

## THE SOUTHERN FLORIDA AVIFAUNA

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### ABSTRACT

In this paper we consider primarily the breeding avifauna of southern Florida; its history as interpreted from fossils, late Pleistocene geological events and existing distribution patterns; and, evidence, in the form of recent range changes, that suggests continuing adjustment to changing environmental conditions. We also review the available quantitative data on bird populations; discuss the ecology of birds inhabiting the interior wetlands in relation to the annual cycle of flooding and drying; and, examine briefly the effects upon bird populations of several natural and man-caused disturbances.

### INTRODUCTION

We aim to review briefly present knowledge of birds in southern Florida emphasizing faunistic and ecological data. Southern Florida is taken to be the peninsula south of the Caloosahatchee and St. Lucie outlets of Lake Okeechobee, including the Lake itself and the Florida Keys. All comments not further specified apply to this region, but we cite comparative data from many other areas.

We refer to birds in the text by their English common names. This usage has been standardized by the American Ornithologists' Union Check-list (1957, 1973) for North American birds and Bond's (1971) guide for West Indian birds. Owre(1973) notes the exotic species mentioned. These sources provide the scientific name for all species mentioned in text. We also follow the taxonomy adopted by the A.O.U. and Bond (including 1956, 1958..73) even where our information suggests different conclusions. To name two such cases: we doubt that the southern Florida *Ardea* problem is adequately resolved by considering the "Great White Heron" to be a white color phase of the local subspecies of the Great Blue Heron (A.O.U., 1973); and we suspect (Eisenmann, 1962) that the nighthawk with polysyllabic territorial calls that breeds in the Greater Antilles, Bahamas and Florida Keys is a species distinct from the Common Nighthawk of continental North America.

At various points we discuss and contrast water birds and land birds as elements of the regional avifauna. The former are the taxonomic groups mainly associated with aquatic habitats, either fresh-water lakes and marshes, shores, estuaries, or the sea; the latter comprise the hawk-like (including vultures, falcons, and Osprey) and galliform or chicken-like (Bobwhite, Turkey) birds, plus the taxonomic groups from doves through finches. This traditional arrangement is ecologically correct in large part, but a few nominal water birds (Cattle Egret, Killdeer) are mainly terrestrial in habit and a few nominal land birds (Everglade Kite, Osprey, Seaside Sparrow) could be as readily regarded as components of aquatic ecosystems. We also distinguish non-passerine and passerine land birds in some discussions. The former includes the hawk-like birds, galliforms, doves, parrots, cuckoos, owls, goatsuckers, swifts, hummingbirds, kingfishers, and woodpeckers. The passerines, or perching birds, are the generally smaller species that tend to occur in denser populations and include the common songbirds that make up the bulk of the obvious land bird life in most of eastern North America.

### FAUNISTIC AND BIOGEOGRAPHIC CONSIDERATIONS

#### Basic Data and State of the Record

According to A. H. Howell's history of ornithology in Florida (1932: 6-37), the beginning of scientific knowledge of birds in the southern part of the state dates back 150 years, to Titian Peale's Florida Keys visit of 1824. Many later ornithologists worked in the area especially from about 1870 to about 1920. Both the published data and extant specimens are widely dispersed. Howell's "Florida Bird Life" (1932: 476-555), a model of bibliographic excellence, located some 1500 publications on Florida birds, and significant numbers of birds collected in southern Florida are found in almost all major, and many minor, museum collections of the United States and Canada (see Banks, *et al.*, 1973) and in numerous European museums. Howell's book later revised and updated to about 1952 by Sprunt (1954), is the major reference summarizing information about Florida birds.

Robertson (1973) noted recently that the available summary of bird occurrence in Florida has two important defects. The first is obvious and inescapable: it is badly out of date. New data have appeared in print at an increasing rate (particularly in *Audubon Field Notes*, now called *American Birds* and referred to hereafter in text by that name) and have not been summarized critically for

more than 20 years. The second flaw, more serious because less easily remedied, is that the available summary is substantially incomplete. The case of the Carolina Parakeet illustrates the problem. Howell considered it extinct noting that the last Florida specimens were collected in 1901 and the last sight record by an ornithologist was in 1904. In contrast, Hahn (1963) listed 13 Carolina Parakeets collected in Florida after 1901, including individuals from three localities in 1913. Such omissions may reflect the fact that much bird collecting in Florida was by commercial and private collectors who seldom published their findings and whose work thus was unknown to Howell and generally remains today. We have no easy way to learn how significant such missing data are. Although we doubt that the material, if thoroughly known, would change present general concepts of the avifauna, it is almost certain to change our view of many species.

#### Summary of the Southern Florida Avifauna

About 400 species of birds have been reported to occur naturally in southern Florida. By our reckoning, the occurrence of 379 species is reasonably well-documented, but 83 of these (22 percent) are known from fewer than 10 credible records and represent a minor element in the regional avifauna. Table 1 categorizes the remaining 296 species.

*Wintering and Migrant Birds* - About 60 percent of the bird species found more or less regularly in southern Florida occur principally in winter or during migration. Space limits preclude detailed discussion of this part of the avifauna, but we note later the quantitative data available for winter land bird populations. The source of southern Florida's migrant and wintering birds is little known for most species, because relevant band recoveries accumulated over the past 40 years by the Bird Banding Laboratory of the Fish and Wildlife Service have not been studied. Southern Florida wetlands are an important wintering ground for water birds, particularly in winters when water is high in the Everglades and coastal marshes, and weather severe farther north. Water birds that winter in significant numbers include the White Pelican (perhaps most of those that breed east of the continental divide), dabbling ducks, American Coot, Black Skimmer, many species of shorebirds, gulls and terns, and northern populations of many wading bird species that also breed in southern Florida. The wintering land avifauna is diverse, but southern Florida is doubtless less important quantitatively as winter range for land birds than for water birds because its upland area is limited and the extensive wetlands attract few land species. The regular occurrence in winter of many birds whose breeding ranges are far west of Florida (such as Swainson's Hawk, American Avocet, Western Kingbird, Scissor-tailed Flycatcher, Black-throated Grey Warbler, and Western Tanager) is notable.

The extended Florida peninsula would seem to offer migrating birds an easy way to and from the tropics, but, in fact, it is the primary route for the relatively few species that either winter in the West Indies, such as the Cape May Warbler, or that winter in South America and migrate by way of the West Indies, such as the Common Nighthawk, Eastern Kingbird and Bobolink. The main stream of bird migration in and out of eastern North America crosses the Gulf of Mexico and in fall a substantial flight also bypasses Florida to the east. These migrants seldom appear in southern Florida except when storms deflect them from their usual path. Bird migration in southern Florida has received little systematic study, but a mass of anecdotal information exists in print, particularly in *American Birds*, relating ground observations of migrants and mortality of migrants at TV towers and other structures mostly in north Florida to specific weather events.

*Breeding Birds* - Our comments focus on the 116 species that comprise the native breeding avifauna, Table 2 lists this avifauna and summarizes distribution by habitat. Of these, at least five no longer breed in southern Florida. Two former breeders are the extinct Carolina Parakeet and the nearly extinct Ivory-billed Woodpecker. Royal and Sandwich Terns once nested in the Florida Keys and on the Gulf coast (Howell, 1932: 268-269; Robertson, 1964a: 78-79), but neither species does so today, though they are still common wintering birds. We list the Zenaida Dove as a former breeding bird, but its place on the list is tenuously held. The species was named from specimens Peale obtained in 1824, presumably in the Keys, and in 1832 Audubon reported it breeding there in numbers (Howell, 1932: 277-278). Its more recent status is that of a West Indian stray and it is so considered in subsequent discussion. In addition to the species considered extirpated, at least four others, (American Oystercatcher, Snowy Plover, American Kestrel, Scrub Jay) have almost disappeared as breeding birds from southern Florida. And, finally, the evidence of breeding in southern Florida is scanty (fewer than 5 definite records) for at least six additional species (Willet, Ruby-throated Hummingbird, Roughwinged Swallow, Prothonotary Warbler, Grasshopper Sparrow, Bachman's Sparrow).

We omit about 13 native species known or alleged to have nested in southern Florida at least once. It seems clear, at least, that none is a regular member of the breeding avifauna. Supporting evidence appears insufficient in the case of reported nesting of the Brown Booby (Howell, 1932: 88-89), American Flamingo (see Allen, 1956: 39-45), Broad-winged Hawk (Howell, 1932: 178), Rough-legged Hawk (Sprunt, 1954: 114), Common Tern (see Robertson, 1964a: 75-78), Key West Quail-Dove (Howell, 1932: 282-283), Chimney Swift (Howell, 1932: 301), Belted Kingfisher (Howell, 1932: 304), and Barn Swallow (Sprunt, 1954: 309-310). Reported breeding of the White-faced Ibis at Lake Okeechobee (A.O.U., 1957: 55) is evidently a mistake, the records actually pertaining to the Glossy Ibis. American Bitterns (Howell,

1932: 111) and American Coots (Howell, 1932: 213; Stevenson, 1958; Sprunt, 1960) occasionally nest but the actual population status is uncertain. The well-documented recent nesting of the Northern ("Baltimore") Oriole in Key West (Ogden, 1972), some 800 miles south of its normal breeding range, must be viewed as an anomaly. A number of migrant and wintering land birds, often singing males, have been reported from southern Florida in summer, but such isolated records are no proof of breeding. Recent observations (Stevenson, 1968; H.W. Werner, pers. comm.) suggest that the Black Rail probably breeds in southern Florida, but no one has yet found a nest.

#### Comparison with Breeding Avifaunas of Adjacent Areas

Comparisons of the number of bird species that breed in southern Florida with the number that breed in the nearby West Indies, in the rest of Florida and the contiguous Southeast, and in other parts of eastern North America yield some insight on the characteristics and possible history of the regional avifauna. The subject seems best approached by looking at water birds and land birds separately and also further subdividing these groups.

*Water Birds* - Water birds of more or less tropical affinity are strongly predominant among those breeding in southern Florida and the diversity of species exceeds that of most neighboring areas to the north. Southern Florida has the same number of breeding water birds, 43 species, as occurs in the remainder of the state. Five species that breed in southern Florida (Roseate Tern, Sooty Tern, Noddy Tern, and the recent Magnificent Frigatebird and Fulvous Tree Duck) are not known to breed elsewhere in Florida; and, omitting casual nesting records for several ducks, only five water bird species, known to breed in other parts of the state have not been found nesting in southern Florida (Black Rail, American Woodcock, Black Skimmer, and the recent Common Tern (Hallman, 1961) and Caspian Tern).

Florida with 48 species has more breeding water birds than does Alabama (38), Georgia (29), or South Carolina (40). The near West Indies, Cuba and the Bahamas, however, have a breeding water bird fauna of about 60 species (Bond, 1971), markedly more diverse than that of southern Florida. These differences are more readily interpreted if major ecological groups of water birds are considered separately.

*Seabirds* - Of the eight primarily oceanic species that breed in the near West Indies, three (Magnificent Frigatebird, Sooty Tern, Noddy Tern) also nest in southern Florida. All the others (Audubon's Shearwater, White-tailed Tropic-bird, Blue-faced Booby, Brown Booby, Bridled Tern) occur regularly at sea near Florida, and perhaps are absent as breeders mainly because southern Florida has few isolated out-islands and rocks suitable for nesting.

*Species of Estuarine and Coastal Wetlands* - With the exception of the American Flamingo, the breeding water birds of this habitat system are identical in southern Florida and the near West Indies. Flamingos have specialized nesting requirements (they need a place that is free of terrestrial predators) and probably never nested in Florida, although birds from Bahaman colonies once visited Florida Bay regularly in large numbers (Allen, 1956).

*Species of Interior Wetlands* - The major deficit of breeding water bird species as compared with the near West Indies is in the interior wetlands that today comprise by far the most extensive habitat system of southern Florida. Fifteen breeding species of water birds (Table 2) occur mainly in the interior wetlands and all but the Mottled Duck also breed in Cuba, where at least 12 additional species (Least Grebe, Olivaceous Cormorant, 4 ducks, 3 (possibly 4) more rails, 2 coots, and the Jacana) are also associated primarily with interior wetlands (Barbour, 1943; Bond, 1971).

*Land Birds* - Southern Florida has notably few breeding land birds compared to other states of the Southeast. Table 3 compares the southern Florida land avifauna to the southeastern states, several northern states in the East and Midwest, and the three major islands of the Greater Antilles. Figure 1 shows the southward decrease in the numbers of breeding land birds on the Florida peninsula. Points of interest that emerge from this comparison are: 1) Numbers of breeding passerines decrease steadily southward. States located mostly or entirely within the southeastern coastal plain (Florida, Louisiana) have about two-thirds as many breeding passerines as smaller areas in the Northeast. Southeastern states that extend into piedmont and mountain areas (Alabama, Georgia) show less disparity with 20 to 25 percent fewer breeding passerines than occur in areas of comparable size farther north. 2) The southward decrease in number of breeding passerines continues in the Florida peninsula, where southern Florida has only 60 percent of the total known to breed in the state. 3) Despite its featureless terrain and geological youth, southern Florida has about the same number of breeding passerines (but a somewhat different suite of species) as the topographically and ecologically much more diverse and (in part) geologically ancient islands of the western Greater Antilles. 4) Curiously, the number of breeding non-passerine land birds is remarkably constant across a wide latitudinal belt of eastern North America. Of the areas compared, Cuba, depauperate in breeding passerines, has the largest number of breeding non-passerine land birds.

### Characteristics of the Southern Florida Land Avifauna

The most intriguing points about the land birds of southern Florida are the limited number of breeding species in a region of considerable size and ecological diversity, and the fact that most of the breeding land birds are widespread North American forms, although the vegetation (at least in the Keys and along the mainland coast) is predominantly West Indian.

*Avifaunal Impoverishment* - As noted (Table 3) the southeastern coastal plain, and Florida in particular, has a diminished fauna of breeding land birds, especially passerines. Of the land birds breeding in north Florida nearly one-third do not range into southern Florida. In most cases, the southern breeding limits of Florida land birds absent as breeders in southern Florida show no clear relation to physiographic or ecological features. Habitat similar to that they occupy at their Florida range limit commonly extends much farther south in the peninsula.

The same characteristic, breeding range limits that are not readily explained by ecological conditions, is evident within southern Florida, where over 60 percent of the breeding land birds (20 of 37 non-passerines and 25 of 36 passerines, see Table 2) do not occur in all of the apparently suitable habitat. As we discuss later, several species may have colonized southern Florida rather recently and may eventually extend their ranges to more obvious ecological limits. Below we note the main locations within southern Florida where land birds reach breeding range limits.

*Big Cypress* - Land birds that apparently reach their southern breeding limits in the cypress swamps of Collier and northern Monroe counties are the Ruby-throated Hummingbird, Tufted Titmouse, Blue-gray Gnatcatcher, Red-eyed Vireo, Prothonotary Warbler, and Parula Warbler. Most are known from few definite breeding records, but the area is poorly studied and all species, possibly except the Prothonotary Warbler, seem to be present regularly in the breeding season. The Tufted Titmouse may have a still more southerly (relict?) population in the southwest coast mangrove swamps, where Edscorn has reported summer observations (Ogden, 1969, 1970a). Although these species reach the approximate southern extent of cypress swamps in southwest Florida, none is known to breed in the similar cypress belt that extends into southern Florida along the eastern edge of the Everglades.

*Miami Rock Ridge Uplands* - About 18 birds originally reached southern nesting limits in the upland areas of southeastern Florida, namely the Red-tailed Hawk, Short-tailed Hawk, American Kestrel, Bobwhite, Turkey, Mourning Dove (continental population), Red-headed, Downy, Hairy, and Red-cockaded woodpeckers, Purple Martin, Blue Jay, Brown-headed Nuthatch, Eastern Bluebird, Loggerhead Shrike, Pine Warbler, Summer Tanager, and Rufous-sided Towhee. Most are pine forest birds, but the list includes several forest-edge species one of which (the Towhee) may also have sparse breeding populations in the southwest coast mangroves (J. B. Edscorn, pers. comm.). Again, although the pine forest birds occur (or once did) south to the limit of pine on the mainland, none is known to have nested in pinelands of the Lower Florida Keys where the total area of habitat (25 to 40 square kilometers of pine) seems adequate to accommodate populations of any of the missing species.

*Southern Mainland* - Nine species, the Black Vulture, Screech Owl, Great Horned Owl, Barred Owl, Eastern Kingbird, Common Crow, Common Yellowthroat, Eastern Meadowlark, and Boat-tailed Grackle apparently breed south to the limit of suitable habitat on the southern mainland and not in the Florida Keys, but this division is less clear. The three owls may yet be found breeding in the Keys; the Common Crow ranges far south in Florida Bay, chiefly as a predator around water bird rookeries, but it seldom visits the Keys proper and probably doesn't nest; and, potential habitat for Common Yellowthroats is limited in the Keys. We doubt reports of Boat-tailed Grackles from the Keys, because no recent observer has found the species and because Howell's comments (1932: 432) seem to be based entirely upon observations by Bartsch (1914, *et seq.*) who frequently reported Boat-tailed Grackles, but never Common Grackles, which in fact are abundant there.

*Upper Florida Keys* - Finally, about eight land birds nest in the northern and central Florida Keys (mainly the larger islands near the mainland), but not farther south. They are the Swallow-tailed Kite, Burrowing Owl, Chuck-will's-widow, Common Nighthawk (continental population), Common Flicker, Pileated Woodpecker, Carolina Wren, and Brown Thrasher. Several are newly established as breeders, doubtless responding to recent habitat changes in the Keys.

The southern Florida region not only has a limited land avifauna but individual habitats also tend to have few breeding species and low population density (see later discussion). The avifauna is also oddly constituted in that it lacks many distinctive types of land birds. The present generally distributed native land avifauna has no small hawks (*Accipiter*, *Falco*), swifts, hummingbirds, small or mid-sized flycatchers (*Empidonax*, *Contopus*), swallows (other than the semi-domesticated Purple Martin), a single titmouse, no large thrushes, no orioles, and practically no small finches. With the exception of titmice, a group that does not occur in the West Indies, land avifaunas both in the near West Indies and farther north in the southeastern United States have one to several breeding species in each of the above groups. Southern Florida is unique in lacking representatives of many groups that

are prominent in regional land avifaunas throughout most of North America and West Indies. Most of the groups mentioned have special feeding adaptations and in their absence the available resources would seem to be under-exploited. The southern Florida avifauna is therefore unbalanced (MacArthur and Wilson 1967: 177) and presumably subject to invasion.

*Origin of the Avifauna* - In one of the earliest comments on southern Florida natural history, De Pourtales (1877: 138) clearly stated an essential biological characteristic of the region:

"We have here a curious example...of land of comparatively recent origin which has received its flora and fauna from two different and very distinct sources, the West Indies and the North American continent, and, as it seems, the flora chiefly from the former, the fauna mostly from the latter."

De Pourtales perceptive observation holds true even for the land birds of the part of Florida closest to the West Indies. Northern birds account for 64 of the 73 breeding land birds of southern Florida, an overwhelming 88 percent of the avifauna. Only seven land birds (Table 2) are exclusively of West Indian origin, and the two remaining species, Mourning Dove and Common Nighthawk, apparently have invaded southern Florida from both directions.

Extensive evidence, in addition to their dominance in the present avifauna, suggests that the land birds of northern origin have a long history in Florida. The northern element in the Florida avifauna is highly endemic at the subspecies level which argues in favor of a considerable period of residence. In all, about 40 percent of the breeding land birds of southern Florida, 11 non-passerines and 18 passerines, are subspecies that are either limited to Florida or probably developed there (A.O.U., 1957). A number of the Florida subspecies (such as the Everglade Kite, Scrub Jay, Prairie Warbler, and Grasshopper Sparrow) are separated geographically from their nearest relatives as also are such species as the White-tailed Kite, Short-tailed Hawk, Caracara, and Burrowing Owl, local subspecies of which are not limited to Florida. Nearest related populations of several of the disjunct Florida forms now occur in the southwestern United States and Mexico.

Perhaps even stronger evidence of the long predominance of the continental element in Florida is found in the fact that about 35 species of land birds have apparently colonized the West Indies from Florida or elsewhere in southeastern North America. For several species, more than one colonization of the West Indies evidently occurred. A rough tally of the northern continental element mostly in the Bahamas and Cuba shows three instances in which the same subspecies occurs in the West Indies and on the adjacent continent, at least 17 instances in which the West Indian forms are subspecifically distinct, at least 12 instances of West Indian forms regarded as distinct species, and several cases of West Indian forms sometimes considered to be distinct genera. The varying degrees of differentiation of northern continental land birds, some of which are now widespread in the West Indies, suggest that the invasions have occurred over a long period of time. We note the suggestion (Yang and Selander, 1968: 138) that the Common Grackle probably derived from the Pleistocene isolation in Florida of a population of the Greater Antillean Grackle, but we see no reason why the latter species may not instead have originated as a result of an invasion from Florida (cf., Bond, 1948: 221).

The spread of breeding land birds in the opposite direction, from the near West Indies to Florida, is a tale soon told. All nine species (Table 2) are obvious recent immigrants. No geographical differentiation has been detected in the Florida populations of West Indian land birds and several species are thought to have colonized southern Florida within recent decades. The known land avifauna of Florida and the Southeast, recent and fossil, includes nothing that could be called an "old Antillean" element. In the cases where the pattern of subspecies distribution in the near West Indies permits a decision, it is clear that Florida's West Indian Mourning Doves originated in Cuba, while the Common Nighthawks (Paulson, 1966: 14) and possibly the Gray Kingbirds (Brodkorb, 1950) are Bahaman.

#### Pleistocene Conditions and the Southern Florida Avifauna

In the preceding section we outlined salient characteristics of the present bird fauna of southern Florida. With these characteristics in mind, we consider here events of the Florida Pleistocene that probably played a major determining role. We place particular emphasis on the rise and fall of late Pleistocene seas over southern Florida that brought drastic changes in the land area as well as major shifts of vegetation which together determined the nature and extent of habitats available to land birds.

*Geological Background* - The Pleistocene was marked by five major ice advances accompanied by lower sea level and four interglacials with higher sea level (Cooke, 1945; Parker and Cooke, 1944). During glacial periods Florida was a refuge for bird populations forced south by ice, and the greatly expanded land areas of Florida and the West Indies (especially the Bahamas) presumably favored exchange of bird species across the narrow ocean gap between the two regions. The interglacials are of interest here mainly because each invading sea left islands where stranded populations of birds may have differentiated in isolation.

Earlier interglacial seas eliminated southern Florida as bird habitat, except perhaps as a feeding area for offshore and pelagic water birds. Development of the present avifauna undoubtedly began as

soon as there was an appreciable area of continuously emerged land. When this may have been depends critically upon disputed details of the later Pleistocene sequence (see Brooks, 1974). It seems likely that suitable areas first became available as the last interglacial sea receded, but islands in southern Florida may have escaped that submergence.

*Fossil Record* - The only reports of fossil birds that we know of from southern Florida (Bird, 1953; Hirschfeld, 1968) identified bones of six species, all of which still occur in the area, from sinkholes of no great age in tropical hammocks near Homestead. Study of older deposits, mostly in the north-central peninsula by Pierce Brodkorb and his associates, has revealed a rich Pleistocene avifauna. Brodkorb's monumental "Catalogue of Fossil Birds" (1963a, 1964, 1967, 1971), now complete except for passerines, gives Pleistocene records for: 96 species that have also occurred in Florida during historical time, about 43 percent of the known recent avifauna in the groups covered; 6 species still living but not known historically from Florida; and, about 20 paleospecies not known as living birds. In addition, at least 24 living species (all historically Floridian) and at least five paleospecies of passerines are known from the Florida Pleistocene (Wetmore, 1956: 90-102; Brodkorb, 1957, 1959; Ligon, 1965). Numbers of species are certain to change as additional fossil birds are identified (Brewer, 1969) and as material is restudied (Olson, 1974 a,b), but Florida clearly supported one of the most diverse of known Pleistocene avifaunas. The avifauna retained several bizarre types until quite late in the Pleistocene including a peculiar stork (Wetmore, 1956; Brodkorb, 1963a), a large condor (Wetmore, 1956; Brodkorb, 1964), and a giant flightless bird "larger than the African ostrich" of a fossil group otherwise known only from southern South America (Brodkorb, 1963b). Pleistocene fossil birds from the near West Indies are less numerous and are difficult to date, because most are from cave deposits, but they include an unusually high proportion of extinct species, notably large raptors such as eagles and giant barn owls (Wetmore, 1937; Brodkorb, 1955).

Perhaps the main conclusion that can be drawn from the record of fossil birds is that Florida's Pleistocene avifauna seems much like its present avifauna. It differed in having several extreme oddities; a few now-extinct species of decidedly tropical, particularly Mexican, affinities; and, a few northern birds such as the Ruffed Grouse (Brodkorb, 1964), Great Auk (Hay, 1902; Brodkorb, 1960), and Common Murre (Brodkorb, 1960). Representatives of the neotropical and northern groups occur together in some deposits of Illinoian age (Brodkorb, 1957, 1959) and are said to be "interglacial relicts" and "glacial indicators", respectively. Based on the fossil birds and other evidence Brodkorb (1957: 138) surmised "that the climate in northern Florida during the Illinoian glacial stage was at least as cool as that of Virginia today." Records of the Great Auk and Common Murre are from east coast archeological sites with reported radiocarbon dates of about 3000 years B.P., and about 1000 years B.P., leading Brodkorb (1960: 342) to suggest that these occurrences may indicate "two periods of cool climate in Florida prehistory." The Pleistocene fossil record has no clear evidence of interchange of birds between Florida and the near West Indies. No distinctively West Indian bird is known from the well-studied Florida Pleistocene, and collections from New Providence, Bahamas, thought to be early Wisconsin showed more relationship to Cuba and less to Florida than does the present Bahaman avifauna (Brodkorb, 1955).

*Late Pleistocene Paleoeecology* - The plant ecologist in southern Florida can observe many plant successions that involve tens of years, occasional relict distributions that indicate trends of change over a few hundred years (Alexander, 1953), and peat cores that show predominant local vegetation over periods of several thousand years. No direct evidence exists of the nature of southern Florida land vegetation longer than about 5000 years ago. Perhaps because of this, it seems to be generally assumed that a pattern of vegetation somewhat like that of the present persisted throughout the most recent cycle of sea level change. Because very slight differences in elevation often determine plant communities in southern Florida, it seems to us that sea level changes of the magnitude indicated in the geological literature undoubtedly resulted in continuing changes in the pattern of vegetation, and that during the low sea stage of late Wisconsin time the plant cover of southern Florida must have differed greatly from that seen today.

Recession of the last interglacial sea presumably was attended by a southward shift of coastal and inland vegetation belts (see Emery *et al.*, 1967: 1305) comparable to the northward shift that Egler (1952) suggested as the controlling condition of present physiographic succession in southern Florida. It seems certain that any present inland site supported a succession of plant cover types as its condition changed from saline to brackish to freshwater and its position from shoreline to near-shore to inland during withdrawal of the last interglacial sea. Bird life characteristic of these habitats doubtless moved as the vegetation moved. The last submergence apparently reached either the 5-5.5 m (Brooks, 1974) or the 7.5-9 m contour (Cooke, 1945). If the former is correct the Miami Rock Ridge, Florida Keys and other high spots may have persisted as islands through the interglacial. If the latter is correct these areas would have become accessible to colonization by a Caribbean drift flora as the sea withdrew to about 5m above current sea level (ASL) while the present Everglades was still a shallow estuary to the north and west (see Parker and Cooke, 1944: 47). At least 1.5 m ASL the mainland islands would have had a broad northward land connection. By 35,000 years ago, sea level had withdrawn to about its present location (Milliman and Emery, 1968) and the vegetation pattern probably closely

resembled that of today since the paleobotanical record includes no indication of the occurrence of plant communities or even conspicuous plants not found in the region today. The sea continued to fall for an additional 20,000 years to a low 130 meters below present sea level about 16,000 years ago (Milliman and Emery, 1968), and then began to rise, rapidly at first and then more gradually (Scholl, *et al.*, 1969), returning southern Florida to its present landform and plant cover. Our main concern here is to consider the likely condition of the region as bird habitat during the more advanced stages of sea withdrawal, and perhaps the central question is, Did the Everglades exist at that time?

The few authors who have considered late Pleistocene paleogeography of southern Florida tend to suggest that lakes and marshes have occupied the Everglades continually since soon after the sea receded (Parker and Cooke, 1944: 49; Davis, 1943: 244-248; Parker and Hoy, 1943: 43), but we see little reason to believe that the present Everglades has existed for much longer than is indicated by its oldest peat deposits (see Robertson, 1955: 335-341, for detailed argument). Given the increase of effective land elevation, solution and subterranean drainage must have eliminated any Everglades-like marshes relatively soon after the sea fell below the present shoreline. We suggest that for an extended period (15,000 years?) during the low sea level of late Wisconsin time at least the southern Everglades and Florida Bay were a limestone upland broadly continuous with the Florida Keys and occupied by upland vegetation. How much the plant cover differed in detail from the present upland vegetation of southern Florida depends mainly upon how much cooler glacial period climate may have been that far south. We would suspect, however, that the principal upland vegetation types and ecological processes (*e.g.*, natural fire) were essentially as known today.

If the above speculations approximate the truth, the habitat available to land birds was much greater during late Wisconsin time and the habitat of the birds of interior wetlands was much reduced.

#### Recent Breeding Range Changes by Peninsular Florida Birds

We summarize here (Table 4) the evidence of change in the breeding range limits of 44 populations in peninsular Florida, distinguishing those that seem primarily the result of man's impact from those not obviously so. We exclude species that have increased (Glossy Ibis) or decreased (Wood Stork, Everglade Kite, Bald Eagle, Snowy Plover, Hairy Woodpecker, and many others) markedly in Florida without notable change of range limits. We also exclude most of the northern land birds that reach range limits in the Big Cypress, although occurrence there of several species is a considerable extension of the breeding ranges previously recognized (Howell, 1932; Sprunt, 1954). The summer bird life of the Big Cypress is still rather poorly known and we suspect that these species are not new arrivals in the area.

Most of the information on range changes has accumulated since publication of the most recent summary of Florida ornithology (Sprunt, 1954), and we cannot within reasonable space credit the source of each datum that contributes to overall knowledge of the subject. Much of the record derives from field work by Henry M. Stevenson and his associates as briefly noted in more than 50 seasonal summaries of bird occurrence in Florida that Dr. Stevenson has edited in *American Birds* from 1953 to date.

The 44 populations include 9 water birds and 35 land birds; 29 instances of range extension and 15 of range loss. The range changes by water birds have no characteristics of special note. Except for the Cattle Egret and Fulvous Tree Duck, both notorious long-distance colonizers, the range extensions are relatively minor and human predation almost certainly caused the range losses by four species. Range changes by land birds, however, show interesting differences in the pattern of recent change between West Indian and continental species.

Ten of the 11 land birds that have lost an appreciable amount of breeding range in peninsular Florida are continental species the range limits of which have shifted northward, and, for eight of these, habitat destruction or other human disturbance appears inadequate to account for the range losses. Concerning species that have disappeared from southeastern Florida it should be noted that most either were gone prior to the wholesale removal of native upland vegetation in recent decades, or inhabited areas that have not been greatly disturbed. Of the 15 range extensions by continental land birds, southward advances by six species seem unlikely to be the result of man's modification of habitat. But, the more notable recent range extensions in Florida by continental species (such as those of the Burrowing Owl, Brown-headed Cowbird, Blue Grosbeak, and Indigo Bunting) almost certainly represent exploitation of new habitat created by man. As Rohwer and Woolfenden (1969) have suggested, the gradual southward spread of other continental species in the peninsula may indicate that they are adapting to the present climate.

In contrast, the Zenaida Dove is the only land bird of West Indian origin that may have lost range. All other West Indian land birds known to breed in Florida have extended or consolidated their ranges in recent years. Three land birds, the Yellow Warbler and subspecies of the Mourning Dove and Common Nighthawk apparently have colonized southern Florida from the West Indies in recent decades, and three additional species (Smooth-billed Ani, Gray Kingbird, Black-whiskered Vireo) have extended their breeding ranges well beyond the limits of typically West Indian habitats. Although originally derived from the continent, the Prairie Warbler (also extending its range northward) may reasonably be associated with the West Indian element in this context, because it is an endemic Florida subspecies that inhabits a tropical vegetation type.

The recent spread of several West Indian birds into and within southern Florida suggests that additional species may become established. If so, the new colonizers seem most likely to be found among

the 21 West Indian species that have already reached southern Florida by their own wing power (Table 5). We omit the Least Grebe, American Kestrel (Cuban subspecies), Jacana, Blue-headed Quail-Dove, Black Swift, Cuban Bullfinch (see Stimson, 1961), and Melodious (=Cuban) Grassquit (see Austin, 1963), because evidence of their natural occurrence in Florida seems inadequate. We list the Scaly-naped Pigeon and Tawny-shouldered Blackbird, although we suspect that the Florida records may be based on escapes, and also list the Zenaida Dove now only a casual visitor.

Because so many exotic birds are imported into southern Florida (Owre, 1973), one must weigh carefully the possibility that supposed West Indian casuals are in fact escaped cage birds. The record itself (Table 5), particularly the definite seasonal pattern of occurrence of some species suggests natural dispersal. Also, if, as we suspect, most West Indian birds that reach southern Florida originate in the Bahamas rather than Cuba, the fact that the Bahamas have long-standing and well-enforced controls on the export of native birds (A. Sprunt, IV, pers. comm.) is significant. Recent summaries (Banks and Clapp 1972; Clapp and Banks, 1973) show no birds imported to the United States from the Bahamas, and, indeed, no imports of any species listed in Table 5 except White-cheeked Pintail and Bananaquits from South America. The summaries of course also show no recent imports from Cuba. But, Cuban proclivities for caging wild songbirds are well-known (Barbour, 1943), and many such birds no doubt accompanied the mass migrations of Cubans to southern Florida in the later 1800's and more recently.

It is a minor axiom of avian geography that in the simplified milieu of islands, birds tend to lose traits (for extreme example, flight) that they need to compete in more complex ecological situations found on larger land masses. Thus the view that birds evolved on islands are unable, or seldom able, to invade continents. Bond (1934, 1948, 1963) has maintained consistently that this applies in the case of West Indian birds in relation to North and South America and substantial evidence from present distributions (such as the West Indian land birds that occur along the Caribbean island fringe of Central America, but not on the adjacent continent) supports his argument. Bond stated (1948: 221) "...it is unlikely that a genus peculiar to these islands could invade any continental area." We speculate above (see also Paulson, 1966: 13-14) that several such genera are potential invaders of Florida. We suggest that the supposed competitive inferiority of island birds is irrelevant in southern Florida where the present breeding land avifauna is depauperate. Indeed, the only West Indian forms that would encounter close ecological competitors in southern Florida are those of relatively recent continental origin that may originally have colonized the near West Indies from Florida.

We think that the Masked Duck, a hummingbird, Bahama and Cave swallow, Bananaquit, Stripe-headed Tanager, and Black-faced Grassquit are the pick of the list of potential colonizers. It appears that all would find unexploited ecological opportunities in southern Florida and that all now reach Florida frequently enough to have a chance of establishing viable breeding populations. Some possibility may also exist that climatically preadapted West Indian subspecies, such as Pine Warblers from the Bahamas or American Kestrels from Cuba, might reinvade the continent in the now virtually birdless pineland of the Lower Florida Keys. Rapid obliteration of this pine forest by land developers, however, may soon negate the latter speculation. For the species named earlier, it isn't likely that suitable habitat will disappear from southern Florida.

#### Suggested Explanation of the Present Avifauna

To this point, we have reviewed the composition and principal characteristics of the southern Florida avifauna, noted geological events that may have influenced its development, and discussed recent range changes and the occurrence of West Indian birds that may be potential colonists of southern Florida. These data suggest a possible explanation of the existing avifauna and perhaps allow prediction of its future course.

*Water Birds* - Coastal and estuarine species require little comment. They are basically tropical, but nearly all species now have extensive ranges both north and south of southern Florida. Ample habitat doubtless persisted in or near Florida through all the ups and downs of sea level during the Pleistocene. Few recent breeding range changes of note are evident among species of this group and little evidence exists that Florida was the theater of much of their evolution. Differentiation of coastal-estuarine water birds in Florida seems limited to several subspecies of the Clapper Rail, probably the white morph of the Great Blue Heron and, less probably, the white morph of the Reddish Egret.

At first glance, it appears that the expansive Everglades should support a more diverse water bird fauna than it does. As noted, Cuba has more species in a smaller area of interior wetlands, but this may result mostly from the fact that Cuba is older and well-placed to receive immigrant marsh and quiet water birds from both Florida and Central America. Two possible factors, one historical and one ecological, may contribute to the scarcity of breeding water birds in southern Florida's interior wetlands. As we argued earlier, the Everglades in its present incarnation probably is a recent feature. Evidence from sediments suggests that mini-Everglades existed in Florida Bay and other coastal lagoons at an earlier stage of the Holocene sea rise (Hoffmeister, 1974), but even such transient interior wetlands as these were relatively recent and southern Florida may have been entirely without an Everglades for an extended period of late Wisconsin time. Secondly, most present interior wetlands are (or were naturally) seasonal marshes and it may be that the productivity of such habitats is exploited most efficiently by mobile populations of wading



birds, most species of which are also, and perhaps primarily, estuarine. This may help account both for the abundance of wading birds in southern Florida and for the rather few species that are primarily associated with the interior wetlands. These arguments are less satisfactory for Florida at large, where the ecological diversity of interior wetlands is greater, but bird species diversity remains low. Although a large proportion of the present water bird species of interior wetlands are known from the Florida Pleistocene, the fossil record does not suggest that Florida then had a much more diverse fauna of these sorts of water birds.

*Land Birds* - The main question that emerged from previous discussion is, Why does southern Florida have so few species of breeding land birds? Several authors (Simpson, 1964; MacArthur and Wilson, 1967) have suggested that peninsulas have fewer species than adjacent mainland because the narrowed land connection reduces both the likelihood of initial invasion and the possibility for replacement of populations extirpated on the smaller peninsular land mass. We see two reasons, however, to doubt that Florida's present landform is a sufficient explanation of Florida's few breeding land species. First, with the late Wisconsin sea 130 m below present sea level, land connection to the continent, and the peninsula itself, was roughly three times wider than it is now. Initial invasions by continental species should have been little retarded and should have resulted in a widespread continental fauna, at least of upland forms, on the greatly expanded late Wisconsin land mass of Florida. Second, the depauperate and unsaturated southern Florida avifauna is merely the extreme case of the general avifaunal impoverishment of lowland southeastern North America (Robertson, 1955; Rohwer and Woolfenden, 1969; Cook, 1969; Tramer, 1974). Such a "peninsular effect" could scarcely apply to the entire coastal plain.

We suggest that recent breeding range changes involving retreat of continental species and advance of West Indian species in Florida may provide a clue to the avifaunal impoverishment of the Southeast. Ornithologists in western Europe and northeastern North America began to realize nearly a century ago that northward extension of the breeding ranges of many birds was related to climatic amelioration in formerly glaciated areas. It may be less generally appreciated that range changes similarly determined by warming climate might occur in regions remote from glaciers. The pattern of recent range change by birds in Florida (especially those not obviously influenced by man) suggests to us that a climatic trend that favors West Indian forms and disadvantages continental forms may be the controlling factor.

The striking lack of diversity of the southern Florida breeding land avifauna seems understandable only by reference to the changes of land area, vegetation and climate from late Wisconsin time to the present. In our view, southern Florida (and, to a diminishing degree northward, the entire Southeast) exists today as a sort of avifaunal vacuum, the hiatus between a continental land avifauna withdrawing before an unfavorable climatic trend and a West Indian land avifauna delayed in reaching vacant and suitable habitat by a sea barrier and perhaps also by intrinsic qualities that make island birds poor colonizers of mainland areas. Cook (1969: 71) advanced a similar argument, without specific reference to Florida, in suggesting that the successive glacial periods tended to eliminate the sub-tropical fauna of the Southeast, because these forms had no contiguous land area for refuge to the south, and that subtropical elements re-invade during the warmer interglacials. The southern Florida avifauna may now be in the early states of such an interglacial invasion.

Other possible explanations of the southern Florida land avifauna appear untenable. Exclusion by interspecific competition is not convincing as a general argument. Only two pairs of possible close competitors occur within southern Florida. The tropical Gray Kingbird perhaps replaces the continental Eastern Kingbird on the Florida Keys and the two tend to be ecologically segregated on the mainland, the former species coastal and the latter inland, but they do co-exist locally. Ranges of the closely related Black-whiskered and Red-eyed vireos apparently are not in broad contact at present, but may become so if northward and inland spread of the Black-whiskered Vireo continues. In these two cases, the presence of a potentially competing continental species has not prevented the establishment and spread of a West Indian invader. Thus MacArthur's (1972: 137) generalization that the southern edges of species' ranges are often limited by competition does not hold in the case of southern Florida. Diffuse competition can scarcely apply to Florida, because within habitat species diversity and population density (see beyond) are also much reduced.

Another conceivable view is that southern Florida has a limited land avifauna simply because many birds haven't yet had time to reach the region. This argument fails completely for species that dispersed south from the North American continent. Land habitats began to appear in southern Florida at least as early as the onset of the last glacial period. Thus the region has been available to birds four or five times longer than the glaciated regions of eastern North America that now support land avifaunas much more diverse than that of southern Florida. Evidence mentioned earlier also suggests that many continental land birds have a long history in the region. The question of sufficient time for invasion may, on the other hand, have some validity in the case of West Indian land birds.

Somewhat as with the time factor, geographical barriers have doubtless been of little importance to the dispersal from the north but of significance to invasion from the south. The Everglades is the only physiographic feature that might be regarded as a barrier to the dispersal of continental species. At present it is a considerable impedance to some birds of upland habitats, but we believe it is much too recent to have figured importantly in the history of the land avifauna. Considering dispersal of birds from the south, the narrow ocean gap that separates southern Florida from the near West Indies must have delayed northward dispersal by West Indian land birds and perhaps it is an impassable limit for some

species. Many authors have suggested that hurricanes play a significant role in the dispersal of birds across oceanic barriers, but the fact that so few West Indian land birds have colonized typically West Indian habitats in southern Florida argues strongly that hurricanes have not been effective.

Having eliminated competition, time and accessibility as likely general explanations of the absence of land birds that reach limits north of southern Florida, we conclude that the regional environment is unsuitable, or no longer suitable, for these species. The evidence from recent range changes seems to show that the environmental inadequacies involve both climate and habitat. Breeding ranges of some continental species have receded in the absence of obvious or sufficient habitat change. These instances may represent the effects of postglacial warming and perhaps they are the closing episodes of a pattern that was more prevalent a few thousand years ago. Northward range extension by several West Indian land birds may illustrate the other side of the same phenomenon. Although we question Tramer's thought (1974: 128) that lack of habitat diversity may explain the low avifaunal diversity of the Southeast, the southward spread of some continental land birds in Florida in the wake of habitat modification indicates that habitat previously was limiting for these species.

Evidence to support the ideas advanced here might come from the withdrawal of additional northern species or the establishment of breeding populations in southern Florida by additional West Indian species. In an undisturbed situation, we would predict continuation of the trends evident from recent natural range changes. Unhappily, this experiment in biogeography is unlikely to run its course. Because of massive environmental change by man, particularly the almost establishment of a diverse exotic avifauna (Owre, 1973), it probably will never be known to what extent Nature indeed abhorred the avifaunal vacuum it developed in southern Florida.

#### ECOLOGICAL CONSIDERATIONS

##### Quantitative Data on Southern Florida Birds

Present knowledge of the size of bird populations in southern Florida varies from accurate, long-term records of the population changes of several rare species to extremely limited information on the total abundance of birds in particular habitats and the trend of numbers of most species. In view of the on-going major environmental changes in southern Florida, ornithological research is obviously challenged to obtain much more, and much more precise, quantitative data on bird populations.

*Populations of Breeding Land Birds* - Table 6 summarizes all the studies we know of from peninsular Florida and the near West Indies that measured total numbers of land birds breeding in a given area. Censuses 1-10 in Table 6 covered areas that nominally are pine forests of various types, censuses 11-16 covered broad-leaved forests, censuses 17-21 covered natural forest-edge situations, and censuses 22-26 covered several kinds of man-made habitat. We deleted nesting water birds from censuses 11, 12, 15, and 20 and changed totals accordingly, but the number of breeding pairs involved was trivial except in the case of census 20. Considering the meager list of 26 breeding-bird censuses, it is plain that the data are inadequate for all habitats and nil for several major types of habitat.

All studies used the territory-mapping method in which a measured area gridded with markers is surveyed repeatedly during the breeding season and any evidence of nesting (such as singing males, nests, or dependent young) is plotted on field maps. Various authors have discussed this census technique and its shortcomings (Williams, 1936, 1947; Kendeigh, 1944; Aldrich, 1947; Pough, 1947). It is best-suited to measure numbers of the smaller, seasonally monogamous birds that engage in conspicuous territorial behavior. It is less adequate or altogether ineffective for measuring numbers in wide-ranging species, colonial species and species that depart markedly from monogamous mating systems.

Only brief discussion of the quantitative data is possible here. It seems evident from the descriptions of habitat and the species of birds that several pine forest and broad-leaved forest areas are more appropriately considered forest-edge, and we have treated them so (other than censuses 3, 5, 7-10, 13-16) in the comments that follow. Censuses 1-2 and 4-6 covered areas where pines were small or widely scattered and broad-leaved shrubs made up much of the vegetation; several areas also adjoined or included broad-leaved forest. It is notable that mature sand pine scrub, census 3, lacked most characteristic pine forest species. Broad-leaved forests of censuses 11 and 12 included many shrubby openings.

Pine forest censuses from mainland southern Florida show a breeding avifauna of about 15 species and an average population density of 45 breeding males per 40 hectares. These results are similar to the average population density found in pine flatwoods areas of southeastern Georgia, 42 breeding males per 40 hectares (Aldrich and Burleigh, 1946; Fleetwood, 1947a, b, 1948), but community diversity, about 22 breeding species, was somewhat greater in the Georgia areas. The pinelands of the Lower Florida Keys support an extremely low breeding population that includes no typical pine forest birds. On the basis of one census, pine forest on Great Abaco, Bahamas, has a breeding population that is less diverse than that of southern Florida, but more than twice as dense.

Nine censuses of areas in mainland peninsular Florida that we consider forest-edge habitats show an average density of about 110 breeding males per 40 hectares. Florida Keys areas have lower populations and fewer species. Vegetation of forest-edge areas, including those lumped here under that category, is so diverse that close comparison with bird populations of forest-edge habitats elsewhere is unrewarding.

Inspection of data from roughly comparable areas north of Florida in the eastern United States (*American Birds*) suggests that bird populations of forest-edge habitats in Florida are about one-third lower and perhaps no more than half as diverse.

The three available censuses of broad-leaved forests on the Florida mainland, all from the work of Woolfenden, *et al.*, in the Tampa area, have an average population density of 144 breeding males per 40 hectares and an average diversity of 16 breeding species. Breeding population density in one census from the Florida Keys is an order of magnitude lower. Comparison of the Tampa data with those from other broad-leaved forests of the southeastern United States (Woolfenden and Rohwer, 1969; Rohwer and Woolfenden, 1969) showed decidedly lower bird population density and species diversity in Florida. Kendeigh (1944) stated that population densities of 200 to 300 breeding males per 40 hectares and a breeding avifauna of about 30 species was typical of the deciduous forests of eastern North America.

To summarize, the diversity of breeding land birds is lower in mainland Florida than it is in comparable habitats elsewhere in eastern North America and is much reduced in all habitats of the Florida Keys. Species diversity in forest-edge in southern mainland Florida seems about the same as found in comparable habitats of the central and northern peninsula. Breeding population density is also markedly lower in Florida than it is in the adjacent southeastern coastal plain in broad-leaved forests and in forest-edge, but apparently not in pine flatwoods. Several southern Florida habitats, such as mature tropical hardwood forest, pine forest of the Lower Florida Keys and mature mangrove forest (Robertson, 1955), support extremely low populations of breeding land birds and have few generally distributed breeding species. Tramer (1974; 126-127) stated that bird species diversity within sample areas of forest habitat remained essentially constant from 45° N southward in the eastern United States even though the total diversity of breeding land birds on a regional basis decreased sharply. He stated further that, within the 45° to 25° belt, variation of within-habitat diversity resulted from local moisture and edaphic factors which affect vegetation structure. It seems plain from the above discussion that forest breeding bird diversity is much reduced in Florida (see also Tramer's (1974) Fig. 1) and that this reduction is a reflection, not of edaphic, but of historical biogeographic factors.

*Wintering Birds* - Winter bird censuses and Christmas Counts, sponsored by the National Audubon Society and published in *American Birds*, provide most of the quantitative data on wintering birds in southern Florida. Moseley (1969, 1970, 1971, 1972), in the only winter bird censuses conducted in southern Florida, found 14 to 24 species in densities of 192 to 293 birds per 40 ha in a Deerfield Beach park. Lowest density occurred during the severe winter drought of 1971 which suggests that prevailing hydrologic conditions significantly affect even the land birds of upland suburban areas. Winter censuses of natural habitats are available for central Florida areas near Tampa Bay (Wass, 1955 a,b), Lake Placid (Woolfenden, 1968, 1970 a, b, c, d) and Vero Beach (Kale and Webber, 1969 a, b). Altered habitats censused in central Florida in winter include a citrus grove (Kale and Webber, 1969 c) and a grazed pasture near DeLand (Loftin, 1970, 1971).

Studies that permit comparison of wintering and breeding bird population on the same areas (Table 7) have particular interest. As the authors of these studies also noted, population density was usually much higher and species diversity substantially greater in winter. Thus habitats in peninsular Florida that appear to be understocked with breeding birds have considerable value as wintering areas for land birds that breed in other parts of North America. We doubt, however, that wintering land birds are sufficiently numerous or localized to depress breeding populations.

Data assembled by Christmas Counts, one-day tallies during the holiday season of the numbers and kinds of birds within a circle 24 km in diameter, provide a mass of information of widely varying quality on the abundance and distribution of wintering birds. Since the first southern Florida Christmas Count in Miami in 1904, 242 counts have been held at 30 locations. Counts that have covered the same area for a period of 10 or more years are Coot Bay (23 years), Dade County (14), Fort Lauderdale (16), Fort Myers (17), Key Largo-Plantation Key (19), Key West (19), Lower Keys (22), Marathon (15), Monroe Station (11), Naples (12), Sanibel-Captiva Islands (12), Stuart (15), and West Palm Beach (22). Poorly controlled, or uncontrollable, variables of weather, number and ability of observers, counting methods, and coverage make Christmas Count data difficult to analyze quantitatively; and, in addition, the significance of any one-day tabulation is open to some question (Stewart, 1954; Arbib, 1967). Counts of more recent years that include greater detail on weather, habitat, time afield, and methods of coverage have considerable value for study of bird population trends and winter distribution (Arbib, 1967; Robertson, 1968), particularly because some of the variables of coverage can be controlled by weighting number of birds seen according to number of party-hours of observation. Several recent studies have utilized Christmas Count data (Bock and Smith, 1971; Bystrak, 1971), including one in Florida (Schreiber and Schreiber, 1973).

*Wading Birds* - Ten species of herons (excluding Cattle Egret), two ibises, a spoonbill and a stork nest in southern Florida. These species have particular historical significance and ecological importance. Although the record is woefully incomplete, more quantitative information is available on their population levels than for any other group of birds. Wading bird populations have changed drastically over the past century due to human activities, primarily hunting and habitat alteration. The total number of wading birds in southern Florida at various times can be crudely estimated as:

1870	2,500,000
1910	500,000
1935	1,200,000
1960	300,000
1970	150,000

Robertson (1965) discussed the principle causes of these fluctuations. The late 1870's saw the end of the primeval abundance of wading birds with the initiation of commercial plume-hunting which lasted for 30 to 40 years. With the cessation of hunting but the wetland habitat largely intact, the remnant populations of most species rebounded, reaching a new peak of abundance in the 1930's when Robert P. Allen and the National Audubon Society began detailed study of these birds. Since then, the progressive loss and deterioration of wetland habitat reduced wading bird numbers to about 10 percent of the reported level in the 1930's. A generally complete survey of southern Florida by the National Park Service and National Audubon Society in 1972 showed 128,400 breeding wading birds.

The underlying causes of these changes can be seen by comparing population levels in Florida Bay and coastal areas with those of the interior Everglades (Table 8) of Everglades National Park. (Note that this comparison does not include all southern Florida nesting populations of these species.) Whereas birds nesting in estuarine areas have increased in the past 30 years and are probably near carrying capacity, those nesting in interior wetlands of Everglades National Park have declined as their habitat became smaller and more unstable. Current and past population data on various species of wading birds follow.

The Roseate Spoonbill was severely reduced by plume hunting in the 1880's and thereafter. The Florida population was 513 birds in 1941 (Allen, 1942). The current population of about 2200 birds is restricted to Florida Bay. There has been a tendency towards westward movement of nesting colonies in the Bay, probably in response to destruction of former feeding areas along the Florida Keys. The present population is stable or increasing slightly.

The White Ibis was historically and remains today the most abundant wading bird in southern Florida. As Kushlan and Kushlan (in prep.) describe the changing abundance of this species, it suffered little from plume hunters, although colony disruption occurred, and continued abundant through the 1930's. In this period an average of 420,000 birds and a maximum near 660,000 birds nested in the southern Everglades. This represented 90 percent of the White Ibis nesting in 16 colonies through out Florida. The population declined thereafter and the traditional southern Everglades mangrove-edge colonies were especially reduced as nesting there became increasingly intermittent. For example, White Ibises nested in the southern Everglades in only 7 of the last 16 years. Complete surveys of southern Florida nesting colonies in the early 1970's found the following number of nesting birds: 1971 - 1600; 1972 - 60,300, including 35,600 in a single colony (Kushlan, 1973 a); 1973 - 40,200. The total southern Florida nesting population is therefore about 60,000 birds subject to considerable year to year variation.

The Glossy Ibis was rare in Florida as late as the 1930's. More recently it has increased in the state and also has extended its breeding range as far north as Long Island. Except for sporadic early records, nesting in southern Florida has been confined to Lake Okeechobee. Surveys of Lake Okeechobee in the early 1970's found no nesting in 1971 and 100 birds nesting at King's Bar in 1972. A significant colony movement into southern Florida occurred in 1973 when 1200 nested in Conservation Area 3 (Kushlan and Schortemeyer, 1974). The maximum southern Florida nesting population is probably less than 1500 birds of a Florida total of about 3500 birds.

The Wood Stork was little affected by plume hunting and remained abundant into the 1930's when the southern Florida nesting population exceeded 75,000 birds and the species nested in single colonies that exceeded 50,000 birds (Holt, 1933). The population declined irregularly through the 1950's in response to progressive loss of habitat. In the 20 years prior to 1961, nesting succeeded in 13 or 14 years, and, as of 1961, the total Florida population was more than 20,000 all but 2,000 of which nested in southern Florida colonies at Corkscrew Swamp and in the southern Everglades. Since the 1960-61 nesting season, the population has declined rapidly as few years had substantial reproductive output. This decline has been monitored closely by the National Park Service and National Audubon Society and is summarized in Table 9. As of 1974, a successful year, the southern Florida breeding population was 5800 birds, a 93 percent reduction since the 1930's and a 69 percent reduction since 1961.

The "Great White Heron", with the exception of a recent record from Charlotte Harbor (Bancroft, 1969), nests only in Florida Bay, the Florida Keys and, sparingly, in the Ten Thousand Islands. The population was much reduced by 1885 (Pierce, 1962) and reached a reported low point of about 150 after the 1935 Labor Day Hurricane (Sprunt, 1954: 24). The present population is about 2500 adults distributed as follows: 1750 in Everglades National Park; 500 in Lower Keys National Wildlife Refuges; 150 elsewhere on the Keys; and 100 elsewhere in southern Florida. The population is increasing slowly and near carrying capacity but is subject to periodic reduction by hurricanes. For example, hurricane Donna in 1960 killed about 40 percent of the Florida Bay population, but the loss was largely regained within two years.

The egrets and small herons (Great Egret, Snowy Egret, Louisiana Heron, and Little Blue Heron) today number around 40,000-50,000 birds. All were reduced by plume-hunting, recovered and then declined due to environmental pressure. Unfortunately, few recent data are available for the various species but they

appear to be decreasing, especially since the early 1960's, with the Snowy Egret probable declining most drastically.

The Reddish Egret was severely reduced and perhaps extirpated in Florida by plume-hunting and has increased slowly since the mid-1930's. Despite some evidence of recent return to its former Gulf Coast range (Bancroft, 1971), the Florida population of about 300 birds still nests primarily in Florida Bay.

*Other Rare, Endangered or Localized Species* - Although quantitative information on wading birds is incomplete, much less is known about most other threatened species. In this subsection we review population data on species for which some information is available.

The Brown Pelican has declined in most parts of its North American range but appears generally stable in Florida with a statewide nesting population of about 16,000. A statewide census conducted in 1968, 1969, and 1970 (Williams and Martin, 1970) showed that Brown Pelicans nested in 21 colonies in southern Florida, notably at Miguel Key, Estero Bay and Everglades City on the west coast and 18 locations in the Florida Keys. Williams and Martin placed the southern Florida breeding population at 946, 850, and 1245 respectively during the three years of census. The variation was mostly due to the timing of the Florida Keys censuses which located 746, 570 and 1090 birds. Probably 1100 can be considered a conservative estimate of numbers nesting in the Keys and 1300 for southern Florida as a whole. In an analysis of Christmas count data, Schreiber and Schreiber (1973) found that the wintering population in the Coot Bay area has remained generally stable, but the species has apparently increased on the Keys.

The Magnificent Frigatebird summers in Florida forming roosts numbering several hundred to several thousand birds. Harrington, *et al.* (1972) described how the proportion of adult males and females varies from area to area. Nesting in Florida was confirmed only in 1969, when a colony of about 100 pairs was found on the Marquesas Keys (Ogden, 1969). Forty nests were found in 1970 and about 100 in 1971 (Ogden 1970 a, 1971).

The Sooty Tern occurs worldwide on warmer seas. The tropical Atlantic form of this pelagic species nests in the United States intermittently and in small numbers on islands off Texas and Louisiana and regularly at Dry Tortugas. Robertson (1964 a) summarized population estimates from 1902 through 1956. Prior to protection in 1903, commercial eggging and disturbance had reduced the population to around 5000 adults. The population increased thereafter and is now estimated to number 80,000 breeding adults. The movements and behavior of Tortugas Sooty Terns have been discussed by Robertson (1969) and Dinsmore (1972).

The Roseate Tern nests in Florida only in the Florida Keys and at Dry Tortugas. Population estimates of the Tortugas colony from 1917 through 1963 were summarized by Robertson (1964 a). The maximum population there was 450 birds in 1959, but nesting is subject to frequent failure due to storm tides and predation. Other recent nesting records from the Florida Keys indicate four nesting sites used intermittently by 10 to several hundred birds. The total Florida population is 250 to 300 breeding pairs, possibly maintained by recruitment from more successful Bahaman colonies.

The Noddy Tern is a pantropical seabird which in Florida nests only at Dry Tortugas. Population estimates from 1902 through 1962 were tabulated and discussed by Robertson (1964 a). The nesting population has shown wide fluctuations with a low of fewer than 300 birds as recently as the late 1940's. The fluctuations are not well-understood but resulted in part from predation by rats and damage to bushy vegetation by hurricanes. The population has increased slowly over the past 25 years and now numbers approximately 3000 breeding adults.

The endemic Florida subspecies of the Everglade Kite is the North American race of a species widespread in the New World tropics including Cuba. The remnant population, which occurs primarily in Lake Okeechobee, the Conservation Areas and Everglades National Park, was estimated to be down to not more than 100 and probably less than 60 birds by 1950 (Sprunt, 1950). Censuses conducted by the Fish and Wildlife Service placed the minimum population at 20 in 1966 (Steiglitz and Thompson, 1967), 47 in 1967 and 56 in 1970 (P.W. Sykes, Jr, pers. comm). In 1969 the total population was estimated to be about 120 (Dept. Interior, 1973). Kites have recently reinvaded their former range in the St. John's marshes where a nest was found in 1972 for the first time since the 1930's. In 1973, 22 nests were found in southern Florida, all at Lake Okeechobee with an additional 6 nests in the St. John's marshes (Sykes, pers. comm).

The Short-tailed Hawk is a relict tropical species found in the United States only in Florida. Little is known about population numbers in southern Florida. Moore, *et al.* (1953) presented data showing an increase in sightings from 1932 to 1951, but Ogden (1974) in his detailed study of the biology of the species noted that it is typically scarce throughout its lowland range. Four nesting locations are known in southern Florida (Ogden, 1974: Fig. 1) where nearly the entire Florida population winters.

The Bald Eagle as a breeding species in southern Florida is almost entirely an inhabitant of coasts and estuaries (younger birds and adults outside the winter breeding season often range inland) and its population has declined in the face of coastal development. The present estimated breeding population of southern Florida is 66 to 77 pairs distributed as follows: Lower Florida Keys, 2 to 4 pairs; in and near Everglades National Park, 13-year average of 52.7 pairs, range 49 to 55 pairs; Gulf coast of Collier and Lee counties north of the Park to the Caloosahatchee, 8 to 12 pairs; east coast north of the Park to the St. Lucie Canal (probably none between Palm Beach and southern Biscayne Bay), 1 to 3 pairs; interior, mainly eastern edge of the Big Cypress, 2 to 5 pairs. The species has survived better in southern Florida than it has anywhere else in the state, but the present population probably is reduced by at least 40 percent from original numbers and coastal nesting sites outside the Park, the upper Ten Thousand

Islands and possibly the Lower Keys are likely to be abandoned within the next decade, Productivity data indicate that the Park population is reproducing at a rate adequate to maintain its numbers (Sprunt, *et al.*, 1973).

The Osprey population in Florida Bay has been censused by J.C. Ogden who found 141 active nests in 1968 and 138 in 1969 (Ogden, 1970 b). This population is stable (Henny and Ogden, 1970) or slightly increasing. The entire population in and near Everglades National Park is estimated to be 200 nesting pairs.

The Florida Sandhill Crane is a rare disjunct subspecies that nests primarily north of southern Florida. While the northern Florida populations have been studied extensively (Williams, 1972), less is known about southern Florida birds. In the Loxahatchee National Wildlife Refuge, Thompson (1970) found 61 nests during five years of censusing from 1964 through 1968.

The "Cape Sable" Seaside Sparrow is an endangered subspecies found only in extreme southern Florida. Historically it nested in prairies inland of the Gulf coast mangrove zone south of Carnestown, Collier County, and inland to the Everglades, and on Cape Sable (Stimson, 1956). Harold W. Werner (1971, unpubl.) has documented the present status of this bird. His surveys conducted in 1970 and 1973-74 found a 95 percent reduction in the Gulf coast population since the early 1950's. In the Ochopee colony, Werner found 10 singing males in 1970, 5 in 1973 and 1 in 1974. The 5 to 10 acre colony on Cape Sable with at least 11 birds found in 1970 (Werner, 1971) may no longer be extant. The recently discovered population in Taylor Slough (Ogden, 1972) contains over 1000 birds (Werner, pers. comm.).

#### Ecology of Wading Birds

In this section we discuss the ecology of the long-legged wading birds of the order Ciconiiformes, namely the Wood Stork, White Ibis, Roseate Spoonbill, Great Blue, Green, Snowy and Reddish egrets, and Least and American bitterns. We do not comment on the primarily terrestrial Cattle Egret (see Jenni, 1969; Browder, 1973; and Fogarty and Williams, 1973). The ecology of three wading birds has been studied in some detail in southern Florida: Roseate Spoonbill (Allen, 1942), Wood Stork (Kahl, 1962, 1964; Kushlan, Ogden and Higer, in press; Ogden, Kushlan and Tilmant, 1974, in prep.), and White Ibis (Kushlan, in prep. a). Most of the existing ecological information on southern Florida herons is summarized in the contributions of R.P. Allen and A.J. Meyerriicks to Palmer (1962).

*Seasonality* - Distribution and activity of wading birds in southern Florida show a marked seasonality. Florida, especially southern Florida, supports substantially increased numbers of wading birds in winter. Great Blue Heron, Black-crowned Night Heron, Green Heron, and Least and American bittern populations that nest throughout the East and Midwest winter in and south of Florida. Wintering White Ibis, Great and Snowy egrets, Yellow-crowned Night, Little Blue and Louisiana herons are derived from Atlantic and perhaps Gulf coast breeding populations. For most of the latter species, migration to Florida in winter is a return to the area from which their recent range expansions originated. These birds enter Florida in fall and migrate north again from February to April.

Other species migrate into southern Florida to nest. Wood Storks are present in numbers only in winter and spring, arriving in November and returning north after they complete nesting, as late as June, but usually earlier. Roseate Spoonbills show similar seasonality, but seem to move into southern Florida from the south, particularly from Cuba. They arrive in late September through October and nest primarily from November through January. Unlike Wood Storks, some adult and many juvenile Roseate Spoonbills remain in southern Florida through the summer. Reddish Egrets also remain throughout the year but additional birds from the West Indies apparently visit the Florida coast in summer. All North American ciconiiforms but one occur in southern Florida in winter and all these, with the probable exception of the American Bittern, are also represented by nesting populations.

Another aspect of the seasonality of wading birds is intra-regional movement. This phenomenon has been documented for the Wood Stork (Ogden, Kushlan and Tilmant, 1974; Browder, 1974) and the White Ibis (Kushlan, in prep. a) but occurs also in the herons. Everglades Wood Storks arriving in southern Florida in November feed first in drying marshes just inland from the Gulf Coast, then move to similar southern coast feeding grounds, and finally to the Everglades in the spring. Corkscrew Swamp Storks have an analogous sequence of movements in the Big Cypress Swamp ending in spring in the marshes around Lake Okeechobee. White Ibis, and the smaller herons, follow a complex pattern of movements through the coastal marshes, Big Cypress and Everglades. In all cases this movement corresponds to the pattern of water level decline in the dry season, with birds exploiting a succession of suitable feeding areas as various parts of South Florida dry. With the onset of the rainy season, many wading birds especially White Ibis migrate to coastal roosts and feeding grounds and many may, like the Wood Stork, leave southern Florida but there is no direct evidence for this. During high water periods, only the larger herons (Great Blue Heron, Great Egret) and the small species (Green Heron, Least Bittern) that feed from emergent vegetation remain in any numbers in the Everglades.

*Nesting Seasons* - There is a general division of wading bird breeding populations into winter (November-February) and spring (March-June) nesters. Birds that nest and feed in Florida Bay, and the larger species with prolonged development periods tend to nest in winter whereas smaller species of inland hab-

itats nest in spring. Specifically, in Florida Bay, Roseate Spoonbills and Reddish Egrets begin nesting in October and December respectively. "Great White" and Great Blue herons, which breed in Florida Bay in small numbers nearly year round, have their peak nesting in early winter with "Great Whites" peaking before Great Blues. Florida Bay Great Egrets also nest in December.

Larger species nesting at inland sites also nest in winter. Great Blue Herons and Great Egrets begin nesting in December but may continue establishing nests through April or May. Wood Storks traditionally nested in November and December, but have delayed nesting into spring in recent years. Smaller herons and White Ibis typically nest in spring.

*Food Availability* - Conventional ecological wisdom holds that bird breeding seasons are timed so that maximum food resources are available to feed the young. Although there is little information on food availability in Florida Bay, the winter nesting of herons and other piscivorous birds such as Ospreys, Bald Eagles, Brown Pelicans, and most Double-crested Cormorants, implies that winter is the optimal nesting time there for birds utilizing such resources. Alternatively, food may be nearly constant year-round and other factors may dictate nesting season. Inland wading bird nesting firmly supports the rule. The typical winter and spring nesting seasons of inland wading birds coincides with the drying of the vast interior wetlands of southern Florida.

Drying begins in early winter and continues at an increasing rate through May or June until, in the usual year, much of the interior is dry. Drying progresses from supratidal marshes near the coast to shallower areas of the Big Cypress Swamp and the open Everglades marsh, and finally to remnant Everglades pools, the deeper sloughs of the Big Cypress and ponds within the mangrove belt. Fish and aquatic invertebrates become more available to wading birds as water becomes shallower and as immigration causes fish densities to increase in the deeper pools. The Wood Stork, because it feeds by tactile groping, is the species most dependent on the availability of highly concentrated fish in residual pools. Wood Stork nesting is apparently controlled by food availability which in turn is a function of water level recession (Kahl, 1964) and fish concentration. A receding water level is so important that time of nesting is correlated with the rate of decline, and small increases in water level will cause Wood Storks to desert rookeries (Kushlan, Ogden and Higer, in press). Herons probably also depend, to a lesser degree, upon dry season food concentration. White Ibis rely heavily on drying wetlands for successful spring nesting, but this species depends more on the availability of shallow water *per se* than on highly concentrated food supplies (Kushlan, in pres. a).

*Hydrologic Determinants of Nesting Success* - Wading bird populations that nest inland are presumably adapted to the typical dry season pattern of water level fluctuation, a slow winter decline followed by a rapid drop in April and May and a rapid rise with the onset of the rainy season in early June. Deviations from this pattern, both man-caused and natural, now occur about as frequently as the typical situation. Droughts brought on by an early dry season, less than normal winter rainfall, or a late wet season seriously disrupt wading bird nesting. In general, most inland and coastal heron colonies fail to form or nest unsuccessfully in years of general and early drought. White Ibis also fail to nest or nest in smaller numbers in drought years but may postpone nesting until summer when smaller colonies form along the coast. Wood Stork nesting traditionally failed in drought years and the storks left southern Florida, as do many species of wading birds under such conditions. Since 1962, however, Everglades Wood Storks have nested successfully only three times, all in drought years. We suggest that this reflects changed conditions in the highly altered interior wetland ecosystem of southern Florida. Drought also affects other birds of interior marshes such as the Anhinga, Everglade Kite and Limpkin which tend to disperse from southern Florida or fail to nest during droughts.

Prolonged high water apparently benefits smaller herons such as the Least Bittern (Kushlan, 1973 b) and other marsh birds such as Limpkins and Pied-billed Grebes, but most wading birds are adversely affected. High water levels in 1970 led to winter nesting of Pied-billed Grebes at a pond in the Big Cypress but inhibited use of the pond by wading birds (Kushlan, 1972). Heavy rainfall and year-round surface water discharge caused a protracted period of high water in the Everglades from 1968 through 1970. Whereas prior to this period, Wood Storks had nested successfully in years of high surface water discharge (Robertson, 1964 b), nesting failed in these years because no drying occurred. White Ibis and other species were similarly affected. Conversely during this period, Limpkins increased in numbers (J.C. Ogden, pers. comm.). Thus extended periods of high water have an impact on bird populations as drastic as that of drought.

*Food Ecology* - Although the relation of wading bird nesting to food availability is known in the broad stroke, details of food ecology, including data on food actually consumed and on the competitive relationships of wading birds, are generally unavailable. Knowledge of food consumption is lacking primarily because it requires analysis of stomach contents or regurgitation samples, and two of the classical studies of wading bird ecology in South Florida dealt with rare or diminishing species, Allen (1942) on Spoonbills and Kahl (1964) on Wood Storks, and provide little such information.

In Florida Bay and adjacent habitats fish, crustaceans and insects apparently provide most of the food of Roseate Spoonbills (Allen, 1942). Observations by Recher (1972) in Florida Bay indicate that "mullet", "mojarra" and "killifish" are the most common foods of Snowy Egrets and Louisiana Herons, while

"lizardfish", "pipefish" and "eels" were taken by Little Blue Herons.

Few data exist on the prey taken by herons in interior wetlands, but recent studies have clarified the food habits of the Wood Stork and White Ibis. Ogden, Kushlan and Tilmant (in prep.) collected regurgitated food from nestling and adult Wood Storks and compared these samples with quantitative measurements of prey available at sites where Wood Storks were feeding. Despite their non-visual foraging behavior, Wood Storks appear to select larger fish and certain species. Fish comprise nearly the entire diet, and, although more than 30 prey species occurred in the samples, five groups (sunfish and four other species of fish) made up 84 percent of the biomass and number of prey consumed. Many of the most abundant fish in the areas where Wood Storks fed were insignificant in the diet. The food of the White Ibis in southern Florida (Kushlan, in prep. a) differs in various habitats, especially between inland and coastal localities. Crayfish and crabs respectively are the dominant dietary component at these locations. White Ibis also prey upon aquatic insects, mollusks and in all more than 50 species of organisms. They consume fish only from dense concentrations and even there fish are represented in the diet below their availability in the environment. Thus the White Ibis can be considered a generalized feeder, yet one that tends to specialize on crustaceans.

Competition for food among wading birds has been little studied in southern Florida. The Wood Stork and White Ibis obviously consume very different prey, but the situation in herons probably is more complex. The best exposition of the mechanisms by which competition may be avoided by herons in Florida Bay is a popular article by Meyerriecks (1962). He shows that various species forage at different depths and by different techniques and therefore presumably utilize different segments of the available resources. A similar tendency for differences was shown by a quantitative analysis of heron foraging in a pond in the Big Cypress Swamp (Kushlan, in prep. b). Herons varied in size, feeding location or behavior. There was also a difference in timing of use of the pond. Black-crowned Night Heron and Little Blue Heron feeding peaked before the onset of utilization by the mixed species aggregation and may have eliminated from the pond by members of the aggregation.

*Environmental Impact* - One of the most important aspects of wading bird ecology is the impact of these birds on the environment and their role in ecosystem function. Certainly such large predators numbering formerly, in the millions and presently in the low hundreds of thousands of individuals must have a dominant influence on energy flow in the ecosystem. In fact, the nearly unique ability of the South Florida ecosystem to support such large numbers of 14 species of superficially similar secondary and tertiary consumers on a resource base that is reduced in species diversity by biogeographic factors is generally unappreciated.

Study of the functional role of wading birds in southern Florida ecosystems has only begun. The impact of a wading bird aggregation on the fish community of a pond has recently been studied (Kushlan, in prep. b). Analysis of the changes in the fish community before and after an episode of mixed-species predation showed that wading birds consumed 75 percent of the available biomass of fish. More important is the apparent function of this predation. In a year when extended high water forced wading birds to abandon the area before the pond became shallow enough for feeding, a fish kill eliminated 93 percent of the biomass and all but 6 of the 26 species of fish (Kushlan, 1974). In contrast, predation reduced fish biomass less and did not eliminate any species. The implication is that wading bird predation can crop fish populations to levels compatible with survival through a normal dry season. Thus while concentrated fish are necessary for successful nesting of wading birds, the predation pressure of the birds may serve as a mechanism to sustain the prey stocks themselves.

The impact and role of wading birds in the energetic structure of the south Florida ecosystem is little known at present. However the massiveness of this impact can be seen in the energy requirements for nesting of the two best known species. If White Ibis and Wood Storks nested in the number that they did in their most successful of recent years, 1972 and 1974, respectively, they would together require in excess of 3 billion kilocalories or approximately 2500 metric tons of food (Kushlan, in prep. a). As the impact of the remaining 12 species of wading birds is not known and the secondary productivity of South Florida habitats has not yet been studied, the meaning of this energy requirement to the total system is undeterminable.

#### Effects of Natural and Man-Caused Disturbances

Recurring natural disturbances, particularly the extreme intensities of hurricanes, fires, floods, droughts, and freezes, dominate the southern Florida environment. Their influence doubtless long antedates man in the region, but modern man's activities have complicated (without truly controlling) the effects of some natural disturbances and man has introduced equally pervasive, if sometimes less obvious, environmental disturbances of his own. We discussed earlier how extremes of water level variation affected the wading bird populations of interior wetlands. Here we look in a cursory way at the effects upon birds of other major natural and human disturbances. Concerning the natural disturbances, it is important to realize that the avifauna presumably evolved in their presence and is more or less adapted to them. Any species that were altogether intolerant of recurring disturbances by hurricanes, fires, etc., must have disappeared long ago.



*Hurricanes* - Hurricanes have two contrasting facets of ornithological interest. They are widely believed to be a major agent in both the extinction and colonization of birds, particularly of land bird populations on islands. Because most of the West Indies and southern Florida lie within the Atlantic tropical cyclone belt, hurricanes have been invoked frequently to explain anomalous patterns of bird distribution or the otherwise unaccountable absence or disappearance of species on Caribbean islands. It appears to us that the record of hurricanes and birds in Florida provides little support for either of the above views, and that the supposed West Indian examples of extinction or colonization of birds caused by hurricanes are not well-proved.

Intense hurricanes in southern Florida cause locally heavy mortality of birds along low coasts and on islands, especially among nesting or roosting concentrations of water birds (Robertson and Paulson, 1961; Robertson and Muller, 1961; Owre, 1967). But, despite evidence that hurricanes often kill large numbers of birds, we can find no evidence in southern Florida of a bird population that was extirpated even briefly or locally by a hurricane (see "Great White Heron" and "Cape Sable" Seaside Sparrow).

Huntington and Barbour (1936), in one of the few West Indian observations of the effects of a specific storm, found that many land birds were much less numerous at Soledad, Cuba, several months after a hurricane and referred to "the almost complete disappearance" of some species from Bahaman islands following severe storms. Such instances can be matched in southern Florida, but are examples of heavy mortality, not extirpation. Suggestions that West Indian hurricanes may account for impoverished avifaunas on some islands (Bond, 1946), the local disappearance of bird species (Paulson, 1966), and even the fact that some species found in Bahaman cave deposits have not persisted in the area (Wetmore, 1937) seem to be entirely speculative. It cannot be doubted that small, isolated populations are vulnerable to extinction; nor do we doubt that hurricanes are a possible agent of extinction. We suggest, however, that hurricanes are a longstanding fact of life for the birds that inhabit the Caribbean hurricane belt, and we suspect that the principal way in which hurricanes may extirpate bird populations is indirect, through habitat change (see Craighead and Gilbert, 1962), rather than by sudden annihilation. Outside the usual tropical cyclone belt, as in Grenada (Bond, 1959) and Tobago (French, 1973) direct effects of the occasional hurricane upon bird populations may well be more severe.

Perhaps because birds have at times been seen in numbers in the calm central eye of a hurricane, Bond (1934, 1948, 1963) and other authors have attributed discontinuous distributions of many West Indian land birds to the vagaries of hurricane transport, including some suggested movements (*e.g.*, Florida to the Bahamas, Greater Antilles to islands of the southwest Caribbean) requiring storm tracts that rarely occur. The one case of inter-island colonization associated with a specific storm involved the hurricane of 3 September 1930 thought to have transported the American Kestrel, Mourning Dove, White-winged Dove, and Smooth-billed Ani from Hispaniola to Mona Island (Bond, 1946). It must be noted, however, that Mona lies up-range of Hispaniola along the tract of this storm (Cry, 1965: 95), hence the birds presumably could not have been carried in the eye of the hurricane.

Data for the last 100 years (Cry, 1965; Dunn, 1965; Sugg, 1966, 1967; Sugg and Pelissier, 1968; Sugg and Herbert, 1969; Simpson and Sugg, 1970; Simpson and Pelissier, 1971; Simpson and Hope, 1972; Simpson and Herbert, 1973; Herbert, 1974) show that 112 tropical storms crossed or passed near the coast of peninsular Florida after first crossing or passing near the coast of Cuba or the Bahamas. Any of these storms may conceivably have carried birds from the near West Indies to Florida and, because birds thus transported might not be found until long after the storm, it is almost impossible to show that hurricanes were not involved. Analysis of 134 bird records of known date for the past century (most of these shown in Table 5) suggests, however, that hurricanes have not been a major vector of West Indian birds to southern Florida.

To begin with, the positive evidence of hurricane transport of West Indian birds to southern Florida is minimal. Fewer than 20 records in the sample can be associated, even speculatively, with a specific tropical storm. Assuming, as seems reasonable to us, that most West Indian casualties were found within a year of their arrival, 57 of the records (43 percent) occurred within the one-year periods (1 June through 31 May) that included and followed the 36 hurricane seasons of the past century in which no tropical storms crossed from the near West Indies to Florida. Assuming, as also seems reasonable, that effective transport required that the storm center cross coastlines on both sides of the Straits of Florida, eliminates an additional 23 records (17 percent) that occurred in years when storms merely passed near one or both coasts. Other records can be questioned on the basis that a given storm did not cross the West Indian range of the bird species found in southern Florida during the year that followed the storm.

We do not suggest that hurricanes never carry West Indian birds to Florida, but merely that hurricane transport, particularly of small land birds, seems to have been accepted rather uncritically in this instance and in general. During hurricanes most land birds seek shelter on or near the ground (Sutton, 1945; many more recent observations in *American Birds*), and, despite the enormous energy of hurricanes, the common vision of such birds being swept away by the winds is probably incorrect. It seems obvious that no small bird could survive long in the vortex of a hurricane, and it is generally assumed that birds are transported in the eye of the storm. The slow forward movement of tropical storms (storm centers commonly take 12 hours or longer to cross the sea gap between Florida and the West Indies) thus becomes a critical factor in the potential hurricane transport of small birds. The species most commonly encountered in the eye of hurricanes seem to be seabirds, land birds that feed on

the wind such as the swifts and swallows, and migrants that may have had sufficient fat reserves to sustain extended flight. The subject clearly needs more study, but we suggest that the likelihood of successful colonization across a sea barrier as the result of a hurricane is much smaller. If specific weather events figure in the occurrence of West Indian birds in Florida, we suggest that directional airflows, such as autumnal northeast storms, are more likely to be involved than hurricanes.

*Fire and Other Natural Factors* - Fires, both natural and man-caused, occur commonly in the interior wetlands and pine forest vegetation types of southern Florida, but direct mortality of birds as a result of fire is probably limited almost entirely to nestlings of species that nest on the ground or in low vegetation. As with hurricanes, the indirect effects of fire upon vegetation are undoubtedly of greater importance to bird populations than any mortality that may result from the fire. In general, fire tends to maintain pine and marsh vegetation against invasion by hardwood shrubs and should favor birds of more open areas at the expense of forest-edge species. Emlen's study (1970) of bird populations in unburned and recently burned pine forest suggested, however, that even the indirect effects of a single fire may be insignificant.

Occasional cold spells in southern Florida damage native vegetation and sometimes cause heavy mortality of fish, and from central Florida northward in the Southeast these episodes may also result in serious losses to wintering populations of insectivorous birds. In southern Florida, the stress imposed by freezes is usually too brief to have serious effects on bird life. Resident and migrant land birds that feed on insects and fruit probably are more severely stressed after hurricanes, which commonly defoliate coastal forests, than by the infrequent freezes. Serious red tide incidents occur periodically along the central Gulf Coast of Florida, but are relatively infrequent in southern Florida and none is known to have affected birds. Disease no doubt causes steady, inconspicuous losses to bird populations, but the only large-scale avian mortality from disease reported from southern Florida was an outbreak of fowl cholera that killed about 5000 American Coots and about 100 water birds of other species (Klukas and Locke, 1970).

*Habitat Change* - Man's principal impact on southern Florida bird life has come through large-scale alteration of habitat, in extreme cases amounting to the virtual obliteration of native vegetation over extensive areas. Effects have been greatest in uplands near the coast, but the area of estuarine interior wetlands has also been reduced significantly. The fate of the rockland pine forest of southern Dade County illustrates how recent and complete the habitat changes have been in some instances. Comparison of aerial photographs of 1940 and 1972 shows that urban and agricultural development removed nearly 90 percent of the pine forest south of Sunset Drive (South Miami), excluding about 25 km<sup>2</sup> of pine within Everglades National Park, mostly within the past 20 years. Nearly all that remains consists of thinned stands of mature pines in suburban yards, where the expectancy of further life is about 10 to 15 years for individual trees and scattered, small patches of natural forest most of which have a dense understory of exotic hardwoods. As reproduction of pine is rare in either situation, disappearance of theremnant stands within about 20 years is predictable even without additional disturbance by man.

Other southern Florida vegetation types that have been reduced in area by 50 percent or more include sand pine scrub, the cypress belt along the east edge of the Everglades, tropical hammock forests, both of the southeast coast and the Upper Florida Keys, and beach and sand dune vegetation along both coasts. Other habitats, such as the prairie types northwest of the Everglades, have been extensively altered by removing saw palmetto and replacing native grasses with introduced pasture grasses.

Quantitative data on the effects upon bird populations of these massive habitat changes are lacking for southern Florida. Studies in central Florida (Table 7) indicate that some man-made habitats, such as citrus groves, support fairly dense and diverse populations of native birds. In general, suburban habitats (Woolfenden and Rowher, 1969: 12-25) have much higher total bird populations than the natural communities that they replaced, but a much lower diversity of species. General observations in southern Dade County indicate that, with the removal of pine forest, some former pine forest species (Blue Jay, Common Grackle) have become primarily birds of suburban habitats; many species (raptors, Chuck-will's-widow, Hairy Woodpecker, Eastern Kingbird, Common Crow, Loggerhead Shrike, Pine Warbler) have largely disappeared; and others, including some that did not originally inhabit pine forests (Smooth-billed Ani, Bobwhite, Mourning Dove, Eastern Meadowlark, Boat-tailed Grackle, Red-winged Blackbird) have increased in the habitat provided by pastures and abandoned farmlands.

*Exotic Birds* - As recent studies by O. T. Owre and his students (Owre, 1973; Carleton, 1971) have pointed out, man-created suburban habitats of southeast Florida are dominated by a vegetation liberally selected from the flowering and fruit-bearing plants of the world tropics, and provide ecological niches made-to-order for many of the exotic birds that escape or are released from the stream of birds imported through Miami. Besides longer established exotics, such as the Starling and House Sparrow, the breeding land avifauna of southeast coast suburban areas now includes the Canary-winged Parakeet and at least five additional species of parrots, Red-whiskered Bulbul, Hill Myna, Spotted-breasted Oriole, Blue-gray Tanager, and Java Sparrow. Exotic birds frequently seen at large, but not yet known to breed could easily double the present list. A few additional species are locally established elsewhere in southern and central Florida, principally in suburban areas. The future course of the establishment and spread of

exotic birds and their possible competition with native species is unpredictable, but potential problems, both of damage to crops and displacement of native birds, are evident.

*Other Man-Caused Disturbances* - Birds in southern Florida thus far have largely escaped the more serious effects of several disturbances man has introduced in the environment. Lighthouses off the Florida Keys have long taken their toll of migrating birds (Merriam, 1885), including some kills of major proportions (Bennett, 1909), but few kills at TV towers, the modern hazard to migrant birds, have occurred in southern Florida. Oil spills critically threaten marine and estuarine water birds in many areas and are a potential threat in southern Florida, but we know of only one serious recent incident. Oil dumped from a freighter grounded near Dry Tortugas in January, 1964, killed several hundred water birds of about 10 species (N.P.S., 1964). Because relatively little pesticide sampling of birds has been done in and near southern Florida (Schreiber and Risebrough, 1972; Krantz, *et al.*, 1970; Wiemeyer, *et al.*, 1972; Lincer and Salkind, 1973; Ogden, *et al.*, 1974), and because the sources and fate of organochlorine chemicals (DDT and other chlorinated pesticides, polychlorinated biphenyls) in Florida ecosystems are incompletely understood, it is much too early to assess effects on bird populations. Disturbingly high levels of persistent organochlorides have been found in the eggs of several estuarine birds, but no decline in southern Florida populations of the species considered most susceptible (Brown Pelican, Bald Eagle, Osprey) can be unambiguously charged to chemical contamination. Misuse of the highly toxic, but non-persistent, organophosphate pesticides has caused occasional massive direct bird mortality in southern Florida, as in the recent kill of some 10,000 Robins near Homestead (Lee, 1972; Stevenson, 1972).

#### Summary

This paper reviews present knowledge of southern birds emphasizing faunistic and ecological data. The presently available published summaries of Florida birds are both dated and incomplete. Especially important among the missing data are unreported specimens in museum collections.

About 60 percent of the southern Florida avifauna consists of migrant or winter resident species. Southern Florida wetlands are an important wintering ground for water birds. Upland habitats are less significant to wintering birds, but a review of available quantitative data suggests a notable increase in abundance and diversity of land birds in winter.

The native breeding avifauna is composed of 116 species. Contrasted with nearby states, Florida has a more diverse fauna of water birds, but it has fewer species of breeding water birds in the interior wetlands than occur in Cuba. Southern Florida has relatively few land birds reflecting a pattern of progressive southward decrease in the diversity of breeding passerines through the southeastern coastal plain and the Florida peninsula. This impoverished avifauna is characterized by domination by birds of continental origin, by range limits that show little relation to ecological features, by lack of replacement by similar species southward, and by a small contingent of species of West Indian origin.

Southern Florida was eliminated as land bird habitat during full interglacial periods of the Pleistocene. However the Pleistocene fossil record from northern Florida suggests that the Pleistocene avifauna was much like the present avifauna. We suggest that during the last glacial period Florida was populated by an upland, continental fauna and that the Everglades is a relatively recent feature related to lowered land elevation relative to sea level.

Forty-four bird populations have undergone recent change of breeding range limits. The general pattern is withdrawal of continental species, except for some exploiting man-made habitat changes, and expansion of the ranges of West Indian species. Future West Indian invasions and range expansions are likely. The depauperate land bird fauna seems explainable only as the early stages of a dynamic shift from a continental to a West Indian avifauna controlled by changing climatic conditions.

Review of quantitative information on southern Florida breeding birds shows that the southern Florida avifauna is not only impoverished but lacks a number of adaptive types and has much lower breeding bird densities in broad-leaved forest and forest-edge habitats, although not in pinewoods, than occurs in similar habitats elsewhere in the Southeast. Quantitative data on wading bird species and other rare, endangered or localized species are also reviewed.

Wading bird populations are characterized by seasonal influx of wintering birds and intra-regional migrations in response to lowering water levels during the dry season. Species utilizing the interior wetlands nest during the dry season when food becomes available by the concentration of aquatic animals in remnant pools as water levels fall. The success of wading bird nesting, particularly of the highly sensitive Wood Stork, depends on the seasonal hydrologic cycle and is disrupted by both droughts and extended high water.

Hurricanes seem to have played little role in transporting West Indian birds to Florida and have not directly extirpated bird populations, although dramatically altering some habitats. Neither fire, frost, nor disease seriously affect southern Florida bird populations. However man-caused changes, particularly habitat annihilation, have had profound effects.

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TABLE 1

SUMMARY OF THE STATUS OF BIRDS THAT OCCUR  
REGULARLY IN SOUTHERN FLORIDA

Category	Number of Species
<u>Wintering and migrant species</u>	<u>180</u>
Water birds	74
Land birds	106
Non-passerine	14
Passerine	92
<u>Breeding species</u>	<u>116</u>
Water birds	43
Land birds	73
Non-passerine	37
Passerine	36
<u>Total species</u>	<u>296</u>

TABLE 2  
BREEDING AVIFAUNA OF SOUTHERN FLORIDA

Species	Habitat <sup>1</sup>	Comment
WATER BIRDS -		
Pied-billed Grebe	7	More common in wet years.
Brown Pelican	8	-
Double-crested Cormorant	7, 8	-
Anhinga	7	-
*Magnificent Frigate-bird	8	Marquesas Keys; 1st nested, 1969.
Great Blue Heron	7, 8	"Grt. White H." mainly 8.
Green Heron	1, 7, 8	-
Little Blue Heron	7, 8	-
Cattle Egret	6a, 7, 8, 9b	First nested, 1953.
*Reddish Egret	8	Mainly in Florida Bay.
Great Egret	6, 7, 8	-
Snowy Egret	7, 8	-
Louisiana Heron	7, 8	-
Black-crowned Night Heron	7, 8	-
Yellow-crowned Night Heron	7, 8	-
Least Bittern	7, 8	-
Wood Stork	7, 8	-
*Glossy Ibis	6, 7, 8	-
White Ibis	6, 7, 8	-
*Roseate Spoonbill	7, 8	Nests only in Florida Bay.
*Fulvous Tree Duck	7, 8	First nested, 1965.
Mottled Duck	7	-
Wood Duck	2, 7	-
Sandhill Crane	6, 6a, 7	-
Limpkin	7	-
King Rail	7	-
Clapper Rail	1, 9	-
Purple Gallinule	7	-
Common Gallinule	7	-
*American Oystercatcher	9	Rare breeder on Gulf coast.
Snowy Plover	9	Gulf beaches, now very rare.
Wilson's Plover	2, 9a	-
*Killdeer	6a, 9a, 9b	Extending south; 1st nested, 1939.
*Willet	9	Few definite nesting records.
Black-necked Stilt	7, 8, 9, 9a	-
Laughing Gull	9, 9a, 9b	-
*Gull-billed Tern	7, 2, 9a	-
*Roseate Tern	9, 9a	-
Sooty Tern	9	Nests only at Dry Tortugas.
Least Tern	9, 9a	-
Royal Tern	9	Extirpated; last nested c. 1890.
Sandwich Tern	9	Extirpated; last nested c. 1890.
Noddy Tern	9	Nests only at Dry Tortugas.

TABLE 2--continued

Species	Habitat <sup>1</sup>	Comment
LAND BIRDS (Non-passerine) -		
Turkey Vulture	general	See footnote 4.
*Black Vulture	general	Not in Florida Keys.
*Swallow-tailed Kite	1, 2, 3, 3a, 5, 5a	-
Everglade Kite	7	-
*Red-tailed Hawk	3, 5	Not in Florida Keys
Red-shouldered Hawk	1, 2, 3, 5	-
*Short-tailed Hawk	1, 2, 3, 5	Few nest in southern Fla.
Bald Eagle	7, 8	-
Osprey	7, 8	-
Carcara	6, 6a	Few nest in southern Fla.
*American Kestrel	3	May no longer nest in so. Fla.
*Bobwhite	5, 3a, 5, 5a	Not in Florida Keys. <sup>5</sup>
*Turkey	2, 3, 4, 5	Not in Florida Keys.
3+ White-crowned Pigeon	1, 4	Mainly in Florida Keys.
+ Zenaida Dove	1 <sup>2</sup>	Nesting, Keys, 1832; extirpated?
+ Mourning Dove	3, 3a, 5, 5a	-
Ground Dove	5, 5a, 9	-
Carolina Parakeet	2, 4, 5	Extinct; last seen c. 1915.
*Mangrove Cuckoo	1, 4, 5	Slow spread north and inland
Yellow-billed Cuckoo	3, 5	-
+ Smooth-billed Ani	5, 5a	Rapid increase and spread north.
Barn Owl	5, 5a	-
*Screech Owl	3, 3a, 5, 5a	Rare or absent in Keys.
*Great Horned Owl	2, 3, 4, 5	Not in Florida Keys.
Burrowing Owl	6, 6a	Nesting in Keys since early 1960s.
*Barred Owl	2, 3, 4, 5	Rare or absent in Keys.
*Chuck-will's-widow	3, 4, 5	-
+ Common Nighthawk	3, 6, 6a, 9, 9a	Est. in Keys since early 1940's.
*Ruby-throated Hummingbird	2, 5	Few definite nesting records.
*Common Flicker	3, 3a, 5, 5a	-
*Pileated Woodpecker	1, 2, 3, 4, 5	-
Red-bellied Woodpecker	2, 3, 3a, 5, 5a	-
*Red-headed Woodpecker	2, 3, 3a, 5, 5a	-
*Hairy Woodpecker	3	Becoming scarce; not in Keys.
*Downy Woodpecker	3, 3a, 5, 5a	Not in Florida Keys.
*Red-cockaded Woodpecker	3	Big Cypress; gone in southeast Fla.
Ivory-billed Woodpecker	2, 3	Extirpated; last seen c. 1938.
LAND BIRDS (Passerine) -		
*Eastern Kingbird	3, 5	Not in Florida Keys.
+ Gray Kingbird	1, 5, 5a	Spreading inland.
Great Crested Flycatcher	3, 3a, 4, 5, 5a	-
*Rough-winged Swallow	6a, 9a	Few definite nesting records.
*Purple Martin	5a	All known nest in bird houses.
*Blue Jay	3, 3a, 5, 5a	Not in Florida Keys.
Scrub Jay	Fla. scrub	Now rare in southern Fla.

TABLE 2--continued

Species	Habitat <sup>1</sup>	Comment
*Common Crow	1, 2, 3, 5, 7, 8	Not in Florida Keys.
*Fish Crow	1, 2, 5, <u>5a</u> , 7, 8	Spreading south on east coast.
*Tufted Titmouse	1, <u>2</u> , 4	-
*Brown-headed Nuthatch	3	Big Cypress; gone in southeast.
*Carolina Wren	4, <u>5</u> , 5a	-
Northern Mockingbird	3, 3a, 5, <u>5a</u>	-
*Brown Thrasher	5a	Spread into so. Fla. since 1930s.
*Eastern Bluebird	2, <u>3</u>	Big Cypress; gone in southeast.
*Blue-gray Gnatcatcher	2	Big Cypress.
*Loggerhead Shrike	3, 5, 6, 6a	Not in Florida Keys.
White-eyed Vireo	5, 5a	-
+ Black-whiskered Vireo	1, 4, 5a	Spreading north and inland.
*Red-eyed Vireo	2, 4	-
*Prothonotary Warbler	2, 5	Few nesting records; recent?
*Northern Parula Warbler	2, 4	-
+ Yellow Warbler	1	Spread into Keys since 1940s.
*Pine Warbler	3, 3a	Not in Florida Keys.
Prairie Warbler	1	Disjunct endemic subspecies.
Common Yellowthroat	5, 7	Not in Florida Keys.
*Eastern Meadowlark	3, 3a, 5a, 6, 6a, 7	Not in Florida Keys.
Red-winged Blackbird	1, 2, 5a, 6, 6a, 7, 8, 9b	-
*Boat-tailed Grackle	6, 6a, <u>7</u> , 9b, 8	Not in Florida Keys.
Common Grackle	<u>3</u> , <u>3a</u> , 5, <u>5a</u> , 7, 8	-
*Summer Tanager	3, 3a	Not in Florida Keys.
Cardinal	5, 5a	-
*Rufous-sided Towhee	5, 5a	Not in Florida Keys.
*Grasshopper Sparrow	3, 6	Few definite nesting records.
*Seaside Sparrow	6, 7	"Cape Sable" Seaside Sparrow.
*Bachman's Sparrow	3, 6	Few definite nesting records.

<sup>1</sup>Habitat Code - Underlining indicates the habitat of primary importance. 1) Mangrove forest and scrub; 2) Cypress forest; 3) Pine forest; 3a) Suburban pine, scattered to fairly dense pine stands in lawns; 4) Closed hardwood forest, both the hardwood hammocks of upland sites and Everglades tree islands dominated by red bay (*Persea borbonia*), holly (*Ilex cassine*) and other swamp forest species; 5) Forest edge, natural brushy vegetation of many types interspersed with open areas; 5a) Suburban forest edge, landscape plantings, citrus and other groves and brushy growth, mainly of exotic plants, on vacant lots, old fields and other disturbed land; 6) Grasslands, prairies and higher marsh with relatively short hydroperiods; 6a) Man-made grasslands, such as improved pastures, airports and golf courses; 7) Interior wetlands; 8) Coastal and estuarine wetlands; 9) Natural beaches and mudflats including vegetated areas along beaches; 9a) Man-made bare ground, such as new fill, spoil banks and gravelled roofs of buildings; 9b) Cultivated and recently fallow agricultural land.

<sup>2</sup>Asterisks preceding species names indicate that the bird does not breed in all areas of apparently suitable habitat in southern Florida.

<sup>3</sup>Plus signs preceding species names indicate the land birds of wholly or partly West Indian origin that breed in southern Florida.

TABLE 2--continued

<sup>4</sup>The Turkey Vulture of extreme southern Florida is said to be the same subspecies that occurs in tropical North America (Barleight, 1938; A.O.U., 1957: 98), but it possibly is a Pleistocene relict (Wetmore, 1956) once more widespread in the southern U.S., rather than a recent invader from the West Indies.

<sup>5</sup>We omit the so-called "Key West" Bobwhite (Howe, 1904: 168; Howell, 1932: 194; Aldrich, 1946: 500) the few records which, all from Key West at about the same time, strongly suggest a temporary population of escaped or introduced birds.

TABLE 3

## DIVERSITY OF NATIVE LAND AVIFAUNAS

Location <sup>1</sup>	Area (km <sup>2</sup> )	Elevation (m)	No. species of breeding land birds		
			Total	Passerine	Non-passerine
Maine	80,393	1,600	131	95	36
Michigan	147,687	610	152	109	43
Massachusetts	20,375	1,067	123	89	34
Kentucky	103,247	1,265	119	85	34
South Carolina	78,490	1,082	111	73	38
Alabama	132,292	732	121	80	41
Georgia	151,471	1,463	125	86	39
Louisiana	116,970	168	105	68	37
Florida	140,539	72	104	61	43
<u>Southern Florida</u>	<u>44,755</u>	<u>15</u>	<u>73</u>	<u>36</u>	<u>37</u>
Cuba	114,525	1,996	82	33	49
Hispaniola	76,483	3,170	77	36	41
Jamaica	10,961	2,256	70	35	35

<sup>1</sup>Data derived from following sources: Me. - Palmer, 1949; Mi. - Wood, 1951; Ma. - Griscom and Snyder, 1965; K. - Mengel, 1965; S.C. - Sprunt and Chamberlain, 1949; La. - Lowery, 1960; Al. - Imhof, 1962; Ga. - Barleight, 1958; Fl. and S. Fl. - all current information; Cuba - Bond, 1971, Barbour, 1943; Hisp. - Bond, 1971, Wetmore and Swales, 1931; Jam. - Bond, 1971. For older references it is probable that a few land birds (probably <10 in all cases) have been added to the avifaunas in recent years.

TABLE 4  
BREEDING RANGE CHANGES BY PENINSULAR FLORIDA BIRDS

## A.-Range advances

## 1.-Probably not primarily in response to man's impact on environment

Species	Range Change	References, Comments
*Magnificent Frigatebird	To Marquesas Keys, mid-1960's, probably from near West Indies.	See Ogden, 1969.
Fulvous Tree Duck	To Lake Okechobee, Everglades, SE coast. First nested, 1965. Some may be escapes. Presumably from either SW U.S. or Cuba.	See Ogden and Stevenson, 1965; Bond, 1971: 43.
Mississippi Kite	Spread into northern peninsula, now nesting south at least to Gainesville.	See Ogden, 1971, 1972, 1973; cf., Sprunt, 1954: 97.
Caspian Tern	Nesting in Tampa area since 1962. Possibly also Merritt Is.	See Woolfenden and Meyerrieks, 1963; Ogden, 1973.
*White-crowned Pigeon	Becoming more widespread in interior of Everglades N. P. in summer.	Loss of feeding habitat in Upper Keys may be a factor.
*Mangrove Cuckoo	Spread north to Miami area. Also inland in S Fla. where now numerous records. Now resident, perhaps formerly only present in summer.	See Stimson, 1964a; cf., Sprunt, 1954: 272.
Great Crested Flycatcher	Nesting Lignumvitae Key, but not in Lower Keys, 1951-2; pair with young, Key West, 1973. Apparently invaded Fla. Keys since 1930's.	See Robertson, 1955; Ogden, 1973; cf., Sprunt, 1954: 232.
Yellow-throated Vireo	South along Peace River to vicinity Fort Meade; earlier south to Orlando area.	See Stevenson, 1968; Mason, 1952; cf., Sprunt, 1954: 366.
*Black-whiskered Vireo	Has spread north on Atlantic coast to at least New Smyrna and on Gulf coast to at least Cedar Key, possibly St. Marks. Also, widely inland in extreme S Fla. and inland at sites near coast farther north. Now many records (specimens) from coasts of W Florida., Ala. and Ia.	See Nicholson, 1950b, 1950c, 1953; Robertson, 1962, 1968; Stimson, 1964b; Imhof, 1963, 1964, 1965, 1966; Stewart, 1965; Colehour, 1970; cf., Howell, 1932: 350. Advance related to spread north of mangroves along coast, but now has far outranged mangroves.
Prothonotary Warbler	Found southern Big Cypress, 1966; breeding, 1970.	See Stevenson, 1966; Ogden, 1970. Apparent advance <u>c.</u> 165 km south (cf., Sprunt, 1954: 376), but Big Cypress birds poorly known.
*Yellow Warbler	First found near Key West, 1941; now common resident outer Fla. Keys and Fla. Bay, north on east coast to Miami area.	See Greene, 1942; Ogden and Stevenson, 1965. Mainly inhabits fringing growth of red mangrove ( <i>Rhizophora</i> ).
Prairie Warbler (Fla. race)	North on Gulf coast to Cedar Key, and probably to St. Marks area.	See Stevenson, 1957, 1960; Ogden, 1972; cf., Sprunt, 1954: 410.
Louisiana Waterthrush	Has extended breeding range into Fla. panhandle and Tallahassee region, with one nesting record at Gainesville.	See Austin, 1965.
Yellow-breasted Chat	Now many summer records in northern peninsula, but apparently no definite breeding records south of former known range.	cf., Sprunt, 1954: 422. Possibly related to man-caused habitat change.

## 2.-Probably primarily in response to man's impact on environment

Cattle Egret	First known nesting, Lake Okechobee, 1953; now ubiquitous. Almost certainly colonized Fla. from the West Indies.	Almost altogether a species of altered habitats except in nesting.
Killdeer	Spread throughout mainland SE Fla. since mid-1950's. Numerous nesting records.	cf., Sprunt, 1954: 162; Kushlan and Fisk, 1972.
*Mourning Dove (Greater Antillean race)	First collected in Fla. Keys, 1953. Nesting at Dry Tortugas since 1962, but subspecies there still uncertain. Becoming more common in Keys.	See Aldrich and Duvall, 1958; Robertson and Mason, 1965.
*Smooth-billed Ani	Considered casual by Howell (1932: 290) and still a rarity to Sprunt (1954: 245-246), but has spread explosively since early 1960's. Now abundant along east coast north at least to Vero Beach with many records farther north, and on Gulf coast.	Largely limited to man-made forest-edge situations where now one of the most common land birds in much of SE Fla.
Burrowing Owl	Spreading northward in northern peninsula since 1950's. Also invaded Fla. Keys to Key Vaca, early 1960's.	See Neill, 1954; Idgon, 1963; Paulson and Stevenson, 1962; Stevenson, 1963. In pastures, airports, golf courses, and other cleared land.



TABLE 4--continued

Species	Range Change	References, Comments
Common Nighthawk (Continental race)	Spread into Upper Keys, early 1960's. Present southern range limit in Keys uncertain.	See Sutherland, 1963; Robertson, 1961, 1962. Relationship with the following form still needs study in Keys.
+Common Nighthawk (Bahaman race)	First reported from Key West, 1942. Spread north to Key Largo by 1961. Numerous records on southern mainland, but no known nesting there.	See Greene, 1943; Nicholson, 1950a; Stevenson, 1958; Ogden, 1973; and above references.
Chimney Swift	A recent slight advance in SW Fla. to Fort Myers area, but former range limit not well-described.	See Stevenson, 1967.
+Gray Kingbird	Now widespread breeder on southern mainland, chiefly in towns. Several summer inland records farther north.	See Grimes, 1953. <u>in</u> extension in NE Fla., where coastal spread probably not man-caused. Inland spread in S Fla. related to land-clearing and perhaps to consequent disappearance of Eastern Kingbird.
Rough-winged Swallow	Spread (sparsely) through central third of peninsula since 1950's. Nesting in quarries, on structures, canal banks, etc.	Stevenson, 1957, 1960; Robertson, 1962; Ogden, 1969; cf., Sprunt, 1954: 306.
Barn Swallow	Recent nesting records at Payne's Prairie, nests in culverts. Other northern peninsula localities?	See Ogden, 1972, 1973.
Brown Thrasher	Populations in southern third of peninsular Fla. are sparse, but has nested on Key Largo.	cf., Sprunt, 1954: 343.
Brown-headed Cowbird	Not known as breeder to Sprunt (1954: 446-447), but has spread rapidly through panhandle since mid-1950's (Weston, 1965: 123-124) and invading northern half of peninsula.	See Stevenson, 1960, 1966, 1968; Ogden and Stevenson, 1965; Ogden, 1971. Southward dispersal of juveniles in early summer complicates interpretation of records.
Blue Grosbeak	Has spread into northern half of peninsula (or at least become much more common) within past 15 years.	See Stevenson, 1956, 1964, 1966; Robertson, 1962; Ogden and Stevenson, 1965; Ogden, 1971, 1972, 1973.
Indigo Bunting	Apparently in process of occupying most of peninsula since spread first noted south of Tallahassee in mid-1950's. Spread almost certainly related to replacement of pine forest by fields, pastures and brushy forest-edge.	See especially Johnston, 1965. Also Stevenson, 1956, 1960, 1964, 1968; Ogden and Stevenson, 1965; Robertson, 1962; Ogden, 1969, 1972, 1973.

## B.-Range Losses

## 1.-Probably not primarily in response to man's impact on environment

Broad-winged Hawk	Perhaps never widespread in peninsular Fla., but no recent nesting records south of Gainesville.	See Ogden, 1971, 1973; cf., Howell, 1932: 178.
American Kestrel	Gone from SE Fla. by g. 1940 (Miami is the type locality of <i>E. a. palula</i> ), and now a very scarce breeder in southern two-thirds of peninsula.	See Ogden, 1972, 1973; cf., Holt and Sutton, 1926 and Howell, 1932: 190-191.
+Zenaida Dove	Breeding Fla. Keys, 1832, <i>vide</i> Audubon. Not found by any later observer.	An enigma, see text comment. Conceivably extirpated by hunting.
Common Crow	Reportedly once widespread in Fla. Keys, but not so today.	cf., Howell, 1932: 341.
White-breasted Nuthatch	Once resident in northern half of peninsula, but apparently no recent Fla. breeding record and few records of any kind.	cf., Howell, 1932: 345.
Brown-headed Nuthatch	Gone from SE Fla. where once locally common.	cf., Holt and Sutton, 1926. Logging may have been a factor, but the species doesn't require mature pine.
Gray Catbird	Apparently no longer breeds in Florida (Stevenson, 1967).	cf., Howell, 1932: 357.
Eastern Bluebird	Gone from SE Fla., where it nested on Long Pine Key as recently as 1952 (Robertson, 1955). Miami is the type locality of <i>E. a. grata</i> .	cf., Howell, 1932: 366.
Summer Tanager	Now rare as a breeder in SE quarter of peninsula, but present in Miami area to at least mid-1950's.	See Stevenson, 1955, 1956; cf., Howell, 1921.
Reddish Egret	Nested on coasts of much of the peninsula in 1800's (Howell, 1932: 104; Allen, 1942-55) but now largely limited to Fla. Bay.	Perhaps beginning to reclaim former Gulf coast range (Bancroft, 1971). Decline of this and the following species caused by plume-hunting.
Roseate Spoonbill	A widespread breeder in southern peninsula in late 1800's. Now nests only in Fla. Bay.	cf., Howell, 1932: 120; Allen, 1942: 7.
Royal Tern Sandwich Tern	Once nested Fla. Keys and Gulf coast.	See text comment. Commercial eggging probably caused the disappearance of these species.
Red-cockaded Woodpecker	Gone from SE Fla. where a few persisted near Homestead until g. 1965.	Removal of mature pine forest undoubtedly caused its disappearance.
Scrub Jay	East coast populations largely gone south of Palm Beach. SW Fla.?	cf., Howell, 1932: 339. Decline caused by obliteration of habitat.

\*West Indian species or subspecies.

TABLE 5

WEST INDIAN BIRDS RECORDED FROM FLORIDA BUT NOT KNOWN TO BREED

Species	No. of Records in Florida	Probable Source	Comment
Bahama Duck (= White-cheeked Pintail)	>10	Bahamas	Has occurred almost annually in recent years. Several recent specimens and photos. Extreme dates: 23 Dec. - 2 May.
Masked Duck	>15	Cuba	Several recent specimens and photos. Extreme dates: Nov. - 13 Apr.
Caribbean Coot	3	Cuba	All in winter of 1973-74. Specimen, numerous photos. Also several apparent Carib. Coot X Am. Coot hybrid... (W. J. Bolte, pers. comm.).
Red-necked Pigeon (= Scaly-naped Pigeon)	2	Cuba	Both specimens from Key West.
Zenaida Dove	8	Bahamas or Cuba	Photos, but no Fla. specimen in this century. Extreme dates: 30 Sept. - 24 Apr.
Key West Quail-Dove	5	Bahamas or Cuba	Published photo (Nelson, 1966). Extreme dates: 15 Sept. - 12 Nov; 1 in May.
Ruddy Quail-Dove	4	Cuba	Specimen, Dry Tortugas (Robertson and Mason, 1965). Extreme dates: 8 Dec. - May.
Antillean Palm Swift	1	Cuba	2, Key West, July-Aug., 1972, published photo (Ogden, 1972).
Emerald Hummingbird (= Cuban Emerald)	7	Bahamas or Cuba	No specimens or photos, but several detailed observations (Stimson, 1944; Cruickshank, 1964). Year-round, several in summer.
Bahama Woodstar	2	Bahamas	Photos. One spring and one fall record.
Loggerhead Kingbird	2	Bahamas or Cuba	Some question of specific identity existed (Stevenson, 1972), but photos seem to support this identification. At same Fla. Keys locality in two consecutive winters.
Bahama Swallow	8	Bahamas	No Fla. specimen in this century. Extreme dates: 7 Apr. - 11 Dec.

TABLE 5--continued

Species	No. of Records in Florida	Probable Source	Comment
Cave Swallow	12	Cuba	Mostly Dry Tortugas, where regular in spring in recent years. Several mainland records, and recent Fla. specimens (Stevenson, 1965; Dinsmore, 1968). Extreme dates: 28 Feb. - 26 July.
Cuban Martin	3	Cuba	Practically impossible to identify in the field. Perhaps a subspecies of the Purple Martin (Bond, 1971).
Bahama Mockingbird	1	Bahamas; limited range in Cuba	Sight record only; Dry Tortugas, 3 May 1973 (P. A. Buckley, pers. comm.).
Thick-billed Vireo	2	Bahamas	Sight records only (Stevenson, 1961; Robertson and Mason, 1965).
Bananaquit	>25	Bahamas; limited range in Cuba	Mostly SE coast and Keys, where a rare, regular winter resident in recent years. Often sings. Extreme dates: 1 Nov. - 23 Mar.; also May?, 18 Aug.? Many photos. Almost surely the Bahaman subspecies (Robertson, 1968).
Bahama Yellowthroat	1	Bahamas	Loxahatchee Nat'l. Wildl. Ref., 19 Oct. 1968; caught in mist-net, escaped (Sykes, 1968).
Stripe-headed Tanager	>30	Bahamas	All records from SE coast and Keys, where recorded in all months except Aug. through Oct. Often sings; nesting suspected, but not proved. Both Bahaman subspecies may occur, but the one specimen (Stevenson, 1963) was <i>S. g. zena</i> .
Tawny-shouldered Blackbird	2	Cuba	Key West, 27 Feb. 1936, 2 specimens (Demeritt, 1936); Marathon, 25 May 1955 (Sprunt, 1963).
Black-faced Grassquit	6	Bahamas; limited range in Cuba	Mostly SE Fla., but several records from interior. No seasonal pattern evident. Several recent specimens (Browning, 1964; Robertson, 1968).

TABLE 6  
POPULATION DENSITY OF BREEDING LAND BIRDS IN FLORIDA

I. Natural Habitats

Description and Size of Study Area	Location	Years Studied	No. Breeding ♂♂/40 ha	No. Breeding Species	Density of Most Common Species (♂♂/40 ha)
1. Longleaf pine-turkey oak association (10 ha)	NW of Gainesville, Alachua Co.	1958-1962	$\frac{84^1}{(64-96)}$	$\frac{7.8}{(6-10)}$	B-g. Gnatcatcher, $\frac{26.4}{21.6}$ ; Sum. Tanager, $\frac{21.6}{10.6}$ ; Tufted Titmouse, $\frac{10.6}{7.2}$ ; Grt. Crest. Flycatcher, $\frac{7.2}{7.2}$ ; Yellow-thr. Vireo, $\frac{7.2}{7.2}$ .
2. Slash pine-turkey oak association (8 ha)	Archbold Biol. Sta., Highlands Co.	1969	100	14	R-s. Towhee, 50; Blue Jay, 12.5; M. Dove, 7.5; Chuck-will's-widow, 7.5; Red-bell. W'pecker, 7.5; Grt. Crest. Flycatcher, 7.5.
3. Sand pine scrub (8 ha)	Archbold Biol. Sta., Highlands Co.	1969	80	9	R-s. Towhee, 45; Blue Jay, 12.5; Car. Wren, 5; Grt. Crest. Flycatcher, 5; White-eyed Vireo, 5.
4. Scrubby flatwoods (8 ha)	Archbold Biol. Sta., Highlands Co.	1969	125	13	R-s. Towhee, 75; Scrub Jay, 10; Grt. Crest. Flycatcher, 7.5; Blue Jay, 7.5; M. Dove, 5; Car. Wren, 5; White-eyed Vireo, 5.
5. Recently burned scrubby flatwoods (8 ha)	Archbold Biol. Sta., Highlands Co.	1969	50	12	R-s. Towhee, 20; Bobwhite, 10; Gr. Dove, 10; Scrub Jay, 5; E. Meadowlark, 5.
6. Low flatwoods with bayhead (4 ha)	Archbold Biol. Sta., Highlands Co.	1969	120	11	Car. Wren, 20; White-eyed Vireo, 20; Pine Warbler, 20; Cardinal, 20; R-s. Towhee, 20.
7. Old second-growth rockland pine forest (10 ha)	Long Pine Key, Dade Co.	1951-1952	$\frac{55.5}{(55-56)}$	$\frac{15}{(13-17)}$	Pine Warbler, $\frac{12}{11}$ ; Red-bell. W'pecker, $\frac{11}{5}$ ; E. Meadowlark, $\frac{7}{4.5}$ ; N. Mockingbird, $\frac{5}{4.5}$ ; E. Kingbird, $\frac{4.5}{3.5}$ ; Bobwhite, $\frac{4}{3.5}$ ; E. Bluebird, $\frac{3.5}{3.5}$ .
8. Young second-growth rockland pine forest (10 ha)	Long Pine Key, Dade Co.	1951-1952	$\frac{34.5}{(33-36)}$	$\frac{15.5}{(14-17)}$	Bobwhite, $\frac{6.5}{5.5}$ ; Red-bell. W'pecker, $\frac{5.5}{4}$ ; Pine Warbler, $\frac{4}{4}$ ; Blue Jay, $\frac{4}{4}$ ; N. Mockingbird, $\frac{4}{4}$ ; Log. Shrike, $\frac{4}{4}$ ; Com. Grackle, $\frac{2}{2}$ .
9. Mature rockland pine-palm forest (20 ha)	Big Pine Key, Fla. Keys, Monroe, Co.	1951-1952	$\frac{5.5}{(5-6)}$	$\frac{3}{(3-3)}$	Red-bell. W'pecker, $\frac{2}{2}$ ; Gray Kingbird, $\frac{2}{1.5}$ ; Cardinal, $\frac{1.5}{1.5}$ .
10. Old second-growth <u>Pinus caribaea</u> pine-yard (10 ha)	S of Marsh Harbour, Great Abaco, Bah.	1952	92	13	Pine Warbler, 22; Olive-capped Warbler, 17; Stripe-headed Tanager, 9; Black-faced Grassquit, 8; Hairy Woodpecker, 6; Thick-billed Vireo, 6; Grt. Ant. Pewee, 5; B-g. Gnatcatcher, 5; Log. Kingbird, 4; Yellow-thr. Warbler, 4.
11. Live oak-cabbage palm coastal hammock (14 - 20 ha)	Near Vero Beach, Indian River Co.	1966-1968	$\frac{124.3}{(108-141)}$	$\frac{15.7}{(14-18)}$	Cardinal, $\frac{50.7}{11.3}$ ; Car. Wren, $\frac{38}{11.3}$ ; Red-bell. W'pecker, $\frac{11.3}{11.3}$ .
12. Oak-palm-hickory hammock and maple swamp (24 ha)	W of Vero Beach, Indian River Co.	1966-1969	$\frac{122.5}{(107-130)}$	$\frac{16}{(14-18)}$	Car. Wren, $\frac{38.3}{12.8}$ ; Cardinal, $\frac{28.7}{12.8}$ ; Red-bell. W'pecker, $\frac{12.8}{12.8}$ ; White-eyed Vireo, $\frac{12}{6.8}$ ; Yellow-billed Cuckoo, $\frac{6.8}{6}$ ; Grt. Crest. Flycatcher, $\frac{6}{6}$ .
13. Live oak-cabbage palm hammock (13.5 ha)	Hillsborough River State Park, Hillsborough Co.	1967-1968	$\frac{186}{(183-189)}$	$\frac{15.5}{(15-16)}$	Car. Wren, $\frac{45}{31.5}$ ; Parula Warbler, $\frac{34.5}{31.5}$ ; Red-eyed Vireo, $\frac{31.5}{30}$ ; Cardinal, $\frac{30}{13.5}$ ; B-g. Gnatcatcher, $\frac{13.5}{13.5}$ .
14. Mixed oak ridge (12 ha)	Sawgrass Lake area, Pinellas Co.	1964	154	9	Car. Wren, 50; Cardinal, 50; Yellow-billed Cuckoo, 20; Blue Jay, 17; Brown Thrasher, 10; Screech Owl, 7.
15. Wet maple swamp (39 ha)	Sawgrass Lake area, Pinellas Co.	1964	111	5	Car. Wren, 51; Cardinal, 40; Yellow-billed Cuckoo, 20.
16. Mature tropical hammock (7.3 ha)	Lignumvitae Key, Fla. Keys, Monroe Co.	1952	14	5	Black-whiskered Vireo, 11; Grt. Crest. Flycatcher, 3.

TABLE 6--continued

Description and Size of Study Area	Location	Years Studied	No. Breeding ♂♂/40 ha	No. Breeding Species	Density of Most Common Species (♂♂/40 ha)
17. Small tropical hammock and shrubby pinewoods (10 ha)	Dark Hammock, Long Pine Key, Dade Co.	1951-1952	<u>83.5</u> (77-90)	<u>13.5</u> (12-15)	Cardinal, <u>20.1</u> ; Red-bell. W'pecker, <u>11</u> ; Pine Warbler, <u>12.5</u> ; White-eyed Vireo, <u>10</u> ; Grt. Crest. Flycatcher, <u>7</u> ; Car. Wren, <u>5.5</u> ; Blue Jay, <u>5</u> .
18. Burned-out tropical hammock (8 ha)	Royal Palm Hammock, Dade Co.	1951-1952	<u>125.5</u> (120-131)	<u>10.5</u> (10-11)	Cardinal, <u>42</u> ; Car. Wren, <u>28.5</u> ; White-eyed Vireo, <u>23</u> ; Red-bell. W'pecker, <u>15</u> ; Grt. Crested Flycatcher, <u>6</u> .
19. Coastal hammock scrub and buttonwood ( <i>Conocarpus</i> ) (6.8 ha)	Near Flamingo, Monroe Co.	1951-1952	<u>100.5</u> (87-114)	<u>7.5</u> (7-8)	White-eyed Vireo, <u>42.5</u> ; Cardinal, <u>25.5</u> ; Red-bell. W'pecker, <u>21</u> ; Grt. Crest. Flycatcher, <u>2</u> ; Yellow-billed Cuckoo, <u>4.5</u> .
20. Scrubby mangrove island (51.2 ha)	North West Key, Fla. Bay, Monroe Co.	1952	33	5	R-w. Blackbird, 19; Prairie Warbler, 9; White-crowned Pigeon, 2; Gray Kingbird, 2; Osprey, 1.
21. Disturbed tropical hammock (12 ha)	Big Pine Key, Fla. Keys, Monroe Co.	1951	61	7	White-eyed Vireo, 22; Cardinal, 20; Red-bell. W'pecker, 8; Gr. Dove, 3; Yellow-billed Cuckoo, 3; Black-whiskered Vireo, 3.

II. Altered Habitats

22. Active citrus grove (16.2 ha)	W of Vero Beach, Indian River Co.	1967-1969	<u>194.3</u> (188-200)	<u>11.7</u> (11-13)	Bobwhite, <u>41</u> ; Cardinal, <u>34.3</u> ; Mockingbird, <u>32.7</u> ; Gr. Dove, <u>17</u> ; R-s. Towhee, <u>15.3</u> ; R-w. Blackbird, <u>14.3</u> ; M. Dove, <u>13</u> ; E. Meadowlark, <u>11</u> .
23. Long-abandoned key lime grove	Lignumvitae Key, Fla. Keys, Monroe Co.	1951	58	7	Cardinal, 16; Black-whiskered Vireo, 12; Yellow-billed Cuckoo, 7; Red-bell. W'pecker, 7; Grt. Crest. Flycatcher, 7; White-eyed Vireo, 7.
24. Suburban pine area (18.4 ha)	Gulfport, Pinellas Co.	1963	607	11	House Sparrow, 330; M. Dove, 150; Mockingbird, 35; Blue Jay, 33; Com. Grackle, 13; Cardinal, 13.
25. Suburban oak area (7.1 ha)	St. Petersburg, Pinellas Co.	1963	526	8	House Sparrow, 217; Blue Jay, 114; M. Dove, 103; Mockingbird, 40; Cardinal, 29.
26. New suburban area (15.2 ha)	St. Petersburg, Pinellas Co.	1963	203	6	House Sparrow, 127; Mockingbird, 24; M. Dove, 23; Blue Jay, 16; Cardinal, 8.

<sup>1</sup>Underlined numbers are averages. Numbers in parenthesis show range of total population density and number of breeding species recorded in the various years of study.

References: Census #1: Woolfenden and Allen, 1958; Woolfenden, Allen, and Birkenholz, 1959; Allen, Birkenholz and Jenni, 1960; Jenni, Allen and Frost, 1961; Jenni, Birkenholz and Ligon, 1962. #2-6: Woolfenden, 1969. #7-10, 16-21 and 23: Robertson, 1955. #11-12 and 22: Kale and Webber, 1968 a, b, c; Webber and Kale, 1969 a, b. #13: Woolfenden, 1968. #14-15: Rohwer and Woolfenden, 1969. #24-26: Woolfenden and Rohwer, 1969.

TABLE 7

## COMPARISON OF WINTER BIRD AND BREEDING BIRD DENSITIES IN FLORIDA HABITATS

Location	Habitat	Year	Number of Species			Density (Birds/40 ha)		
			winter	summer	<u>winter</u> summer	winter	summer	<u>winter</u> summer
Archbold Biological Station <sup>1</sup>	Live Oak-Cabbage Palm Hammock	1967-68 <sup>4</sup>	33	16	2.06	411	366 <sup>5</sup>	1.12
Vero Beach <sup>2</sup>	Live Oak-Cabbage Palm Coastal Hammock	1966-67	41	15	2.73	1494	286	5.22
		1967-68	37	19	1.95	412	252	1.63
		1968-69	34	17	2.00	530	220	2.41
	Oak-Palm-Hickory Hammock and Maple Swamp	1966-67	48	17	2.82	1058	220	4.18
		1967-68	48	17	2.82	761	254	3.00
		1968-69	41	19	2.16	1017	254	4.00
Citrus Grove	1966-67	39	12	3.25	595	380	1.57	
	1967-68	39	13	3.00	500	390	1.28	
Archbold Biological Station <sup>3</sup>	Slash Pine Turkey Oak Association	1969-70	31	14	2.21	370	100	3.70
	Recently Burned Scrubby Flatwoods	1969-70	18	12	1.50	240	100	2.40
	Scrubby Flatwoods	1969-70	19	13	1.46	195	250	6.78
	Sand Pine Scrub	1969-70	25	9	2.78	390	160	2.44

<sup>1</sup>From Woolfenden, 1967, 1968b.<sup>2</sup>From Kale and Webber, 1968a, b, c, 1969a, b, c.<sup>3</sup>From Woolfenden, 1969, 1970a, b, c, d.<sup>4</sup>Includes nesting season of 1967 and winter season of 1967-68.<sup>5</sup>Includes only nesting birds.

TABLE 8

A COMPARISON OF BREEDING POPULATIONS OF WADING BIRDS ON THE SOUTHERN COAST  
AND FLORIDA BAY AND INTERIOR WETLANDS OF EVERGLADES NATIONAL PARK  
IN 1930'S AND 1960'S

Species	Mid-1930's	Mid-1960's
Florida Bay and Coasts		
Great Blue Heron	-	1,100
Great Egret	300	2,500
Small Herons	1,000	5,000
White Ibis	1,500	3,500
Interior Everglades		
Great Blue Heron	-	0-200
Great Egret	25,000	500-5,000
Small Herons	90,000	1,000-7,500
White Ibis	420,000	0-5,000

TABLE 9

THE NUMBER OF WOOD STORKS NESTING AND NUMBER OF YOUNG BIRDS PRODUCED  
FROM 1956-57 THROUGH 1973-74 IN THE SOUTHERN EVERGLADES AND  
CORKSCREW SWAMP COLONIES

Year	Southern Everglades <sup>1</sup>		Corkscrew Swamp <sup>2</sup>	
	Nesting Population	Production	Nesting Population	Production
1956-57	2,080	0	0	0
1957-58	200	0	1,000	925
1958-59	2,000	2,200	8,000	9,000
1959-60	5,000	2,870	10,000	14,500
1960-61	6,200	2,000	12,000	17,000
1961-62	0	0	0	0
1962-63	2,000	1,000	6,000	2,000
1963-64	3,000	0	0	0
1964-65	4,000	200	2,600	0
1965-66	5,200	500	8,000	3,500
1966-67	3,800	2,000	7,360	7,350
1967-68	4,200	200	10,000	0
1968-69	3,000	0	7,000	340
1969-70	2,500	0	3,800	0
1970-71	2,000	150	2,400	1,500
1971-72	1,900	400	3,000	200
1972-73	1,800	200	0	0
1973-74	2,000	1,900	3,800	3,500

<sup>1</sup>Information from files of the Everglades National Park.

<sup>2</sup>Information from Kahl (1964) and from files of the National Audubon Society and Everglades National Park.

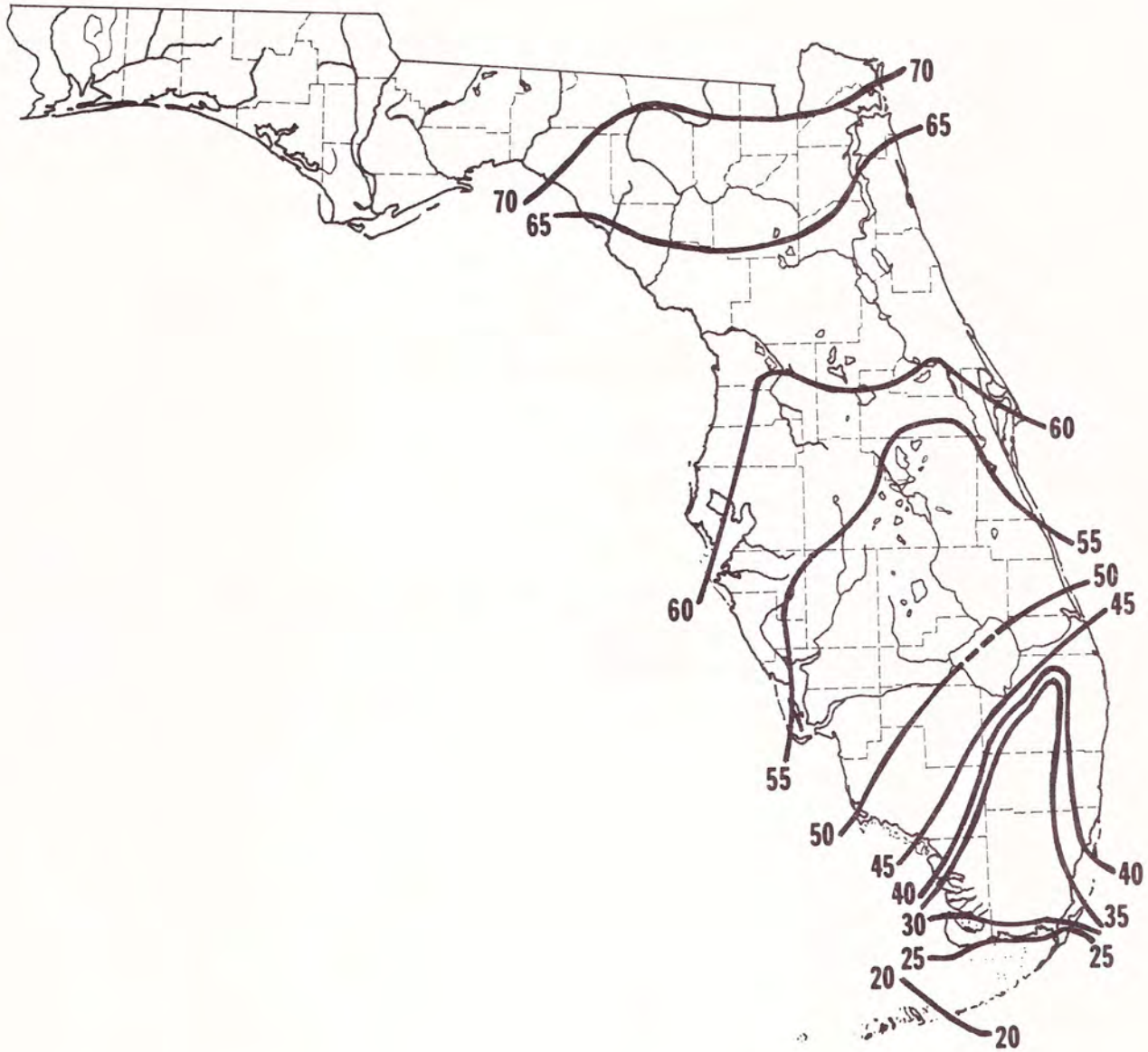


Figure 1. Species density of breeding land birds in Florida.