Estuaries Vol. 15, No. 2, p. 147–157 June 1992

The Relative Importance of Biotic and Abiotic Vectors in Nutrient Transport

KEITH L. BILDSTEIN
Department of Biology
Winthrop College
Rock Hill, South Carolina 29733
and
The Belle W. Baruch Institute for Marine Biology
and Coastal Research
University of South Carolina
Columbia, South Carolina 29208

ELIZABETH BLOOD
School of Public Health
and
The Belle W. Baruch Institute for Marine Biology
and Coastal Research
University of South Carolina
Columbia, South Carolina 29208

PETER FREDERICK
Department of Wildlife and Range Science
School of Natural Resources
University of Florida
Gainesville, Florida 32611

ABSTRACT: The mass of nutrients (nitrogen, phosphorus, potassium, and calcium) imported during 1984 and 1985 to the North Inlet Estuary, Georgetown County, South Carolina, by precipitation and runoff was compared with that imported by a colonial-nesting wading bird, the white ibis (*Eudocimus albus*). From late March through late June of both years, breeding ibises imported nutrients to the North Inlet Estuary study site from freshwater bottomland forest swamps, where they fed on crayfishes (Procambaridae). Although 1984 was a relatively wet year, in 1985 the ibis breeding season was preceded by a severe winter–spring drought. In 1984 ibises nested in higher numbers, had higher per-pair breeding success, and imported 11 times more nutrients than in 1985. Nutrient input from atmospheric sources was substantially lower in 1984 than in 1985. The 1984 ibises imported 9% as much nitrogen, 33% as much phosphorus, 0.4% as much potassium, and 0.3% as much calcium to the estuary as did atmospheric sources. In 1985 nutrient input from ibises amounted to only 0.2% of the nitrogen, 2.9% of the phosphorus, and $\ll$1% of the potassium and calcium imported by atmospheric sources. Our results show that nutrient inputs to estuaries from colonial-nesting wading birds can be substantial when compared with those from atmospheric sources and can vary considerably among years. They also suggest that nutrient regimes in estuaries with large assemblages of wading birds may differ significantly from those lacking such colonies.

Introduction

Nutrient availability affects primary productivity in salt-marsh ecosystems (Pomeroy et al. 1981). Although nutrient processing in coastal ecosystems has been the focus of several recent studies (i.e., Pomeroy and Wiegert 1981; Dame et al. 1986), the relative importance of biotic and abiotic vectors of nutrients has received scant attention. Here, we report the results of a study conducted in a South Carolina estuary that compares annual fluxes of nitrogen, phosphorus, potassium, and calcium from atmospheric sources with those from a common, and sometimes abundant, wading bird, the white ibis (*Eudocimus albus,* Order Ciconiiformes). We also compare the magnitudes of these nutrient inputs with the potential tidal input from a bay abutting the site's southern border.

Our study was conducted in response to suggestions that avian populations may affect nutrient processing by moving nutrients between ecosys-

0160-8347/92/020147-11$01.50/0

tems when birds feed in one area and roost or nest in another (Sturges et al. 1974; Morales and Pacheco 1986). Although the results of previous studies indicate that avian populations do not impact nutrient processing significantly *within* ecosystems via their role as accelerators of nutrient cycling (Sturges et al. 1974; Wiens and Innis 1974; Wiens and Dyer 1977; Bedard et al. 1980), several studies suggest that birds can play a substantial role in nutrient processing by moving nutrients *between* ecosystems, especially when their mobility is coupled with communal roosting or nesting. Thus, colonial nesting wading birds have the potential of being significant biotic vectors (sensu Forman 1981) of nutrients when large numbers of them breed in one ecosystem and feed in another. When compared with the movement of nutrients by physical vectors, the movement of nutrients by birds appears to be of minor importance on a region-wide basis (Hutchinson 1950; Golovkin and Pozdynakova 1966; Bedard et al. 1980). Even so, studies conducted at communal roosting and nesting assemblages indicate substantially enhanced local nutrient availability as the result of the deposition of excreta (Ritchie 1920; Hutchinson 1950; Golovkin and Pozdynakova 1966; Weir 1969; Zelickman and Golovkin 1972; McColl and Burger 1976; Onuf et al. 1977).

From 1975 to 1989 between 2,000 and 20,000 pairs of white ibises nested annually on Pumpkinseed Island, a 9-ha marsh island in Winyah Bay, along the southern border of the North Inlet Estuary near Georgetown, South Carolina (Osborn and Custer 1978; Bildstein et al. 1990). From late March through early June, most of the ibises breeding at the site fly inland to feed on crayfishes (Family Cambaridae) in bottomland forest, with birds commuting up to 40 km one way several times daily between their feeding sites and the breeding colony. The long-distance flights inland, which result in ibises importing nutrients from freshwater habitats to the estuary, occur because nestling ibises require freshwater prey for normal growth and development (Johnston and Bildstein 1990). Later in the season, after the young have fledged, ibises shift to feeding on brackish-water fiddler crabs (*Uca* spp.) in the North Inlet Estuary, before departing in late summer–early fall for their wintering grounds (Bildstein et al. 1981; Bildstein 1983). As a result of the large numbers of individuals feeding on the marsh from early spring through early fall, ibises annually comprise 17% of the avian biomass in the estuary (Bildstein et al. 1982).

Stinner (1983) reported that phosphorus and calcium input from a colony of white ibises breeding in the oligotrophic Okefenokee Swamp in southern Georgia was ten times that imported by precipitation and stream flow. Our study compares the relative magnitudes of nutrient input from ibises and atmospheric sources in a eutrophic coastal ecosystem over a two-year period that included both a relatively wet year and a drought year, and discusses these findings in terms of landscape ecology.

Methods

Study Site

The study was conducted on the 6,030-ha North Inlet Estuary and associated forested watershed (3,200-ha estuary and 2,830-ha forested uplands), directly northeast of Winyah Bay and east of Georgetown, South Carolina (33°20′N, 79°10′W) (Fig. 1). The high-salinity estuary, typical of estuaries in the southeastern coastal plain (Pritchard 1967), is dominated by smooth cordgrass (*Spartina alterniflora*), and consists of about 60% salt marsh; 10% mud flats, sandbars, and oyster reefs; and 30% open water (Forth 1978).

The upland watershed is dominated by 25-year-old loblolly pines (*Pinus taeda*), with intermittent oaks (*Quercus* spp.) and red maple (*Acer rubrum*). The understory is dominated by scattered wax myrtle (*Myrica cerifera*) (cf. Barry 1980). Soils are Spodosols, with Aeric Haplaquods in drier portions and Typic Haplaquods in wetter areas. Organic horizons average 15 cm; the organic-mineral horizon averages 35 cm, with the underlying mineral soil primarily consisting of weathered sands intermixed with shell deposits. Topographic relief is <1 m km^{-1} (Blood et al. 1989).

Approximately 989 ha of forest contribute freshwater runoff directly to the 3,200-ha North Inlet Estuary study site (outlined in Fig. 1). Freshwater input from upland streams is typically $<1\%$ of the tidal prism. Four forested wetlands drain into the North Inlet Estuary (Fig. 1). Watershed E, a 53-ha watershed (outlined in Fig. 1), was selected to measure export to the marsh from the costal pine forest via a first-order intermittent stream with a sandy substrate. The upper portion of the study stream contains substantial debris and is usually coated with an organic floc. The lower portion is shallow, with few debris dams and no flocculent organic matter (Blood et al. 1989).

White ibises in the area breed at the southern edge of the estuary on Pumpkinseed Island, a 9-ha, tidally inundated, marsh island located in Mud Bay, a shallow northeastern extension of Winyah Bay (Fig. 1). The island, which is vegetated with black needlerush (*Juncus roemerianus*), salt marsh bulrush (*Scirpus robustus*), big cordgrass (*S. cynosuroides*), smooth cordgrass, and a narrow strip of marsh elder (*Iva frutescens*), has served as a colony site since at least 1967 (Bildstein et al. 1990).

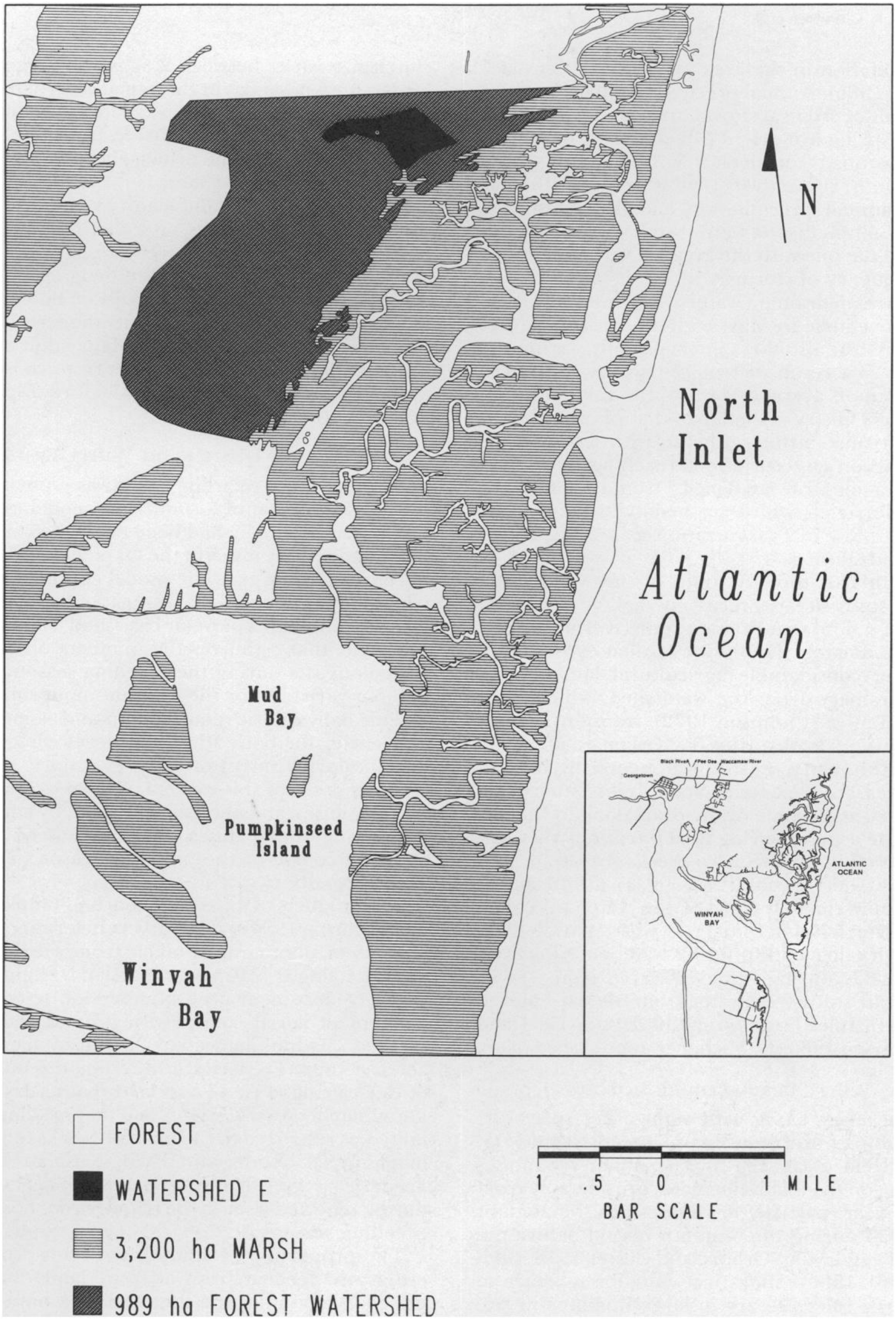

Fig. 1. Map of North Inlet Estuary and Winyah Bay, South Carolina, depicting the 989-ha forested watershed, Watershed E, the 3,200-ha North Inlet Estuary study site, and Pumpkinseed Island (site of the white ibis breeding colony).

Precipitation in the area averages 130 cm yr^{-1} (NOAA 1985). Annual precipitation patterns vary as a result of tropical storms and hurricanes. Winter and spring are drier (20% and 21% of annual precipitation, respectively), with 5 and 4 storms each month, respectively. Fall is wetter, with 24% of the annual precipitation and 4 storms each month. Summer is the wettest season (35% of rainfall), and the one with the greatest variation in size and frequency of storms.

The stream draining watershed E normally flows from November to May, with an average rate of 0.02 $m^3 s^{-1}$. It also flows intermittently during the summer as a result of tropical storms and hurricanes. Runoff averages 41% of the rainfall input. Stream chemistry is similar to that of other blackwater streams in the southeast, with dissolved organic carbon concentrations reaching 62 mg l^{-1}, and averaging 21.6 ± 0.8 mg l^{-1} from 1983 through 1985. Nutrients, which are mainly in the organic form, are low in concentration as are suspended solids and silicates.

Winyah Bay, directly south of the North Inlet Estuary study site, is a relatively shallow bay (mean depth of 4.6 m) that drains a four-river watershed of approximately 47,000 km^2 (Allen et al. 1984), including considerable agricultural land. Freshwater drainage from the watershed, which averages 425 $m^3 s^{-1}$ (Johnson 1972), transports a sizeable nutrient load to the bay (Allen et al. 1982, 1984). Although most freshwater entering Winyah Bay appears to bypass the North Inlet Estuary (Allen et al. 1984), some of the drainage into the bay enters the estuary during tidal intrusions via sheet flow as well as through two creeks that drain into Mud Bay (Kjerfve et al. 1981; Fig. 1). On an annual basis, approximately 25% of the water exchange in the North Inlet Estuary is with Winyah Bay. Although a tidal node prevents water entering from Winyah Bay on high tides (Kjerfve et al. 1981), during our study freshwater from the bay entered the North Inlet Estuary on 130 days in 1984 and on 93 days in 1985 (N. Michener unpublished data).

White Ibis Breeding Biology

White ibises, along with eight other species of wading birds, breed on Pumpkinseed Island (Fig. 1) (Bildstein et al. 1982). The number of ibises breeding on the island fluctuates considerably from year to year, partially in response to the amount of rainfall during the 6-month period before the onset of egg-laying (Osborn and Custer 1978; Bildstein et al. 1990). Migrating white ibises return to the North Inlet Estuary in large numbers in late March (Palmer 1962; Sprunt and Chamberlain 1970). Ibises begin egg-laying in early April, and the first young hatch in late April–early May. Mean clutch size varies between 2 eggs and 3 eggs, and birds whose nests fail in the egg and early-nestling stages (usually as a result of tidal inundation [Frederick 1987]) often renest. Aside from tidal inundation, starvation is the principal cause of nestling mortality (Frederick 1985).

Nestlings, which are ambulatory within 7–10 days of age, are fed by adults on a diet dominated by crayfishes. They do not leave the island until they are almost 7 weeks old. After fledging, juvenile ibises feed on their own, principally on fiddler crabs in the North Inlet Estuary and on other crustaceans in freshwater wetlands inland. Many adult and recently fledged juvenile ibises return to roost each evening on Pumpkinseed Island before dispersing in late summer.

Nutrient Input From White Ibises

Nutrient input by white ibises was estimated using a modification of a simulation model (Stinner 1983) that originally had been developed to study nutrient input by ibises in the Okefenokee Swamp, in southern Georgia. The model consists of a nutrient-input submodel that estimates nutrient input by white ibises on a per-pair basis, and a population submodel that estimates the numbers of ibises at the colony site during the breeding season.

Input variables for the nutrient-input submodel include daily caloric requirements and assimilation efficiencies for both adult and developing young ibises, caloric content of ibis prey, caloric and nutrient content of ibis excreta, nutrient content of nestling ibises, and percent time spent by adult and developing young ibises on Pumpkinseed Island over the course of the breeding season (Table 1 and Appendix 1).

The numbers of ibises breeding on Pumpkinseed Island during 1984 and 1985 were determined from a series of photographs taken from a fixed-wing aircraft flying at 150 m over the island. Flights were timed to document peak numbers of nests. Comparisons of aerial counts with ground counts of marked quadrats indicate >95% accuracy of the aerial counts (Frederick 1987). For the purposes of our calculations, we assumed that each pair of ibises hatched two nestlings and that nestling mortality was restricted to the first two weeks following hatching (cf. Rudegeair 1975; Kushlan 1977b; Frederick 1985). Nestling mortality was assessed during repeated visits to the island throughout both breeding seasons.

The proportion of adult ibises flying from the estuary to feed in freshwater wetlands was estimated by counting the ibises feeding on a 45-ha census plot during the 1984 and 1985 breeding seasons, and assuming that the ratios of the number of birds feeding on the entire estuary to the num-

TABLE 1. Input variables for the simulation model used to determine per-pair nutrient input by white ibises breeding on Pumpkinseed Island in 1984 and 1985.

Input Variable	This Study	Stinner (1983)
Caloric requirements of adults (kcal/day/bird)	162.6	164.6
Caloric requirements of nestlings from hatching to 40-days-old (kcal)	8,620	8,620
Assimilation efficiency		
Adults	79.7%	79.7%
Young	79%	68%
Caloric content of prey (kcal/g dry-weight)		
Crayfish	4.10	4.05
Fiddler crabs	2.30	—
Caloric content of excreta (kcal/g dry-weight)		
Crayfishes/fiddler crabs	2.02/1.34	2.48[a]
Percent nutrient content of excreta		
Crayfishes/fiddler crabs		
Nitrogen	5.4%/3.6%	—
Phosphorus	1.9%/1.9%	8.3%
Potassium	0.38%/0.30%	1.5%
Calcium	10.9%/19.1%	10.0%
Percent of time spent by adults at the colony site:		
7-d postmigration period	54%	0%
10-d courtship period	81%	54%
21-d incubation period	54%	77%
Days 1–14 of nestling period	75%	54%
Days 15–40 of nestling period	27%	54%
20-d fledgling period	27%	54%
Percent of time spent by fledglings at colony site:	75%	54%

[a] Predominantly crayfish.

TABLE 2. Input variables for the simulation model used to determine the numbers of ibises importing nutrients to Pumpkinseed Island in 1984 and 1985.

Input Variable	1984	1985
Number of pairs breeding on Pumpkinseed Island[a]	12,973	1,976
Percent of breeding pairs feeding off of the North Inlet Estuary		
March	97%	71%
April	94%	45%
May	97%	74%
June	98%	81%
Number of hatchlings per pair	2.0	2.0
Number of 14-day-old nestlings per pair[b]	1.3	0.8
Number of fledglings per pair	1.3	0.8

[a] Based on aerial surveys on May 14, 1984 and May 4, 1985.
[b] The model assumes that all nestling mortality occurred during the 14 days following hatching (see text for explanation).

ber feeding on the census plot were similar to those recorded in 1979 and 1980, when the census plot and the entire estuary were monitored concurrently (cf. Henderson 1981; Bildstein et al. 1982). (Subsequent counts of birds feeding throughout the estuary in 1988 and 1989 [Bildstein unpublished data] support the validity of this approach.) Estimates derived from our calculations closely agreed with the ratios of crayfishes to fiddler crabs in regurgitant samples collected from nestling white ibises in 1984 and 1985.

The results of the nutrient input submodel were integrated with the population submodel (Table 2) to produce estimates of nutrient input to Pumpkinseed Island by the breeding population of white ibises.

To assess the sensitivity of Stinner's original model (Stinner 1983) to our modifications, we compared our output on a per-pair basis with that derived using the unmodified model.

During the summer 1982, nitrogen concentrations in the Mud Bay water column near the ibis colony site on Pumpkinseed Island averaged 54% higher than the already nutrient-rich waters of Winyah Bay (Allen et al. 1984). However, as Pumpkinseed Island is 1.5 km south of the North Inlet Estuary, we conservatively assumed that only 25% of the nutrients deposited on the island by ibises were eventually transported to the study site by tidal activity.

Nutrient Input From Abiotic Sources

Gross precipitation for chemical analysis was sampled using five gauges consisting of polypropylene bottles fitted with 16.5-cm diameter funnels, placed at 45 openings adjacent to the forest stand. Volumes were calibrated throughout the study using standard rain gauges. Following each storm, samples were collected for analysis, and gross volume was converted to depth over the watershed.

Water flow in the stream was measured with a Parshall flume, and water height was converted to volume from a stage-to-discharge relationship constructed for the stream. Samples were analyzed following each storm.

Precipitation and streamflow samples were analyzed for total nitrogen and phosphorus and for potassium and calcium. All samples were maintained at 4°C until analysis. Approximately 200 ml of each sample were filtered through precombusted Whatman GF/F glass-fiber filters. Aliquots for total nitrogen and phosphorus and for cations were stored separately. Total N and P were measured by colorimetric test with a Technicon Autoanalyzer II or Orion Scientific Autoanalyzer System, using Technicon Industrial Method No. 329-74W, following persulfate digestion (Glibert et al. 1977). Cation analyses were by flame atomic absorption.

Preliminary univariate analyses indicated the need for log transformation to normalize the chemical data. Data used to calculate annual flux for precipitation and stream flow came from 67

TABLE 3. Nutrients imported to the North Inlet Estuary by white ibises, 1984 and 1985.

	Input from					
	Excreta		Nestling Carcasses		Total Input	
Nutrient (kg)	1984	1985	1984	1985	1984	1985
Nitrogen	636.3	57.4	3.8 (0.6%)[a]	0.7 (1.2%)[a]	640.1	58.1
Phosphorus	223.9	20.2	2.5 (1.1%)	0.4 (2.1%)	226.4	20.6
Potassium	44.8	4.0	1.7 (3.7%)	0.3 (6.9%)	46.5	4.3
Calcium	1,284	115.8	1.0 (0.1%)	0.2 (0.2%)	1,285	116.0

[a] Percent of total input.

storms occurring from January 1, 1984 through December 31, 1985. Rainfall and stream fluxes were calculated by multiplying volume by mean constituent concentration for each storm. We approximated the contributions of nine storms for which we did not collect stream samples by averaging the concentrations of the storms preceding and following the missed events and using these averages in conjunction with storm volume to determine flux.

The amounts of nutrients flowing into Winyah Bay were calculated by combining U.S. Geological Survey discharge data for the Pee Dee, Black, Lynches, and Waccamaw rivers with monthly (nitrogen and phosphorus) or bimonthly (cations) concentrations in the discharge (Bennett et al. 1984, 1985).

Results

Nutrient Input From White Ibises

Estimates of the amounts of nutrients imported by white ibises are given in Table 3. In 1985 nutrient input from ibises was only 9% of what it had been in 1984. Most of the difference (94%) resulted from an 85% drop in the size of the ibis breeding population in 1985 (Table 2). The remaining 6% of the decline occurred because of a 41% drop in per-pair nutrient input to the estuary. This decrease, in turn, resulted from a combination of substantially lower nestling survivorship (2%) (Table 2), and less off-estuary feeding in 1985 (4%) (Table 4).

TABLE 4. Numbers of white ibises feeding on the North Inlet Estuary during the 1979 and 1980 breeding seasons, and estimated numbers for 1984 and 1985.

	Numbers of Birds		
Month	1979–1980[a]	1984[b]	1985[b]
March	694	852 (3.3)[c]	1,128 (28.5)
April	1,343	1,648 (6.4)	2,182 (55.2)
May	626	768 (3.0)	1,017 (25.7)
June	464	569 (2.2)	754 (19.1)

[a] Based on twice-a-month aerial censuses of the marsh.
[b] Numbers are estimated based on the assumption that the ratio of the number of birds feeding on the entire marsh to the number feeding on a 45-ha census plot was the same in 1984 and 1985 as in 1979 and 1980.
[c] Percent of breeding population.

Sensitivity Testing of the Model Used to Generate Estimates of Nutrient Input From White Ibises

Despite considerable differences between the values we used for a number of input variables and those used by Stinner (1983) in her application of the model, in 1984 our per-pair estimate of the amount of excreta imported by ibises was only 10% higher (3,634 g versus 3,276 g) than it would have been had we employed Stinner's (1983) original values. In 1984 the magnitude of the difference increased to 52% because of declines in our estimates of nestling survival and relative use of off-estuary foraging sites (Tables 1 and 5). Even so, these differences are small compared with the effect of substituting Stinner's original (1983) values for the nutrient content of excreta with those used in this study (Tables 1 and 5). When these substitutions are made, differences of at least 250% occur between our estimates for phosphorus and potassium input and those derived using the original values (Table 5). Differences in estimated calcium input are considerably less (Table 5).

The reasons for the substantial differences in the phosphorus and potassium content of ibis excreta are unclear, but our values for birds on both fiddler crab diets and zoo diets (a mixture of horse meat, fish meal, and shrimp meal) are in essential agreement with those for birds on a crayfish diet. The nutrient content of bird excreta can vary by an order of magnitude, even among species consuming apparently similar diets (cf. Bedard et al. 1980). Our values for both nitrogen and phosphorus fall at the lower end of the range of values for mainly piscivorous coastal and sea bird species (Hutchinson 1950; Powell et al. in press). This, together with the higher values for phosphorus and potassium derived by Stinner (1983) for ibis excreta in the Okefenokee Swamp, suggests that our estimates of nutrient input by white ibises are conservative.

TABLE 5. Differences in estimates of the amounts of excreta and nutrients imported to the North Inlet Estuary by breeding white ibises resulting from the use of different values for input variables in Stinner's (1983) nutrient-input model.

Amount Imported Per-Pair (g dry wgt)	Based on Input Variables from				
	This study[a]		Stinner	Percent Difference	
	1984	1985	1983	1984	1985
Excreta	3,634	2,150	3,276	−10%	+52%
Nitrogen	196	116	—	—	—
Phosphorus	69.0	41.8	272	+294%	+567%
Potassium	13.8	8.17	49.1	+256%	+501%
Calcium	396	234	327	−17%	+40%

[a] See Tables 1 and 2 for a comparison of the values of input variables used in this study and in Stinner (1983).

Nutrient Input From Abiotic Sources

Gross precipitation, which was 8% below the 30-yr mean during our study, was slightly higher in 1984 (119 cm) than in 1985 (115 cm). Rainfall during winter 1983–1984, spring 1984, and summer and fall 1985 was above the 30-yr mean. Rainfall during summer 1984, winter 1984–1985, and spring 1985 was below average (Table 6).

We calculated the 30-yr average discharge of our stream to be 52 cm (based on 30-yr mean rainfall and assuming 40% runoff). Runoff for 1984 was 13% above this mean, while runoff in 1985 was 34% below average. Runoff from November to May was 52.3 cm in 1983–1984, but only 11.2 cm in 1984–1985 (Table 6).

Although precipitation on the North Inlet Estuary was slightly higher in 1984 than in 1985, the nutrient content of precipitation was substantially higher in 1985 than in 1984. As a result, phosphorus, potassium, and, especially, nitrogen inputs from rainfall, but not from stream flow, were substantially greater in 1985 than in 1984 (Table 7). This was not so for Winyah Bay, where nutrient input via freshwater flow was considerably greater in 1984, especially during the ibis breeding season (Table 8).

Increased nutrient input from rainfall and stream flow into the North Inlet Estuary study site in 1985 (Table 7), coupled with a decrease in nutrient input from ibises (Table 3), resulted in a sizeable shift in the relative annual contributions of nutrients imported to the estuary by these vectors (Table 7). And, in both years, the combined nutrient input from these two sources (i.e., white ibises and local precipitation) is several orders of magnitude less than the amount of nutrients imported into Winyah Bay from its watershed (Table 8), some of which eventually enters the North Inlet Estuary (see above).

Discussion

The total amounts of nitrogen, phosphorus, potassium, and calcium imported to the North Inlet Estuary by white ibises, rainfall, and stream flow appear to vary considerably among years. Nitrogen and phosphorus input from rainfall at the North Inlet Estuary falls at the low end of the range of values for ten sites in North America, Europe, and Africa (Valiela et al. 1978). Even so, rainfall and stream flow appear to import considerably more nutrients overall than do white ibises. This is especially true for potassium and calcium (Table 7). Nevertheless, in one of the two years of our study ibises contributed substantial amounts of both nitrogen and phosphorus to the estuary (Table 7).

Because ibises import nutrients during spring and summer, a time of rapid *Spartina* growth on the marsh, the impact of ibises on primary productivity is probably disproportionate to the relative magnitude of their nutrient flux (cf. Bedard et al. 1980). On the other hand, rainfall and stream flow disperse nutrients more broadly throughout the estuary while ibises deposit almost all of their input on Pumpkinseed Island at the southern edge of the site. Also, nutrient-rich fresh water draining from agricultural areas into Winyah Bay, directly south of our study site, is an additional, and potentially massive, source of nutrient input that is not included in our model (Table 8). Most of the nutrient-rich fresh water entering Winyah Bay appears

TABLE 6. Seasonal rainfall on the North Inlet Estuary and runoff in watershed E during 1984 and 1985.

Year	Rainfall (cm)	Runoff (cm)
1984		
Winter	34.4 (31)[a]	15.2 (45)
Spring	38.4 (42)	37.1 (242)
Summer	15.4 (−41)	0.8 (−91)
Fall	31.0 (1)	6.5 (−47)
1985		
Winter	17.2 (−34)	2.9 (−72)
Spring	15.8 (−41)	8.3 (−23)
Summer	42.1 (63)	6.4 (−39)
Fall	39.6 (28)	9.6 (−22)

[a] Percent above or below 30-year average rainfall or runoff. The 30-year average runoff was calculated as 40% of rainfall.

TABLE 7. Nutrients imported to the North Inlet Estuary by abiotic and biotic sources, 1984 and 1985.

Nutrients	Year	Abiotic Input (kg) Rainfall	Stream Flow	Total	Biotic Input (kg) Ibis Excreta	Ibis Carcasses	Total	Combined Input (kg)	% Biotic
Annual input									
Nitrogen	1984	3,211	3,001	6,212	636.3	3.8	640.0	6,852	9.0%
	1985	21,245	2,008	23,253	57.4	0.7	58.1	2,311	0.2%
Phosphorus	1984	399.8	69.0	468.8	223.9	2.5	226.4	695.2	33.0%
	1985	573.7	108.7	682.4	20.2	0.4	20.6	703.0	2.9%
Calcium	1984	12,831	346,486	359,317	1,284	1.0	1,286	360,603	0.4%
	1985	21,044	237,832	258,876	115.8	0.2	116.0	258,992	0.04%
Potassium	1984	1,734	12,206	13,940	44.8	1.7	46.5	13,987	0.3%
	1985	6,920	9,404	16,324	4.0	0.3	4.3	16,329	0.03%
Input during the ibis breeding season[a]									
Nitrogen	1984	1,738	1,690	3,427	636.3	3.8	640.0	4,067	15.7%
	1985	10,833	135.4	10,968	57.4	0.7	58.1	11,026	0.5%
Phosphorus	1984	168.6	52.6	221.2	223.9	2.5	226.4	447.6	51.0%
	1985	193.1	19.4	212.4	20.2	0.4	20.6	233.0	8.8%
Calcium	1984	2,913	155,041	157,954	1,284	1.0	1,286	159,240	0.8%
	1985	6,010	53,239	59,249	115.8	0.2	116.0	59,365	0.2%
Potassium	1984	852.6	2,921.7	3,774	44.8	1.7	46.5	3,821	1.2%
	1985	3,623	1,899	5,522	4.0	0.3	4.3	5,526	0.1%

[a] Assumed to be March, April, May, and June.

to bypass the North Inlet Estuary. However, some of this water does enter the marsh as sheet flow during extremely high spring tides and wind-driven intrusions (Kjerfve and Proehl 1979; Dame et al. 1986). If significant amounts of nutrients enter the marsh during tidal inundations when ibises are not present on Pumpkinseed Island, the relative importance of input from ibises would decrease substantially. Nevertheless, our results suggest that wading birds can function as significant biotic vectors of nutrients in estuarine ecosystems.

Ibises imported less than one-tenth as much nutrients to the North Inlet Estuary in 1985 as they had in 1984 because of declines in their (1) breeding population, (2) per-pair breeding success, and (3) relative use of inland feeding sites. All three shifts apparently occurred in response to a 60% decline in the amount of rainfall within the region during the six-month period preceding the onset of egg-laying in 1985 (Bildstein et al. 1990). As a result of lower rainfall during the winter and early spring of 1985, crayfish availability in parched inland freshwater wetlands declined to the point that many ibises returning to coastal South Carolina in March 1985 failed to initiate courtship and mating behavior. Those that did breed in 1985 suffered the consequences of the reduced availability of their freshwater prey when many nestlings died of starvation or excessive salt loading as parents shifted to feeding them brackish-water prey such as fiddler crabs (Bildstein et al. 1990; Johnston and Bildstein 1990).

TABLE 8. Freshwater input of nutrients into Winyah Bay, 1984 and 1985.

Nutrient	Year	Freshwater Input (kg × 10^6) Annual	Breeding Season
Nitrogen	1984	19.4	9.57
	1985	9.97	1.97
Phosphorus	1984	1.89	1.10
	1985	0.73	0.14
Calcium	1984	71.5	35.1
	1985	53.5	9.20
Potassium	1984	31.7	14.8
	1985	27.4	4.50

The decline in the amount of nutrients imported by white ibises in 1985 compared with 1984, coupled with concurrent increases in rainfall-induced fluxes of all nutrients except calcium, resulted in a substantial shift in the relative magnitude of these biotic and abiotic vectors of nutrient flow (Table 7). Although we have modelled nutrient input by white ibises for only two years, the difference in the numbers of birds breeding at the site in 1984 and 1985 appears to be typical of the colony. During a 10-yr period between 1979 and 1988, for example, the coefficient of variation for the number of birds breeding at the site was 60%, with the number of pairs of ibises breeding on Pumpkinseed Island ranging over an order of magnitude (from a low of <2,000 in 1985 to a high of >20,000 in 1987; Bildstein et al. 1990). Thus, substantial annual shifts in nutrient input by this species are probably typical. Coefficients of variation for nutrient input from precipitation and stream flow during an 8-yr period from 1978 through 1985 are 20% and 42%, respectively.

Studies of the movement of nutrients across ecosystem boundaries are a relatively new phenomena associated with the emerging discipline of "landscape ecology" (cf. Forman 1981; Wiens et al. 1985). Our work suggests that the relative magnitudes of abiotic and biotic nutrient fluxes into an estuarine ecosystem can shift dramatically among years. Researchers exploring the relative importance of such vectors in ecosystem functioning will need to consider the possibility of substantial annual variation in these transport mechanisms.

Acknowledgments

Our studies of nutrient fluxes in the North Inlet Estuary have been supported by grants from the Winthrop College Research Council and Faculty Development Fund and the Whitehall Foundation (K. L. Bildstein); Sigma Xi, The Explorers Club, The Frank M. Chapman Memorial Fund, and the Tokyo Broadcasting Corporation (P. Frederick); South Carolina Sea Grant Consortium (E. Blood); and by an NSF-LTER grant to the Belle W. Baruch Institute for Marine Biology and Coatal Research. We thank F. J. Vernberg for his continued support and enthusiasm, D. Allen for logistic support, and S. McDowell for collecting ibis excreta. We sincerely appreciate the comments of J. Hobbie and two anonymous reviewers, which helped us substantially improve the final version of this manuscript. Contribution No. 825 of the Belle W. Baruch Institute for Marine Biology and Coastal Research.

Literature Cited

Allen, D. M., S. E. Stancyk, and W. K. Michener (eds.). 1982. Ecology of Winyah Bay, SC, and potential impacts of energy development. Publ. 82-1, Belle W. Baruch Institute, University of South Carolina, Columbia, South Carolina. 275 p.

Allen, D. M., S. E. Stancyk, and W. K. Michener (eds.). 1984. Pollution ecology of Winyah Bay, SC: Characterization of the estuary and potential impacts of petroleum. Publ. 84-1, Belle W. Baruch Institute, University of South Carolina, Columbia, South Carolina, 271 p.

Association of Official Analytical Chemists. 1980. Official Methods of Analysis. 13th ed. Association of Official Analytical Chemists, Washington, D.C.

Barry, J. M. 1980. Natural Vegetation of South Carolina. University of South Carolina Press, Columbia, South Carolina. 214 p.

Bedard, J., J. C. Therriault, and J. Berube. 1980. Assessment of the importance of nutrient recycling by seabirds in the St. Lawrence Estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 37:583–588.

Bennett, C. S., R. D. Hayes, K. H. Jones, and T. W. Cooney. 1984. Water resources data South Carolina water year 1984. USGS Water-Data Report SC-84-1. U.S. Geological Survey, Columbia, South Carolina. 392 p.

Bennett, C. S., R. D. Hayes, K. H. Jones, and W. W. Cooney. 1985. Water resources data South Carolina water year 1985. USGS Water-Data Report SC-85-1. U.S. Geological Survey, Columbia, South Carolina. 412 p.

Bilby, L. W. and E. M. Widdowson. 1971. Chemical composition of growth in nestling blackbirds and thrushes. *British Journal of Nutrition* 25:127–134.

Bildstein, K. L. 1983. Age-related differences in the flocking and foraging behavior of white ibises in a South Carolina salt marsh. *Colonial Waterbirds* 6:45–53.

Bildstein, K. L., R. Christy, and P. DeCoursey. 1981. A preliminary analysis of energy flow in a South Carolina salt marsh: Wading birds. *Colonial Waterbirds* 4:96–103.

Bildstein, K. L., R. Christy, and P. DeCoursey. 1982. Size and structure of a South Carolina salt marsh community. *Wetlands* 2:118–137.

Bildstein, K. L., W. Post, P. Frederick, and J. W. Johnston. 1990. The role of freshwater wetlands in the breeding ecology of White Ibises in coastal South Carolina. *Wilson Bulletin* 102:84–98.

Blood, E. R., W. T. Swank, and T. Williams. 1989. Precipitation, throughfall and streamflow chemistry in a coastal loblolly pine stand, p. 61–78. *In* R. R. Sharitz and J. W. Gibbons (eds.), Freshwater Wetlands and Wildlife, 1989, CONF-8603101, DOE Symposium Series No. 61, USDOE Office of Scientific and Technical Information, Oak Ridge, Tennessee.

Dame, R., T. Chrzanowski, K. Bildstein, B. Kjerfve, H. McKellar, D. Nelson, J. Spurrier, S. Stancyk, H. Stevenson, J. Vernberg, and R. Zingmark. 1986. The outwelling hypothesis and North Inlet, South Carolina. *Marine Ecology-Progress Series* 33:217–229.

Dunn, E. H. 1975. Growth, body components and energy content of nestling double-crested cormorants. *Condor* 77:431–438.

Forman, R. T. T. 1981. Interaction among landscape elements: A core of landscape ecology, p. 35–48. *In* S. P. Tjallingii and A. A. de Veer (eds.), Perspectives in Landscape Ecology. Proceedings of the International Congress of the Netherlands Society of Landscape Ecology. Veldhoven, The Netherlands.

Forth, C. M. 1978. A comparative analysis of the foraging behavior of two species of Ardeids: *Egretta thula*, the Snowy Egret and *Casmerodius albus*, the Great Egret. M.S. Thesis. University of South Carolina, Columbia, South Carolina. 71 p.

Frederick, P. 1985. Mating strategies of White Ibis. Ph.D. Dissertation. University of North Carolina, Chapel Hill, North Carolina. 97 p.

Frederick, P. 1987. Chronic tidally-induced nest failure in a colony of White Ibises. *Condor* 89:413–419.

Glibert, P. M., F. D'Elia, and Z. Mlodzinska. 1977. A semi-automated persulfate oxidation technique for simultaneous total nitrogen and total phosphorus determination in natural water samples. *Woods Hole Oceanographic Contribution 3954.* Woods Hole, Massachusetts.

Golovkin, A. N. and L. E. Pozdynakova. 1966. Effect of marine colonial birds on the biogenic salts in the Murmansk precoastal waters, p. 265–289. *In* E. N. Pavlovskii (ed.), Fish-Eating Birds and Their Significance in Fish Economy. Nauka, Moscow, USSR (Translated for the Fish and Wildlife Service, U.S. Department of the Interior, and the National Science Foundation, Washington, D.C., by Franklin Book Programs Inc., Cairo, Illinois, 1976.)

Henderson, E. G. 1981. Behavioral ecology of the searching behavior of the White Ibis (*Eudocimus albus*). M.S. Thesis. University of South Carolina, Columbia, South Carolina. 72 p.

Hutchinson, G. E. 1950. Biochemistry of vertebrate excretion. *Bulletin of the American Museum of Natural History* 96:1–554.

Johnson, F. A. 1972. A reconnaissance of the Winyah Bay estuarine zone, South Carolina. South Carolina Water Resources Commission Report 4., Columbia, South Carolina. 36 p.

Johnston, J. W. and K. L. Bildstein. 1990. Dietary salt as a physiological constraint on White Ibises breeding in an estuary. *Physiological Zoology* 66:190–207.

Kjerfve, B. and J. A. Proehl. 1979. Velocity variability in a cross-section of a well-mixed estuary. *Journal of Marine Research* 37:409–418.

KJERFVE, B., L. H. STEVENSON, J. A. PROEHL, AND T. H. CHRZANOWSKI. 1981. Estimation of material fluxes in an estuarine cross-section: A critical analysis of spatial measurement density and errors. *Limnology and Oceanography* 26:325–335.

KUSHLAN, J. A. 1977a. Population energetics of the American White Ibis. *Auk* 94:114–122.

KUSHLAN, J. A. 1977b. Growth energetics of White Ibises. *Condor* 79:31–36.

MCCOLL, J. G. AND J. BURGER. 1976. Chemical input by a colony of Franklin's Gulls nesting in cattails. *American Midland Naturalist* 96:270–280.

MORALES, G. AND J. PACHECO. 1986. Effects of diking a Venezuelan savanna on avian habitat, species diversity, energy flow, and mineral flow through wading birds. *Colonial Waterbirds* 9:236–242.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1985. Local climatological data for Georgetown, South Carolina (30 year summary, 1951–80). National Climatic Data Center, Asheville, North Carolina.

O'CONNOR, R. J. 1984. The Growth and Development of Birds. John Wiley and Sons, New York. 315 p.

ONUF, C. P., J. M. TEAL, AND I. VALIELA. 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. *Ecology* 58:514–526.

OSBORN, R. G. AND T. W. CUSTER. 1978. Herons and Their Allies: Atlas of Atlantic Coast Colonies, 1975 and 1976. USFWS OBS-77/08. US Fish and Wildlife Service, Washington, D.C. 211 p.

PALMER, R. S. 1962. Handbook of North American Birds. Vol. 1. Loons through Flamingos. Yale University Press, New Haven, Connecticut. 567 p.

POMEROY, L. R. AND R. G. WIEGERT. 1981. The Ecology of a Salt Marsh. Springer-Verlag, New York. 271 p.

POMEROY, L. R., W. M. DARLEY, E. L. DUNN, J. L. GALLAGHER, E. B. HAINES, AND D. M. WHITNEY. 1981. Primary production, p. 39–67. *In* L. R. Pomeroy and R. G. Wiegert (eds.), The Ecology of a Salt Marsh. Springer-Verlag, New York.

POWELL, G. V. N., W. J. KENWORTHY, AND J. W. FOURQUREAN. In press. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bulletin of Marine Science.*

PRITCHARD, D. W. 1967. What is an estuary: Physical viewpoint, p. 3–5. *In* G. H. Lauff (ed.), Estuaries. Publ. No. 83, American Association for the Advancement of Science, Washington, D.C.

RITCHIE, J. 1920. Animal life in Scotland. Cambridge University Press, Cambridge, England. 550 p.

RUDEGEAIR, T. J. 1975. The reproductive behavior and ecology of the White Ibis. Ph.D. Dissertation. University of Florida, Gainesville, Florida. 147 p.

SPRUNT, A., JR. AND E. B. CHAMBERLAIN. 1970. South Carolina Bird Life. University of South Carolina Press, Columbia, South Carolina. 657 p.

STINNER, D. H. 1983. Colonial wading birds and nutrient cycling in the Okefenokee Swamp ecosystem. Ph.D. Dissertation. University of Georgia, Athens, Georgia. 129 p.

STURGES, F. W., R. T. HOLMES, AND G. E. LIKENS. 1974. The role of birds in nutrient cycling in a northern hardwoods ecosystem. *Ecology* 55:149–155.

VALIELA, I., J. M. TEAL, S. VOLKMANN, D. SHAFER, AND E. J. CARPENTER. 1978. Nutrient and particulate fluxes in a salt marsh ecosystem: Tidal exchanges and inputs by precipitation and groundwater. *Limnology and Oceanography* 23:798–812.

WEIR, J. S. 1969. Importation of nutrients into woodlands by Rooks. *Nature* 221:487–488.

WIENS, J. A. AND M. I. DYER. 1977. Assessing the potential impact of granivorous birds in ecosystems, p. 205–266. *In* J. Pinkowski and S. C. Kendeigh (eds.), Granivorous Birds in Ecosystems. Cambridge University Press, Cambridge, England.

WIENS, J. A. AND G. S. INNIS. 1974. Estimation of energy flow in bird communities: A population bioenergetics model. *Ecology* 55:730–746.

WIENS, J. A., C. S. CRAWFORD, AND J. R. GOSZ. 1985. Boundary dynamics: A conceptual framework for studying landscape ecosystems. *Oikos* 45:421–427.

ZELICKMAN, E. A. AND A. N. GOLOVKIN. 1972. Composition, structure, and productivity of neritic plankton communities near the bird colonies of the northern shores of Novaya Zemlya. *Marine Biology* 17:265–274.

Received for consideration, January 5, 1990
Accepted for publication, May 13, 1991

APPENDIX 1. Derivation of the input variables used in the simulation model to determine per-pair nutrient input by white ibises on Pumpkinseed Island in 1984 and 1985.

Input variable Derivation
Caloric requirements of adult and recently fledged ibises:
Calculated using a time-activity budget for ibises presented in Kushlan (1977a), together with existence metabolism (i.e., the energy expended to maintain a constant weight with limited motor activity) equations in Wiens and Dyer (1977).
Caloric requirements of developing ibises:
Based on data presented in Kushlan (1977b).
Mean assimilation efficiencies of adult ibises:
Based on data presented in Kushlan (1977a).
Mean assimilation efficiencies of nestling ibises:
Based on the results of a feeding study conducted at the study site (Johnston and Bildstein 1990).
Caloric content of prey (fiddler crabs and crayfishes):
Determined using a Parr adiabatic oxygen bomb calorimeter.
Caloric and nutrient content of ibis excreta:
Determined by the Agricultural Services Laboratory, Georgia College of Agriculture, Athens, Georgia, using standard Association of Official Analytical Chemists techniques (Association of Official Analytical Chemists, 1980).
Dry weight of 1- to 14-day-old nestlings:
Based on data presented in Dunn (1975) for nestling double-crested cormorants (*Phalacrocorax auritus*), an altricial bird with a developmental pattern similar to ibises. (Similar values have been reported for other altricial species [summarized in O'Connor 1984].)
Nitrogen content of nestling ibises:
Based on a value given in Sturges et al. (1974) for the adults of 20 species of small passerines.
Phosphorus, potassium, and calcium contents of nestlings:
Based on values for nestling birds presented in O'Connor (1984) that had been calculated from data in Bilby and Widdowson (1971) for newly hatched nestling European blackbirds (*Turdus merula*), an altricial species with a developmental pattern similar to ibises. (Unfortunately the mineral content of young birds is hardly studied.)
Excreta for nutrient analysis:
Obtained from two 1-year-old hand-reared white ibises (1 male and 1 female) housed in a 3 × 3 × 3 m outdoor pen lined with polyethylene. (The birds were fed a diet of either fiddler crabs or crayfishes for 24 h before excreta were collected. Birds were then maintained on each of the two diets for the next 2 d and excreta collected twice daily: once in early morning before the birds were fed, and again in late afternoon.)
Percent time spent by adults and recently fledged juvenile ibises at the colony site during the 98-d breeding period:
Calculated from >4,000 h of observations of ibises on Pumpkinseed Island made during two breeding seasons.