded to the inland colonies of Chew Mill and Blackwater, and the coastal colony of Harris Neck. Feathers from St. Simons Island had carbon isotopic compositions that spanned nearly the entire range of values reported for the other colonies. Feathers from sibling storks were similar in isotopic composition; their differences ranged from 0.2 to 1.1‰ for $\delta^{13}C$, and from 0.1 to 0.4‰ for $\delta^{15}N$.

Carbon isotopes

Collectively, down feathers from the four colonies displayed a wide range in $\delta^{13}C$ (–27.5 to –13.3‰). On the average, feathers from the inland colonies were 6–11‰ lower in $\delta^{13}C$ than those from the coastal colonies (see Table 1 for summary statistics). The average $\delta^{13}C$ for feathers from Chew Mill and Blackwater were similar, although the statistical significance of the relationship was marginal (t=1.86, 12 *df*, P=0.088).

The average $\delta^{13}C$ values for down feathers from the coastal colonies were higher than those from the inland localities, with feathers from Harris Neck being the highest of the four colonies studied. The average $\delta^{13}C$ of feathers from Harris Neck and St. Simons Island were similar (t=1.66, *10 df*, P=0.127). All other comparisons of average $\delta^{13}C$ values for down feathers were statistically significant (HN vs. CM: t=10.43, 10 *df*, $P=10^{-6}$; HN vs. BW: t=10.81, 5 *df*, $P=10^{-4}$; SS vs. CM: t=3.34, 7 *df*, P=0.012; SS vs. BW: t=3.96, 6 *df*, P=0.007, where HN Harris Neck, CM Chew Mill, BW Blackwater, and SS St. Simons Island).

Table 1 Average and range of values for $\delta^{13}C$ and $\delta^{15}N$ (‰) of down feathers from wood storks and food items in regurgitant

Colony	No.[a]	Average $\delta^{13}C$ ($\pm 1\sigma$[b])	Range	Average $\delta^{15}N$ ($\pm 1\sigma$)	Range
Feathers					
Inland colonies					
Chew Mill	7	–25.05±1.17	–26.11 to –22.92	11.13±0.60	10.39 to 12.35
Blackwater	7	–26.11±0.94	–27.49 to –24.89	8.35±0.66	7.90 to 9.57
Coastal colonies					
Harris Neck	5	–15.18±2.12	–17.93 to –13.31	11.70±0.37	11.08 to 11.99
St. Simons Is.	7	–18.84±4.47	–26.02 to –13.99	11.35±0.91	9.53 to 12.07
Food items					
Inland colonies					
Chew Mill	11	–28.06±1.11	–29.35 to –26.11	9.03±0.97	6.59 to 10.01
Blackwater	6	–27.32±2.81	–32.34 to –24.75	5.88±3.29	–0.23 to 8.84
Coastal colonies					
Harris Neck	11	–18.39±6.02	–28.03 to –13.69	8.31±1.29	6.42 to 10.14
St. Simons Is.	28	–15.45±0.99	–17.39 to –13.44	9.64±1.33	6.00 to 11.23

[a] Number of samples
[b] SD of the mean

Nitrogen isotopes

The $\delta^{15}N$ of down feathers from all four colonies ranged from 7.9 to 12.4‰ (Table 1). The average $\delta^{15}N$ for feathers from the colonies of Chew Mill, St. Simons Island and Harris Neck were not statistically different (CM vs. SS: t=–0.53, 12 *df*, P=0.604; CM vs. HN: t=–1.81, 10 *df*, P=0.100; SS vs. HN: t=–0.80, 10 *df*, P=0.441). However, feathers from Blackwater were isotopically distinct (BW vs. CM: t=8.14, 12 *df*, $P=10^{-6}$; BW vs. SS: t=7.10, 12 *df*, $P=10^{-5}$; BW vs. HN: t=–10.25, 10 *df*, $P=10^{-6}$).

Correlation of carbon and nitrogen isotopes

The *K*-nearest-neighbor test was used to determine the statistical significance of inter-colony relationships between feather groupings in $\delta^{13}C$–$\delta^{15}N$ space (Rosing et al. 1998). Results from adjusted pairwise comparisons included: CM vs. BW: P=0.0008; CM vs. HN: P=0.0009; CM vs. SS: P=0.016; BW vs. HN: P=0.0014; BW vs. SS: P=0.0096; HN vs. SS: P=1.000. These results suggested that feathers from each colony were isotopically distinct, except for those from Harris Neck and St. Simons Island, which could not be discriminated from each other based on $\delta^{13}C$ and $\delta^{15}N$.

Relationships between the $\delta^{13}C$ and $\delta^{15}N$ of feathers within a colony were evaluated using a Pearson's simple correlation test statistic. No relationships were observed between $\delta^{13}C$ and $\delta^{15}N$ for feathers from either inland colony (CM: r^2=0.002, n=7; BW: r^2=0.107, n=7), but a strong correlation existed for feathers from St. Simons Island (b=14.85±0.52, m=0.18±0.03, 6 *df*, r^2=0.904). Although the narrow range of values limited the statistical significance of the relationship, feathers from Harris Neck also exhibited a similar positive correlation between $\delta^{13}C$ and $\delta^{15}N$ (b=14.03±0.72, m=0.15±0.04, 5 *df*, r^2=0.779).

Table 2 Common and scientific names for prey items collected from regurgitant of nestling wood storks

Scientific name	Common name
Freshwater species	
Low-level consumer	
	Crayfish
Upper-level consumer	
Amia calva	Bowfin
Aphredoderous sayanus	Pirate perch
Centrarchus macropterus	Flier
Esox americanus	Redfin pickerel
Ictalurus sp.	Bullhead
Lepomis gibbosus	Pumpkinseed sunfish
L. gulosus	Warmouth
L. marginatus	Dollar sunfish
Umbra pygmaea	Eastern mudminnow
Saltwater species	
Low-level consumer	
Callinectes sapidus	Blue crab
Peneaus sp.	Shrimp
Upper-level consumer	
Cyprinodon variegatus	Sheepshead minnow
Fundulus heteroclitus	Mummichog
Leiostomus xanthurus	Spot
Mugil curema	White mullet

Wood stork foraging patterns

Prey species composition

Prey items collected from the regurgitant of nestling storks are reported in Tables 2, 3. Individual food items included crustaceans (*Callinectes sapidus*, *Peneaus* sp. and crayfish), detrivorous and omnivorous fish (*Fundulus heteroclitus* and *Mugil* sp.), and piscivorous fish

Table 3 Weights and $\delta^{13}C$ and $\delta^{15}N$ (‰) for prey items recovered from the regurgitant of nestling wood storks from palustrine (*fw*) and estuarine (*sw*) wetlands in Georgia

Nestling	Prey item	*n*[a]	Weight (g)	$\delta^{13}C$	$\delta^{15}N$
Chew Mill (fw)					
–	*Amia calva*[b]	1	6.4	–26.75	8.89
–	*Ictalurus* sp.[b]	1	5.8	–28.30	10.01
–	Crayfish[b]	4	17.2	–27.51	6.59
–	*Lepomis marginatus*[b] (30.0 mm)[c]	1	0.4	–28.72	8.11
–	*L. marginatus*[b] (36.0 mm)	1	0.9	–28.18	9.47
–	*L. marginatus*[b] (51.0 mm)	1	2.3	–27.05	9.81
–	*L. marginatus*[b] (56.0 mm)	1	2.6	–29.35	9.44
–	*L. marginatus*[b]	15	33.3	–29.41	9.21
–	*Esox americanus*[b]	4	36.0	–26.11	8.71
–	*Lepomis gulosus*[b]	3	27.1	–29.25	9.64
–	*Lepomis* sp.[b]	1	8.4	–28.03	9.43
Weighted average				–28.00	8.89
Blackwater (fw)					
053	Crayfish[b]	5	34.0	–24.75	6.20
054	Crayfish[b]	2	8.7	–24.92	5.14
059	Crayfish[b]	1	3.5	–28.46	–0.23
055	*Centrarchus macropterus*[b]	4	54.4	–32.34	6.91
053	*Aphredoderous sayanus*[b]	5	18.2	–26.73	8.40
054	*A. sayanus*[b]	6	18.8	–26.72	8.84
Weighted average				–28.39	6.90
Harris Neck (sw)					
093	*Umbra pygmaea*[b]	7	30.1	–28.03	7.02
059	*Fundulus heteroclitus*	9	18.2	–15.19	9.25
128	*F. heteroclitus*	3	8.1	–13.69	9.66
142	*F. heteroclitus*	2	2.6	–15.07	10.14
093	*Lepomis gibbosus*[b]	7	17.5	–28.03	7.42
093	*Esox americanus*[b]	1	4.5	–26.90	6.42
136	*Cyprinodon variegatus*	3	4.2	–17.23	6.99
128	*Peneaus* sp.	5	1.6	–14.24	7.37
142	*Peneaus* sp.	1	0.3	–14.13	8.72
093	*Leiostomus xanthurus*	7	34.6	–14.77	8.90
142	*L. xanthurus*	11	17.4	–15.06	9.50
Weighted average				–19.80	8.34
St. Simons Island (sw)					
123	*Callinectes sapidus*	2	27.6	–17.39	8.10
079	*F. heteroclitus*	1	1.0	–16.22	11.23
101	*F. heteroclitus*	14	18.5	–16.19	9.68
102	*F. heteroclitus*	15	23.5	–15.80	9.84
111	*F. heteroclitus*	11	13.2	–14.38	10.14
114	*F. heteroclitus*	1	1.2	–14.15	10.88
121	*F. heteroclitus*	10	9.3	–16.32	10.11
123	*F. heteroclitus*	23	60.4	–15.15	10.72
123	*F. heteroclitus* (23.0 mm)	1	0.1	–13.44	10.05
111	*F. heteroclitus* (30.0 mm)	1	0.1	–16.37	9.33
111	*F. heteroclitus* (32.0 mm)	1	0.4	–14.36	10.35
101	*F. heteroclitus* (36.0 mm)	1	0.2	–15.31	9.62
101	*F. heteroclitus* (37.5 mm)	1	0.6	–15.93	8.90
102	*F. heteroclitus* (38.0 mm)	1	0.6	–16.21	10.34
102	*F. heteroclitus* B (38.0 mm)	1	0.5	–16.03	10.11
123	*F. heteroclitus* (38.5 mm)	1	0.6	–13.70	11.00
102	*F. heteroclitus* (53.0 mm)	1	1.7	–16.20	9.32
111	*F. heteroclitus* (53.0 mm)	1	1.6	–16.14	9.79
101	*F. heteroclitus* (58.0 mm)	1	1.9	–15.62	9.85
123	*F. heteroclitus* (58.5 mm)	1	3.0	–15.10	10.86
123	*F. heteroclitus* (59.0 mm)	1	3.7	–14.36	9.81
101	*F. heteroclitus* (60.0 mm)	1	1.5	–16.37	10.04
102	*F. heteroclitus* (60.0 mm)	1	2.5	–15.88	11.01
111	*F. heteroclitus* (60.5 mm)	1	2.5	–14.91	10.32
123	*Peneaus* sp.	1	0.3	–16.57	6.00
111	*Peneaus* sp.	3	0.5	–14.83	9.02
101	*Peneaus* sp.	1	0.3	–15.68	6.10
111	*Mugil curema*	2	2.2	–13.95	7.36
Weighted average				–15.70	9.90

[a] Number of individuals in sample
[b] Freshwater prey item
[c] Fork length (in parentheses)

(e.g., *Leiostomus xanthurus*, *Aphredoderous sayanus*, *Lepomis* sp. and *Esox americanus*). The most common freshwater species collected (by weight, here and below) were *Lepomis* sp., crayfish, and *Centrarchus macropterus* while the predominant saltwater food items were *F. heteroclitus*, *Leiostomus xanthurus* and *Callinectes sapidus*.

Inland colonies. Prey items collected from the inland colonies were exclusively freshwater species. Of these, crayfish were the only crustacean collected. At Chew Mill, five fish species made up almost 90% of the prey; these included: *Lepomis* sp. (53%), *E. americanus* (26%), and *Amia calva* and *Ictalurus* sp. (~5% each). The remaining 10% of prey were crayfish.

Fewer prey species were recovered from regurgitant at Blackwater. Two species of fish, *Centrarchus macropterus* and *Aphredoderous sayanus*, made up over two-thirds of the food items collected, while crayfish made up the remaining third of prey from this colony.

Coastal colonies. All of the food items recovered from the regurgitant of St. Simons Island nestlings were saltwater species, with 16% being crustaceans (*Callinectes sapidus* and *Peneaus* sp.), and the remainder *F. heteroclitus* and *Mugil* sp. Only 62% of the prey recovered from Harris Neck were saltwater species, with approximately two-thirds of these being *L. xanthurus*, and the remain-

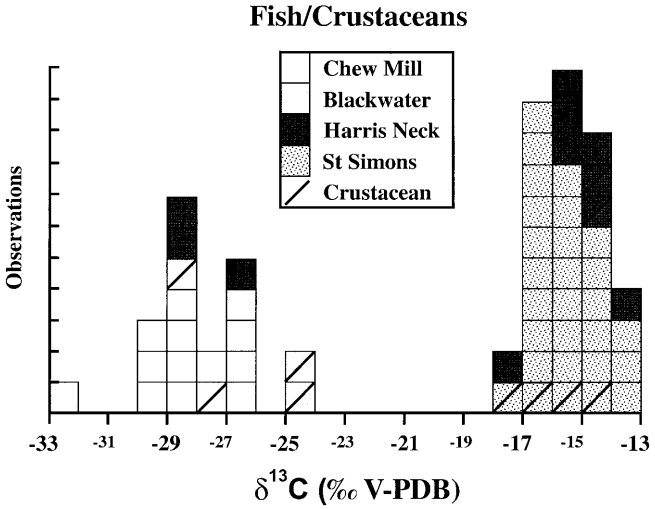

Fig. 3 Histogram of $\delta^{13}C$ values for prey items recovered from the regurgitant of nestling wood storks. Slashes designate crustaceans. The number of observations (*y*-axis) may or may not be representative of the frequency of prey types because several individuals were combined for a single analysis in some cases

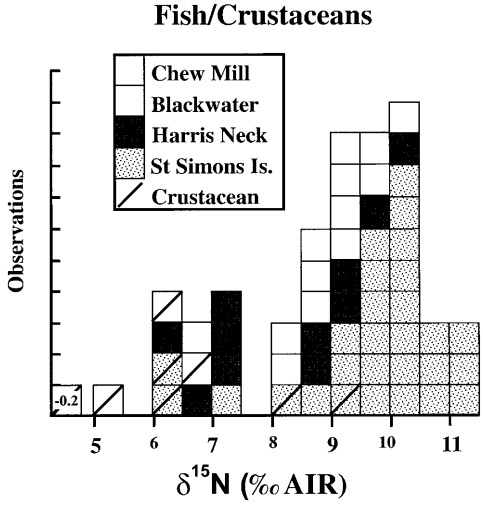

Fig. 4 Histogram of $\delta^{15}N$ values for prey items recovered from the regurgitant of nestling wood storks. Box at far left represents a single sample that plotted off the *x*-axis. All other aspects of the histogram are similar to Fig. 3

der *F. heteroclitus*, but also *Cyprinodon variegatus* (<5%). Less than 2% of the saltwater prey items from Harris Neck were crustaceans (*Peneaus* sp.). Of the freshwater species collected at Harris Neck, 58% were *Umbra pygmaea*, 34% were *Lepomis gibbosus* and 9% were *E. americanus*.

Stable isotope content of prey

The stable isotope compositions of prey items are reported in Table 3 and plotted in Figs. 3, 4. Most food items were combined according to species prior to isotopic analysis, resulting in isotopic compositions that represented the total integrated mass of regurgitant collected. In some instances (e.g., *F. heteroclitus* from St. Simons Island), selected food items were analyzed individually to test for potential relationships between size or weight and isotopic composition, but no statistically significant relationships were observed.

Carbon isotopes. Food items had a broad range in $\delta^{13}C$, extending from –32.3 to –13.4‰, and exhibited a distinctly bimodal distribution (Fig. 3). Prey items formed two groupings with ranges of –32.3 to –24.8‰ and –17.4 to –13.4‰, respectively. Prey from Chew Mill and Blackwater had isotopic compositions that fell within the low-$\delta^{13}C$ grouping, while prey from St. Simons Island all fell within the high-$\delta^{13}C$ grouping. Prey items from Harris Neck had a sufficiently wide range in $\delta^{13}C$ to fall within both groups of data.

Nitrogen isotopes. The $\delta^{15}N$ of prey items from the four colonies ranged from –0.2 to 11.2‰ (Fig. 4), with a distribution skewed towards more positive values (9–10‰).

Table 4 Chi-square tests to compare observed wood stork foraging destinations with those expected as a function of wetland aerial coverage (*E* expected number of foraging points based on the relative area of the corresponding wetland type, *O* observed number of foraging points occurring within that wetland type)

Foraging	St. Simons Island		Harris Neck[a]	
	% Total area	*E*/*O*	% Total area	*E*/*O*
Estuarine	52	14/17	86	27/25
Palustrine	48	13/10	14	4/6
	P=0.25		*P*=0.35	

[a]All points (*n*=5) associated with a managed feeding pond next to colony were removed from the analysis. If points associated with the managed feeding pond were used, the expected number of points would be significantly different from that observed

Unlike carbon isotopes, the distribution of $\delta^{15}N$ values did not show a bimodal distribution but rather a broad continuum. The ranges in $\delta^{15}N$ for prey were generally similar and relatively broad among colonies, with prey from Blackwater being slightly lower in $\delta^{15}N$ than prey from the other three colonies.

Aerial tracking

A total of 58 foraging excursions were documented for adult wood storks from coastal colonies by following birds in a fixed-wing aircraft (Table 4). Of the 31 foraging excursions originating from Harris Neck, 25 were made to estuarine sites and 6 were made to palustrine sites. This contrasts with excursions that originated from St. Simons Island, where 17 out of 27 trips were made to estuarine sites, with the remainder (10 forays) to palustr-

ine sites. Using the pooled data on individual forays and a GIS database of wetland types, the ratio of actual estuarine to palustrine wetlands within the Harris Neck and St Simons Island foraging ranges were 0.86 and 0.52, respectively. When compared to the ratio of foray-types that storks completed, chi-square tests determined that stork foraging flights were distributed according to wetland availability within each colony's total foraging area along the coast.

Discussion

Nestling storks were chosen as the focus of this study primarily because their feathers record dietary history that occurred solely at the site of natal origin. This required the carbon and nitrogen of feather keratin to have been supplied by parents that foraged in nearby estuarine and palustrine wetlands. To determine the percentage of prey-types (saltwater vs. freshwater) in the diet from the carbon and nitrogen isotopes in feathers, the relationship between the isotopic content of feathers and diet must be known. Based on the results of the captive wood stork feeding trial and published data for other bird species, $\varepsilon_{feather\text{-}diet}$ values of 3‰ were used to relate feathers and foods for *both* carbon and nitrogen isotopes. These values were selected to simplify the corrections required for interpretation of the isotopic records; in both cases, uncertainty in the estimation of ε was less than the distribution of isotopic values for field samples measured in this study.

Carbon isotopes in feathers and food resources

Inland isotopic signatures

Using the range in $\delta^{13}C$ observed for down feathers from the inland colonies (–27 to –23‰) and an $\varepsilon_{feather\text{-}diet}$ of 3‰, the predicted range in $\delta^{13}C$ for food resources was –30 to –26‰. This range was similar to that observed for C_3 plants that make up the base of the food web in inland environments (Smith and Epstein 1971; Rounick and Winterbourn 1986). Other studies have documented similar ranges in $\delta^{13}C$ for wetland biota from inland environments of South Carolina and Georgia. McArthur and Moorhead (1996) determined that riparian and aquatic plant species along a creek near Chew Mill varied between –35 and –28‰, while aquatic macrophytes collected from nearby ponds ranged from –28 to –23‰ (C.S. Romanek, unpublished work).

Coastal isotopic signatures

The predicted ranges in $\delta^{13}C$ for food resources from feathers of Harris Neck and St. Simons Island were –21 to –16‰ and –29 to –17‰, respectively. The predicted range for Harris Neck was consistent with biota derived primarily from estuarine wetlands along the Georgia coast. Haines (1976a, 1976b) and Haines and Montague (1979) determined that primary producers and consumers from Georgia salt marshes ranged from –26 to –12‰ in $\delta^{13}C$, while low-trophic-level consumers (shrimp and crabs) had values that ranged from –23 to –12‰. Hughes and Sherr (1983) and Kneib et al. (1980) determined that the $\delta^{13}C$ of estuarine fish such as *F. heteroclitus*, *Mugil cephalus* and *Leiostomus xanthurus*, which rely primarily on low trophic-level producers and consumers, had $\delta^{13}C$ values between –22 and –14‰, broadly reflecting the $\delta^{13}C$ of the available carbon base. Predators like the wood stork, which forage in the intertidal zone of estuarine environments, should be characterized by $\delta^{13}C$ values that are ultimately related to the isotopic composition of prey items that characterize these food webs, and our data suggested that this was indeed the case.

Nitrogen isotopes in feathers and food resources

Using an $\varepsilon_{feather\text{-}diet}$ of 3‰ for nitrogen and the observed range in $\delta^{15}N$ for down feathers (Table 1), the predicted range in $\delta^{15}N$ for food resources of nestling wood storks from all four colonies was ~5 to 9‰. This range was compatible with the $\delta^{15}N$ observed for potential prey of estuarine and palustrine wetlands (Nadelhoffer and Fry 1994; Michener and Schell 1994), although this was not surprising given the wide and overlapping range of $\delta^{15}N$ observed for prey in aquatic ecosystems. The dynamic nature of wetlands, which can vary spatially and temporally in $\delta^{15}N$ (Yoshioka et al. 1994; France 1995; Boon and Bunn 1994), requires additional habitat-specific knowledge to decipher the nitrogen isotope records embodied in feather keratin.

It is not known whether the ecosystems in which adult wood storks foraged were similar in structure and $\delta^{15}N$ content, but if this were the case then the ~3‰ difference between feathers from the inland colonies would predict distinct feeding patterns, with nestlings from Chew Mill subsisting primarily on upper trophic-level consumers (piscivorous fish) and nestlings from Blackwater being fed lower trophic-level consumers (crayfish). Alternatively, if these wetlands were isotopically distinct then the difference would be related to nitrogen bases that were inherently different in their nitrogen isotopic composition (Vander Zanden and Rasmussen 1999).

The combined carbon and nitrogen isotope data provided insights into foraging strategies that could not be determined from the isotope systematics of a single element. A strong correlation existed between the $\delta^{13}C$ and $\delta^{15}N$ of down feathers from the coastal colonies. The relatively high $\delta^{13}C$ of estuarine wetlands can be used to define the $\delta^{15}N$ signature of the estuarine environment. The $\delta^{15}N$ for feathers enriched in ^{13}C was ~11–12‰ for nestlings from both Harris Neck and St. Simons Island, suggesting that adults from these two colonies foraged in common (or at least similar) estuarine wetlands; this is reasonable given the close geographic proximity of the two colonies (<35 km).

While the estuarine $\delta^{15}N$ signature could be determined straightforwardly, the $\delta^{15}N$ signature for the palustrine component of the coastal diet was more difficult to ascertain. Assuming that coastal storks foraged in common freshwater wetlands, the $\delta^{15}N$ of the palustrine signature could be predicted from the distribution of $\delta^{13}C$ values for feathers from the coastal colonies. The $\delta^{15}N$ of nestling feather SS095 from St. Simons Island (9.5‰; Fig. 2) is instructive in this manner as it had a $\delta^{13}C$ signature (–26.0‰) that was uniquely characteristic of freshwater wetlands. This $\delta^{15}N$ was also the lowest of any feather collected from the coast and it fell within the range of values observed for the inland colony of Blackwater. To evaluate these relationships further, regurgitant from nestling birds was identified and analyzed for its isotopic content.

Stable isotopes and prey items in stork regurgitant

Inland colonies

Prey items recovered from the regurgitant of nestlings at Chew Mill and Blackwater were all freshwater species. The $\delta^{13}C$ of these prey ranged from –32 to –25‰, with no preferential distributions noted among lower trophic-level (crayfish) and higher trophic-level (piscivorous fish) consumers (Fig. 3). The range in $\delta^{13}C$ for prey from Chew Mill (–29 to –26‰) was identical to the range predicted from feathers (Table 1). This suggests that in this colony regurgitant accurately reflected the source of carbon being incorporated in feather keratin. Prey items from Blackwater had a wider range in $\delta^{13}C$, with *C. macropterus* having the lowest $\delta^{13}C$ (–32‰) and crayfish the greatest $\delta^{13}C$ (≤–25‰) of all freshwater prey. Based on down feathers, the predicted range in $\delta^{13}C$ for food resources (–30 to –28‰) again fell within the observed range of $\delta^{13}C$ for dietary items in regurgitant.

The $\delta^{15}N$ of prey further clarified the feeding habits of inland wood storks. Crayfish comprised almost one-third of the prey items in regurgitant at Blackwater compared to only 10% at Chew Mill. These percentages were reflected in the $\delta^{15}N$ of feathers. As lower trophic-level consumers, crayfish should have $\delta^{15}N$ values that are lower than prey of higher trophic status (e.g., piscivorous fish). Prey from Chew Mill were predominantly upper trophic-level consumers (e.g., *Amia calva, E. americanus, Lepomis marginatus*), and they had $\delta^{15}N$ values (7–10‰) that bracketed the $\delta^{15}N$ of the diet predicted from feather keratin. Prey from Blackwater had $\delta^{15}N$ values (–0.2 to 9.0‰) that again bracketed the predicted diet, but in this case the diet was weighted heavily toward lower-trophic-level consumers (e.g., crayfish). The differences between the $\delta^{15}N$ of lower- and upper-trophic-level consumers were generally similar among colonies, suggesting that the nitrogen bases and trophic structures of these inland ecosystems were similar. These results suggested that wood storks were feeding at different trophic levels within these two inland ecosystems. The cause for this is unclear, but it may be related to the relative availability of prey types at each colony.

Coastal colonies

Food resources were potentially more difficult to interpret from the down feathers of coastal nestlings because the foraging ranges of adult storks included both estuarine and palustrine wetlands. Based on the distribution of species in regurgitant, it was predicted that storks from St. Simons Island foraged solely in estuarine wetlands while storks from Harris Neck foraged in both estuarine and palustrine wetlands. This contrasted sharply with interpretations based on the $\delta^{13}C$ of feathers, which suggested that nestlings from both coastal colonies assimilated carbon from estuarine and palustrine resources. In fact, the $\delta^{13}C$ of feather SS095 from St. Simons Island was sufficiently low to conclude that all of its carbon originated from freshwater resources.

Saltwater prey from both coastal colonies displayed a range in $\delta^{13}C$ characteristic of marine sources (–17 to –13‰). Only one saltwater prey item from St. Simons Island (*Callinectes sapidus*) had a $\delta^{13}C$ (–17.4‰) compatible with feathers from any nestlings at this colony (siblings; Fig. 2). All remaining prey were greater in $\delta^{13}C$ and all feathers were lower in $\delta^{13}C$, clearly identifying freshwater prey as a component of the diet that was not found in regurgitant samples. Regurgitant from Harris Neck, on the other hand, contained freshwater prey with a palustrine $\delta^{13}C$ signature (~–28‰ for *U. pygmaea* and *L. gibbosus*), yet feathers from this colony displayed clear estuarine isotopic signatures.

Relationships between stable isotopes in feathers and GIS

Discrepancies between predictions of foraging patterns based on regurgitant composition and the stable isotopic content of feather keratin were reconciled through the aerial tracking of adult wood storks from the coastal colonies. Direct observations revealed that 81 and 63% of the foraging excursions made by adults from the Harris Neck and St. Simons Island colonies, respectively, were to estuarine wetlands. When these data were interpreted within the context of a GIS database of wetland types, 86 and 52% of the area within the Harris Neck and St. Simons Island foraging ranges were estuarine wetlands. Therefore over the course of the study, storks foraged in wetlands according to their relative abundance along the coast. The percentages of prey types (estuarine vs. palustrine) in regurgitant from these same colonies did not accurately reflect the integrated foraging activities over the time interval during which the sampled feathers were grown. Saltwater prey constituted approximately 60% of the regurgitant recovered from nestlings at Harris Neck and 100% of the regurgitant from St. Simons Island (Table 3). The distribution of

observed forays more accurately reflected the predictions from the stable isotope content of feather keratin than the species composition of prey from regurgitant, the latter representing only the prey composition of each bird's most recent meal.

Aerial tracking and the isotopic composition of feathers provided internally consistent data sets since foraging excursions were documented over the critical time interval of feather growth. Contradictions between regurgitant composition and the isotopic content of feathers occurred because regurgitant and feathers recorded information on different time scales. Regurgitant provided only an instantaneous snapshot of the foods a stork last consumed while feathers recorded an integrated signature of assimilated foods over the entire period of feather growth. A single analysis of regurgitant may or may not be representative of the integrated diet or even of those materials metabolized by an individual.

Implications for conservation strategies

The stable isotopic composition of wood stork feathers records reliable dietary information that is not easily obtained by other means. Using this method, the foraging ecology of individual birds can be targeted for analysis without undertaking lengthy, expensive, and time-consuming procedures. The $\delta^{13}C$ and $\delta^{15}N$ of feathers can document, at relatively low cost, a variety of foraging strategies. Further, the $\delta^{13}C$ signature of feather SS095 from a St. Simons Island nestling documented a unique and persistent freshwater foraging preference that extended throughout the time interval of feather growth (~1 month) while other nestlings from the same colony showed more variable contributions of freshwater and saltwater prey to the diet. Such high-resolution records of foraging ecology suggest that, as in the case of coastal breeding white ibis (*Eudocimus albus*; Bildstein 1993), freshwater wetlands are an important habitat for wood storks during annual breeding activities. Preservation of these wetlands will serve to enhance conservation efforts for this endangered species in coastal regions of the southeastern United States.

Acknowledgements C.S.R. would like to thank Eric Peters for suggesting the application of stable isotopes to ecosystem research at the Savannah River DOE Site, and C.P. Chamberlain for providing guidance on sample preparation. Additionally, Dr. Merav Ben-David is acknowledged for providing help and guidance in the statistical analysis of data using the *K*-nearest-neighbor program. The support and cooperation of Sherry Branch and the staff of the Aviculture Department of Sea World, Orlando, Florida allowed the estimation of isotope enrichment factors for the captive storks in their collection. This work would not have been possible without the aid of Joan Gariboldi, Heather Brant and Carol Eldridge of SREL, and John Robinette (USFWS) and Mike Harris (GDNR). The USFWS and Georgia Department of Natural Resources are acknowledged for financial support. This work was also funded in part by the U.S. Department of Energy (Financial Assistance Award DE-FC09–96SR18546) to the Savannah River Ecology Laboratory through the University of Georgia Research Foundation, Inc.

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