
NUTRIENT TRANSPORT by WADING BIRDS in the EVERGLADES

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ABSTRACT

The effect of nutrient accumulation resulting from deposition of feces in colonies of colonially breeding and roosting wading birds is estimated in this chapter for breeding and nonbreeding ciconiiform birds in the Everglades ecosystem, by modeling energy consumption and feces deposition rates and by using existing measurements of size, energy, and nutrient content of prey items from the Everglades. Current populations of breeding and nonbreeding birds are estimated to consume 4.9 fewer tonnes of prey (dry mass) per year than the much larger populations of the 1930s and 1940s, equivalent to an estimated 14.6 million fewer prey items per year. This difference translates into 455 fewer tonnes of feces deposited in roosts and colonies per year, roughly equivalent to 59 fewer tonnes nitrogen and 5.6 fewer tonnes phosphorus. Nonbreeding birds are estimated to account for only 1.5% of the difference in nutrient flux attributable to birds between the two periods, indicating that the differences are due to reductions in energy-intensive breeding attempts. Although even the largest historical populations are estimated to have redistributed only a very small fraction of the total annual deposition of phosphorus and other nutrients in the marsh, loading rates at colonies can be extremely high. Loading rates at historical colony sites could have been as high as 120 g phosphorus $m^{-2} \cdot yr^{-1}$ (approximately 3000 times the estimated historic atmospheric deposition rate), while current colonies are estimated to have rates of only 0.9 g phosphorus $m^{-2} \cdot yr^{-1}$ (more than 20 times the historic atmospheric deposition rate). Evidence from the Everglades and other ecosystems suggests that high nutrient concentrations in the vicinity of colonies has a strong effect on the productivity and species composition of aquatic fauna and flora. This

may have strong feedback effects for survival of young wading birds, which characteristically develop foraging skills at or near colony sites. Recent relocation of large colonies from the estuarine zone to the freshwater Everglades implies that nutrient input to the estuary has decreased significantly. Nutrient-rich colonies probably serve as islands of refugia for nutrient-tolerant species in the oligotrophic Everglades and may serve to significantly affect the variability in biodiversity of the marsh. Sources of error tend to be in the direction of overestimation of nutrients transported, and in this regard, the amount of food required by nestlings is a central and poorly understood variable.

INTRODUCTION

Populations of animals can serve as important vectors of nutrient flow, both by transporting nutrients between ecosystems (Morales and Pacheco, 1986; Bildstein et al., 1992) and by recycling and redistributing nutrients within ecosystems (Meyer et al., 1983; Powell et al., 1991). Both processes are accomplished by the consumption of food in one location and the excretion of nutrients, in the form of feces, in the same or another location.

The redistribution and in many cases concentration of nutrients may have an impact on the nutrient budgets of entire ecosystems, particularly those which are naturally oligotrophic. Meyer et al. (1983) reported that schools of fish which fed away from a coral reef contributed between 30 and 48% of the total ammonia and between 59 and 90% of the total particulate phosphorus to coral heads. Nutrient concentration by animals can also be dramatic in nesting colonies of birds, which often forage at great ranges from their colonies, but deposit a large proportion of their feces at communal breeding sites, often islands. Bildstein et al. (1992) found that white ibises (*Eudocimus albus*) imported 33% as much phosphorus and 9% as much nitrogen into a South Carolina salt marsh as did atmospheric sources. In the oligotrophic Okefenokee Swamp in southern Georgia, Stinner (1983) found that white ibises contributed 10 times as much phosphorus and calcium to the ecosystem as were imported by stream flow and atmospheric deposition.

Such concentration of nutrients also may strongly affect local community structure. Bird colonies have been shown to increase nutrient concentrations and phytoplankton in the Barents Sea (Golovkin, 1967; Golovkin and Garkavaya, 1975). A number of studies have found that locally high concentrations of nutrients due to bird colonies can profoundly alter both the vegetation in the colony site (Dusi et al., 1971; Weseloh and Brown, 1971; Wiese, 1978; Stinner, 1983; Allaway and Ashford, 1984) and the plant and animal communities surrounding the colony. Bosman and Hockey (1986) determined that seabird deposition of feces in South African colonies resulted in the production of thick, intertidal algal mats not present on nearby unenriched intertidal zones. The mats, in turn, created foraging habitat for a number of shorebird species. Onuf et al. (1977) found that mangroves in wading bird (Ciconiiformes) colonies in a Florida estuary were more productive than those on adjacent noncolony islands and that leaves of colony trees were grazed by insects at higher rates than those on noncolony trees. Powell et al. (1991) found that seagrass beds surrounding colony islands in Florida Bay were denser than beds surrounding nearby noncolony islands. In addition, species composition

of seagrasses around the colony islands was different from the noncolony islands, probably as a result of the elevated sediment nutrient levels near colonies. Because seagrass density was positively correlated with densities of demersal invertebrates and fishes in Florida Bay (Sogard et al., 1987), these changes in vegetation surrounding marine wading bird colonies have potential for structuring aquatic animal communities.

Wading birds have historically been important consumers of fishes, invertebrates, and anurans in the Everglades ecosystem (Robertson and Kushlan, 1974; Ogden, 1978, 1994; Frederick and Spalding, 1994), and the size alone of even conservatively estimated historic breeding assemblages suggests that these birds played an important role in nutrient relocation and liberation within the ecosystem (Harris, 1988). Because virtually no records exist to indicate the size of Everglades wading bird populations prior to the turn of the century (Kushlan et al., 1984), estimates made during the early 1930s will be used here as indicators of prehistoric populations and ecosystem conditions.

Wading birds have declined precipitously as breeders in the Everglades since the 1930s, although large populations of waders continue to winter in the Everglades (Hoffman et al., 1991). In addition, Ogden (1978) noted that wading birds have shifted the center of their breeding distribution northward within the southeastern United States, as well as toward freshwater areas within the Everglades

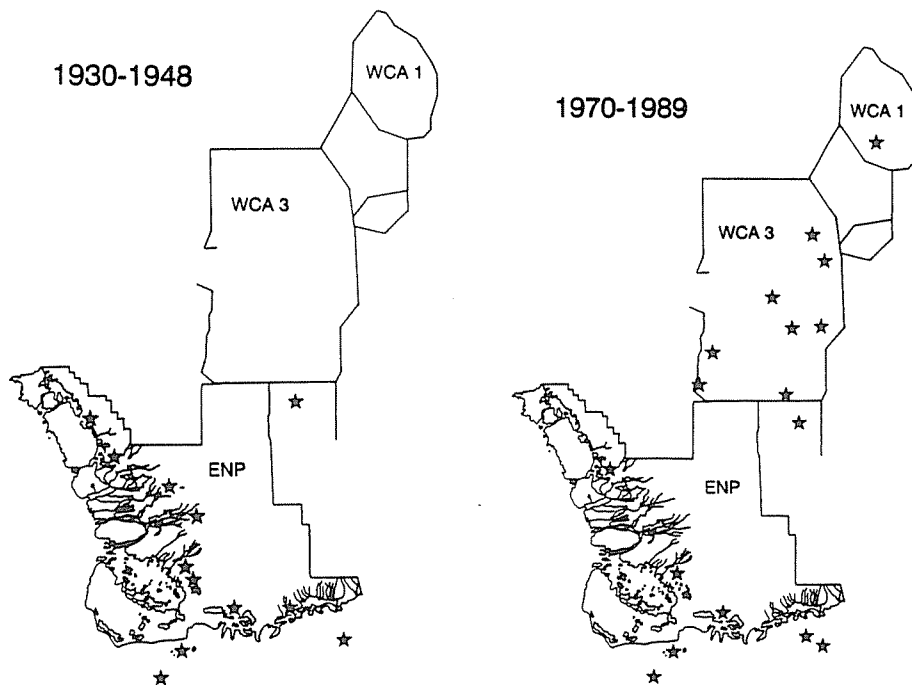


Figure 23.1 Map of the study area, showing boundaries of Water Conservation Areas 1 and 3 and Everglades National Park. Stars represent locations of colonies containing at least 150 nests, reported at any time during 1930–48 and 1970–89. Compared with earlier conditions, colonies are presently shifted away from estuarine sites and centered in the freshwater marshes, particularly the Water Conservation Areas.

(Figure 23.1). The size of breeding assemblages has also decreased. Between 1934 and 1948, at least 10 breeding assemblages were reported to contain in excess of 10,000 nests (Ogden, 1978; Kushlan et al., 1984). During the period from 1978 to the present, no colonies contained in excess of 7000 nests.

These changes in seasonal abundance, breeding status, breeding location, and breeding assemblage size may have had profound impacts on nutrient transport by birds within the ecosystem and, in particular, upon nesting sites as islands of nutrient enrichment within an otherwise oligotrophic wetland. Here, nutrients consumed and deposited at colony and roost sites in the Everglades are estimated for a variety of wading bird species, as well as differences in nutrient flux attributable to wading birds during the past 60 years.

METHODS

Numbers of Wading Birds

Numbers of wading birds breeding in the freshwater and estuarine Everglades (current Water Conservation Areas 1, 2, and 3, Everglades National Park [not including islands in Florida Bay], and northeast Shark River Slough) (Figure 23.1) were estimated from a number of survey reports and historical summaries (Allen, 1958; Kushlan, 1974; Kushlan and White, 1977; Ogden, 1978; Kushlan et al., 1984; Ogden et al., 1987; Frederick and Collopy, 1988; Everglades National Park Research Center records; National Audubon Society Research Department records). Locations of colonies also were compiled from these reports. Recent estimates of numbers of wintering, summering, and nonbreeding wading birds were derived from systematic aerial surveys conducted since 1985 (Hoffman et al., 1991). The numbers of breeding wading birds used for estimation of energetics are shown in Table 23.1.

Nutrient Consumption and Excretion

Nutrient consumption by wading birds was estimated from energetic requirements of adults and young, and excretion was estimated as the nonassimilated portion of energy consumed. Assimilation efficiencies were taken from three studies in which ciconiiform species were hand-raised and fed *ad lib* into adult-

Table 23.1 Numbers of Wading Bird Nesting Attempts per Year Used in Comparisons of Historical and Current Nutrient Transport (see text for sources)

Decade or year	Wood storks	White ibis	Great egrets	Tricolored herons	Snowy egrets	Little blue herons	Total
1930s	4,000	100,000	4,000	15,000	10,000	2,500	135,500
1940s	4,000	48,000	4,000	15,000	10,000	2,500	83,500
1975	1,330	12,956	3,267	3,500	4,500	2,000	27,553
1986	275	2,503	1,751	1,133	1,319	437	7,418
1987	100	4,130	2,005	537	1,383	723	8,878
1988	220	4,250	2,478	267	200	135	7,550

hood (Kahl, 1964; Kushlan, 1977; Johnston and Bildstein, 1990). In all cases, a 79% assimilation efficiency was used for both adults and young.

Energy Required by Adults

Daily adult energetic needs were calculated for white ibises from Kushlan's (1977) activity budget, for wood storks (*Mycteria americana*) directly from Kahl's (1964) estimates, and for other species from mass-dependent metabolic equations by Wiens and Dyer (1977). Estimates of daily existence energy needs for adults of all species were used directly to estimate nonbreeding energy needs. Total energy consumption by nonbreeding birds (including nonbreeding, wintering, or migrating birds) was estimated as daily existence needs for each species times the number of nonbreeding bird-days for each species. For years since 1985, species-specific abundances were used from the 1985–88 Systematic Reconnaissance Flight surveys for the Water Conservation Areas (Hoffman et al., 1991) and Everglades National Park (M. Fleming, unpublished). For years prior to 1985, there is little useful information concerning numbers of nonbreeding birds. To estimate the month-specific numbers of nonbreeding bird-days during the period prior to 1985, the monthly ratios of nonbreeding to breeding birds from 1985 to 1988 (Hoffman et al., 1991) were applied to the size of the breeding population in each year prior to 1985. Because historic nesting conditions are generally agreed to have been more attractive than during the last decade, and because several of the species expanded their breeding range northward during the period of record, it is reasonable to assume that this method overestimates historic nonbreeding populations relative to current ones.

For wood storks and white ibises, Kahl (1964) and Kushlan (1977), respectively, calculated the increase in energy required for breeding activity by adults. Daily existence needs of other species were then multiplied by these factors to arrive at adult daily breeding energy. Number of days of breeding activity for adults of each species was taken from Bent (1926), Kahl (1964), Wiese (1975), Rudegeair (1975), and Kushlan (1974). Daily adult breeding energy was multiplied by the number of days of nesting to achieve total energy needs of adult breeding birds.

Energy Required by Young

Energy needs of developing young white ibises and wood storks were based on models presented by Kushlan (1977) and Kahl (1964), respectively. Energy needs of young great egrets (*Casmerodius albus*), tricolored herons (*Egretta tricolor*), snowy egrets (*E. thula*), and little blue herons (*E. caerulea*) were calculated by summing weight-specific energy needs over the period of growth, using equations for energy needs of growing birds presented by Kendeigh et al. (1970). Age-specific weights for these species were taken from data presented by Black et al. (1984) and Werschkul (1979).

Excreta and Nutrient Deposition

Energy of excreta was estimated as the nonmetabolizable portion (21%) of energy consumed. It was assumed that young deposited all excreta at colony sites

until the development of sustained flight abilities, which was assumed to occur at 80 days for wood storks, 65 days for great egrets, and 45 days for white ibises, snowy egrets, tricolored herons, and little blue herons (Palmer, 1962; Kahl, 1964; Wiese, 1975; Rudegeair, 1975; Werschkul, 1979; Black et al., 1984; Frederick and Collopy, 1988; Bancroft et al., 1991; Frederick et al., 1993). It was also assumed that young of all species had a 20- to 30-day period of postfledgling attachment to the colony, during which the young spent only nights at the colony (13 h), depositing an estimated 54% of their daily (24 h) excreta. A constant rate of excretion was assumed in all calculations of excreta production. Because most nonbreeding, adult wading birds roost communally at night, it was also assumed that 54% of their daily excreta was deposited at roost sites. Using activity budget and breeding phenology data from a number of sources (Bent, 1926; Kahl, 1964; Rudegeair, 1975; Wiese, 1975; Werschkul, 1979; Frederick, 1987; Bildstein et al., 1992), it was estimated that breeding adults deposited 54% of daily excreta in the colony during precourtship and during incubation, 81% during courtship and egg laying, 75% during early nesting stages, and 27% during late nesting and postfledging periods.

Excreta were assumed to contain an energy value of $8372 \text{ J} \cdot \text{g}^{-1}$ (dry mass), a value intermediate to $5860 \text{ J} \cdot \text{g}^{-1}$ measured by Stinner (1983) and $8372\text{--}10,046 \text{ J} \cdot \text{g}^{-1}$ measured by Bildstein et al. (1992), to translate excreted energy into dry mass of excreta. Nutrient analyses of white ibis feces by Stinner (1983) and Bildstein et

Table 23.2 Nesting Energy Costs (kJ) and Other Constants Used in Calculation of Nutrient Transport by Wading Birds

	Wood storks	White ibis	Great egrets	Tricolored herons	Snowy egrets and little blue herons
Energy required by adults, per nesting attempt	619,952	101,628	134,140	63,037	63,037
Energy required to grow 1 young	133,533	36,083	66,926	26,937	26,937
Young fledged/nest	2.25	2.0	2.0	2.0	2.75
Total energy per nesting attempt	868,532	173,794	267,992	116,911	116,911
Daily nonbreeding energy per adult	1,884	682	703	322	322
Dry weight (kg) excreta per nesting attempt	23.75	3.22	3.86	1.77	1.77
Other constants					
Composition of feces (%)	Nitrogen	Calcium	Phosphorus		
White ibis	5.0	15.0	1.9		
Piscivorous waders	13.0	15.0	1.9		
Assimilation efficiency	79%				
Energy value of prey (kJ/g dry mass)					
Fish	21.2 J/g				
Crayfish	17.03 kJ/g				

al. (1992) and of fish-eating waders by Dusi et al. (1971) were used to estimate the nutrients deposited by all wading bird species (Table 23.2).

No attempt was made to estimate the deposition of nutrients in colonies due to mortality of young, because Bildstein et al. (1992) found that carcasses of young contributed less than 1% of total nutrient deposition in a large white ibis colony which exhibited mortality rates similar to Everglades colonies (Frederick and Collopy, 1988).

Energy consumption was translated into weight of prey consumed through caloric measurements of Everglades fishes and crayfishes (Kushlan et al., 1986). Mean sizes of prey consumed by Everglades wading birds were taken from Bancroft et al. (1988), G. T. Bancroft (unpublished data), Ogden et al. (1978), Kushlan and Kushlan (1975), and P. C. Frederick (unpublished) to derive numbers of crayfishes (principal food of white ibises) and fishes (all other species) consumed.

RESULTS

On a per bird basis, nesting wood storks require by far the most energy, consuming at least 4.8 times the amount required by white ibises and over 6 times the amount required by the small *Egretta* herons (Table 23.2).

Estimated consumption of prey necessary to fuel both reproductive efforts and nonbreeding activities is shown in Figure 23.2 for several points in the recent past; Figure 23.3 shows the amounts of nutrients deposited in colony and roost sites by wading birds. Both parameters show dramatic declines since the 1930s, along with breeding population decreases. It is estimated that wading bird populations currently consume 4901 tonnes less prey (89% reduction, dry mass) per year

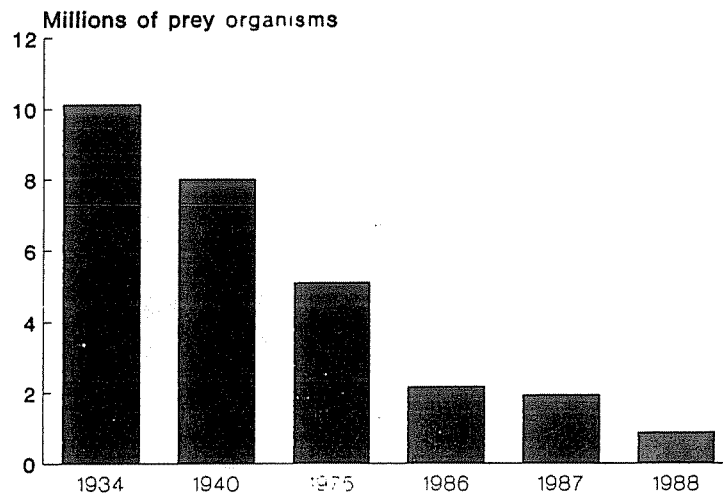


Figure 23.2 Estimated annual consumption of prey by wading birds during breeding and nonbreeding activities in six different years.

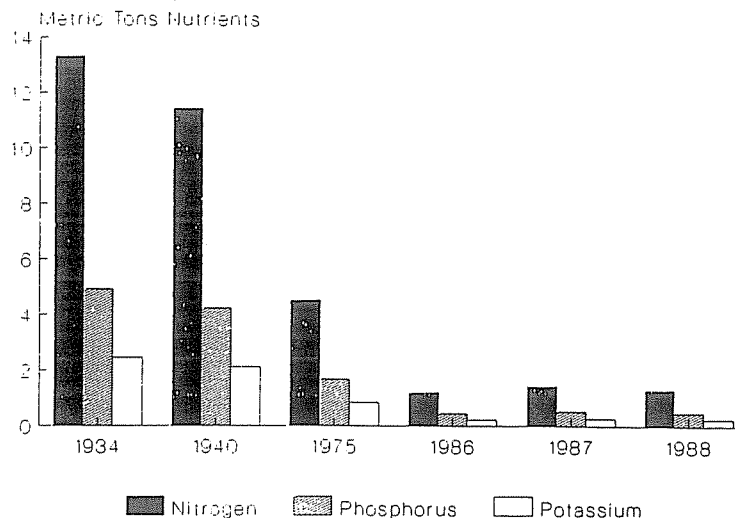


Figure 23.3 Estimated mass of nutrients (in tonnes dry mass) transported to breeding colonies and roosts by wading birds and deposited in the form of feces. Changes in deposition are a function of both changes in numbers of birds using the Everglades and changes in numbers of birds breeding there.

than 1930s populations did, amounting to 14.6 million fewer individual prey items eaten (87% reduction). It is also estimated that current populations of wading birds leave 455 tonnes less feces per year at colony and roost sites, a difference that represents an estimated 59 tonnes of nitrogen and 8.6 tonnes of phosphorus per year.

The majority of this reduction in consumption of prey items and transport of nutrients can be traced to reductions in breeding activity, rather than changes in the size of nonbreeding populations (Figure 23.4). Since the 1930s, reductions in dry mass of excreta transported to roost sites by nonbreeding birds amount to only 1.5% of the total reduction in deposition to colony and roost sites. This stems from the fact that nesting attempts are inherently much more costly in energy than nonbreeding activities. This finding is probably even more robust than stated, because historic nonbreeding populations are likely to have been overestimated relative to current ones. It seems clear that the decline in wading bird breeding has resulted directly in a greater than 90% reduction in predation by the wading bird guild.

The differential reduction in numbers of each species breeding (Table 23.1) has led to changes in the contributions of each to total nutrient transport (Figure 23.5). While white ibises are still the dominant contributor to nutrient flux by wading birds, their annual contribution has decreased by an order of magnitude. Wood storks, originally the second-ranked contributor, have become ranked third, behind great egrets. Although numbers of nesting great egrets have not changed dramatically since the 1940s, their relative importance as nutrient vectors has increased from moving less than 5% of all nutrients moved by waders to more than 40%.



Figure 23.4 Excreta deposited in colonies by breeding birds and growing young (solid) compared with deposition in roosts by nonbreeding birds (open) as a function of time. In all years the vast majority of deposition is contributed through reproductive effort.

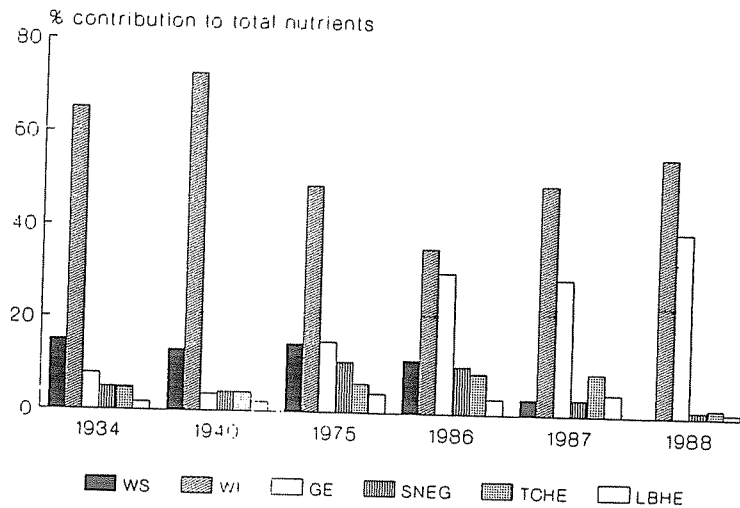


Figure 23.5 Historic and current contribution of individual wading bird species to the deposition of nutrients in the Everglades.

DISCUSSION

The findings presented in this chapter suggest that even large historical populations of wading birds contributed little to the overall flow of nutrients within the Everglades marshes. The estimated 5.07 tonnes of phosphorus annually deposited in colony sites by wading birds during years of peak abundance in the early 1930s is less than the 3% of total historic annual phosphorus inputs to the entire

ecosystem from rainfall estimated by Davis (1994). Wading birds, then, can be seen as inconsequential movers of nutrients relative to annual inputs, at least on the scale of the Everglades and associated estuarine areas.

This conclusion is bolstered by the fact that potential sources of error in the estimates in this chapter are likely to lead to an overestimation of nutrient transport by wading birds. In an effort to err consistently, the highest values have been used to estimate energy needs and excretion rates, leading to a liberal estimation of nutrient transport and concentration. This is particularly true of nestling food consumption, which is based largely on studies of captive hand-reared birds, all of which were fed *ad lib*. Because wading birds have been noted for frequent brood reduction, which is largely dependent on available food (Mock et al., 1987), and chronic competition among nestlings for food, it is reasonable to suppose that food satiation of nestlings is rare in the wild. Mock et al. (1987) may have reported the only measurements of food amounts consumed by wild nestlings. Their measurement of $1453 \text{ kJ} \cdot \text{d}^{-1}$ for broods of great egrets 21 days or less of age is less than 20% of the energy needs calculated through weight-specific growth equations (which are based on *ad lib* feedings). This example suggests that the current estimation of energy consumption by young could lead to overestimation of food consumption and excretion by young of up to 80%. Because individual energy consumption rates of young have a large effect on total estimates of nutrient transport, it is likely that this potential source of error overwhelms other sources. The nesting energy figures in this chapter should therefore be treated as maxima. The huge difference in food consumption between captive fed and wild nestlings also suggests that digestive efficiencies or growth rates are different between the two. If wild birds typically have higher digestive efficiencies than the figures used from captive-reared birds, then production of excreta and probably nutrient content of excreta has been overestimated. However, the digestive efficiency of 79% is at the upper end of measured digestive efficiencies for birds.

Even considering these potential sources of error, it is obvious that large quantities of nutrients can be concentrated in very small spaces through wading bird defecation. Two examples are instructive. In his most conservative estimate, Allen (1958) reported the approximately 16-ha 1934 Shark River colony to contain over 250,000 nests (Ogden, 1978). Using Allen's species breakdowns and excreta deposition factors from the study described in this chapter, it is estimated that this colony site would have received at least $331 \text{ g} \cdot \text{m}^{-2} \text{ yr}^{-1}$ nitrogen and $120 \text{ g} \cdot \text{m}^{-2} \text{ yr}^{-1}$ phosphorus in 1934. This level of phosphorus deposition is approximately 3000 times the historic annual areal input estimated by Davis (1994). While the Shark River colony was considered at the time to be abnormally large for the Everglades (Ogden, 1978), it may serve as an example of the upper limit of nutrient loading by wading birds. The far smaller, less dense Alley-North (Rescue Strand) colony of 1987 represents a more common and more typical example of a recent nesting aggregation. This 352-ha freshwater colony had approximately 5450 nests in 1987. Using the composition of nests given by Frederick and Collopy (1988), it was calculated that the colony received $20.3 \text{ g} \cdot \text{m}^{-2} \text{ yr}^{-1}$ nitrogen and $0.90 \text{ g} \cdot \text{m}^{-2} \text{ yr}^{-1}$ phosphorus. This estimated phosphorus input is 20 times the historical annual areal input (Davis, 1994). The difference in phosphorus input between the Alley-North and the Shark River colonies is on the order of 120 times.

The works of Davis (1994) and D. Scheidt (unpublished National Park Service report) suggest that such levels of nutrient loading can have a significant effect on species composition and productivity of freshwater and estuarine marsh macrophyte communities. Browder et al. (1994) have described dramatic changes in freshwater marsh periphyton and invertebrate communities associated with elevated nutrient concentrations. In estuarine mangrove situations similar to many of the large historically important Everglades colony locations, elevated nutrient levels due specifically to bird feces can increase productivity of mangroves (Onuf et al., 1977) and change both species composition and productivity of seagrass beds (Powell et al., 1991; Sogard et al., 1987). Increases in local productivity may have important feedback effects on the survivorship of juvenile wading birds by providing highly productive foraging habitat close to the colony where juveniles develop their feeding skills (Rodgers and Nesbitt, 1979).

Thus, while nutrient redistribution and concentration by wading birds is, and was historically, a relatively small part of the entire Everglades nutrient budget, the local concentrations of nutrients dramatically altered the nutrient character of the colony islands themselves. The extent to which nutrient enrichment at colonies may affect downstream communities undoubtedly varies with size of colony, enrichment concentrations, plant uptake rates, and water flow rates. At a small (400 pair) mixed-species colony in a shallow central Florida marsh impoundment, J. Burney (personal communication) found that increases in phosphorus and ammonia from the colony were not detectable beyond 300 m from the colony edge. In a situation of higher volume and flow of surrounding water, Powell et al. (1991) found that effects of breeding bird colonies on aquatic vegetation could not be detected beyond about 200 m from the colony edge. It seems prudent to propose that the effects of nutrient enrichment, at even very large colony sites, are limited to the immediate vicinity of the colony (certainly less than 1 km downstream) and are best described as "islands" of enrichment.

It is unclear how long such local alteration of plant, and possibly animal, communities in and surrounding colonies might persist following the cessation of excretion inputs. Dramatic changes in species composition of macrophytes are still apparent 6 years after nutrient dosing experiments in central Shark River Slough (D. Scheidt, personal communication). Similarly, the Broad River colony site in coastal Everglades National Park, last used in 1940, is still clearly distinguishable (P. C. Frederick and G. V. N. Powell, personal observation) as an area of luxuriant mangrove growth, despite the passage of over 50 years and at least two major hurricanes. J. C. Ogden (personal communication) reports that the Lane and East River colony sites in coastal Everglades National Park are still distinctly greener than surrounding mangroves even though it has been more than 10 years since the last heavy use of the colony by birds. These observations suggest that locally abundant nutrient input by wading birds is bound quickly into soils and vegetation and is retained and recycled at the site of deposition for long periods.

While this seems plausible for some colony sites, it may not be true of those which have strong surrounding currents, tidal overwash, and quite different surrounding soils and macrophyte communities. Lund (1957) found that nutrient concentrations in sediment samples were not elevated at two estuarine colonies in Everglades National Park (Duck Rock and East River) but were elevated in the

immediate vicinity of the Cuthbert Lake colony. Lund attributed the difference to local sediment types.

Because a number of large colony sites are documented to have been used repeatedly over a period of many years (Kushlan et al., 1984), historic patterns of nutrient loading by breeding birds may have resulted in the creation of long-term, i.e., periods of 3–15 years (if continued use by birds is the criterion), islands of refugia for species with high nutrient requirements or tolerances, such as cattail (*Typha* sp.) (Davis, 1994), in an otherwise oligotrophic marsh.

The changes in distribution, colony size, and numbers of breeding wading birds over the last 50 years have undoubtedly had important ramifications for such refugia-dependent species. It is suggested here that the dramatic reductions in numbers of breeding birds have significantly reduced the number of patches where species disadvantaged by low nutrient conditions can survive. The reduction in availability of the special conditions surrounding colonies may have significantly reduced heterogeneity in composition and abundances of both plant and animal communities within the freshwater and estuarine Everglades. The movement of large colonies away from estuarine sites suggests that these effects were most pronounced in the estuarine zone.

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