

## The FAUNAL CHAPTERS: CONTEXTS, SYNTHESIS, and DEPARTURES

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### ABSTRACT

Salient themes of the chapters on animal ecology are discussed here, and aspects of the historical/biogeographical setting essential to understanding the Everglades fauna and the prospects for its restoration are described. The Everglades is located at the distal end of a long peninsula, at an important biogeographical boundary, and in a region where sea level rise has been the dominant geological process of the past 15,000 years. Interaction of these forces determined the characteristics of its present biota: relatively species poor, of mixed continental and Antillean origin, and with endemism and small populations strongly concentrated in the reduced area of uplands. In the 1920s through 1960s, the Everglades probably served as the major source of repopulation of wading birds throughout the eastern United States. Now, as chronicled in many chapters of the faunal section, nesting in the area has become a demographic sink for wading birds produced elsewhere, although the Everglades still functions as an important feeding area for wintering and transient populations. Re-establishment of productive wading bird nesting populations is a key measure of the success of Everglades restoration. Hypotheses and interpretations of the restoration needs of Everglades wading birds center on revitalization of short-hydroperiod marshes to cue earlier breeding and repair of the diminished productivity of the estuarine system. However, despite considerable study, wading bird restoration remains hampered by inadequate information, especially concerning the ecology of food organisms. At least several hundred species of nonnative animals are established in developed, coastal areas adjoining the Everglades. More and more of these species appear to be extending into undisturbed habitats where the effects of their presence are at present largely unknown. Information on

movement and home range suggests that the Everglades system, in and of itself, is probably too small to sustain viable populations of many of its more mobile animals. This is particularly true of the reduced and still shrinking upland areas, many species of which may be virtually impossible to restore and maintain.

## INTRODUCTION

The original purpose of this chapter was to extract the essence of the preceding series of chapters presenting research on animal ecology. However, it is necessary to consider new information revealed by the onward flow of events and study. Most of the new observations highlighted in this chapter were made by the researchers who presented chapters on the same subjects.

In addition to new data from ongoing studies, abrupt changes of scene in the Everglades itself have also demanded comment. During most of the preparation of this volume, southern Florida was in the second year of a 3-year drought and had not experienced a significant tropical storm in 25 years. The drought was broken in the 1991–92 hydrological year, and now a remarkably wet El Niño winter has followed the epic autumn of hurricane Andrew. Although it is not yet clear that these perturbations will be studied with the sophistication they deserve, their mere occurrence has provided insights into Everglades ecology.

Finally, in preparing this chapter it was decided not to simply rehash the constituent chapters and attempt to connect them. The chapters, after all, engage a wide diversity of subjects and speak capably for themselves. Instead, they are used as springboards or guides to other discussion. Thus, in the material that follows, one section examines the concepts and questions that arise more or less directly from the suite of chapters on wading birds that make up most of the faunal segment. The other four sections are stand-alone essays that do not follow in a natural sequence. Rather, they engage subjects that are discussed little or not at all in this volume, but are central to consideration of the Everglades fauna and critical to any views of restoration. While this may present the reader with a sort of karst topography of subjects, it is more useful to fill gaps than provide continuity of reading. If there is a unifying theme, it is to provide historical and geographical context to the reader's view of the faunal ecology of southern Florida.

## HISTORICAL FACTORS and the PRESENT EVERGLADES FAUNA

Aspects of Holocene geographical and ecological change in southern Florida that have largely determined the composition and status of the present Everglades fauna are reviewed here. In particular, the following are considered: (1) Florida's peninsular landform, initially four times wider and much more elevated than it is now (Webb, 1990, Figure 4.8), (2) Florida's geographical location near a significant biogeographical boundary, and (3) Florida's postglacial history of steadily rising sea level, the proximate force that drives the ecogeographical change. These influences have combined to create a south Florida landscape that has been highly unstable at the upper temporal scale of a few thousand years (deAngelis and White, 1994),

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with a rather dynamic "succession" of communities from upland to freshwater wetland to coastal swamp to estuarine to marine, as sea level rose. These ongoing changes are central to understanding the composition and future of the present regional fauna.

### Peninsularity

It has frequently been noted that the species diversity of vertebrate animals often decreases from proximal to distal regions of long peninsulas. Simpson (1964) termed this phenomenon the "peninsular effect" and reasoned that it might occur because extinction rates tended to increase and immigration rates to decrease with increasing distance from the mainland along a peninsula. The enunciation of this concept sparked examination of peninsular faunas, and Florida, being conspicuously a peninsula, has figured extensively in this discussion.

All four classes of vertebrates in Florida exhibit progressively declining species density (i.e., the number of native breeding species in a representative area) from north to south in the peninsula. This result has been reported from analyses of the faunas of fishes (Loftus and Kushlan, 1987), reptiles and amphibians (Duellman and Schwartz, 1958; Kiester, 1971; Busack and Hedges, 1984), birds (Cook, 1969; Tramer, 1974; Robertson and Kushlan, 1974), and mammals (Simpson, 1964; Layne, 1974). The pattern and degree of north-to-south decline in species density varies considerably between groups. For example, the number of species of breeding landbirds declines precipitously from >70 in the extreme northern peninsula to about 25 at the extreme southern end of the peninsula and <20 in the Lower Florida Keys (Robertson and Kushlan, 1974, Figure 1). Conversely, Dalrymple (1988) pointed out that the principal deficiency in the species composition of herpetofauna of Long Pine Key, Everglades National Park was the lack of salamanders, while species density in groups such as snakes and anurans was more similar to that found in comparable areas much farther north in the peninsula.

Although Florida's vertebrate fauna seems to exhibit the hypothesized peninsular effect, the universality (even the reality!) of the phenomenon has come to be widely questioned. Specifically for Florida, several authors (Tramer, 1974; Wamer, 1978; Busack and Hedges, 1984; Means and Simberloff, 1987) have argued that the southward decline of species density principally reflects a similar decline in habitat diversity and productivity from top to bottom of the peninsula. Attention is sometimes drawn to the much reduced area of uplands in southern Florida, known as "the Everglades effect" (Means and Simberloff, 1987), as a factor contributing to reduced species diversity of terrestrial vertebrates.

Two lines of evidence based on change in the breeding ranges of Florida landbird species over the past 60 years or so seem to bear on questions of peninsularity. First, about 25 species have shown significant southward extensions of their breeding ranges in the Florida peninsula within the period of scientific record (Robertson and Kushlan, 1974; Stevenson, 1976; Robertson and Woolfenden, 1992). Most of these breeding range expansions have been closely associated with anthropogenic or extensively altered habitats new to the peninsular landscape. Thus, it appears reasonable to suppose that many of these species had previously reached a habitat-determined southern range limit in the peninsula. Second, about

ten bird species (plus several mammals) have apparently disappeared from their southern breeding range extremities in the Florida peninsula within the period of scientific record. Most of these species were close or obligate associates of the diminished and fragmented stands of upland vegetation (especially pine forest) near the southern end of the peninsula. These instances would appear to represent the type of local extinctions without replacement which Simpson (1964) visualized as the mechanism of his "peninsular effect." (See the final section of this chapter and Tables 28.1 and 28.2 therein for additional discussion.)

In summary, the present Everglades system has fewer vertebrate species than occur in areas of similar extent farther north in peninsular Florida. Two principal explanations have been suggested to account for these differences: (1) effects of the narrowed peninsular landform tend toward an increased likelihood of local extinction and a decreased likelihood of colonization and recolonization, as in entirely insular environments, or, specifically for Florida, (2) the southward decrease in habitat diversity and productivity adequately explains the reduced species density of vertebrates in southern Florida. Documented recent changes of breeding range by landbird species in Florida (as discussed later in this chapter) lend some support to each of these explanations. However, comment on this subject must consider the probable state of the peninsula itself and its biota throughout the postglacial cycle of sea level change. The Florida peninsula at earlier stages in this approximately 20,000-year process differed greatly from the peninsula of today (Webb, 1990, Figures 4.8 and 4.9) and peninsular effects on the fauna doubtless also differed.

### Location at a Zonal Boundary

As De Pourtales (1877) noted more than a century ago, southern Florida is unusual in that it has predominantly West Indian plant communities (especially uplands and coastal swamps) whose vertebrate inhabitants are mostly North American species. His comment calls attention to a second pervasive influence on the present Everglades fauna, namely, southern Florida's location at the biogeographical frontier between temperate North American and Antillean tropical biotas. Through the various cycles of Pleistocene glacial-interglacial sea levels, the water gap that separated outermost Florida from Cuba and the Bahamas apparently was never much narrower than it is today (Hoffmeister, 1974). Thus, any biotic interchange between the two juxtaposed land masses occurred across a seaway roughly 65–125 km wide at its narrowest. Prevailing winds and ocean currents at present certainly favor transport from the West Indies toward Florida, and these, along with the contribution of migrant birds, no doubt account for the large West Indian component in the flora and the invertebrate fauna of southern Florida (Snyder et al., 1990). Few vertebrates other than birds figured in the exchange, however. For example, the Antillean mammals self-introduced to southern Florida (Layne, 1974) are comprised of only two rare species of bats and the West Indian manatee (*Trichechus manatus*); the Antillean reptiles native to southern Florida (Duellman and Schwartz, 1958) are the reef gecko (*Sphaerodactylus notatus*) and the American crocodile (*Crocodylus acutus*). It appears probable that no North American mammals or reptiles crossed in the opposite direction.

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Only in the case of the land avifauna do present distributions indicate sufficient traffic in both directions to give some insight into the history of the exchange process. Robertson and Kushlan (1974) found evidence for an earlier (last glacial maximum?) flow of landbird species from the continent into the Bahamas and Greater Antilles and a smaller (currently ongoing) movement from the Bahamas and Cuba into southern Florida. The former movement resulted in the establishment in the West Indies of 25–35 landbird species originally of North American origin. Examples include the sandhill crane (*Grus canadensis*), ivory-billed woodpecker (*Campephilus principalis*), brown-headed nuthatch (*Sitta pusilla*), blue-gray gnatcatcher (*Polioptila caerulea*), and pine warbler (*Dendroica pinus*). These West Indian populations are now considered at least subspecifically distinct from their closest continental relatives (Bond, 1956), and ecologically, the group is associated predominantly with pine forest and savanna habitats in the West Indies. The apparently more recent influx in the opposite direction has established about a dozen West Indian landbirds on the continent, with most species more or less restricted to southern Florida. Examples include the snail kite (*Rostrhamus sociabilis*), white-crowned pigeon (*Columba leucocephala*), gray kingbird (*Tyrannus dominicensis*), and black-whiskered vireo (*Vireo altiloquus*). Without exception, these species are considered identical to West Indian populations, and ecologically, they tend to be associated with coastal habitats. Recent records of breeding in southern Florida by the West Indian cave swallow (*Hirundo fulva*) (Smith et al., 1988) and probable breeding by the shiny cowbird (*Molothrus bonariensis*) (Smith and Sprunt, 1987) strongly suggest that species flow toward the continent is continuing. The present breeding land avifauna of southern Florida appears to be unsaturated (i.e., it lacks representative species of a number of trophic guilds) and presumably is open to further invasion (Robertson, 1955; Robertson and Kushlan, 1974).

In summary, evidence from the presence and differentiation of North American species of landbirds in the West Indies suggests that this influx occurred during Pleistocene glacial maxima, especially the most recent glacial cycle. During glacial intervals, uplands on either side of the Florida Straits were near their greatest extent, and most of the invading landbirds (at least those that survive at present) were apparently species adapted to upland (in some cases montane) and xeric habitats. In contrast, the lesser but continuing flow of West Indian landbirds to southern Florida appears to be much more recent and comprised of coastal species. Because sea level rise and anthropogenic effects have so greatly reduced the extent of native upland habitats, North American upland species in southern Florida have been lost more rapidly than new West Indian landbirds have been acquired (see the last section in this chapter). All or parts of the Everglades uplands now lack several bird species typical of southeastern U.S. pine forests that are still numerous in the much more extensive pine areas of the northern Bahamas.

### Rising Sea Level

In this brief segment, two points will be emphasized: (1) although sea level rise is often a slow, ongoing geological process, its effects on biotic communities are detectable on a temporal scale of decades to a few centuries in low-lying coastal

areas such as southern Florida, and (2) overall, rising sea level in the past few thousand years has driven biotic succession in a single general direction—reducing the proportion of area in upland communities and increasing areas of freshwater wetlands, coastal swamps, and estuaries as southern Florida has gradually submerged (see also the final section of this chapter).

Egler (1952) may have been the first to suggest that sea level rise might be of concern to practicing plant ecologists in the region, and more recent studies have amply confirmed this insight. Several studies show that the rate of sea level rise in southern Florida has been most rapid in the intermediate, postglacial past at roughly 7000–2000 years before present (YBP). Study of sediments also indicates this interval as a time of major changes in the regional landscape.

Evidence from peats (Gleason and Stone, 1994) indicates that the Everglades wetland first existed in its present condition and location in about 5000 YBP. At about the same time, buried beds of mangrove peat extending up to several miles offshore mark a major estuarine or marine zone of vegetation along the Gulf coast (Spackman et al., 1966). Conversely, freshwater peats at the bottom of the sedimentary column suggest that an earlier “Everglades” once existed in Florida Bay (Davies and Cohen, 1989). This proto-Everglades evidently met its demise due to rising sea level at between 4500 and 3000 YBP (Wanless and Tagett, 1989).

These results suggest that although relatively youthful in its present setting, the freshwater wetlands and estuaries of the Everglades have a somewhat longer history of more or less orderly retreat in the face of rising sea level. Although there is little description of upland plant material from the sediment studies, upland vegetation of some sort presumably was the predominant plant cover of southern Florida at the lowest sea stages of the present cycle. The present Everglades uplands appear to be fragments of this former landscape, now perched upon the highest remaining elevations.

The retreat of uplands before the sea’s advance is currently observable and very much a factor to be considered in the near future of the Everglades. Alexander (1974) found dead trunks of still-rooted slash pine (*Pinus elliottii*) in a red mangrove (*Rhizophora mangle*) swamp on northern Key Largo, and Ross et al. (in press) measured reduction in area of a pine upland on Sugarloaf Key from successive series of aerial photographs. Ross et al. also provide evidence that the loss of upland plants is specifically due to the effects of saltwater intrusion. Given the rapid rate of effective sea level rise in the southern Florida area (Wanless et al., 1994), the continued loss of uplands and freshwater areas is quite likely to have major effects on the remaining fauna, particularly those communities associated with uplands.

### WADING BIRDS: REGIONAL CONTEXT and ECOSYSTEM INTERACTIONS

The study of wading birds has special relevance for the Everglades for a number of reasons. Wading birds were arguably the focus of the first scientific investigations in the Everglades, and the sheer length of the breeding record has provided powerful clues to understanding how ecological relationships have changed in the

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### The Everglades

Wading birds are the most common and diverse group of birds in the southeastern United States, using the wetlands for nesting and raising young. The range of species here is broad, including many species that are found in other parts of the Everglades. The Everglades show a high degree of adaptability.

The present Everglades in the United States is a range of habitats and white water north of the Rodgers Creek as described by (1981). Situated in the Ogden et al. into virtual Most of the centered (al., 1984) late 1970 Post, 199 have relocated commun *albus*) as plume-hunter it is possible in the environn ties in the vulnerab Regar that for flexibility

ecosystem. Wading birds have historically been a numerically dominant group of predators in this wetland and have likely had effects on the ecosystem that may be measured at the community level. Finally, the human empathy evoked by the grace of these animals has been (and remains) a telling force in mobilizing support for preservation and restoration of the Everglades, in ways that other wetland animals do not.

### The Everglades: A Critical Link in a Far-Flung Wetland Chain

Wading birds are highly mobile and even nomadic animals and form perhaps the most obvious linkages between the Everglades and other ecosystems in the southeastern United States and the Caribbean. It is essential to realize that the birds using the Everglades are not a population specific to that ecosystem, but are wide-ranging consumers, with variable breeding site fidelity. The large ambit and plastic breeding site fidelity in many wading bird species is a strong indication that these species have evolved to take advantage of highly variable wetland conditions, over ranges much larger than the Everglades. Certainly the relatively young age of the Everglades (see earlier) largely excludes the possibility that wading birds would show adaptations that are specific to a southern Florida existence.

The present-day choices for breeding by the wading bird species seen in the Everglades include the coastal plain of much of the southeastern and mid-Atlantic United States, as well as large parts of the Mississippi valley (Byrd, 1978). However, this range is in large part a recent phenomenon. Wood storks (*Mycteria americana*) and white ibises (*Eudocimus albus*) were virtually unknown as breeders in states north of Florida prior to the 1920s (Wayne, 1922; Sprunt, 1922; Ogden et al., 1987; Rodgers et al., 1987), and glossy ibises (*Plegadis falcinellus*) were extremely rare as breeders in the United States before the turn of the century (Bent, 1926; Ogden, 1981). Since the 1970s, a large proportion of the southeastern wood stork population has begun breeding in South Carolina and Georgia (Rodgers et al., 1987; Ogden et al., 1987), and glossy ibises have by now expanded their breeding range into virtually every Atlantic coastal state, including Maine (Hancock et al., 1992). Most of the breeding activity by North American white ibises was probably centered in the Everglades during the 1930s and 1940s (Ogden, 1978; Kushlan et al., 1984), but shifted to central and northern Florida and the Carolinas during the late 1970s and 1980s (Custer and Osborn, 1975; Ogden, 1978; Kushlan et al., 1984; Post, 1990). At present, the majority of breeding white ibises in the United States have relocated yet again to southern Louisiana (B. Fleury and T. Sherry, personal communication). Extensive northward range expansions of great (*Casmerodius albus*) and snowy egrets (*Egretta thula*) have also been documented since the plume-hunting era at the turn of the century (Byrd, 1978; Ogden, 1978). Although it is possible that the recent range shifts toward the north were set in motion by environmental degradation in the Everglades and other Florida wetlands, uncertainties in the timing and magnitude of the range shifts make this hypothesis eternally vulnerable.

Regardless of the causes of these changing breeding ranges, it is quite possible that for several species, the present breeding situation may actually offer more flexibility than the historic one. The current range of breeding locations available

for wood storks and white ibises is now geographically much more dispersed than in the early part of this century and must surely encompass a greater range of possible breeding conditions than formerly. In addition, this greater dispersion of the population is predicted to buffer these populations from catastrophic events such as severe weather and outbreaks of disease.

Among the potential breeding sites in the southeast, the Everglades remains unique in that it is annually guaranteed a large wintering group of wading birds because of its geographic location and climate. This situation gives the Everglades both an inherent advantage in attracting breeding wading birds if conditions are appropriate and a special potential for affecting the condition and health of a wintering population from the entire southeast (Bancroft et al., 1992). These properties are largely a result of physical location—there are few other large wetlands in the United States that stay warm all winter, and none other than the Everglades that are en route to the wintering locations in the Greater Antilles. Thus, the presence of an annual wintering population in the Everglades will probably be relatively robust to all but the most drastic of anthropogenic changes.

Given the large numbers of white ibises and wood storks that were documented breeding in the Everglades during the early and middle part of this century, it is not unreasonable to suspect that the Everglades was a major source of recruitment for these species in the southeast. Similarly, the Everglades had to have been a critical source for the regeneration of populations of great and snowy egrets following the decimations of the plume-hunting era and for roseate spoonbills following the extremely low population levels recorded in the 1930s (Allen, 1942; Powell et al., 1989; Kushlan et al., 1984). Thus, there is a strong possibility that the Everglades has served as a springboard for both population and range expansions.

The current situation seems to be the opposite, with breeding in the Everglades so frequently unproductive or catastrophic for many of the species that the ecosystem may instead be a demographic sink for birds produced from other areas. The exceptions to this rule are the great egret and the roseate spoonbill (*Ajaja ajaja*), both of whose populations seem to be stable or increasing in the Everglades. A related question is whether the larger southeastern populations of other species are also declining. There is good evidence that the wood stork population in the southeast has declined since the 1930s and 1940s (Ogden and Nesbitt, 1979; Ogden et al., 1987), and both white ibises and snowy egrets declined by as much as 50% as breeding birds in the state of Florida between the late 1970s and the late 1980s (Runde, 1991). For all but the wood stork, however, regionwide censuses have been so infrequent and geographically spotty that true population sizes are impossible to determine.

Wading birds also connect the Everglades with Caribbean wetlands. Band recoveries suggest that large numbers of great and snowy egrets, glossy and white ibises, and little blue herons (*Egretta caerulea*) breeding in the United States depend heavily on the Greater Antilles (particularly Cuba) for wintering habitat (Byrd, 1978; Ryder, 1978; P. C. Frederick, unpublished data).

This information suggests that the Everglades has had, and to some extent retains, critical functions for wading bird populations ranging over much of the southeastern United States and the Caribbean. While the Everglades is often accorded recognition for the numbers of wading birds it attracts, it is rarely

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appreciated that changes in the Everglades could have direct effects on wetland bird populations from as far away as New Jersey, Louisiana, and Cuba.

### Population Declines and Functional Relationships: Have Wading Birds Been Studied to Death?

The long history of research and monitoring of wading birds in the Everglades is so often mentioned that one might easily suppose a near perfect understanding of breeding dynamics. It should be emphasized that wading bird ecology in the Everglades is understood largely from a relatively few reliable records of breeding numbers and foraging distributions (Kushlan et al., 1984; Hoffman et al., 1990; D. M. Fleming, unpublished; Ogden, 1994) and that little is in fact known about the ecological relationships and specific mechanisms which explain the resultant patterns.

The evidence concerning this latter statement is embarrassingly abundant. Despite the intensive and extensive evaluations of present and past breeding conditions presented in this book, we still have no firm idea of which conditions and processes once allowed an order of magnitude more birds to breed in the ecosystem than do at present.

One hypothesis suggests that the historical Everglades landscape had sufficiently large amounts of short-hydroperiod marshes in almost any year that birds could find food in all but the most extreme surface water conditions (Browder, 1976; Bancroft et al., 1994; Ogden, 1994; Fleming et al., in press; D. M. Fleming, personal communication). These marshes are hypothesized to have offered considerably better early winter feeding conditions than are now available and thus were able to cue earlier breeding by the birds. This is an attractive explanation in part because there are estimated to have been large amounts of short-hydroperiod marsh lost to anthropogenic changes (Browder, 1976; Gunderson and Loftus, 1993; D. M. Fleming, personal communication; Fleming et al., in press) and because it is known that wading birds (at least in the presently degraded system) frequently use higher elevation marshes prior to breeding (Kushlan, 1976; Hoffman et al., 1990).

One difficulty with this idea is that there are still enormous tracts of shallowly flooded, short-hydroperiod freshwater marshes available in most years in northern Water Conservation Areas 1 and 3, the Rotenberger tract, the wetlands east of Krome Avenue and west of developed Miami, the Pennsuco wetlands, most of Big Cypress National Preserve, the Holey Land, Northeast Shark River Slough, and much of Shark River Slough and the Stairstep area. It is not clear that the short-hydroperiod wetlands which have disappeared had different attributes or dynamics than the present ones do, nor why the latter do not seem to perform an early cueing function for the birds. Loftus et al. (1992) suggest that the lowering of the water table and the consequent effects of repeated drying in the rocky glades to the east of Shark River and Taylor sloughs during this century have reduced the capacity of these wetlands to function as refugia for aquatic animals. This lack of hydrological connectedness between refugia and higher elevation marshes is probably mimicked in many areas by the barriers presented by the presence of levees and canals and may well have impacts on survival of, and speed of recolonization by,

aquatic animals. These "unconnected" higher elevation marshes could be sufficiently impacted to be of little value for wading birds.

However, even if "unconnected" short-hydroperiod wetlands no longer function as they once did, the remaining area of well-connected short-hydroperiod wetlands appears to be quite large (Big Cypress National Preserve, Northeast Shark River Slough, Stairstep area, northern Water Conservation Areas 3, 2, and 1), and it remains unclear why these rather large chunks of land cannot fulfill the former role of the short-hydroperiod wetlands now lost. It seems likely that short-hydroperiod wetlands must have performed a central cueing function for multispecies wading bird breeding in many years in the predrainage Everglades, especially those years with rapid drying (as currently occurs). However, unless short-hydroperiod wetlands have all been similarly degraded in some fashion since historical times, it is unclear why early breeding should not continue to be cued by the remaining acreage. The drastic reduction in numbers of wading birds and the absence of early breeding therefore seem difficult to pin on the loss of short-hydroperiod wetlands alone.

A second group of hypotheses suggests that it was some set of attributes of the now degraded coastal zone which allowed large numbers of birds to breed (Walters et al., 1992; Bjork and Powell, 1993). This "coastal degradation" hypothesis derives support from several points. First, all of the large historical colonies were in the estuarine zone, and accounts exist of prebreeding foraging aggregations in estuarine and coastal areas (Kushlan et al., 1984; Ogden, 1994; W. B. Robertson, Jr., unpublished aerial survey results). Second, it is becoming obvious that the present estuarine zone has been and remains severely stressed by reduced freshwater flows (McIvor et al., 1994); the corollary is that historical freshwater flows might well have generated vastly greater secondary productivity than is now evident. While this part of the hypothesis is to some degree lacking empirical evidence in the Everglades, it derives much support from studies of estuaries elsewhere (Walters et al., 1992; Bildstein, 1990). Third, the several computer-generated views of historical hydrology agree that flows to the estuary were vastly greater than at present and that most of the freshwater marshes were also much wetter (Walters et al., 1992; Fennema et al., 1994). The length of hydroperiod and depths of water backcast to be in much of the natural Everglades system even suggest that all but the highest elevation marshes of the freshwater area were in most years too deep for wading bird foraging. Nesting may have been concentrated on the coast in part because it had both high productivity and consistently shallow foraging opportunities early in the breeding season.

The estuarine zone may have offered other advantages for feeding which have since degraded. Bjork and Powell (1993) have recently demonstrated that annual changes in sea level are critical for allowing rapid surface water recession in the estuarine zone of northern Florida Bay in the early winter months, a phenomenon which attracts large aggregations of wading birds. Bjork and Powell note that the rise in effective ocean level since the 1930s has been large (Wanless et al., 1994), perhaps large enough to have lessened the extent or changed the timing of this early breeding season drying dynamic. This hypothesis could be tested as future modeling efforts develop the ability to backcast water behavior in the coastal zone.

Other changes may also have been at work. Bancroft et al. (1994) suggest that

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the average size of fishes available to wading birds may have decreased as a result of shortened hydroperiod in much of the coastal zone. This hypothesis fits with the fact that the present estuarine zone can still cue early and successful breeding by roseate spoonbills in most years, yet fails to do so for wood storks feeding in the same locations. It may be that the average size of fish available is currently too small for wood storks to capture efficiently (Ogden et al., 1976). Ogden (1994, personal communication) has repeatedly asked which aspect of the coastal zone allowed early summer colonies and large summer roosts of ibises to occur well into the 1960s. According to current wisdom, this would have been a season of high and rising water, when prey in marshes should be extremely disaggregated and foraging conditions most difficult. Clearly, key information about prey movements, prey population behavior, and foraging dynamics is missing.

Although coastal and inland processes have been treated separately for clarity of presentation, they should by no means be seen as mutually exclusive. Indeed, in most coastal/freshwater wetland mosaics that have been studied, the alternating availability of food by year and season at inland and coastal sites seems to be critical to maintaining breeding populations of wading birds (Kushlan, 1977; Bildstein et al., 1990; Bildstein, 1990), and there is no apparent reason why this was not true in the predrainage Everglades.

A final set of hypotheses suggests that one or more effects of droughts set the stage for large amounts of food to become available to wading birds in ensuing seasons, in either fresh or estuarine situations. This hypothesized wading bird response occurs some period of time *after* the drought and is distinct from wading bird response to rapid drying and prey concentration at the *beginning* of a period of drying (Kushlan et al., 1975; Frederick and Collopy, 1989).

At least half of the years in the decade 1930–40 were extremely dry in the lower Shark River Slough drainage, and many of these drought years also produced extensive fires in the estuarine/freshwater ecotone (National Audubon Society warden reports; Ogden, 1978, 1994). These descriptions do not seem to fit the profile of the extremely wet, long-hydroperiod Everglades of the natural system computer scenarios, and Robert Porter Allen's contention (in Ogden, 1978; W. B. Robertson, personal communication) that the conditions during these years may have been anomalous is reiterated here. These dry years (1930, 1932, 1935, 1938) were interspersed with the wetter years (1931, 1933, 1934, 1940) in which very large numbers of wading birds bred (Ogden, 1994), giving the impression that the strong nesting effort was in fact associated with some aspect of the preceding droughts.

The surprisingly large nesting response by wading birds noted in the freshwater Everglades in 1992 may be a modern-day example of this process. The 1992 spring nesting season followed the first full wet cycle after the severe drought of 1989–91 and showed by far the largest nesting response recorded in 17 years (over 27,000 nests) (Frederick, 1993). This remarkable nesting season included early and successful breeding by white ibises, rare nestings by wood storks in Water Conservation Area 3, and the first freshwater nestings recorded for roseate spoonbills in Florida since 1910 (R. Bjork, personal communication). Drying patterns and weather during 1992 were favorable for nesting, but surface water recession rates were by no means exceptional in the context of the preceding 10 years and

therefore do not seem to offer an explanation for the strong response. The most obvious difference about the season was that white ibises were feeding predominantly on small fishes in the Water Conservation Areas. This species is normally very poor at capturing fishes and may only do so during periods of very high fish abundance (Kushlan, 1974).

One explanation for this abundance of fish is that the severe drought killed off most of the large predatory fishes and other aquatic predators, allowing the proliferation of the "forage" fishes that have much shorter reproductive cycles (Kushlan, 1976). Another hypothesized mechanism is that the extended drying of the marsh surface enhanced primary productivity of the marsh through the release of nutrients by oxidation and fires, leading to increased productivity of wading bird prey. The regularity of drought and large fires in the lower Shark River Slough drainage during the 1930s, and the ensuing large nesting response, would certainly fit with this mechanism. These fires and drying may also explain poorer responses by wading bird in future years by longer term damage to the marsh surface (W. Loftus, personal communication). Perhaps the most extreme form of this hypothesis was voiced by Robert Porter Allen, who suggested more than once (W. B. Robertson, personal communication; Kushlan et al., 1984) that the large headwaters aggregations of wading birds in the 1930s were a direct result of environmental changes in the Everglades through "excessive" drying and fires.

Fires may also benefit birds by altering plant communities and even by creating soil depressions (Gunderson and Snyder, 1994; Davis et al., 1994). In the northern Everglades in 1992, wading birds fed extensively in burned-out depressions in the peat, following the fires of the preceding drought period (Frederick, 1993; Hoffman et al., 1994). These depressions are much shallower and more extensive than alligator ponds and may possess unique qualities for concentrating and holding prey animals. The relationship between drought, fires, secondary productivity, and wading bird foraging seems to demand future research.

It should be noted that fire and drought can only be viewed as a nutrient-liberating disturbance (and a possible primer for wading bird production) when it occurs infrequently in the context of longer hydroperiod cycles. Several pieces of evidence show that longer flooding periods lead to higher biomass, densities, and species richness of marsh fishes (Loftus and Eklund, 1994).

Several of these potential explanations also begin to beg larger questions about how food becomes available. Prey becomes available to wading birds through a mixture of two processes: prey abundance (density or standing stock of animals) and prey availability (how easily animals are caught). Were the large historical aggregations fueled by vastly higher standing stocks of prey animals, allowing successful foraging under a range of conditions, or were hydrodynamics (depths, drying patterns) simply more conducive to the capture of animals? Although neither process can be completely discounted, rapid drying rates do not seem to have been important in cueing breeding during the early and middle part of this century in southern Florida (Ogden, 1994). Similarly, the summer roosts and colonies in the coastal zone (mentioned earlier) seem contrary to the importance of hydrodynamics in making food available.

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standing of wading bird breeding ecology and that wading birds are far from being "studied to death" in the Everglades. It is also painfully clear that many of these questions can be traced to a poor understanding of the ecology of aquatic prey animals in the estuarine and freshwater parts of the ecosystem. There is currently no systematic monitoring of aquatic animal populations outside of a few sites in Everglades National Park, and very little research is devoted to understanding the ecology of small fishes and macroinvertebrates. As a dramatic example, next to nothing is known about the only species of crayfish (*Procambarus alleni*) in the Everglades, which is a central food item for most wading birds and many fishes, anurans, and reptiles. Until work on prey animals can be expanded, our power to predict wading bird responses in the ecosystem must remain in a rudimentary state.

It should also be emphasized that the much publicized declines of breeding wading birds in the Everglades have probably been paralleled by declines of many other kinds of more poorly monitored aquatic fauna. Anecdotal accounts of collectors and hunters and personal recollections suggest that many species of snakes, turtles, and anurans are far less abundant now. Similarly, next to nothing is known about trends in insect populations, a remarkable lack in one of the only subtropical protected areas in the United States. The lack of data on these animals reveals (as previously) the strong bird- and mammal-centric emphases in faunal monitoring and research, which is an unhealthy situation.

### EXOTIC ANIMALS and the EVERGLADES ECOSYSTEM

Since about 1970, the remnant fauna of native vertebrates in southern Florida's overdeveloped coastal strips has been extensively replaced by assemblages of exotic species. Large-scale importing of animals (especially fishes and birds, but also reptiles and amphibians), a thriving cottage industry in wild animal culture, and many private and public collections and exhibits provide opportunities for escape or deliberate introduction. Mild climate and an endless suburban sprawl vegetated with plantings from throughout the tropics tend to maximize a free animal's chances of survival. Although biologists were quick to anticipate the developing problem, their concerns and pleas for regulation (Courtenay and Robins, 1973; Owre, 1973) have been thoroughly overrun by events. Thus, "The fresh waters of southern Florida may host the greatest diversity of non-native fish species of any comparably sized region on earth" (Loftus, 1987), and "Unfortunately, few places on earth rival suburban southern Florida in number and variety of free-flying, non-native birds" (Robertson and Woolfenden, 1992).

A large proportion of the free-living exotic animals encountered in southern Florida are of more or less tropical origin. For example, about half of the reported exotic avifauna is made up of species from the New World tropics, with the remainder divided about equally among the Palearctic, Afro-tropical, Oriental, and Australian zoogeographic realms (Robertson and Woolfenden, 1992). The ongoing faunal introductions into southern Florida constitute an immense and unsupervised experiment in community ecology, but one whose opportunities for study have been little exploited. With few exceptions (e.g., Belshe, 1961; King, 1966; Carleton

and Owre, 1975; Wenner and Hirth, 1984), the history and ecological relations of exotic animal populations in southern Florida have not been studied in detail. Interactions with native fauna tend to be poorly known and speculative. Observations, especially of fishes and birds (summarized by Loftus and Kushlan [1987] and Robertson and Woolfenden [1992]), suggest that the species composition of the exotic community and the status of individual populations are highly unstable. Several instances are known in Florida of nonnative species which flourished and expanded their ranges and then, more or less unaccountably, suffered abrupt declines or disappeared. Examples include the Jack Dempsey (*Cichlasoma octofasciatum*) among fishes (Loftus and Kushlan, 1987) and the budgerigar (*Melopsittacus undulatus*), canary-winged parakeet (*Brotogeris versicolurus*), and spot-breasted oriole (*Icterus pectoralis*) among birds (Robertson and Woolfenden, 1992). In addition to coping with a new environment, every exotic doubtless confronts the possibility that the next introduction may be a species that either preys on it or competes more successfully for the same resources. The following accounts summarize the diversity and status of the nonnative element in the Everglades region for each class of vertebrates. A number of nonnative invertebrates are also reported to be established in southern Florida, but (to the authors' knowledge) no comprehensive list of species exists.

### Fishes

Most of the exotic fishes known from southern Florida have been found first in canals near the Atlantic coast. The obvious reason is that most of the facilities from which such fishes might escape or be released are in the coastal area. In addition, exotics may be able to establish more readily in the disturbed and often polluted canal habitats. Today, nonnatives dominate the ichthyofauna at many such sites. Once established in a canal, it is possible for fishes to reach almost any part of southern Florida without leaving the canal system. Much of the concern about the presence of nonnative fishes has centered on whether they would tend to stay confined to canals or would spread into the Everglades marshes. It now seems evident that many of the exotic fishes are indeed invading the marshes, perhaps at an accelerating rate since the dual disturbances of severe drought followed by a strong hurricane.

In their review of the fishes of southern mainland Florida, Loftus and Kushlan (1987) reported that 10–12 species of exotic fishes were thought to be established in southern Florida and noted that three of these species had occurred in natural wetlands, albeit in relatively small numbers. They commented hopefully, "...most exotic species seem unable to successfully colonize the marsh system of the southern Everglades." By the early 1990s (Courtenay et al., 1991; W. F. Loftus, personal communication), 15–17 species of exotic fishes were considered established in southern Florida and 7 or more species were in the Everglades. Two of the nonnatives most widely distributed in the southern Everglades, the predacious pike killifish (*Belonesox belizanus*) and the omnivorous Mayan cichlid (*Cichlasoma urophthalmus*), may be somewhat preadapted, because their natural ranges include similar marsh systems on the Yucatan peninsula (Loftus, 1987; Loftus et al., 1992).

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## Reptiles and Amphibians

As with the fishes, the exotic herpetofauna of southern Florida has increased in recent decades, but many fewer species have shown the ability to penetrate unaltered natural habitats. Duellman and Schwartz (1958) reported 12 exotic species (9 lizards and 3 frogs), of which only the greenhouse frog (*Eleutherodactylus ricordii*), the Cuban treefrog (*Osteopilus septentrionalis*), and the brown anole (*Anolis sagrei*) were commonly found in natural areas. Thirty-five years later (Wilson and Porras, 1983; W. Meshaka, personal communication) the list of more or less established exotics has more than doubled to include 20 lizards, a snake (*Ramphotyphlops*), a turtle (*Psuedemys scripta*), a crocodylian (*Caiman crocodylus*), and four frogs. However, only the same three species previously known (Dalrymple, 1988), plus possibly a Cuban gecko (*Sphaerodactylus elegans*) (W. Meshaka, personal communication), occur to any extent in native habitats.

## Birds

Southern Florida's exotic avifauna is remarkably diverse, but (as of 1993) still closely limited to the heavily developed coastal strips. In Florida at large, about 150 species of nonnative birds have occurred in the wild and about 60 species have reportedly nested in the wild. In the urbanized coastal uplands that embrace the Everglades, the respective totals are about 130 and 45 species (Robertson and Woolfenden, 1992). In many coastal neighborhoods, especially of southeastern Florida, exotic landbirds now are probably more speciose and abundant than the remaining native avifauna. However, the nonnatives are still almost entirely absent from extensive tracts of wild lands in the Everglades-Big Cypress system. Thus, no more than about 20 species of nonnative birds are known to have occurred in Everglades National Park (Robertson et al., 1984; Robertson and Woolfenden, 1992), and only two species, the European starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus*), both limited to developed enclaves, are known to nest within the park. Preliminary observations suggest that hurricane Andrew did not have strong adverse effects on the populations of exotic birds in its path. In fact, individuals that probably escaped from damaged aviaries made at least a temporary addition to the free-flying avifauna. For example, a Homestead neighborhood in the central storm path still had most of its prehurricane exotics plus records of four or five additional species within 6 months after Andrew (J. C. Ogden, P. W. and S. A. Smith, personal communication).

## Mammals

The small size of southern Florida's fauna of nonnative wild mammals may mainly reflect a lower level of input from the import trade and fewer amateur enthusiasts than do other vertebrates. Layne (1974) listed only ten species of introduced mammals that may have had persistent populations, and fully half of these were of somewhat uncertain occurrence in southern Florida or were very localized. However, three species of nonnative mammals, all present in southern Florida for at least many decades, are widespread in natural habitats. Nine-banded armadillos (*Dasybus novemcinctus*), which probably spread from introductions in

central Florida in the 1920s (Neill, 1952), are common in sandy uplands of the Big Cypress but scarce or absent in wetter parts of the system. The black rat (*Rattus rattus*), frequent around rubbish dumps and buildings, is also extensively naturalized in coastal plant communities, including mangrove swamps. Feral populations of domestic hogs (*Sus scrofa*), commonly augmented by stock released for hunting, are generally distributed in the Big Cypress and elsewhere in the system usually occur around the fringes of uplands.

### Concluding Comments: Effects and Prospects

Although the data are patchy and mostly qualitative, some information exists on the impact of nonnative vertebrates in the habitats of southern Florida. As Loftus and Kushlan (1987) pointed out for fishes, the degree of dominance of exotic species at a given site tends to be inversely proportional to the distance of the site from the Atlantic coast. In the developed coastal strips, the fauna of freshwater fishes, lizards, and landbirds is extensively dominated by nonnative forms. Kushlan (1986a) reported on the decline of native fishes and the greatly increased preponderance of exotic fishes in one Dade County canal between 1964 and 1982. In both developed and more natural habitats, predator-prey interactions that involve native and nonnative species are commonly observed. Thus, Takekawa and Beissinger (1983) reported that snail kites (*Rostrhamus sociabilis*) feeding over flooded farm fields apparently preyed on *Pomacea bridgesi*, an aquatic snail introduced from South America. They suggested that this snail might become a significant alternative food source for the kites, because of its ability to thrive in areas with reduced water quality. Geanangel (1986) noted that ospreys (*Pandion haliaetus*) concentrated at phosphate pits in central Florida to feed on exotic *Tilapia* sp., and a number of observers (Loftus, 1979) have reported aggregations of wading birds actively feeding on the exotic walking catfish (*Clarias batrachus*). The frequent occurrence of pike killifish, Mayan cichlids, and spotted tilapia (*Tilapia mariae*) in regurgitations of nestling great egrets and tricolored herons suggests that these exotic fishes make up a substantial part of the food biomass of young wading birds in some Everglades heronries (P. C. Frederick, personal observation). On the other side of the coin, nine-banded armadillos are known to prey extensively on terrestrial invertebrates and small vertebrates; feral hogs at times root into alligator (*Alligator mississippiensis*) and turtle nests to feed on the eggs (D. M. Fleming, personal communication), and the introduced Cuban treefrog regularly preys on native species of *Hyla* (W. Meshaka, personal communication).

The possible competitive interactions between exotic and native vertebrates have been the topic of much speculation, but have been studied relatively little. *Anolis sagrei* is thought to compete with the native green anole (*A. carolinensis*) and to have excluded it in some areas. Competitive exclusion probably also figured in the increasing dominance of exotic vertebrates in developed areas, but direct disturbance of native habitats must have played the major role. Some widespread species groups of exotics, such as fishes of the family Cichlidae, often have biological characteristics (e.g., advanced parental care, herbivory) that may enable them to outcompete native analogues, such as largemouth bass (*Micropterus salmoides floridanus*) and sunfish (Centrarchidae) at least locally (W. F. Loftus,

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personal communication). However, compared to the native fishes, the exotics may produce more available food per unit area of marsh in prey packages more effectively handled by wading birds.

Any present attempt to assess the overall threat posed by nonnative animals to the integrity of the Everglades ecosystem seems futile. Information available on most individual cases is scanty and largely anecdotal, and the subject suffers from a dearth of useful hypotheses. In addition, thought may tend to become paralyzed by the obvious, perhaps insurmountable, difficulty of effective countermeasures. For example, how would one go about removing a well-established, widely dispersed, exotic fish from among all the other fishes in the Everglades? In a hazy, undetailed, nonrigorous sense, one generality seems to emerge from the sparse database: the Everglades, where it is functionally more or less intact, shows considerable resistance to invasion by nonnative species, but with continuing challenges, this faculty tends to break down. However, it is not even clear that the martial images are fully appropriate. The Everglades region has been considered species poor for various groups of animals. Perhaps some exotic species do not so much "invade" as sift into the cracks. In the end, two points are rather obvious: (1) nonnative animals are present by human agency, and at best they are intrusive and unnatural, to be deplored and, if possible, removed, and (2) as long as the "challenge" species continue to be drawn erratically from a grab bag of all the world's fauna, major displacement of native species in natural areas, if not already underway, will surely occur.

#### ANIMAL MOBILITY and the SCALE of the EVERGLADES LANDSCAPE

Despite being considerably reduced from its original extent and variously degraded, an extensive area of wild land still exists in the Everglades–Big Cypress region. The most hopeful aspect for Everglades restoration is simply the presence of a large, contiguous block of country that has not been ruinously diverted to other uses. As of 1993, the relatively intact (or at least restorable) portion of the Everglades–Big Cypress system measured about  $140 \times 190$  km, with an area of roughly  $20,000 \text{ km}^2$ . Thus, the region is, or still has the potential to become, one of the larger natural preserves on earth. Yet, despite its size, one inevitably wonders to what extent the Everglades region is large enough to encourage the activities of its principal animal populations.

For animals with very small range size, the Everglades seems big enough to provide habitat for the foreseeable future. Tree snails of the genus *Liguus*, for example, occur in isolated hammocks and occasionally in undisturbed pine forests. These animals probably rarely move (except by human purpose) between hammocks or traverse large distances across more open habitat (Pilsbry, 1946). The limits to their existence seem to be catastrophic events that occur within the boundaries of the Everglades, such as fires, hurricanes, and rising sea level. Similarly, it is likely that robust populations of many insects and other invertebrates can be maintained in some degree of perpetuity within the scale of the Everglades.

The Cape Sable seaside sparrow (*Ammospiza maritima mirabilis*) is an example of an endemic vertebrate whose lifetime needs may well be served by the

short-hydroperiod marshes and prairies that fringe uplands of the southern Everglades and Big Cypress. Adults (at least adult males) are so sedentary that they rarely move more than a few hundred meters unless forced to do so by flooding or marsh fires (Kushlan et al., 1982; Werner, 1975; Werner and Woolfenden, 1983). Even dispersing juveniles may move no more than several kilometers to form new territories (Werner, 1975). Because the historical range of this species is contained almost entirely within Everglades National Park, the ecosystem is by definition large enough to contain a viable population. The major threat for the Cape Sable seaside sparrow is probably habitat loss due to rising sea level. It remains to be seen whether new habitat will be formed at successively higher elevations and whether the birds will move into it.

It is unclear how large an area is needed by most of the species of freshwater fishes, because very little information on their movements and ecological needs is available. Although it is obvious that many of the smaller fish species are able to colonize previously dry areas from local alligator holes and depressions with considerable speed, it is unclear what the upper limits to these recolonization movements might be and whether this occupation of new territory is accomplished by long-distance movement of individuals or by the leap-frogging of successive generations from an original group of survivors. It is therefore difficult to guess how large an Everglades is needed to maintain healthy populations of most freshwater fishes and, specifically, whether dikes and canals constitute important barriers to movement. Many of the more wide-ranging vertebrates in the Everglades may be genetically vulnerable because of reduced chances of interchange with other populations. Even those with relatively sedentary habits and small territory sizes may be at risk. The breeding land avifauna of Long Pine Key in Everglades National Park has lost about a quarter of its former species during this century (see next section). Although individual breeding territory sizes of these species are generally small, the roughly 30 km<sup>2</sup> of pine forest on Long Pine Key may simply be below the minimum area that many landbird populations require for a high probability of survival. For example, no historical record of any of the characteristic breeding birds of southern Florida mainland pine forests exists for the approximately 9-km<sup>2</sup> pine area of the Lower Florida Keys (Ross et al., in press; Howell, 1932; Robertson and Woolfenden, 1992). Conversely, the approximately 400-km<sup>2</sup> pine forest of Big Cypress National Preserve (J. R. Snyder, personal communication) appears to lack only one species (American kestrel [*Falco sparverius*]) of the expected breeding avifauna (Patterson and Robertson, 1981; D. Jansen, personal communication; K. D. Meyer, personal communication).

The Everglades in its present extent seems far too small to support extremely wide-ranging mammals such as the Florida panther (*Felis concolor coryi*). Six radio-collared individuals from eastern Everglades National Park showed home ranges of about 350–750 km<sup>2</sup> for five females and a home range of about 2000 km<sup>2</sup> for a semi-nomadic subadult male, and subadult males at times have undertaken cross-country forays that spanned straight-line distances of up to approximately 100 km (Smith and Bass, 1994; D. S. Maehr, personal communication). These movements frequently bring panthers into contact with roads and other boundaries of the Everglades, resulting in a high incidence of roadkills and other accidents (Smith and Bass, 1994) (see next section). The greater Everglades ecosystem in its present state

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The solution to these problems of isolation seems to be the ability to move to other locations for foraging and breeding. Thus, manatees (Anon., 1989), wading birds (Kushlan, 1986b; R. B. Bjork and G. V. N. Powell, unpublished data; see also previously in this chapter), and snail kites (Bennetts et al., 1994) all possess the ability to move from the Everglades into more suitable locations as habitat conditions warrant. All three show seasonal patterns of movement, but it is known that movements at least for the birds may also be triggered by foraging or breeding conditions (Bancroft et al., 1994; Beissinger and Takekawa, 1983; R. B. Bjork and G. V. N. Powell, unpublished data). These habits not only provide flexibility in adjusting to conditions within the Everglades, but they also must provide greatly increased opportunities for genetic mixing with a larger population. These movements allow snail kites and wading birds to function within a wetland mosaic from several times to an order of magnitude larger than the Everglades, respectively, and manatees to move through an aquatic mosaic one order of magnitude larger than that of the Everglades.

It is not surprising that examination of these species suggests that the present Everglades ecosystem is too small to meet the lifetime requirements of viable populations of a number of wide-ranging species. It is equally true, however, that the Everglades remains a key core area for many of the species for which it is strictly too small as an island reserve (panthers, wading birds, and migratory songbirds). It can only be concluded that the persistence of many of the more widely ranging animals of the Everglades depends at least as much upon linkages with areas outside the Everglades as it does upon changes and management within the Everglades. The restricted nature of present and potential future corridors for overland movement, however, seems to favor only animals that can leave the system entirely in response to seasonal or annual conditions.

### RESTORING the EVERGLADES: WETLANDS and UPLANDS

The highly variable wetland-upland complex of the Everglades forms an integrated, heterogenous landscape. However, it is often forgotten that today's Everglades is a composite of two terrains that differ greatly in age and history. It was noted earlier that the Everglades wetland is relatively youthful in its present setting. Its oldest peats date back to about 5000 YBP (Gleason and Stone, 1994). In contrast, the upland component of the landscape consists of eroded remnants of a much older upland which reached its greatest extent at the last glacial maximum about 20,000 YBP (Webb, 1990). The total upland area and vegetation of southern Florida has been shrinking as a result of rising sea level since about 14,000 YBP (Robbin, 1984), and recent data (Alexander, 1953, 1974; Ross et al., in press) indicate that the process is continuing.

Everglades restoration is the dominant theme of conservation in southern Florida, and, understandably, thinking about restoration has focused on hydrological remedies for the diminished productivity and size of regional wetlands. Thus, most of the chapters in the faunal section deal with aspects of the ecology of

wetland animals. Their authors are almost unanimous in asserting that population recovery for various species requires a return to freshwater hydropatterns more like those attributed to the original Everglades in the natural system hydrology model (Fennema et al., 1994). More specifically, they prescribe (1) increased wet season flows to flood and revive productivity of the short-hydroperiod marshes of the southern Everglades, along with (2) sufficient dry season flow to hold surface water in deeper sloughs in most years (Fleming et al., in press; Loftus and Eklund, 1994; Loftus et al., 1992; Ogden, 1994). Only one faunal chapter (Smith and Bass, 1994) addresses animal populations of the uplands and upland fringes in any detail. Some more general aspects of the ecology of upland animal species in the Everglades system will be discussed briefly here, and two case histories will be presented. It will be suggested that the regional wetland and upland habitats and faunas differ markedly in their history, their present condition, and especially their potential for restoration.

### Setting the Scene

For purposes of this discussion, wetlands (mainly sawgrass [*Cladium jamaicense*], spikerush [*Eleocharis* spp.], and water lily [*Nymphaea odorata*] marshes and cypress [*Taxodium distichum*] strands) are defined as areas with fairly deep peat and/or marl substrates flooded for 6 months or longer in recent average years. Uplands (mainly pine forest and hardwood hammocks) are areas of limestone rockland (Snyder et al., 1990) seldom (or only peripherally) flooded in average years. Between the wetlands and uplands is a series of transitional, predominantly herbaceous communities (wet prairie, mixed prairie, scrub cypress, *Muhlenbergia* prairie, rocky glades, etc.) with hydroperiods in recent average years ranging from about 6 months to less than 1 month. Hydrological restoration presumably would tend to shift the average wetland/transitional interface (i.e., the line of 6-month flooding) a certain distance upslope and tend to further reduce the extent of uplands.

Some of the salient differences between the Everglades wetlands and uplands are outlined in Table 28.1. As suggested therein, the historical differences between the two landscape elements are reflected by striking differences in the characteristics of the upland and wetland biota. Thus, endemism of both plants and vertebrate animals is strongly concentrated in the limited, older upland area and is little evident in the expansive, much younger wetlands. Moreover, vertebrate species represented by relatively small populations appear to be much more numerous in the upland habitats. Finally, the uplands, but not the wetlands, are known to have lost vertebrate species within the period of scientific record (Table 28.1).

### Wetland Faunal Restoration Prospects

Biologically, the restoration of Everglades wetlands appears eminently feasible (see Table 28.1). Although considerably smaller than it used to be, the natural area is still very large and is potentially one of the largest wetland preserves on earth. Parts of the area are degraded in various ways, but most is relatively intact or at least restorable. Also, the area exists as a contiguous piece virtually without internal

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**Table 28.1** Some Comparisons of Wetland and Upland Components of the Everglades–Big Cypress Ecosystem

| Parameter   | Wetlands                            | Uplands <sup>a</sup>                                 |
|---|-------------------------------------|--|
| <b>Historical</b>                                     |                                     |  |
| Time of most recent greatest extent                   | Mid-19th century prior to drainage  | ca. 20,000 YPB                                       |
| Estimated percent natural area lost since 1900        | ca. 40–50%                          | ca. 80%  |
| <b>Physical</b>                                       |                                     |  |
| Estimated present size of restorable natural area     | ca. 20,000 km <sup>2</sup>          | ca. 1,000–1,500 km <sup>2</sup>                      |
| Internal habitat continuity                           | One continuous area                 | Very fragmented; internal gaps up to ca. 50 km       |
| External habitat continuity                           | Narrowly disjunct; gaps of 25–40 km | Widely disjunct; gaps of 100–200 km                  |
| <b>Biological</b>                                     |                                     |  |
| Botanical endemism <sup>b</sup>                       | None known [?]                      | ca. 40 taxa <sup>e</sup>                             |
| Vertebrate endemism <sup>c</sup>                      | 2–3 subspecies                      | 20–25 subspecies and species <sup>e</sup>            |
| Known local loss of breeding vertebrates <sup>d</sup> | None known                          | ca. 10 species                                       |
| Relict and sedentary populations                      | Few                                 | ca. 75, most of the endemics plus a number of others |

<sup>a</sup> Pine forests, hammocks, and higher herbaceous rocklands; wetlands = the rest of the landscape.

<sup>b</sup> Avery and Loope (1980), Snyder et al. (1990).

<sup>c</sup> Duellman and Schwartz (1958), Layne (1974), Stevenson (1976), Snyder et al. (1990).

<sup>d</sup> Robertson (1955), Layne (1974), Robertson and Kushlan (1974).

<sup>e</sup> Includes Florida Keys.

barriers other than levees and other water control structures. While these significant anthropogenic barriers may restrict movements of fishes and other truly aquatic animals, the blocks of land within each basin seem large relative to the probable movements of fishes.

Most importantly, the Everglades wetland still has its full historical complement of vertebrate animals. Although the two federally listed endangered species of these wetlands, the wood stork (ca. 6000 adults) (J. C. Ogden, personal communication) and snail kite (733 individuals in 1992 census) (Bennetts, 1993), are now rare as breeders in Everglades National Park, their populations are still relatively large and have shown signs of being able to save themselves by their mobility (see preceding section). This same mobility demands, however, that effective conservation of these species must take place at scales much larger than the Everglades. It seems that there is no obvious biological reason why restoration of Everglades wetlands should fail. Given time and the experimental flexibility afforded by the system of water control structures, it does not appear that wetland restoration should even be particularly difficult. The only real problem is political—the need to resolve competing uses of resources and competing visions of the future.

### Upland Restoration Prospects

Quite unlike the wetlands, the prospects for restoring or even maintaining many of the species of the Everglades uplands seem dim and stem largely from relatively recent reductions in the amount and continuity of upland habitats in southern Florida. The recent history of the Florida panther in the southeastern Everglades illustrates the abrupt changes of fortune that can befall small populations in fairly constrained habitat. Barely two years after concluding that the nine individuals in the southeastern Everglades constituted a stable element in the Florida panther population (Smith and Bass, 1994), the Florida panther effectively became extinct (no known reproductive females) in southern Florida east of Shark River Slough (Bass, 1991). Population biologists had been very concerned about the threat that close inbreeding and genetic depression posed to this small, semi-isolated population, but the actual extinction event seems to have been a series of isolated accidents.

Undoubtedly, this disappearance of the Florida panther from a part of its remnant range is only temporary. The species may reintroduce itself by crossing Shark River Slough from the southern Big Cypress (see preceding section), or, if natural dispersal fails, reintroduction of animals from the captive population or from other wild populations would seem likely. However, the point of interest in this event for the panther and other high-risk upland vertebrates is that local extinctions seem likely to be fairly frequent in populations at the ends of peninsulas of fragmented habitat, such as the Everglades uplands. Recruitment along coastal corridors from the more extensive uplands farther north in Florida once must have tended to balance deficits in these terminal populations. No shred of a functional Atlantic upland corridor exists today. Hurricane Andrew eliminated even the illusion of widely spaced stepping stones of native upland habitats along a swath 25 mi wide in southeastern Florida. A rather tenuous and interrupted corridor of uplands still present on the western edge of the Everglades is becoming increasingly fragmented.

Breeding birds of the rockland pine forest of Long Pine Key in Everglades National Park provide perhaps the clearest case of a progressive loss of species diversity in Everglades uplands. Long Pine Key is the extreme terminus of the limestone ridge along the southeast coast of Florida. It is an archipelago of pine-forested, rocky islands surrounded by Everglades marsh. Avifaunal data are available from the 1920s (Holt and Sutton, 1926; Howell, 1921, 1932), from the early 1950s (Robertson, 1955), and more or less continuously in more recent decades (Robertson and Kushlan, 1974). These data indicate that in the 1920s Long Pine Key and nearby pine areas to the east supported practically all the breeding landbirds expected in pine forests of the coastal plain of the southeastern United States, but that by the early 1990s at least ten species appeared to be gone from the area. This amounts to a 26% loss from the known breeding avifauna of 38 species. The landbirds thought to have become extinct on Long Pine Key within the period of scientific record and their probable dates of disappearance are listed in Table 28.2.

Robertson and Kushlan (1974) found that habitat disturbance on Long Pine Key seemed totally inadequate as an explanation for most species losses there. Of the species concerned, only the red-cockaded woodpecker is likely to have been displaced by lumbering in parts of Long Pine Key in the 1930s and 1940s. Near total

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| Species   | Year of Disappearance |
|---|-----------------------|
| American Osprey<br>( <i>Falco sp.</i> )                           | 1920s                 |
| Wild turkey<br>( <i>Meleagris gallopavo</i> )                     | 1920s                 |
| Ground dove<br>( <i>Columbigallina passerina</i> )                | 1920s                 |
| Hairy woodpecker<br>( <i>Picoides villosus</i> )                  | 1920s                 |
| Red-cockaded woodpecker<br>( <i>Picoides borealis</i> )           | 1920s                 |
| Eastern kingbird<br>( <i>Tyrannus tyrannus</i> )                  | 1920s                 |
| Brown-headed nuthatch<br>( <i>Sitta pygmaea</i> )                 | 1920s                 |
| Eastern bluebird<br>( <i>Sialia sialis</i> )                      | 1920s                 |
| Loggerhead shrike<br>( <i>Lanius ludovicianus excubitorides</i> ) | 1920s                 |
| Summer tanager<br>( <i>Piranga a. a.</i> )                        | 1920s                 |

<sup>a</sup> E. Lewis

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**Table 28.2** Bird Species Formerly Breeding in Pine Forests of Long Pine Key, Everglades National Park, and Now Apparently Extirpated

| Species   | Last reported     | Comment   |
|---|-------------------|---|
| American kestrel<br>( <i>Falco sparverius</i> )         | ca. 1940          | Also absent from Big Cypress pinelands                                    |
| Wild turkey<br>( <i>Meleagis gallopavo</i> )            | Mid-1970s         | History in area not clear; reintroduced once                              |
| Ground dove<br>( <i>Columbina passerina</i> )           | 1980s?            | Always scarce in area; a few still present in local farmlands             |
| Hairy woodpecker<br>( <i>Picoides villosus</i> )        | 1991 <sup>a</sup> | Becoming rare in Big Cypress  |
| Red-cockaded woodpecker<br>( <i>Picoides borealis</i> ) | Early 1940s       | Persisted near Homestead to ca. 1964; still about 40 clans in Big Cypress |
| Eastern kingbird<br>( <i>Tyrannus tyrannus</i> )        | ca. 1990?         | Nested commonly in 1950; still present in area?                           |
| Brown-headed nuthatch<br>( <i>Sitta pusilla</i> )       | Uncertain         | Present in 1920s; gone by early 1950s                                     |
| Eastern bluebird<br>( <i>Sialia sialis</i> )            | Mid-1960s         | Fairly common and nesting in early 1950s                                  |
| Loggerhead shrike<br>( <i>Lanius ludovicianus</i> )     | Uncertain         | Nested in 1950s; a few still present in Homestead area                    |
| Summer tanager<br>( <i>Piranga rubra</i> )              | 1920s?            | Nested in Miami area up to ca. 1970s; becoming rare in Big Cypress        |

<sup>a</sup> E. Lewis, personal communication.

removal of pine forest (for agriculture) on private lands east and northeast of Long Pine Key may have contributed to species loss by eliminating the possibility of local recruitment.

### Upland Restoration Prospects: Summary

Loss of species from the southern end of the peninsular uplands may well have started soon after the upland area attained its fullest extent at the last glacial peak. The process may have been accentuated around 5000 years ago, when the origin of the Everglades separated the southern uplands into eastern and western branches. The progressive loss of species diversity in Everglades uplands seems rooted inexorably in a natural phenomenon: postglacial sea level rise. A local anthropogenic element became significant only within the past four or five decades, as human occupation of southern Florida effectively eliminated recruitment along the northward-connecting corridors of upland. It is not certain what the appropriate conservation response to this kind of environmental degradation may be.

One approach might be to undertake re-establishing the corridors, as Harris (1984) and others have suggested and as Noss (1987) outlined for peninsular

Florida. If this objective were pursued urgently, it might still be possible to establish useful upland wildlife corridors west of the Everglades. It is doubtful that upland corridors are feasible in southeastern Florida, where many areas of the former coastal uplands are densely settled well into the edge of the Everglades.

Another alternative, perhaps the only other action alternative, is a program of intensive, long-term, many-species management. Such an effort would need to include frequent monitoring and the augmentation or re-establishment of failing populations. With some 25 species of vertebrates alone to be considered just as the start, this would be an immense undertaking, but, if adequately supported, could succeed. However, one inevitably wonders how prominent a place on the conservation agenda should be accorded to the re-establishment of outpost populations of species that may be fairly common elsewhere. Philosophically, the answer may be elusive, but practically, such sustained and intensive management is likely to occur only for a few high-profile species.

It seems that it should be readily possible to restore a fully functional Everglades wetland system that will retain viability well into the next century and perhaps beyond. As for the Everglades uplands, a continuing loss of species diversity of vertebrates is anticipated until the uplands at length become principally preserves for rare plants, invertebrates, and those vertebrates that either use very small ranges or are mobile enough to access alternative breeding opportunities outside the Everglades ecosystem.

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