

CHAPTER 12

Monitoring Wetland Ecosystems Using
Avian Populations: Seventy Years of
Surveys in the Everglades

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Birds have frequently been suggested as bioindicators of environmental conditions (Custer and Osborn 1977; Ogden 1993; Erwin et al. 1996; Erwin and Custer 2000). This idea is intuitively attractive because birds are often strong bioaccumulators in the energetic sense, are uniquely mobile, feed at various levels in local food webs, and are usually easy to locate and census. However, considerable criticism has been aimed at the overuse of animals in general, and birds specifically, as bioindicators (Morrison 1986; Temple and Wiens 1989; Niemi et al. 1997). This skepticism is well placed, and stems from several sources. The use of any organism as a reliable bioindicator demands that a cause-and-effect relationship between environmental variation and response in the organism be documented—a criterion that is often lacking in field monitoring studies. For instance, changes in the size of avian breeding populations are often touted as an indicator of the abundance and availability of food sources in the area being monitored. Yet variation in bird populations can be due to various local and distant factors, such as habitat conditions elsewhere, overwinter survival rate, or fecundity in previous years. Thus, it is clear that the monitored response of the bioindicator species must be linked specifically and mechanistically to some measurable aspect of

environmental variability or to the end result of some key environmental process.

The species or attribute serving as an indicator must also be matched in grain and scale with the environment or environmental attribute being monitored (Drury 1980). Birds have been regularly monitored at extremely large geographic scales; the U.S. Breeding Bird Survey, the National Audubon Christmas Bird Count (McCrimmon et al. 1997), and the European Seabirds at Sea program (Stone et al. 1995) are excellent examples. Although these programs produce data that allow an understanding of animal movements and population change over very large time and spatial scales, the results are often spatially and temporally too coarse for detecting the effects of environmental change at the scale of ecosystems or the temporal scale of many management actions. Similarly, there are many bird monitoring programs designed specifically to answer questions about the reproductive ecology and demography of particular species at large scales but which are not designed or able to use bird populations to understand ecosystem processes (Robinson et al. 1995).

Despite these caveats, there are numerous examples of the successful use of birds as bioindicators in a variety of types of ecosystems. Long-term trends of penguin-breeding aggregations have been used to detect changes in fishery resources in the Antarctic (Lemaho et al. 1993), physiological stress indicators in birds have been linked with habitat quality (e.g., Marra and Holberton 1998), and historical records of irruption patterns of passerine birds have been used to infer past climatic events (Kinzelbach et al. 1997).

In this chapter, we describe a long-term monitoring program in the Florida Everglades, which has used various response variables (nesting population size, reproductive success, contaminant loads, location of nesting, and habitat-use patterns) in long-legged wading birds (herons, egrets, ibises, storks, and spoonbills, order Ciconiiformes) as a means to understand ecosystem processes and linkages between the Everglades and other ecosystems. The resulting picture of past and present ecosystem behavior has been used to help set goals and monitoring guidelines for the restoration of critical ecosystem functions (Davis and Ogden 1994; Ogden et al., chap. 5).

The utility of wading birds as a monitoring tool in this ecosystem has been examined previously in some detail (Kushlan and Frohring 1986; Ogden 1993; Walters et al. 1992; Ogden 1994; Bancroft 1989). Our goal in this paper is to critically evaluate what this monitoring program has (and has not) told us about environmental attributes and functions within, and external to, the Everglades ecosystem. We also hope to iden-

tify the factors that have made this program successful, in an attempt to find attributes that might identify similar programs in other ecosystems.

Wading Birds as Biological Indicators

Like many birds chosen to be bioindicators, long-legged wading birds are generally large, highly mobile, top-level consumers in the aquatic food web and have high energetic needs. In addition, many species of wading birds are strongly social and often breed and feed in highly aggregated groups. This, combined with the white or light-colored plumage of many species, makes the finding, counting, and monitoring of these animals in a large ecosystem relatively efficient and accurate. Indeed, it is difficult to imagine any other vertebrate that can be monitored with any accuracy or without extreme cost within the approximately 4,000-square-kilometer landscape of the Everglades (Ogden 1993). Wading birds are also known to forage and breed almost exclusively in wetlands, and, when breeding, to forage within a fairly well-defined range surrounding the colony (Bancroft et al. 1994; Smith 1995). This implies that some aspects of reproduction might be profitably used to reflect local environmental differences within the ecosystem. Breeding-site fidelity is highly variable among species, ranging from storks that return annually to the same colony, to ibises that are extremely nomadic (Frederick and Ogden 1997). Nonetheless, most species seem capable of moving their breeding sites in response to consistently unfavorable conditions.

There is also a large but somewhat diffuse body of evidence that links various aspects of wading bird reproduction to the availability of food. In most large wetland ecosystems in the world, the timing of breeding of wading birds usually coincides with the greatest availability of food. In South Carolina, Bildstein et al. (1990) demonstrated that annual numbers of nesting white ibises (*Eudocimus albus*) were in direct proportion to the availability of crayfishes in freshwater marshes. In the Everglades, Kushlan (1976c) showed that white ibises shifted their timing of nesting to coincide with the time at which available food energy was at a maximum. Similarly, in the Everglades, the Llanos of Venezuela, the Pantanal of Brazil, and the Usamacinta Delta and Yucatan of Mexico, wood storks (*Mycteria americana*) breed only during the dry season, when fishes are trapped in high densities in pools and depressions as a result of rapidly receding waters (Kushlan et al. 1975; Leber 1980; Ogden et al. 1988; Ramo and Busto 1992; Gonzalez 1999; Bouton 1999).

More mechanistic studies have also demonstrated links between the availability of food and reproductive success. For example, Powell (1983)

found that food-supplemented great white herons (*Ardea herodias*) in Florida Bay had significantly higher clutch and brood size than did un-supplemented birds. Hafner et al. (1993) found that increases in productivity of little egrets (*Egretta garzetta*) were associated with increased food availability. In the Everglades, interruptions in food supply have been closely correlated with mass nesting abandonments, whether the interruptions are brought about as a result of drought (Bancroft et al. 1990), cold weather (Frederick and Loftus 1993), or flooding (Kushlan et al. 1975; Frederick and Collopy 1989a; Smith and Collopy 1995; Frederick and Ogden 1997). Growth rates of nestling herons are directly related to food intake rates (Salatas 2000), and growth rates in snowy egrets have been correlated with survival rates of fledglings during the first month of life (Erwin et al. 1996).

Within the Everglades, the relative effects of other potential causes of variation in reproductive success have been investigated in some detail. Losses of nest contents to predation has been found to be surprisingly rare in the central Everglades in most years (Frederick and Collopy 1989b), and effects of both researcher disturbance (Frederick and Collopy 1989c) and availability of nesting habitat (Frederick and Spalding 1994) have been found to be negligible. In a large-scale survey of the importance of disease in Everglades wading birds, only one parasitic disease was found to have any effect on reproduction (Spalding and Forrester 1991). Although this disease (eustrongylidosis, caused by parasitic nematodes of the genus *Eustrongylides*) can cause very high mortality of nestlings in some colonies, the disease seems associated only with the relatively uncommon sites of high nutrient deposition within the Everglades (Spalding et al. 1993).

Thus food availability seems to be strongly linked to nesting success in wading birds in general, and variation in food availability explains much of the variation in nesting success specifically within the Everglades. Studies linking choice of nesting site and timing of nesting with availability of food are less well established for the Everglades, but the evidence (above) suggests that location and timing of nesting may also be used as indicators of prey availability and abundance in wetland ecosystems. This information collectively suggests that the cueing and success of nesting are driven largely by the availability of prey, and that variation in reproductive effort and productivity can, within some limits, be interpreted as an indicator of those ecological and physical features that affect the abundance and availability of prey.

The conditions affecting availability of wetland prey to wading birds are probably numerous, but the density of prey animals and depth of water have often been found to be primary components. Wading birds

take many types of aquatic prey, using a wide variety of foraging tactics and behaviors (Kushlan 1976b, 1978). Nearly all foraging is in shallowly flooded wetlands, and foraging success is highly dependent upon appropriate conditions. Variation in foraging success may be dependent on a variety of characteristics of the foraging site, including prey density (Renfrow 1993; Surdick 1998; Gawlik 2002), water depth (Powell 1987; Renfrow 1993; Gawlik 2002), water temperature (Frederick and Loftus 1993), dissolved oxygen (Hafner et al. 1993), and vegetative density (Surdick 1998). Of these variables, dissolved oxygen probably plays a minor role, since the wetlands of the Everglades marshes are shallow and poorly stratified. Similarly, water temperature is only an important factor in the Everglades during relatively brief periods of cold. Within the Everglades, Surdick (1998) found that water depth, prey density, and vegetative density were the factors most commonly affecting foraging success and choice of foraging sites of four species of wading birds, and that these factors often interacted.

Historical and Contemporary Wading Bird Monitoring

The Everglades is nearly unique in having an exceptionally long written record of wading bird nesting. Perhaps most importantly, a well-documented time series of nesting events was begun prior to the period of the most extreme hydrological manipulations, allowing some sense of wading bird dynamics in the ecosystem before much of the natural hydrological variability of the pre-drainage Everglades had been altered.

The history and nature of this nesting record has been reviewed in detail by Robertson and Kushlan (1974), Ogden (1978), Kushlan and Frohring (1986), and Ogden (1994), and we present an overview here. Although there are several written accounts of wading bird nesting from the latter part of the nineteenth century (Scott 1887, 1889, 1890), the first extended series of annual estimates of the nesting aggregations came from wardens and biologists of the National Audubon Society, who regularly checked breeding colonies and roosts in the coastal areas of what is now Everglades National Park (ENP) between the early 1930s and mid-1940s.

Between the late 1940s and the mid-1960s, there was, with the exception of occasional surveys of wood storks, a hiatus in systematic monitoring of wading bird reproduction. Regular estimates of estuarine breeding colonies were resumed by ENP staff during the late 1960s and were intensified and expanded with the help of National Audubon Society biologists to irregularly include parts of the current Water Conservation Areas (WCAs) of the Everglades through the mid-1980s (see fig. 12-1).

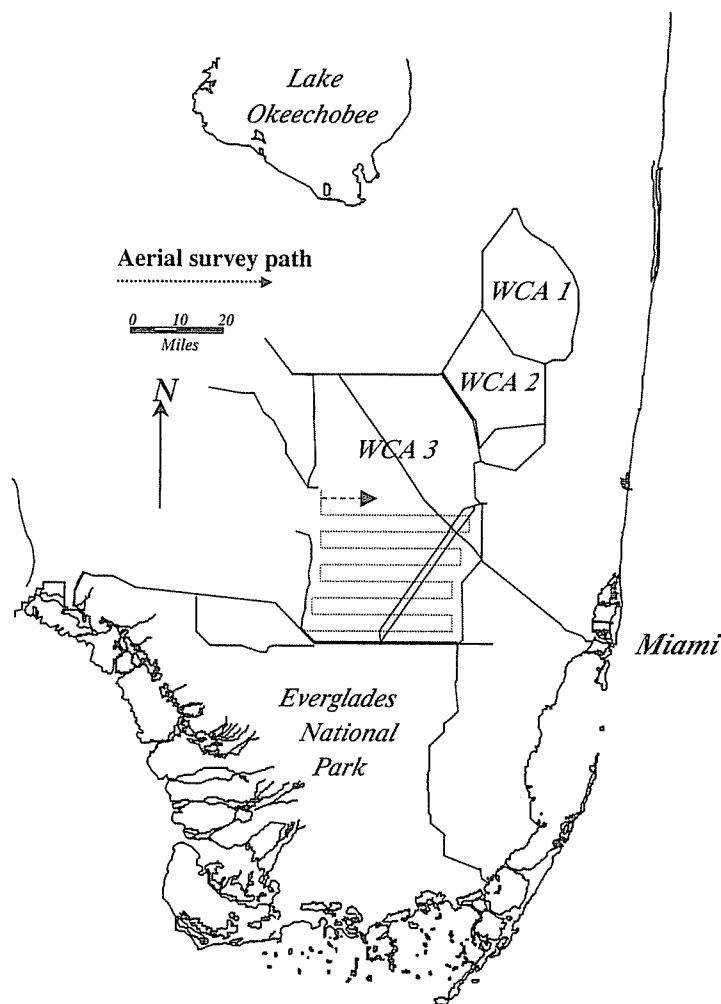


Figure 12-1. Map of the Everglades area showing boundaries of water conservation areas, major urban areas, and landscape features. The approximate flight path of a portion of the systematic aerial surveys for wading bird nesting colonies is shown as a dotted line. Transects are oriented east-west, and spaced 2.6 kilometers apart.

During the same period, the National Audubon Society Research Department (NAS) began annual surveys of wood stork colonies in peninsular Florida and in so doing documented many previously unknown colonies in the central Everglades. These surveys by ENP and NAS were mainly aimed at estimating numbers of birds in large, previously active colonies, and search patterns were not systematic.

Systematic Surveys of Breeding Colonies

Systematic aerial surveys were initiated in the WCAs of the Everglades in 1986 and were adopted in ENP shortly thereafter. These surveys are flown in east-west transects spaced 2.6 kilometers apart (see fig. 12-1). This spacing was determined empirically by flying naive observers near known colonies at decreasing horizontal distances until the colonies were routinely recognized by observers. The surveys are flown once monthly between February and June, and cover the entire mainland Everglades from Florida Bay to northern end of WCA 1. In the WCAs, systematic ground searches are also performed between April and late May of each year by airboat, and each tree island is individually checked for nesting activity. Although the aerial surveys are an efficient means to locate and count large colonies (those with more than one hundred pairs) dominated by white-plumaged birds, they are inefficient for discovering small colonies, particularly those of dark-colored species. Using intensive ground surveys by airboat as a standard, aerial surveys in the Everglades have been shown to miss over 79 percent of all colonies (most of which are very small), and over 30 percent of nesting wading birds (Frederick et al. 1996a). The ground survey program has thus led to the first reliable estimates of dark-colored wading birds in the ecosystem, as well as information on the dispersion of small colonies and solitary nests.

Systematic Surveys of Distribution

Beginning in 1986, systematic aerial estimates of numbers of all wading birds on the marsh surface were initiated. This Systematic Reconnaissance Flight (SRF) program was designed to estimate the geographic distribution and total numbers of all wading birds (breeding, non-breeding, adult, juvenile) within the Everglades ecosystem. Quite distinct from the surveys of breeding colonies, the SRFs are flown at low altitude, and numbers of birds are estimated using strip-transect methodology (Norton-Griffiths 1987; see fig. 12-2). Estimates of total numbers and densities are then derived from the strip counts, which constitute approximately 16 percent of the total area. These surveys have been flown monthly between January and June of 1986 through the present in ENP and the WCAs, and sporadically in Big Cypress National Preserve.

Reproductive Success Studies

Measures of reproductive success have been collected in Everglades colonies at various times and in various manners. Up until the early 1960s, reproductive success was scored only by whether an apparently

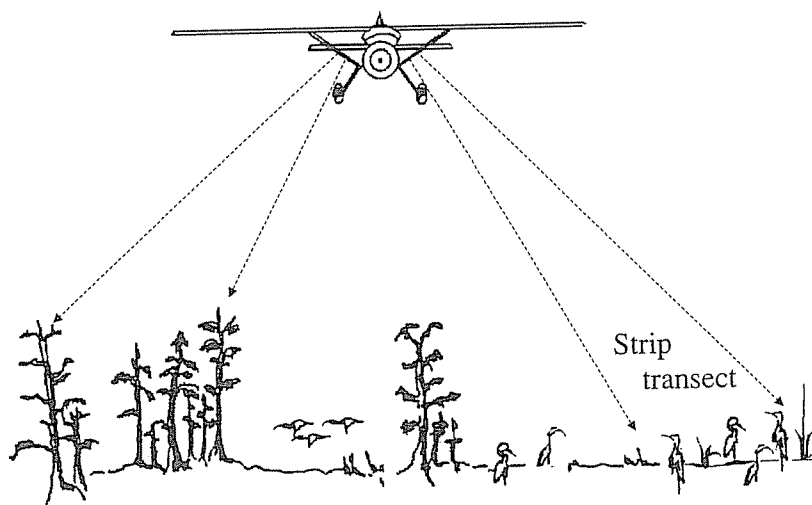


Figure 12-2. Schematic diagram of Systematic Reconnaissance Flight methodology. Flights are conducted at 61 meters in altitude, and observers count birds in strip transects on either side of the aircraft. Estimates of total numbers of birds on the marsh surface are then derived from these strip-counts by taking into account the percentage of the marsh surveyed.

large proportion of the nesting pairs in a colony succeeded or failed. During the late 1960s and 1970s, wood stork productivity was measured as the numbers of young raised per nest start (Ogden 1994). Between 1986 and 1991, repeated checks of marked nests of various species were used to estimate reproductive success and productivity in a large proportion (10–20 percent) of the nests in the southern and central Everglades (Bancroft et al. 1990; Frederick 1995); measurement of these parameters continued in the central Everglades through 1994 and sporadically thereafter (Frederick 1995).

The more recent studies of reproductive success have been linked with studies of foraging movements by reproductive adults (Ogden 1977; Bancroft et al. 1994; Frederick 1995), food habits and energetic requirements of young birds (Bancroft et al. 1994; Williams 1997; Frederick et al. 1999; Salatas 2000), and foraging behavior and foraging habitat (Surdick 1998; Gawlik 2002) to produce a picture of foraging distribution, reproductive success, and reproductive energetics of breeding birds.

Studies of Contaminants

Contaminant studies of wading birds have been sporadically undertaken in the Everglades, beginning with Ogden et al.'s (1974) reports of heavy

metals and organochlorines in eggs, and followed by Spalding and Forrester's (1991) survey of diseases and contaminants. During the 1990s, an intensive investigation of the sources, accumulation points, and effects of methylmercury in the ecosystem's biota led to ongoing annual collections of feather samples from young great egrets and investigations of effects of this contamination (Spalding and Forrester 1991; Sunlof et al. 1994; Beyer et al. 1997; Williams 1997; Bouton et al. 1999; Frederick et al. 1999; Sepulveda et al. 1999; Spalding et al. 2000a,b; Frederick et al. 2000).

What Has Monitoring Revealed about the Ecosystem?

Ogden (1994) summarized a comparison of recent (1974–1989) wading bird nesting with that of the 1930s and 1940s. Between these two periods, the numbers of nesting birds declined by over 90 percent (fig. 12-3). The comparison between the two periods was biased toward finding more birds in the later period, since the more recent survey methodology was systematic and more efficient at finding birds than were the mostly ground-based estimates of the 1930s. The more recent surveys also covered vastly more area—the 1930s estimates were only of coastal colonies and did not penetrate the interior marshes. Thus the 90 percent reduction between the two periods seems conservative. During the period 1930–1946, Ogden (1994) suggested that sixty-nine thousand to eighty-nine thousand birds nested in many years, with peaks of two hundred thousand. The current nesting numbers rarely exceed thirty thousand birds, with peaks of no more than sixty thousand (Frederick and Collopy 1989a; Frederick 1995; see fig. 12-3).

The Importance of Hydrological Variability

One of the most profound puzzles of the Everglades has been that a vast, nutrient-poor wetland system should be capable of supporting a large, concentrated biomass of wildlife. The wading bird monitoring programs have provided evidence of several ecological relationships that explain how the large numbers of wading birds could be supported by a system with such low energy density. The most obvious way is through annual fluctuations in water level, which serve to concentrate aquatic prey animals to the point that they are energetically profitable to consume. This process may create a broad "drying front," which progresses across the landscape as surface water dries during the spring nesting season, allowing wading birds (and other vertebrates) to exploit a moving wave of protein. This annual process has been well documented through aerial



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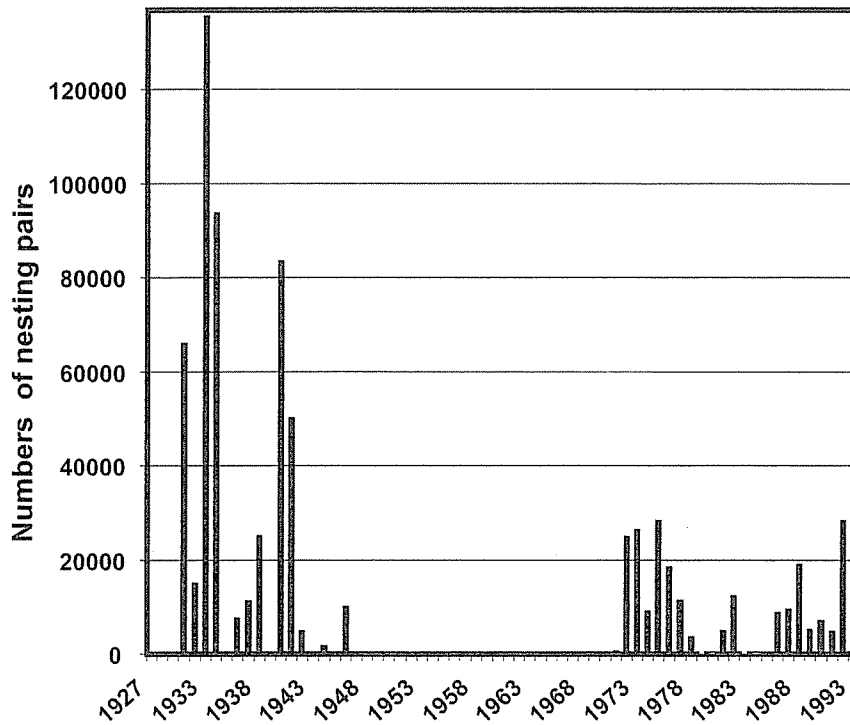


Figure 12-3. Numbers of nesting pairs of all wading bird species surveyed, 1930–1998. Although surveys of wood storks were regularly conducted during the 1950s and 1960s, there were no regular surveys of all wading birds during this time.

surveys designed to monitor numbers of birds (Kushlan 1977; Hoffman et al. 1994).

Other cycles of food availability may be less regular, with return intervals on the order of several to many years. Ogden (1994) noted that during the period of the 1930s, there was far greater interannual variability in colony presence and size than there has been during the most recent thirty years. For instance, during the 1930s and early 1940s, alternate years often showed severe drought with little or no nesting followed by one or more years with extremely large nestings (to over two hundred thousand birds). Ogden suggested that the large nestings of the 1930s and early 1940s were in part dependent upon the alternation of flood and drought. This suggested that there was something about multiyear patterns of hydrological variability that strongly affected nesting.

One prediction from this general observation is that abnormally large nesting events may be more likely following severe droughts than at other

times (Frederick 1998). These events are statistically identified as occurring more frequently than expected. These events have been suggested to have occurred two of the seven years, which are normally large nestings. These events have been suggested to have occurred two of the seven years, which are normally large nestings. These events have been suggested to have occurred two of the seven years, which are normally large nestings.

The idea that nonannual nesting events derives support from more general studies. For example, long-term studies have shown that nesting and hatching success in wading birds and rivers with large flows is higher than those that have low flows.

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Estuarine Pro

The record of nesting events stated that the nesting events (Ogden 1994) during the century, and during the Everglades wetland-marsh interface of 83 percent of the Everglades.

times (Frederick and Ogden 2001). Using the entire nesting record, we statistically identified eight abnormally large nesting events; all but one of these occurred within two years after severe droughts. Similarly, all but two of the severe droughts during the same period were followed by abnormally large nesting events. The biotic mechanisms behind this statistically significant association are unknown, but at least three processes have been suggested: (1) prey are temporarily superabundant following droughts as a result of reliberation of nutrients, (2) prey are superabundant following droughts because predatory fish have been killed off through desiccation (Kushlan 1976a; Walters et al. 1992), and (3) prey are more available following droughts due to more open vegetation (Surdick 1998). These hypotheses have predictions that are specific enough to test with further monitoring of fishes and aquatic macroinvertebrates.

The idea that both prey animals and wading birds depend strongly on nonannual natural hydrological fluctuations for their pulses of productivity derives support from studies of other Everglades biota as well as from more general examples of riverine systems (Junk et al. 1989). For example, long-term stable water conditions in the Water Conservation Areas have been shown to be detrimental to emergent vegetation and to both nesting and hunting success of snail kites (Bennetts and Kitchens 1997), and rivers with flood pulses are known to have more productive fisheries than those that do not (Junk et al. 1989).

Thus the evidence from wading bird monitoring in the Everglades has led directly to recommendations that natural hydrological fluctuation become a priority in water management and has served as part of a growing body of evidence that hydrological fluctuation is necessary to the normal functioning of many types of wetland systems. These examples also highlight the need to understand the mechanisms involved in creating pulses of productivity. This gives further justification for monitoring populations of prey animals at a large-enough scale to enable linkages with the wading bird studies.

Estuarine Productivity

The record of early twentieth-century colony locations also has demonstrated that there has been a major shift in the geographic location of nesting (Ogden 1978, 1994). During the latter part of the nineteenth century, and during the 1930s, all of the major colonies described for the Everglades were in the coastal zone or along the mangrove/freshwater marsh interface. In contrast, by the period 1986–1999, an annual average of 83 percent of the wading bird nests were located in freshwater areas of the Everglades (fig. 12-4). Although turnover in use of colony locations

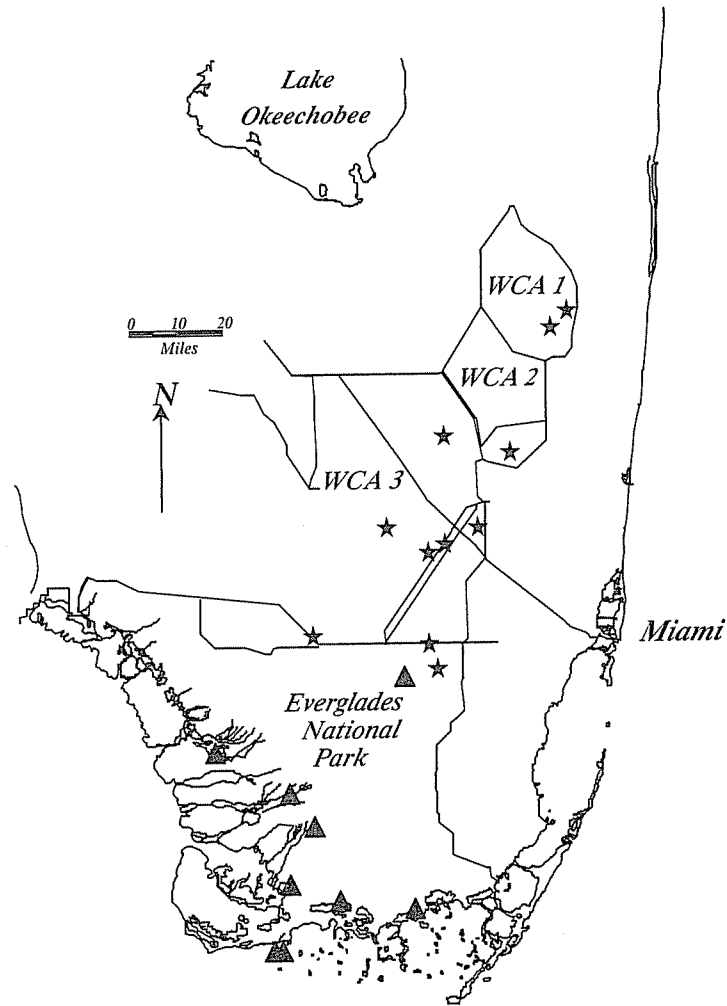


Figure 12-4. Map of the Everglades showing the locations of all colonies more than five hundred pairs. Colonies during the period 1930–1960 are shown as solid triangles and those from 1970–1998 are shown as solid stars. Although the inland colonies may simply have gone undetected during the early surveys, it seems clear that the coastal colonies have disappeared during the recent period.

is common in wading birds (Bancroft et al. 1988; Frederick 1995; Smith and Collopy 1995; Frederick and Ogden 2001), the loss of the entire region of formerly productive coastal colonies was so complete and has been maintained for such a long time (more than thirty years) that the abandonment of the area seemed indicative of a profound change in coastal ecosystem function.

The loss of coastal colonies implied that the coastal foraging habitat or

prey base had become degraded in some fashion, and studies initiated in the 1980s and 1990s on other aspects of the coastal ecosystem have borne this hypothesis out (McIvor et al. 1994). The most profound changes in the coastal zone have probably been driven by an extreme reduction in surface freshwater flows to the region (Smith et al. 1989; Fennema et al. 1994) and have included increases in the salinity of the estuary, decreases in shrimp production (Browder 1985), decreases in sport-fish catches, and decreases in the standing stocks and densities of small "forage" fishes in the coastal marshes and mangrove ecotone (Lorenz 1997). What is most significant about the use of wading bird monitoring information in this story is that the decreases in coastal wading bird colonies were recognized as much as twenty years before evidence from other sources suggested that the productivity of the coastal ecosystem had collapsed (Ogden 1978).

The estuarine zone may also have been productive because it offered wading birds a variety of habitat and wetland types in which to forage that would not be available in the more homogeneous freshwater marshes. The importance of heterogeneous foraging habitats for buffering birds against unpredictable water-level fluctuations has been observed in modern-day studies of coastal-nesting wading birds in the Everglades (Bancroft et al. 1990, 1994) and points to the need to understand fluctuations in prey animal populations in those habitats.

Defining Healthy Hydrological Patterns

Wading bird monitoring studies have also demonstrated important differences in the conditions that have led to productive nesting during historical versus modern periods, and ultimately these observations have led to fundamental changes in surface water management. Ogden (1994) noted that during the 1930s and 1940s large nesting events occurred in years with either wet or dry conditions but that during the modern period, productive nesting occurred only during the drier years. This pattern of nesting in dryer years has been linked to a direct relationship between annual nesting effort and rate of surface water recession for both wood storks (Kushlan et al. 1975) and white ibises (Frederick and Collopy 1989b). An analysis of nest failures in the Everglades during the recent period has similarly shown that abandonment is common whenever a drying water regime is reversed by high rainfall (Frederick and Collopy 1989b).

This difference between historical and modern nesting responses was something of a puzzle. However, monitoring of marsh hydrology and aquatic biota eventually showed that overdrainage of the freshwater marsh resulted in marked decreases in the abundance and standing stock of small fishes and invertebrates (Loftus and Eklund 1994; Loftus et al.

1992). Thus drainage practices have led to short hydroperiod in the freshwater marsh, resulting in depauperate prey animal communities. It then made sense that the wading birds would show progressively greater dependence on drying events through time, because they were using them as a mechanism to concentrate the few prey present. In this case, the combination of changing bird-nesting responses and fish population dynamics were required to fully realize the ramifications of long-term marsh drainage (Walters et al. 1992; Fennema et al. 1994).

It is important to realize that in the absence of the long-term bird monitoring effort, our impression of suitable wading bird foraging conditions would probably be narrowly (and incorrectly) focused on the "beneficial" effects of rapidly falling water for stimulating nesting and increasing nesting success. In fact, this latter impression has been widely held, and has led to management policies that routinely dried much of the marsh surface during the dry season. Thus a negative feedback mechanism probably existed between management that favored annual drying events and consequent increasing dependence of wading birds on drying events.

Tracking Changes in Aquatic Contamination Levels

Wading birds are empirically good accumulators of contaminants for a number of reasons. Wading birds are known to feed at or close to the top of the aquatic food web and show high bioaccumulation potential (Custer and Osborn 1977; Jurczyk 1993; Erwin and Custer 2000). Since the majority of the food gathered by adult wading birds (e.g., white ibises and great egrets) is known to come from distances of 10 kilometers or less from the colony (summarized by Bancroft et al. 1994; Smith 1995), the tissues of young wading birds are known to be composed largely of resources from within this area. The use of young birds therefore largely avoids contamination signals that might come from other parts of the range of these migratory birds. The sampling unit here is the colony site, and although this grain for sampling (20-kilometer-diameter circles) may seem large, it is probably appropriate for monitoring contamination in the aquatic food web of the Everglades ecosystem (rough dimensions 60 by 180 kilometers).

To date, only mercury has been shown to consistently occur in high concentrations in wading birds in the Everglades, though there have been no systematic investigations to date of PCBs or dioxins. The Everglades aquatic food web is highly contaminated with mercury (Frederick 2000), and levels in great egret chicks are in some years higher than has so far been demonstrated for young of any fish-eating bird (Sunlof et al. 1994; Sepulveda et al. 1999). These levels have been shown to be high enough to result in reduced health and altered hunting behavior of juvenile birds

(Spalding et al. 1994; Bouton et al. 1999; Spalding et al. 2000a,b), and there may also be effects on reproduction. Concentrations of mercury in feathers from nestlings have differed markedly and consistently among colonies, and these differences track geographic variation in mercury sampled from mosquitofish (*Gambusia holbrooki*, Stober et al. 1996). In addition, laboratory studies have demonstrated a clear and predictable relationship between mercury consumed and mercury concentration in feathers of young great egrets (Spalding et al. 2000a). Thus, there is empirical evidence from lab and field that feather tissue concentrations are a good indicator of mercury concentration in prey.

In this monitoring program, geographic variation in contamination among colonies has been largely swamped by differences among years, and we have measured a significant decline in mercury concentrations between 1994 and 2000 (73 percent reduction, Frederick et al. 2002). This monitoring system has alerted those studying mercury mass transport and dynamics to look for processes that may have led to this significant decrease in contamination.

Wading birds have thus served an important sentinel role for contaminants in the Everglades (as much by what they have not accumulated as by what they have) and have demonstrated both geographic and temporal differences in concentrations of mercury. Further understanding of the dynamics of mercury at the ecosystem scale is likely to rely in large part on monitoring studies of top-level consumers like wading birds. The success of the mercury monitoring efforts suggests that the birds should also be monitored for other contaminants, since south Florida currently applies more pesticides per hectare, and uses a wider array of pesticides and herbicides, than any other area of the United States.

Linkages between Wetland Ecosystems

Relatively few animals move between the Everglades and other ecosystems. Those that do include the Florida panther (*Felis concolor coryi*), West Indian manatee (*Trichechus manatus*), snail kite (*Rostrhamus sociabilis*), migratory birds, and numerous euryhaline fishes and penaeid shrimps (Browder 1985). Of these, wading birds are probably the longest-monitored both within and outside of the Everglades and in many cases have been the subject of more ecological research. Thus, wading birds are one of the few well-studied Everglades animal groups that have the capability of leaving the ecosystem or of being attracted there from other locations in response to favorable ecological conditions. In this sense, wading birds can function as a true bellwether of environmental conditions among ecosystems in a way that few other species can.

A history of statewide surveys, banding records, and other sources of information indicates that the wading birds that utilize the Everglades are panmictic with, and demographically linked to, wading birds in other wetland areas of the southeast and the eastern Caribbean (Stangel et al. 1990, 1991; Frederick et al. 1996). The Everglades "population" then, is actually not distinct in its genetics or social organization and instead belongs to a loose grouping of animals that occur in a space perhaps as large as the eastern and southeastern United States and the eastern Caribbean. It is important to remember, then, that the dynamics of birds in the Everglades ecosystem may be strongly influenced by conditions in other regions, and, conversely, that management in the Everglades may well influence patterns of distribution and abundance elsewhere.

For example, the Everglades probably served as an important source for the restoration of wading birds in the southeastern United States during the period immediately following the decline of the plume trade (Ogden 1978). The very large nesting aggregations of wading birds documented during the period 1930–1946 were not reported elsewhere in the United States, and several of the species (wood storks, white ibises) were not known to breed outside of Florida at the time. Similarly, very large colonies of great egrets, white ibises, and snowy egrets in Florida during the 1930s immediately preceded the rapid expansion of nesting by these species in the Atlantic coastal plain and Mississippi Valley.

During the last two decades, however, interregional monitoring indicates that this situation may have reversed itself, and the Everglades may now have become a demographic sink rather than source for many species. Wood stork reproductive parameters in the Everglades during the recent period are exceptionally low for the species (Ogden 1994), and it is very unlikely that Everglades wood storks are replacing themselves. Between 1976 and the present, the percentage of the U.S. wood stork population nesting in south Florida dropped from 70 to 13 percent (Coulter et al. 1999). Through a comparison of breeding and Systematic Reconnaissance Flight (SRF) surveys, we have found that during the 1990s an average of 70 percent of adult great egrets, white ibises, and wood storks annually remained as nonbreeders in the Everglades during the breeding season. Although the breeding population appears to be stable or slightly increasing, it is very likely that "sitting out" reproduction in this manner will lead to a sharp decline in recruitment. This suggests that birds breeding in the Everglades may not be reproducing fast enough to cause local recruitment, and that stable populations are maintained instead by new birds from elsewhere. Thus, even an apparently stable population may not be a healthy or self-sustaining one (Temple and Wiens 1989; Sadoul 1997). This example illustrates one of the ways that local

monitoring, even at the ecosystem level, can be extremely misleading if not considered in the context of dynamics in other ecosystems.

The Everglades is in a geographically key position for migrating and wintering wading birds (Byrd 1978; Root 1988), and the SRF surveys have documented especially large numbers of birds using the Everglades during the winter pre-breeding season. These studies have shown that in some years the Everglades may host a substantial proportion of regional populations of some species (Bancroft et al. 1992). The high usage of the area suggests that large numbers of birds are regularly able to assess conditions in the Everglades during the prebreeding period, and the large interannual variance in breeding effort suggests that these migratory birds may include the Everglades as a potential site when deciding where to nest. This scenario bolsters the notion that the numbers of birds nesting in the Everglades is indicative of conditions there, and that wading bird reproduction is a useful bioindicator of restoration.

Events in other ecosystems may also affect wading bird use of the Everglades. For example, white ibises are known to make large-scale shifts in breeding location depending in part on comparing breeding conditions and food resources in past and prospective breeding sites (Ogden 1978; Frederick et al. 1996b; Frederick and Ogden 1997). During the period 1980–1995, the numbers of white ibises in Louisiana increased dramatically, probably in response to a large increase in impoundment acreage devoted to commercial production of crayfishes (*Procambarus* spp., Fleury and Sherry 1992). During the same period, a 50 percent reduction was documented in the total numbers of ibises nesting in Florida (Runde 1991). This suggests strongly that the increase in aquaculture in Louisiana was directly related to decreases in ibises nesting in Florida and in the Everglades.

It therefore seems very important to extend the monitoring of wading birds to sites outside the boundaries of the Everglades ecosystem. This is particularly critical for interpreting changes in wading bird numbers and, eventually, for evaluating the potential for and success of restoration efforts within the Everglades. Monitoring of wading birds throughout their southeastern United States and Caribbean range is far from complete, but useful information can (as above) be gleaned through cooperative efforts with other states and countries.

Assessment of the Everglades Monitoring Programs

We believe that the information presented so far demonstrates that careful, long-term monitoring of an avian species assemblage can be extremely useful in understanding both the past and present dynamics of a

large aquatic ecosystem like the Everglades. Of the Everglades ecosystem features that Davis and Ogden (1994) felt were key to the design of restoration plans, our understanding of nearly all of them has been revealed in part by our understanding of wading bird dynamics. Monitoring of wading birds has demonstrated or helped to demonstrate the importance of large-spatial-extent, habitat mosaics, refugia, sheet flow into the estuaries, seasonal energy pulses, seasonal depth patterns, and long uninterrupted hydroperiods to the functioning of the Everglades. By this standard, we feel that the bird monitoring programs have been an unqualified success. However, there are a number of areas in which these efforts could be improved, and a critical evaluation here may serve to aid in the design of monitoring programs in other ecosystems.

Perhaps the single most obvious weakness of the Everglades avian monitoring program is that there is a poor understanding of processes affecting birds outside the ecosystem. It seems clear that most of the wading bird species in the Everglades wander widely during the nonbreeding season and may frequently be attracted to nest in other locations. Thus the ability to interpret reproductive or population changes in the group of birds using the Everglades may be strongly dependent upon the changing attributes of other wetlands throughout the Caribbean and the southeastern United States. Our ability to distinguish between population changes resulting from factors endogenous or exogenous to the Everglades is poorly developed in large part because comparable monitoring systems elsewhere either do not exist or are incomplete. For example, statewide monitoring of wading bird colonies is occasionally accomplished in Florida, Georgia, South Carolina, Texas, and Louisiana but is conducted infrequently (often five to fifteen years between surveys) and is never performed in all states in the same year. The opportunity to compare responses at these sites with annual fluctuations in the Everglades nesting numbers is therefore extremely rare.

Similarly, the movements of birds to the Caribbean, and in particular to Cuba, are very poorly documented, yet changes in conditions in the Caribbean could strongly influence our interpretation of the dynamics of birds in the Everglades. In Europe, Hafner et al. (1994) found that annual fluctuations in little egrets breeding in the Camargue were partly explained by variation in rainfall in the African wintering grounds for this species. It is probably unrealistic to ever expect the development of simultaneous annual surveys for wading birds throughout the potential range of the Everglades birds, but regular, consistent monitoring in many key areas could greatly expand the ability to interpret dynamics in any one of the wetland locations. The Everglades also lacks any kind of banding

or marking program, which could help identify regular wintering habitats and alternative breeding sites.

The wading bird monitoring programs of the Everglades have been used intensively and extensively as a restoration and research tool in large part because the historical record enabled the establishment of target restoration goals (numbers of wading birds nesting, locations of colonies, and attributes of the ecosystem that nesting is known to depend upon, see Ogden et al. 1997). However, it is not clear that even the "benchmark" period (1931–1946) was representative of a natural, pre-drainage ecosystem. Considerable drainage of the ecosystem had occurred prior to the 1930s (Smith et al. 1989), and some years during the 1930s may have been particularly dry (Frohning et al. 1988). Thus, there is the danger that the use of numbers of wading birds from that period as a restoration target could be misleading. Nonetheless, the period of the 1930s was probably broadly representative of some important characteristics of the pre-drainage Everglades, such as a consistently nesting population, a concentration of nesting in the coastal zone, and high interannual variability in nesting. To avoid the overuse of the 1930s benchmark, restoration targets for wading birds have deemphasized target breeding numbers and focused instead on attributes of productive nesting (timing, location, levels of productivity) and on the ecological functions that are thought to have supported coastal nesting (Ogden et al. 1997).

One of the most common criticisms of waterbird monitoring in general is that censuses are inaccurate, perhaps to the point that change in nesting or total numbers are overshadowed by error resulting from inaccuracies in finding colonies and estimating numbers of birds (e.g., Drury 1980; Frohning et al. 1988; Rodgers et al. 1995). To some extent, the Everglades survey record is buffered from this criticism simply because the change in breeding numbers between early and recent time periods is probably too large (well over one hundred thousand birds) to be the result of inaccuracies in estimation. However, there are important problems that remain with the estimation of large numbers of birds in a large landscape. Within the various Everglades management units, nesting birds are variously estimated by ground surveys, aerial surveys, or both. Given the inaccuracies of using either one of these techniques alone (Frederick et al. 1996a), there is a very real need to standardize estimation procedures throughout the ecosystem.

An evaluation of the utility of the SRF survey system is somewhat premature since much of the data from those systematic surveys are still being analyzed at the time of writing. However, it is true that the majority of insights gained from monitoring wading birds have come directly from

monitoring nesting in various ways, and comparatively little has been derived from the studies of distributional patterns. At the time that the SRF flights were initiated in the mid-1980s, there was great hope that the resulting distribution maps of birds in the Everglades landscape could be used both to determine the ecological attributes necessary for wading bird foraging and nesting, and to assay the success of hydrological restoration efforts. In our view, there has been, and continues to be, only mild progress on the first goal. Although the SRF survey information has been used to identify the fact that birds follow patterns of shallow water and avoid areas of dense vegetation, the grain of the information (2-x-2-kilometer cells) is too coarse to be of much value in finer distinctions of habitat quality. This problem results from an obvious trade-off between geographic extent and detail of surveys, and is one that is likely to be repeated in other extensive ecosystems. This example illustrates that researchers should be very careful about matching the grain of surveys with the question at hand (Begg et al. 1997).

The SRF surveys may have successfully accomplished the second goal—evaluating success of restoration through changes in distributions. One of the most obvious signals of restoration success would be a shift in distribution of birds from the WCAs areas to the coastal zone (Ogden et al. 1997). During the period of SRF surveys (1985–present), no large and consistent shifts of wading bird density distributions have been documented within the Everglades. This reveals that the goal of shifting birds back to the estuarine zone has not been realized, which is not surprising since no large-scale restoration actions have been taken to date. Nonetheless, it is also quite possible that the detection of such large-scale shifts could be accomplished with a far less intensive and expensive program.

The real value of the SRF surveys may lie in their ability to estimate total numbers of birds using the marsh habitat. While the estimates do contain some important biases as a result of the characteristically clumped distribution of birds, there are several robust conclusions that have arisen from this series of population estimates. First, it seems inescapable that the Everglades functions in some years as an important concentration point for wintering wading birds. Second, in conjunction with the breeding bird surveys the SRF counts have resulted in the tentative conclusion that a large proportion of the wading birds remaining in the Everglades throughout the breeding season do not actually attempt to breed. One obvious extension of this finding is that the Everglades may function as a reproductive sink.

One disappointment of the Everglades monitoring program is that there has been little success in matching spatial information about birds with spatial attributes of their prey animals. Such linkages could elucidate the relative importance of changes in prey density to the wading bird de-

clines. The basis of the problem is that it is inherently more costly and logistically difficult to sample fish and invertebrates over a large landscape than it has been to sample birds. For example, during the unanticipated large nesting event of 1992, fish and macroinvertebrate samplings were available from only three locations in the Everglades, and none of them were in the areas where birds nested or fed in high densities. Thus it was impossible to tell whether the large nesting event was related to elevated prey densities. The Everglades fish monitoring program has since been expanded to include over twenty-five sites spread throughout the Water Conservation Areas and Everglades National Park, and it is hoped that this larger network of observation sites will yield a better match with the wading bird distributional studies.

Conclusion

The factors that have led to the overall success of the wading bird monitoring programs may be general, or some cases unique, to the Everglades. To assess the general applicability of the Everglades avian monitoring program to other ecosystems, it seems important to identify the attributes that were essential to the success of the program.

Existence of Historical Baseline Data

The existence of a run of reasonably accurate historical records during a period prior to intensive water management has been the single most valuable attribute of the wading bird program. It is striking, for example, that without the information from the 1930–1946 period there would have been little hint from the birds of the pervasive changes that have taken place in the estuarine zone of the Everglades. It is also sobering to realize that on the basis of the relationships between hydrology and nesting from the recent past (1960–1996), we would have assumed that rapid drying of the marsh surface every year was the key to stimulating nesting. With the inference of the historical period, it became clear that this relationship is probably an artifact of a prey community degraded by years of overdrainage. This example suggests that ecological relationships derived from a current, disturbed ecosystem may be extremely misleading for establishing restoration targets.

The historical data also have compelled us to realize that the natural hydrological variability of the Everglades was in fact key to the ability of the ecosystem to produce the enormous pulses of secondary productivity that fueled the fish and wildlife populations for which the ecosystem was once famous. The historical information has also been central to the develop-

ment of restoration goals, both for target patterns of nesting by wading birds and for ecosystem attributes (timing and minimum flows of water, restoration of flows to the estuary, reconnection of wetland compartments).

The importance of the historical data in the Everglades example speaks very strongly to the need to begin monitoring studies in other ecoregions, particularly those systems that are so far relatively unimpacted by anthropogenic actions. Although the Everglades has been truly and perhaps uniquely blessed with the quality and quantity of historical data on local wading bird population dynamics, similarly useful records are available for many ecosystems, especially for commercially harvested species (e.g., blue crabs and oysters in Chesapeake Bay, salmon in the Columbia River drainage). Even short runs of historical data may be of value in identifying ecosystem attributes and conditions.

Long, Continuous Time Series

Although the historical information has been a critical tool, the sheer length and relative continuity of the Everglades wading bird data set have been of key importance in discerning recurring and changing patterns. The need for long time-series of data for developing trend analyses seems obvious. What is less obvious is the emerging importance of long-term monitoring for detecting rare, trend-setting ecological events in ecosystems. For instance, a minimum of twenty-five years of information has been necessary to detect the powerful effect of severe winters on wetland bird populations in the French Camargue (Johnson 1997; Hafner and Fasola 1997). In the Everglades, the apparent relationship between severe droughts and ensuing bursts of secondary productivity and wading bird nesting relies on evidence of drought events spread out over seven decades of monitoring. Similarly, the differences in patterns shown by nesting birds during the historical and recent periods in the Everglades have demanded at least a decade of continuous data during each era to distinguish the effect of recurrent periods of drought and flood. It is also true that the sheer length of the record has been a strong argument for continuing the program in the face of many other competing funding priorities.

Strong Public Appeal

The initiation and continued public support for monitoring wading birds is directly traceable to their popular appeal. Indeed, the earliest inquiries into the status of breeding wading birds during the late 1800s were the result of public interest in the fate of these animals during the plume-hunting era. The protection of the birds through a network of wardens

and the resulting record of nesting during the 1930s and 1940s was supported directly through funds generated by the public's interest in these programs. This interest continues to the present, and the wading bird monitoring programs continue to enjoy wide public interest as evidenced by the numerous newspaper articles and radio spots that are aired every year on this subject. By comparison, it has been much harder to garner support for monitoring of fishes, invertebrates, and many other aquatic creatures in the Everglades.

Besides being exceptionally beautiful, visible, and evocative animals, these birds are also easy for the public to envision as an indicator of the less-visible and less aesthetically appealing aspects of a wetland ecosystem. In the public eye, they have become symbolic of the health of the Everglades; large numbers of wading birds equates with a healthy ecosystem. Thus the ability to stimulate public support for long-term monitoring may rely in large part on picking a species or group that is inherently popular with humans.

Integration over an Appropriate Spatial Scale

Wading birds are sufficiently mobile to be capable of including the entire Everglades ecosystem when making foraging and nesting decisions. They are also able to collect food and energy over large areas and are tertiary consumers, which is of interest for monitoring both contaminants and prey animal populations. At the same time, the restricted range of foraging during breeding ensures that samples from eggs and young are representative of a specific region of the ecosystem.

Wading Birds Are Biologically Well Understood

Much is known about relationships between wading birds and their environment from studies within and outside the Everglades. This includes a solid linkage between food availability and reproduction, the relative importance of predation to reproductive success, the effects of contaminants, and the responses of birds to various kinds of natural and anthropogenic perturbations. This information is essential to the interpretation of changes in avian population sizes and breeding parameters and their eventual use as indicators of environmental change.

Monitoring Represents a Wide Range of Ecological Needs

Differences in habitat preferences, food habits, and behavior among the dozen or so species of wading birds that are commonly monitored in south

Florida can result in differences among species in responses to environmental conditions (Gawlik 2002). These differences in responses can help to reveal the specific nature of the ecological effects of water management impacts. The use of any single species could not accomplish this goal.

A Range of Spatial and Temporal Scales Is Represented

Mobility and poor site fidelity are characteristic of many species of wading birds that make them good indicators of all levels of environmental conditions. At small time and spatial scales, foraging wading birds may relocate within hours following changes in water depths caused by management practices or sudden rainfall. Mid-scale responses include changes between consecutive years in the location and timing of nesting activity, again in response to regional differences in hydroperiods caused by management practices and annual differences in rainfall. Long-term changes over years or decades are best illustrated by the ecosystem-wide population trends reported for most Everglades wading birds, but may also track changes in contaminants, such as the Everglades mercury example.

Wading Birds Are Easily Monitored

The white species of wading birds have been shown to be easily located, identified, and counted or estimated from low-flying aircraft and as a group are probably far cheaper to monitor than any vertebrate.

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