Avian Use of Fluctuating Wetlands

James A. Kushlan
Department of Biology
University of Mississippi
University, MS 38677

(Keynote Address)

Abstract: This paper reviews evidence to support the hypothesis that water level fluctuation is a dominant characteristic of riparian and wetland ecosystems and that avian populations using such wetlands possess adaptations that permit accommodation to these fluctuations. Hydrologic variability may be seasonal, annual, or irregular, and it may be recurring or irregularly catastrophic. Accommodation may in some cases be permitted by the predictability of the fluctuations. Like wetland vegetation, birds must be responsive to water depth, duration of flooding, and extent and timing of fluctuations. Comparative study of wetland species reveals that suitable strategies may differ among syntopic species. Patterns of prey availability, habitat use, foraging, population movements, and community composition may be similar in many temperate to tropical wetlands. In cool or dry climates, other environmental factors assume a more critical role in limiting avian use of fluctuating wetlands.

INTRODUCTION

Wetland and riparian ecosystems are among the most productive habitats for birds. The impressive concentrations of wintering waterfowl in temperate marshes and the extraordinary species richness and abundance of birds occupying riparian woodlands bear witness to this productivity. Although one-third of the bird species of North America use wetlands (Kroodsma, 1979), the complexity of ecological relationships between birds and wetlands is becoming understood slowly.

FRESHWATER WETLANDS AND WILDLIFE, 1989, CONF-8603101, DOE Symposium Series No. 61, R. R. Sharitz and J. W. Gibbons (Eds.), USDOE Office of Scientific and Technical Information, Oak Ridge, Tennessee.

Many shallow aquatic ecosystems are inherently unstable due to long- and short-term alternation of drought and flood conditions. In this paper I suggest that the pattern of water level fluctuations is a dominant characteristic of riparian and wetland ecosystems and that avian populations using such wetlands possess adaptations that permit accommodation to such fluctuations. If true, we could expect to find that water level fluctuation is a primary factor influencing the occurrence, abundance, and reproductive success of aquatic bird populations and that management of such fluctuation would be crucial to wetland conservation. If environmental fluctuations constrain the ability of birds to survive in wetland ecosystems, understanding their apparent adaptations to these environments should reveal much about their evolutionary responses.

These aspects of aquatic bird ecology and management are becoming increasingly clear. Although aspects of the role of water fluctuation in influencing waterfowl production are appreciated (Uhler, 1944; Johnsgard, 1956; Weller et al., 1958; Harris and Marshall, 1963); only in a few locations, such as in North American prairie marshes (Weller and Spatcher, 1965) and in the Everglades (Kushlan, 1986), have the responses been studied in detail. This biological appreciation has immediate practical implications, and it is manifest that water level manipulation is essential for wetland management (Weller, 1979; Fredrickson and Taylor, 1982; Kushlan, 1987). Adaptation to fluctuating wetlands is a unifying force in the evolutionary history of many bird groups. Consider one such bird, a heron. Its long legs, long neck, long bill, colonial nesting, communal roosting, large repertoire of feeding behaviors, generalized dietary habits, and exceptional mobility preadapt it for use of fluctuating wetlands (Kushlan, 1978, 1981; Hancock and Kushlan, 1984).

In this paper I explore the possible importance of hydrological variability in the ecology of birds inhabiting fluctuating wetland ecosystems, especially summarizing my own studies in an ecosystem that might usefully serve as a model for fluctuating wetlands, the Florida Everglades. From this exploration, specific hypotheses can be generated that might be profitably tested in other wetlands.

HYDROLOGY IN FLUCTUATING WETLANDS

Understanding the response of birds to water level fluctuations requires detailed and quantitative knowledge of wetland hydrology. Water depth in wetland and riparian ecosystems fluctuates in response to variations in rainfall. In swamps and perched bogs, fluctuations are due entirely to in situ rainfall. More commonly in wetlands, water level is the result of the combined effects of local rainfall and downgradient discharge via surface runoff, marsh flow, stream flow, soil interflow, or groundwater seepage.

Water level fluctuations may be moderate or extensive. Perhaps the most dramatic occur in riparian wetlands where water is usually present only in saturated soil but where the floodplain may sometimes be inundated. In North America the extent and effect of riparian flooding differ between the drier West and the well-watered East where the riparian zone supports swamps or marshes having long hydroperiods (Johnson et al., 1985; Harris and O'Meara, this volume).

In most wetlands there is a periodic component to hydrological variation corresponding to relatively wet and relatively dry seasons. For example in the Everglades, water level fluctuates seasonally because, on the average, 85% of the 1250-mm annual total precipitation falls in half of the year. During winter, reduced rainfall leads to a recession of surface waters, a process hastened by increasing evaporation in the spring. At its lowest level, standing surface water may be contracted into the deeper marshes and ponds (Kushlan, 1974a). Similar patterns occur in other temperate and tropical wetlands (e.g., Ewel and Odum, 1984; Kushlan et al., 1985).

Water depth variation also may be caused by rainfall cycles of longer than seasonal periodicity. The annual pattern of water level fluctuation may vary considerably from one year to the next owing to differences in the amount and timing of precipitation. In the Everglades, for example, low rainfall cycles have an approximate 10-year periodicity with a less pronounced periodicity of 5 years superimposed (Thomas, 1974). These year-to-year differences in rainfall result in relatively high and low water conditions in various years.

High and low water conditions may become floods or droughts when their deviation from normal conditions is particularly extensive, perhaps several standard deviations from the long-term mean water depths. These extreme cases may be catastrophic in the sense that they are rare and may exceed the usual accommodative abilities of particular bird species. In many riverine and swamp systems, 50-, 100-, and 400-year flood conditions are calculable. The most striking examples of strong deviations are the irregular floods in riparian zones and high water in marshes caused by infrequent hurricanes.

Study of the ecological effects of water level fluctuation on bird populations can best be carried out by making use of natural and artificial experiments that are proffered by fluctuating wetlands and their managers. Such experimental conditions often arise naturally during a succession of years having differing hydrological conditions. Wetland management has provided additional experimental conditions by drainage and physical compartmentalization of wetlands by levees and canals that change the patterns and timing of water level fluctuations in different parts of a single wetland system (e.g., Kushlan, this volume). By taking advantage of these conditions, studies can be profitably conducted using hydrological parameters as independent variables and biological responses as dependent variables.

An important consideration is the accommodation of birds to wetlands with hydrological predictability. Wetlands have been called pulsed stabilized systems (Odum, 1983) in which fluctuations have some level of predictability in both timing and extent. In the coarse view, a dry season may be expected each year. The extent and timing of the drop in water level may differ annually but as a deviation around a long-term mean. Even catastrophic events, such as severe floods, droughts, and fires, have statistical return times. In the fine view, we can find surprisingly precise statistical relationships. In the Everglades, the pattern of water level increase in the early wet season is statistically correlated with antecedent conditions, and discharge is correlated to past water levels and current rainfall (Kushlan and Jacobsen, in preparation; Thomas MacVicar, personal communication).

We can conclude that such seasonal, annual, and catastrophic changes in water depths could have substantial effects on bird populations. Birds using wetlands must be able to compensate for recurring flood and dry conditions. The biological effects of infrequent events in one year can be compensated for by the restoration of more normal conditions in subsequent years. These disturbances, in fact, may be important in resetting the patterns of ecosystem development of which bird populations are a part. Some of the short- and long-term effects of hydrological variability on birds are due to their effects on patterns of plant community development; others are due to fluctuating water depths per se.

WATER LEVEL EFFECTS ON BIRD HABITAT

Water depth fluctuations and hydroperiods largely determine the character of wetland plant communities and are critical to many birds. Although the types and density of plants vary continuously along hydrologic gradients, they generally can be sorted into associations recognizable by characteristic species that owe their relative abundances to slight differences in elevation and to historical events. Elevation strongly influences such hydrological parameters as timing, depth, duration, and periodicity of flooding. Historical events may be a consequence of the vagaries of seed germination, nearby sources for vegetative colonization, fire, or flooding events.

Water level fluctuations and history affect bird use by virtue of their role in plant establishment. The seeds of most wetland plants require exposure of the soil for germination, and their survival depends on the timing, extent, and duration of the dry period and of subsequent reflooding (van der Valk and Davis, 1978). Thus periodic fluctuations are required to retain most emergent plant communities. Stabilized high water levels lead to the eventual death of emergent plants and their replacement by submersed or floating species. Stabilized low water levels lead to invasion by shrubs and other mesic plants. Much of the reproduction of herbaceous marsh plants is primarily vegetative, and once established, a species may colonize adjacent areas provided hydrological conditions remain appropriate.

The vegetation structure resulting from these processes in turn affects avian use of a wetland in that the various species have distinctive habitat requirements. This may be seen by the habitat use by birds in North American wetlands (e.g., Weller and Fredrickson, 1974; Kushlan, 1978; Weller, 1979; Fredrickson, 1979). The longer-legged species such as great blue herons *(Ardea herodias)* or great egrets *(Casmerodius albus)* feed by wading in shallow open marsh. Swimming species such as waterfowl use deeper zones lacking emergent vegetation. Coots, gallinules, and grebes feed in open water but remain near the cover of reed beds which they use for nesting. Other marsh-edge species are yellow-headed blackbirds *(Xanthocephalus xanthocephalus)* and common yellowthroats *(Geothlypis trichus)*. Least bitterns *(Ixobrychus exilis)*, green-backed herons *(Butorides virescens)*, black terns *(Chlidonias niger)*, red-winged blackbirds *(Agelaius phoeniceus)*, rails, sparrows, and some ducks nest within dense emergent vegetation. Wood ducks *(Aix sponsa)*, grackles, redwings, and wetland warblers nest in swamp trees and often feed in nearby open areas. Swamp trees are also the preferred colonial nesting sites for waterbirds such as herons, ibises, and storks.

The requirements of the various species of aquatic birds are surprisingly specific. This is clearly the case for small species and also for larger species. For example, the habitat preferences of wading birds in the Llanos and in the Everglades were surprisingly coherent (Kushlan et al., 1985). Thus whatever determines vegetation patterns will also, to a large degree, determine bird use of wetlands.

A number of processes can alter aquatic plant communities, and most involve water level fluctuation, either primarily or secondarily. These include the development of natural detention structures such as logjams on effluent streams, fire (Ball and Nudds, this volume), and hydrarch successional processes. Habitats can be changed naturally by the activities of wetland animals such as beavers *(Castor canadensis)* and alligators *(Alligator mississippiensis)*, which locally increase water depth and hydroperiod, and muskrats *(Ondatra zibethicus)* and geese, both of which remove emergent vegetation (Beard, 1953; Kushlan, 1974a; Errington, 1963; Weller and Spatcher, 1965; Reed, this volume). Habitat change can also result from many unnatural processes including artificial flooding and drainage. A simulation study of a wood stork population suggested that population decreases were caused primarily by the lowering of water levels on nearby wetlands (Browder, 1978). Kushlan (this volume) showed the effects of water level management on Everglades bird populations.

From the preceding, it is clear that vegetation characteristics affect avian use of a wetland. Changes in vegetation can result from the interaction of water depth and its fluctuation through plant establishment and survival. Vegetative, and consequently avian, responses to water depth fluctuation are generally predictable, as has been shown for North American prairie marshes (Weller and Fredrickson, 1974). Should water levels stabilize, vegetation would change in predictable ways and initiate a reduction in diversity and abundance of bird populations able to use the wetland.

DIRECT EFFECTS OF WATER FLUCTUATIONS

Fluctuation of water depth per se, rather than vegetation, is the key factor for many birds. Deep water is required for swimming and diving birds, such as grebes, diving ducks, cormorants, and anhingas. Shallow water of specific depths is required by wading birds, which partition feeding sites on the basis of water depth (Kushlan, 1976a). Thus water depth fluctuations can restrict or permit avian habitat use through depth limitations.

Water depth fluctuations also can restrict or permit avian habitat use through control of the abundance and availability of prey. In the southern Florida wetlands, for example (Kahl, 1964; Kushlan, 1974a, 1974b, 1986), the abundance of fish and aquatic invertebrates increases during the deep water season. During the dry season, falling water levels increase their availability to wading birds by concentrating prey in dry season pools. Wading birds take advantage of the abundant and available food supply to nest in the dry season.

The abundance and availability of prey of some aquatic birds depend on high-water conditions in the wet season. The snail kite *(Rostrhamus sociabilis)* consumes aquatic snails that achieve highest populations in deep water marshes (Kushlan, 1975; Sykes, 1983, 1984; Kushlan and Bass, 1983a). Kites possess adaptations to wetland fluctuation including flexible nesting timing, rapid renesting after nest failure, and rapid renesting by serial polygamy (Beissinger, this volume).

Numerous other studies have recently confirmed that prey availability and consumption are correlated with water level fluctuations. The little egret *(Egretta garzetta)* in the Camargue of France changes its foraging sites in relation to food availability determined by water level fluctuations (Hafner and Britton, 1983). Bildstein (this volume) found that the white ibis *(Eudocimus albus)*, which forages in both estuarine and freshwater habitats, required crayfish found in fluctuating freshwater wetlands to nest successfully. Coulter (this volume) found that the total number of foraging sites available to wood storks *(Mycteria americana)* influenced nesting success, and this was related to the seasonal timing of water level fluctuations across the feeding habitat. In some cases the relationships of prey abundance and availability to avian use may be complex. In one area the availability of fish prey to wood storks was related, in addition to the extent and duration of flooding, to the distance from sources of prey recruitment and the size of local predator-fish population, which itself depended on the extent of the previous dry season (Browder, 1978). Jelks and Collopy (this volume) demonstrated a preference by wading birds for semiflooded emergent marshes over higher and lower sites. Similarly, highest densities of waterfowl are found in ephemeral or semipermanent wetlands (Kantrud and Stewart, 1977; Ball and Nudds, this volume). Thus over many types of wetlands, fluctuating water conditions are required for use by aquatic birds.

In some species the pattern of water level fluctuation directly determines breeding season and success as, for example, is the case for the wood stork in Florida (Kahl, 1964; Kushlan et al., 1975; Clark, 1979). In the Big Cypress Swamp, initiation of wood stork nesting depends on when the surface water falls to a certain point. In the Everglades, nest initiation depends on the rate at which water levels fall. In eastern Florida, nest initiation depends on both water level and drying rate. The latter study is particularly interesting because it was a specific test of the hypothesis that the timing of nesting was controlled by hydrological fluctuations. In all cases time of nest initiation greatly affects reproductive success and population stability (Kushlan et al., 1975; Kushlan and Frohring, 1986). Clark (1979) found that the most young were produced in years when early drying accelerated through the breeding season. In all three situations, the fundamental causality involved the timing and extent of water level fluctuations, although the specific operative hydrological parameters may vary in different wetlands.

Some birds can nest in wetlands only during periods of little or no standing water. For example, the Cape Sable seaside sparrow *(Ammodramus maritimus)* population has spread with the expansion of its short-hydroperiod marsh owing to drainage (Kushlan and Bass, 1983b). Its reproduction ceases as water depths increase in the wet season. Wetland habitats (especially riparian wetlands) are often used for nesting by upland birds during seasonal dry periods or droughts (Johnson and Haight, 1985; White et al., this volume; Hamel and Brunswig, this volume). Fredrickson (1979) concluded that fluctuating water levels influence the opportunity for a variety of species to exploit riparian wetlands.

Waterfowl are also directly affected by water level fluctuation, which determines areas available as well as food supplies in those areas. The wetland available to waterfowl in North American prairie marshes depends on spring water cover and depth (Schroeder et al., 1976; Short, this volume). Total waterfowl production is heavily dependent on water levels and is being reduced in years of low water levels (Yeager and Swope, 1956; Rogers, 1964). Food supplies are affected because in the nesting season these waterfowl consume invertebrates, the abundance of which depends on seasonal and multiyear timing and extent of drying (Krull, 1970; Krapu, 1974; Swanson and Meyer, 1977; Flake, 1979; Swanson, 1984). McKnight and Low (1969) found that an 18-fold increase in midge larvae occurred after a period of drying contrasted with the levels found in marshes that were continuously flooded. The high levels of invertebrates are probably the result of a combination of nutrient release and mortality of fish predators (Krapu and Duebbert, 1974) but are ultimately dependent on water levels fluctuating appropriately.

AVIAN STRATEGIES IN FLUCTUATING WETLANDS

Fluctuating water level and its effect on habitat, water depth, and prey availability should require exacting adaptations on the part of resident birds, and it is likely that mechanisms of accommodation might differ among species. One can appreciate the extent of differing adaptations of birds to fluctuating marshes by contrasting two superficially similar species, the white ibis and the wood stork (Bildstein this volume; Kushlan, 1976b, 1977, 1979a, 1979b, 1986; Kushlan and Frohring, 1986; Kushlan and Kushlan, 1979; Kushlan et al., 1975; Ogden et al., 1976). Both are nonvisual tactile foragers but feed differently. The white ibis inserts its bill into the marsh sediment, whereas the wood stork gropes by placing its bill in the water. The prey taken by the two birds barely overlap. White ibis feed on small, demersal, burrowing prey, particularly crayfish and insects. Wood storks feed on relatively large, mobile fish that occur in dense concentrations. As a result, the species choose rather different feeding situations: ibises prefer shallower water than do wood storks.

These distinctions in foraging ecology lead to differences in other responses to water level fluctuations. In southern Florida, the populations of both species shift feeding locations following the seasonal drying of the Everglades. The white ibis is nomadic and nests in various locations depending on where water conditions are appropriate. In contrast, the wood stork is traditional in its use of nesting sites. Its long 4-month nesting season means that water conditions at the time of nesting may not be a good predictor of prey locations several months later. In compensation wood storks nest at traditional centralized sites and travel over 80 km from the nest site to foraging sites. These two species in several ways represent ends of a continuum of aquatic birds which show similar abilities to adapt to water level fluctuations.

Seasonal movement and longer-term shifts of populations, as illustrated by ibis and storks, appear to be a recurring strategy among wetland birds. In the Everglades, population shifts are a response to changing foraging conditions due to water level fluctuations. Similar situations are reported from other tropical and temperate wetlands (Kushlan et al., 1985; Jelks and Collopy, this volume). Waterfowl also make seasonal and sporadic population shifts, all in response to water level fluctuations (Hansen and McKnight, 1964; Henny, 1973; Flake, 1979). Even within a season, waterfowl move among disjunct wetlands to obtain ephemeral food supplies as marsh patches dry (Krapu, 1974; Derrickson, 1978; Dwyer et al., 1979; Weller, 1979). During droughts in the prairie potholes, some waterfowl appear to shift toward tundra wetlands (Hansen and McKnight, 1964).

OTHER WETLANDS

Aquatic bird use of the dry riparian woodlands of western North America is slight. Nonetheless these phreatophytic habitats support extremely high bird diversities and abundances (Carothers et al., 1974; Johnson and Haight, 1985). The importance of water table elevation in controlling transpiration and productivity in riparian systems is well-known (Ritzi et al., 1985). Although the effects of water table elevation and its fluctuation on riparian bird communities remain to be determined, they are clearly more subtle than in better-watered fluctuating wetlands.

In northern peat bogs, water depths are relatively stable over long periods, although long-term fluctuations can affect plant survival, especially survival of swamp trees (Weller, 1979). These peatlands are less affected by seasonal rainfall cycles because the water-holding capacity of the peat results in bogs carrying their own perched water table. Tundra wetlands are similarly less affected by water level variations during the short growing season. However, microgeographic variability in water depth is an important aspect of tundra ecology. Slight elevational differences result in different plant communities and different depths of pools which support the invertebrate production on which shorebirds and waterfowl such as pintail *(Anas acuta)* depend.

Although hydrological fluctuations appear to play important roles in determining avian use of many wetlands, there are two exceptions. The direct effect of water level fluctuations on bird populations appears to be less in more xeric groundwater ecosystems and seems to be more complex in colder climates, where seasonal temperature variations become a more dominating factor.

ROLES OF WATER LEVEL FLUCTUATIONS

Considerable evidence appears to support the general hypothesis that the pattern of water level fluctuation is a dominant characteristic of riparian and wetland ecosystems and that avian populations using such wetlands must possess suites of adaptations that permit accommodation to such fluctuations. Given such an understanding, from examining the relationship of water level fluctuations to avian users, it is worthwhile to formulate more specific hypotheses that might be examined in other contexts. Such hypotheses may provide a framework for studying various hydrological effects and achieving a broader understanding of wetland ecology. These can be stated as follows:

1. The seasonal pattern of water level fluctuation is a dominant force in freshwater wetland ecosystems.

2. Water level fluctuations can control the impact of other important environmental factors.

3. Water level fluctuations in wetlands occur with periodicities and extents that have inherent statistical predictability.

4. Natural catastrophic events occur with predictable return times and can reset population sizes and community structure.

5. Survival and reproductive success of wetland organisms require specific adaptations to fluctuating water levels.

6. Wetland use by animals is based on hydrological conditions that affect water depth, vegetative habitat, prey abundance, and availability.

7. There are limits to the ability of organisms to accommodate to fluctuating conditions that may be exceeded by events whose amplitude is widely deviant from the norm.

8. The variability of fluctuating wetlands may be accommodated by large-scale population movements, either seasonally or from one year to the next, resulting in repeated colonization of and emigration from a wetland site as hydrological conditions change.

9. The packing of species in a community dominated by fluctuating water levels is accomplished by differing fundamental adaptations, but prey or habitat use may overlap because of seasonal superabundances of food.

10. Species having differing fundamental adaptations may be supported in a single system because of seasonal, geographic, or year-to-year variations in the pattern of water level fluctuations.

11. In dry and cool ecosystems, those factors tend to exert relatively more influence than does water level fluctuation.

12. Even in dry and cool systems, water level fluctuations may have important implications for avian use.

CONCLUSIONS

A review of studies of avian use of wetlands suggests that the pattern of water level fluctuation is an important force in many wetland ecosystems. Its importance seems greatest in tropical or subtropical systems having moderate climates and distinct rainfall seasonality and appears to lessen in colder or drier climates. I suggest, however, that many subtle yet important effects of hydrological fluctuation on avian populations remain to be discovered.

The prominence of hydrological fluctuation in explaining behavioral, ecological, and morphological adaptations of aquatic birds suggests that it may be a useful unifying concept. Investigations of the Everglades were based upon evaluating hypotheses concerning the quantitative effect of water level fluctuation on animal population parameters within natural experiments. Such an approach may prove to be useful in other wetlands.

Water level fluctuations in wetlands must be preserved and managed. Precise manipulation of water levels in waterfowl impoundments is increasingly advocated as a management technique to supply food and cover for waterfowl (Weller, 1978; Fredrickson and Taylor, 1982). Many other aquatic bird species depend on the conservation and appropriate management of wetlands (Kushlan, 1979b, 1983). Thus water level management by active manipulation is the appropriate strategy for preserving entire wetland ecosystems (Kushlan, this volume). Water level fluctuation is a dominant process in wetlands and is especially important in maintaining avian populations. Thus, such fluctuations must be perpetuated in wetlands to achieve avian management goals whether they be the propagation of specific bird populations or preservation of natural wetland systems.

LITERATURE CITED

Beard, E. B., 1953, The Importance of Beaver in Waterfowl Management at Seney National Wildlife Refuge, *Journal of Wildlife Management*, 17: 398-436.

Browder, J. A., 1978, A Modeling Study of Water, Wetlands, and Wood Storks, *Wading Birds*, National Audubon Society Report 6, New York, pp. 325-346.

Carothers, S. W., R. R. Johnson, and W. W. Aitchison, 1974, Population Structures and Social Organization of Southwestern Riparian Birds, *American Zoologist*, 14: 97-108.

Clark, E. S., 1979, Factors Affecting the Initiation and Success of Nesting in an East-Central Florida Wood Stork Colony, *Proceedings of the 1978 Conference of the Colonial Waterbird Group*, 2: 178-188.

Derrickson, S. R., 1978, The Mobility of Breeding Pintails, *Auk*, 95: 104-114.

Dwyer, T. J., G. L. Krapu, and D. M. Janke, 1979, Use of Prairie Pothole Habitat by Breeding Mallards, *Journal of Wildlife Management*, 43: 526-531.

Errington, P. L., 1963, *Muskrat Populations*, Iowa State University Press, Ames, Iowa.

Ewel, K. C., and H. T. Odum, 1984, *Cypress Swamps*, University Presses of Florida, Gainesville, Florida.

Flake, L. D., 1979, Wetland Diversity and Waterfowl, *Wetland Functions and Values: The State of Our Understanding*, P. E. Greeson, J. R. Clark, and J. E. Clark (Eds.), American Water Resources Association, Minneapolis, Minnesota, pp. 312-319.

Fredrickson, L. H., 1979, Lowland Hardwood Wetlands: Current Status and Habitat Values for Wildlife, *Wetland Functions and Values: The State of Our Understanding*, P. E. Greeson, J. R. Clark, and J. E. Clark (Eds.), American Water Resources Association, Minneapolis, Minnesota, pp. 296-306.

——, and T. S. Taylor, 1982, *Management of Seasonally Flooded Impoundments for Wildlife*, U. S. Fish and Wildlife Service Resource Publication 148, U. S. Government Printing Office, Washington, D. C.

Hafner, H., and R. H. Britton, 1983, Changes of Foraging Sites by Nesting Little Egrets (*Egretta garzetta* L.) in Relation to Food Supply, *Colonial Waterbirds*, 6: 24-30

Hancock, J., and J. Kushlan, 1984, *The Herons Handbook*, Harper & Row, New York.

Hansen, H. A., and D. E. McKnight, 1964, Emigration of Drought-Displaced Ducks to the Arctic, *Transactions of the North American Wildlife and Natural Resources Conference*, 29: 119-127.

Harris, S. W., and W. H. Marshall, 1963, Ecology of Water-Level Manipulations on a Northern Marsh, *Ecology*, 44: 331-343.

Henny, C. J., 1973, Drought Displaced Movement of North American Pintails to Siberia, *Journal of Wildlife Management*, 37: 23-29.

Johnsgard, P. A., 1956, Effects of Water Fluctuation and Vegetation Change on Bird Populations, Particularly Waterfowl, *Ecology*, 37: 689-701.

Johnson, R. R., and L. T. Haight, 1985, Avian Use of Xeroriparian Ecosystems in the North American Warm Deserts, *Riparian Ecosystems and Their Management: Reconciling Conflicting Uses*, R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre (Eds.), USDA Forest Service, General Technical Report RM-120, pp. 156-160, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado.

——, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre, 1985, *Riparian Ecosystems and Their Management: Reconciling Conflicting Uses*, USDA Forest Service, General Technical Report RM-120, Forest and Range Experiment Station, Ft. Collins, Colorado.

Kahl, M. P., 1964, The Food Ecology of the Wood Stork, *Ecological Monographs*, 34: 97-117.

Kantrud, H. A., and R. E. Stewart, 1977, Use of Natural Basin Wetlands by Breeding Waterfowl in North Dakota, *Journal of Wildlife Management*, 42: 243-253.

Krapu, G. L., 1974, Foods of Breeding Pintails in North Dakota, *Journal of Wildlife Management*, 38: 408-417.

___, and H. F. Duebbert, 1974, A Biological Survey of Kraft Slough, *Prairie Naturalist*, **6:** 33-55.

Kroodsma, D. E., 1979, Habitat Values for Nongame Wetland Birds, *Wetland Functions and Values: The State of Our Understanding*, P. E. Greeson, J. R. Clark, and J. E. Clark (Eds.), American Water Resources Association, Minneapolis, Minnesota, pp. 320-343.

Krull, J. N., 1970, Aquatic Plant-Macroinvertebrate Associations and Waterfowl, *Journal of Wildlife Management*, **34:** 707-718.

Kushlan, J. A., 1974a, Observations on the Role of the American Alligator *(Alligator mississippiensis)* in the Southern Florida Wetlands, *Copeia*, **1974:** 993-996.

___, 1974b, Effects of a Natural Fish Kill on the Water Quality, Plankton, and Fish Population of a Pond in the Big Cypress Swamp, Florida, *Transactions of the American Fisheries Society*, **103:** 235-243.

___, 1975, Population Changes in the Apple Snail *(Pomacea paludosa)* in the Southern Everglades, *Nautilus* **89:** 21-23.

___, 1976a, Wading Bird Predation in a Seasonally-Fluctuating Pond, *Auk*, **93:** 464-476.

___, 1976b, Site Selection for Nesting Colonies by the American White Ibis *Eudocimus albus* in Florida, *Ibis*, **118:** 590-593.

___, 1977, Population Energetics of the White Ibis, *Auk*, **94:** 114-122.

___, 1978, Feeding Ecology of Wading Birds, *Wading Birds*, National Audubon Society Report 6, New York, pp. 249-296.

___, 1979a, Foraging Ecology and Prey Selection in the White Ibis, *Condor*, **81:** 376-389.

___, 1979b, Design and Management of Continental Wildlife Reserves: Lessons from the Everglades, *Biological Conservation*, **15:** 281-290.

___, 1981, Resource Use Strategies in Wading Birds, *Wilson Bulletin*, **93:** 145-163.

___, 1983, Special Species and Ecosystem Preserves: Colonial Waterbirds in U. S. National Parks, *Environmental Management*, **7:** 201-207.

___, 1986, Responses of Wading Birds to Seasonally Fluctuating Water Levels: Strategies and Their Limits, *Colonial Waterbirds*, **9:** 155-162.

___, 1987, External Threats and Internal Management: The Hydrological Regulation of the Everglades, *Environmental Management*, **11:** 109-119.

___, and O. L. Bass, Jr., 1983a, Snail Kite in the Southern Everglades, *Florida Field Naturalist*, **11:** 108-111.

___, and O. L. Bass, Jr., 1983b, Habitat Use and the Distribution of the Cape Sable Sparrow, *The Seaside Sparrow, Its Biology and Management*, T. L. Quay, J. B. Funderburg, Jr., D. S. Lee, E. F. Potter, and C. S. Robbins (Eds.), Occasional Papers of the North Carolina Biological Survey 1983-5, pp. 139-146.

___, and P. C. Frohring, 1986, The History of the Wood Stork in Southern Florida, *Wilson Bulletin*, **98:** 368-386.

___, and M. S. Kushlan, 1979, Observations on the Crayfish in the Everglades, *Crustaceana Supplement*, **5:** 116-120.

___, L. G. Morales, and P. C. Frohring, 1985, Foraging Niche Relations of Wading Birds in Tropical Wet Savannas, *Ornithological Monographs*, **36:** 663-682.

___, J. C. Ogden, and A. L. Higer, 1975, *Relation of Water Level and Food Availability to Wood Stork Reproduction in the Southern Everglades, Florida*, U. S. Geological Survey Report 75-434, Tallahasee, Florida.

McKnight, D. E., and J. B. Low, 1969, Factors Affecting Waterfowl Production on a Spring-Fed Salt Marsh in Utah, *Transactions North American Wildlife and Natural Resources Conference*, **34:** 307-314.

Odum, E., 1983, *Basic Ecology*, Saunders College Publishing, New York.

Ogden, J. C., J. A. Kushlan, and J. T. Tilmant, 1976, Prey Selectivity by the Wood Stork, *Condor*, **78:** 324-330.

Ritzi, R. W., H. Bouwer, and S. Sorooshian, 1985, Water Resource Conservation by Reducing Phreatophyte Transpiration, *Riparian Ecosystems and Their Management: Reconciling Conflicting Uses*, R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre (Eds.), USDA Forest Service, General Technical Report RM-120, pp. 191-196, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado.

Rogers, J. P., 1964, Effect of Drought on Reproduction of the Lesser Scaup, *Journal of Wildlife Management*, **28:** 213-222.

Schroeder, L. D., D. R. Anderson, R. S. Pospahala, G. G. W. Robinson, and F. A. Glover, 1976, Effects of Early Water Application on Waterfowl Production, *Journal of Wildlife Management*, **40:** 227-232.

Swanson, G. A., 1984, Invertebrates Consumed by Dabbling Ducks (Anatinae) on the Breeding Grounds, *Journal of the Minnesota Academy of Science*, **50**: 37-40.

——, and M. I. Meyer, 1977, Impact of Fluctuating Water Levels on Feeding Ecology of Breeding Blue-Winged Teal, *Journal of Wildlife Management*, **41**: 426-433.

Sykes, P. A., Jr., 1983, Recent Population Trend of the Snail Kite in Florida and Its Relation to Water Levels, *Journal of Field Ornithology*, **54**: 237-246.

——, 1984, The Range of the Snail Kite and Its History in Florida, *Bulletin of the Florida State Museum 29*, Gainesville, Florida.

Thomas, T. M., 1974, A Detailed Analysis of Climatological and Hydrological Records of South Florida with Reference to Man's Influence on Ecosystem Evolution, *Miami Geological Society Memoir*, **2**: 82-122.

Uhler, F. M., 1944, Control of Undesirable Plants in Waterfowl Habitats, *Transactions North American Wildlife Conference*, **9**: 295-303.

van der Valk, A. G., and C. B. Davis, 1978, The Role of Seed Banks in the Vegetation Dynamics of Prairie Glacial Marshes, *Ecology*, **59**: 322-335.

Weller, M. W., 1978, Management of Freshwater Marshes for Wildlife, *Freshwater Wetlands*, R. E. Good, D. F. Whigham, and R. L. Simpson (Eds.), Academic Press, New York, pp. 267-284.

——, 1979, Wetland Habitats, *Wetland Functions and Values: The State of Our Understanding*, P. E. Greeson, J. R. Clark, and J. E. Clark (Eds.), American Water Resources Association, Minneapolis, Minnesota, pp. 210-234.

——, and L. H. Fredrickson, 1974, Avian Ecology of a Managed Glacial Marshland, *Living Bird*, **12**: 269-291.

——, and C. E. Spatcher, 1965, *Role of Habitat in the Distribution and Abundance of Marsh Birds*, Iowa Agriculture and Home Economics Experiment Station Special Report No. 43, Ames, Iowa.

——, B. H. Wingfield, and J. B. Low, 1958, Effects of Habitat Deterioration on Bird Populations of a Small Utah Marsh, *Condor*, **60**: 22-224.

Yeager, L. E., and H. M. Swope, 1956, Waterfowl Production During Wet and Dry Years in North-Central Colorado, *Journal of Wildlife Management*, **20**: 442-446.