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FLORIDA KEYS
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On the cover: “Doghouse Key” by Clyde Butcher.
Linkages Between the Snail Kite Population and Wetland Dynamics in a Highly Fragmented South Florida Hydroscape

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INTRODUCTION

The endangered snail kite (**Rostrhamus sociabilis**) is the only avian species that occurs throughout the South Florida freshwater hydroscape and whose population is restricted to these wetlands. Habitat quality for this species is dependent on hydrology and wetland plant communities that support its principal food source, the apple snail (**Pomacea paludosa**). Consequently, there is direct linkage between changes in hydrology and changes in habitat quality for the kite.

The pre-drainage or “natural” South Florida freshwater hydroscape, dominated by the Everglades, was characterized by: (1) its spatial extent, in excess of 3.6 million ha; (2) its spatially continuous sheet flow, emanating variously south of Lake Okeechobee and flowing almost imperceptibly (36 m/hr; Holling et al., 1994) downslope on the flat gradient of about 2 cm/km (Leach et al., 1972); and (3) the resultant heterogeneous landscape mosaic of water depths and habitat types (Davis and Ogden, 1994). The current or “managed” system has been reduced to 1.8 million ha, approximately half its original size. The system is now severely fragmented by compartmentalization into a series of interconnected impoundments designated Water Conservation Areas (WCAs), consisting of 100+ water control structures and approximately 2000 km of dike works and canals. Entire wetland landscapes have been virtually eliminated (Davis et al., 1994), while others have been severely altered as a result of water management practices (Science Subgroup, 1993).

Under the existing management regime for kites, droughts have been portrayed as demographic catastrophes in which both survival and reproduction plummet (Beissinger and Takekawa, 1983; Beissinger, 1986, 1995). Management recommendations have consequently focused primarily on increasing the interval between drydowns and maintaining permanent water levels (e.g., Stieglitz and Thompson, 1967; Martin and Doebel, 1973; Beissinger, 1983, 1995). This effectively results in “freezing” or stabilizing specific hydrologic conditions in large-scale impounded wetland units (principally the WCAs) to provide a critical habitat for the maintenance of this species. However, while this approach may confer some short-term benefits, it is counter to the natural dynamics under which these wetland systems evolved (Leach et al., 1972). It essentially promotes the continued maintenance of a fragmented system of fixed components rather than the interconnected dynamic mosaic targeted by recent restoration efforts (Science Subgroup, 1993).

In this paper we frame the issues of water management needs for snail kites in the context of an adaptive management paradigm (e.g., Holling, 1978; Walters, 1986; Foin et al., 1998). We begin with the management assumptions stated above and follow a progression of kite and habitat responses at various spatial scales, ranging from local, specific sites to the entire region, detailing the subsequent consequences. We conclude with recommendations for a new management paradigm, one that more closely reflects the historic “natural” system within which the kite proliferated (Sykes, 1984).

LINKAGES BETWEEN BIRDS AND HABITAT AT MULTIPLE SCALES

The snail kite is a wetland-dependent species whose population dynamics are a function of changes in carrying capacity of the wetland hydroscape comprising its range. This carrying capacity is subject to acute declines during regional droughts. As stated previously, it is widely held that droughts drastically impact both survival and reproduction of the kite. Our concern is that simplistic single-species management schemes that seek to counter or solve the drought “dilemma” by creating drought refugia within selected prime wetland areas may well compromise the habitat values critical for population recovery and long-term sustainability. This concern is particularly amplified when aspects of temporal and spatial scale are ignored (Bennetts and Kitchens, 1997a).

Most severe droughts are localized to part of the snail kite’s range, rather than extending across its entirety. While droughts resulting in drydowns can cause acute reductions in carrying capacity of local wetland sites, the ability of the snail kite population to sustain itself through time is a function of the total habitat base across the region. The continued persistence of the snail kite
population in the face of the periodic droughts that characterize South Florida will largely depend on the maintenance of a critical network of viable wetlands dispersed across the entire regional hydroscape (Bennets and Kitchens, 1997a,b). The term viable is emphasized to bring attention to the fact that wetlands, by definition, are areas subjected to periodic wet and dry conditions. They are occupied by plant and animal populations specifically adapted to these conditions. These wetland communities are highly sensitive to alterations in hydroperiods, particularly those extending or stabilizing water depths. Recovery time from the deleterious effects of such alterations can be extended.

The general problem concerning current management can be considered a failure to discriminate between survival of individual kites and the requirements for long-term sustainability of the population. Key to this oversight is inadequate consideration of either the bird or the habitat at multiple spatial and temporal scales. It is only in the context of cross-scale linkages that the effects of habitat management on the kite populations become apparent (Bennets and Kitchens, 1997b). The following narrative is a descriptive account linking the biology of snail kites and their habitat at different scales, followed by a consideration of the response of the habitat, and the birds, at these different scales to current management.

**MACROSINGLE: RANGE OR REGIONAL SCALE**

The entire population of snail kites in the U.S. is currently confined to that area of Florida lying south of an east–west line crossing the state at the approximate latitude of Orlando. The area is characterized climatically as subtropical with pronounced wet and dry seasons. Precipitation is approximately 100 cm/year, with the bulk occurring during June to August. While the precipitation averaged over this region is seasonally predictable (Duever et al., 1994), it is spatially variable (MacVicar and Lin, 1984), with some parts of the region experiencing localized droughts while other areas are receiving normal or even above normal precipitation. The landscape is largely a flattened limestone basin overlain to the north by shallow sands and to the south by peat. The regional topographical gradient is extremely flat, declining to the south approximately 2 cm/km with localized topographic discrepancies approaching 1.5 m (Gunderson, 1994). Given its abundant, spatially variable precipitation and slight drainage gradients, much of the landscape is dominated by a mosaic of water and wetlands, or a "hydroscap." The hydroscap used by kites is encompassed within several watersheds, including: (1) its two principal watersheds, the Kissimmee/Okeechobee/Everglades (KOE) and Upper St. Johns River (USJR) basins; (2) portions of the Big Cypress Basin; (3) the Loxahatchee River Basin, principally Loxahatchee Slough and Pal Mar; and (4) portions of the Caloosahatchee River Basin. The Kissimmee chain of lakes (Tohopekaliga, East Tohopekaliga, Kissimmee, Marion, Tiger, Pierce, Jackson, and Hatchineha), Lake Okeechobee, the Water Conservation Areas (3A, 3B, 2A, 2B, and 1 and A.R.M. Loxahatchee National Wildlife Refuge), the Holeyland Wildlife Management Area, and the Everglades National Park are among those areas used by kites in the KOE. The Blue Cypress Marsh Water Conservation Area, Blue Cypress Water Management Area of the USJR, and the West Palm Beach Water Catchment Area of the Loxahatchee River watershed are other important areas used by kites. Numerous other smaller wetlands and water retention units or "peripheral" areas scattered throughout the region are critically important areas in the event of region-wide droughts. Although termed "peripheral," they are regularly utilized. Use is not restricted to drought use only, as been implied by Beissinger and Takekawa (1983) and Takekawa and Beissinger (1989).

The wetlands and associated water bodies composing this hydroscap vary in size from a few hectares to several thousand hectares, totaling more than 1.2 million ha. These wetlands include lacustrine, palustrine, and riverine types and occur within several major physiographic provinces and features. The palustrine wetlands include mosaics of extensive gramminoid marsh strands dominated by sawgrass (*Cladium jamaicense*), with tree islands on isolated topographic highs. Tree islands are dominated variously by woody species, including red bay (*Persea palustris*), dahoon
holly (Ilex cassine), and willow (Salix caroliniana). Wet prairies, dominated by spike and beak rushes (Eleocharis and Rhynchospora spp.), and aquatic sloughs, dominated by fragrant water lily (Nymphaea odorata) and submerged aquatics including bladderwort (Utricularia spp.), occupy the topographic “lows” or troughs interspersed within the strands of sawgrass and tree islands. The lacustrine types occur as littoral areas dominated by extensive coenoclines of spatterdock (Nuphar luteum), and maidencane (Panicum spp.) and are bordered by bullrushes (Scirpus spp.) on the lakeward edge and willow or cattail (Typha spp.) toward the shore.

The snail kite population inhabiting the region is currently estimated at around 3000 birds (Dreitz et al., in press), having steadily increased over time from apparent population lows in the 1950s and 1960s following major droughts. Annual counts since 1969 have varied between 65 and 996, but generally support an increasing population trend over this period, even when adjusted for observer and other biases (Bennets et al., 1999). Observations of birds outfitted with radio transmitters (Bennets and Kitchens, 1997a,b) suggest that kites use the regional hydroscape as an extensive network of habitats. At this scale, the snail kites are quite nomadic and move frequently throughout the region (Figure 6.1). Our data indicate that, on average, birds move from one distinct wetland area to another several times per year. Thus, rather than a meta-population consisting of distinct subpopulations, snail kites in Florida are more of a panmictic population utilizing the entire spatial extent of their range. These extensive movements of individual kites among the various wetland areas and types within the region serve to effectively “connect” these rather spatially and hydrologically fragmented systems in a networked fashion. In addition to the nomadic movement of individuals, the birds congregate variously throughout this network with dramatic temporal shifts

FIGURE 6.1  South Florida showing a summary of inter-wetland movements (solid lines) of adult, radio-tagged snail kites during 1992 and 1993. These movements illustrate a basic habitat network used by snail kites (circles represent major wetland units, squares represent peripheral areas).
in numbers and locations. Depending upon the season, the resultant pattern is a continuum of individual and communal foraging and nesting activities, highly variable in time and space.

**MICROSCALE: INDIVIDUAL BIRDS (AND SNAILS) AT THE LOCAL OR SITE-SPECIFIC SCALE**

At the level of individual birds, we focus primarily on foraging and nesting ecology. Snail kites feed almost exclusively on apple snails. Snail kites are visual hunters and must locate their prey within the water column. They capture their prey by flying low over the marsh and, after sighting a snail, drop to pluck their prey from the top few centimeters of water. Foraging is widely dispersed in areas with sparse vegetation and concentrated along boundaries distinguishing various emergent macrophytes, where patches of coenoclines are interspersed. The latter areas are typically extensive and usually delineate plant communities of different hydroperiod preferences (e.g., spike rushes and water lilies in the Everglades marshes, or maidencane and rushes in the littoral reaches of lakes). In general, foraging areas are shallow and provide an emergent stem density sufficiently sparse to enable kites to see their prey, yet dense enough to provide an emergent substrate for snails concentrating at or near the surface in numbers that attract foraging birds. The snails climb plant stems to the water surface in order to breathe, particularly during warmer periods when water-column oxygen concentrations are reduced. There may be a threshold depth beyond which it is energetically inefficient for snails to make the excursion between the surface and bottom waters for breathing, thus limiting the snails to shallow marsh areas. Likewise, because water depth and temperature vary inversely during the warmer months, snails in deeper waters emerge to breathe less frequently and thus are less often exposed to foraging activities (Darby et al., 1997).

**MESOSCALE: HABITAT OR LANDSCAPE SCALE**

When viewed at an expanded spatial scale, foraging habitats tend to occur in three general categories (Bennetts et al., 1994). For the Everglades marshes, foraging is generally confined to two general vegetation types classified by Loveless (1959) as wet prairies and aquatic sloughs. The wet prairies are further divided into *Eleocharis* - and *Rhynchospora*-dominated prairies, although foraging kites tend to use the former more frequently. Functionally, these are three different coenocline types, spatially arrayed or interspersed along a gradient of hydroperiods ranging from 70 to 99% inundated. Precise hydroperiod discriminations tend to be highly site specific but follow a general trend of 50 to 82% for *Rhynchospora* prairies (peaking at 75%), and 50 to 94% for *Eleocharis* prairies (peaking at 85%) in the Water Conservation Areas (Zaffke, 1983). Aquatic sloughs are dominated principally by fragrant water lily, floating heart, *Nymphaea aquatic* a, and submerged aquatics, including bladderwort. These sloughs tend to be more or less permanently inundated except during exceptionally dry years as defined by Bennetts and Kitchens (1997a) and Bennetts et al. (1999). Foraging in the lake environments outside the Everglades is generally confined to the reaches of the littoral system dominated by extensive stands of maidencane and spike rushes (Bennetts et al., 1994) with hydroperiods ranging from 50 to 90% (Sincok and Powell, 1957). Foraging is focused in the deeper areas of this zone. Deeper areas are dominated by spatterdock that is either a poor substrate for visual hunting or unsuitable for snails. Shallower areas are dominated by cattail or flag (*Sagittaria*) in stands too densely vegetated for visual hunting, and snail densities are reduced.

Nesting habitat has somewhat different constraints. Snail kites tend to nest in woody substrates that are located over water. Nests may occur singularly in isolated woody shrubs such as pond apple (*Annona glabra*), willow, and wax myrtle (*Myrica cerifera*) on microtopographic mounds in the marshes. Communal nests are more often found in the shrub/scrub strands or "tree islands" that are either completely surrounded by water or occur in the trailing edge or "tails" of tree islands where hydroperiods are extended. In the absence of woody vegetation, kites will nest in herbaceous vegetation such as cattail, although nest failure under these circumstances tends to be higher due to nest collapse, especially after wind events (Chandler and Anderson, 1984; Snyder et al., 1989).
This occurs more often in the lacustrine habitats (e.g., Lake Okeechobee), typically at times when shorelines have migrated downslope due to excessively low water conditions, or in lake systems with littoral systems confined by levees and subject to elevated water stages. Kites tend to avoid areas without standing water during the nesting season, presumably due to vulnerability to increased terrestrial predation pressures.

Habitat requirements of the kite can be summarized graphically in relation to a hydrological gradient (Figure 6.2), where foraging habitats tend to occur in coenoclines occupying the wetter areas, and nesting habitat tends to occupy patches in relatively drier habitats. When viewed from a landscape perspective, expanding in spatial extent to another scale, the interspersion and proximal locations of these habitat types become apparent (Figure 6.3). Obviously, foraging habitat is always required, and nesting habitat is required during periods of nesting. One without the other in proximal association will not be suitable habitat, at least for some life-history stages. Given the existing hydrology management paradigms promoting stable, specific water regimes in selected areas of the system, this interspersion of foraging and nesting habitat is at risk of decline. The following sections elaborate this concern.

**HYDROSCAPE, HABITAT, AND KITES: MANAGEMENT AT MULTIPLE SCALES**

**The Hydrologically Altered System**

As stated earlier, the South Florida hydroscape has been dramatically changed in the past 50 years, with wetland areas being reduced from 3.6 to 2.4 million ha (Davis and Ogden, 1994). Water levels and flows that once fluctuated seasonally in response to rainfall and runoff have been dramatically altered in an attempt to reduce effects of flooding and droughts on human activities in South Florida (McPherson and Halley, 1996). The inter- and intra-annual variability of water stages in the remaining principal wetland systems supporting kites has been severely altered. Both peak and minimal stages have been lowered, and the range between peak and minimal stages has been considerably decreased in several areas (Figure 6.4). Due to dams, dikes, and levees, for the first time in the geological history of the Everglades, stages and flows are no longer coupled to rainfall (Figure 6.5). The KOE no longer exists as a single hydrologic unit. Instead, it is subdivided into the Upper Kissimmee Chain of Lakes, Lake Okeechobee (with dredged outlets to both coasts), the remaining Everglades partitioned into three major impoundments (WCAs 1, 2, and 3, serving principally as flood protection and water supply reservoirs), and the Everglades National Park. The massive sheet-flow system that characterized the pre-drainage Everglades (Science Subgroup, 1993; Davis and Ogden, 1994) has been eliminated and replaced by this series of impoundments that effectively step the water level stages from north to south in a fashion that exaggerates the vertical component of the hydroperiod (Figure 6.6). This alteration has resulted in excessive ponding in the southern end of impoundments while over-draining the northern ends (Dineen, 1972; Light and Dineen, 1994).

**Altered Hydrology for Kites: Consequences of the Existing Paradigm**

Descriptive accounts of snail kite populations during the late 1800s and early 1900s indicated that snail kites were relatively abundant in Florida, at least at some locations (Scott, 1881; Bailey, 1884; Wayne, 1895; Howell, 1932). By the 1920s and continuing through the 1950s, virtually all reports described snail kites in Florida as declining or rare (Howell, 1932; Sprunt, 1945; Wachenfeld, 1956). Declines were attributed primarily to widespread drainage that occurred throughout Florida (Howell, 1932; Sprunt, 1945; Sykes, 1983a; Bennett et al., 1994). Since that time snail kite numbers have rebounded from what was considered to be a low of about 50 to 100 birds (Sprunt, 1945) to a current estimate of approximately 3000 birds (V. J. Dreitz, in press). This rebound has been largely
attributed to the creation of the impounded Water Conservation Areas that provided long-hydropereiod marshes in areas substantially affected by drainage (e.g., Sykes, 1983b).

This concept has been extended further into a management paradigm that critical habitat for kites requires maintaining continuous inundation of specific wetland units as refugia from drought (e.g., Stieglitz, 1965; Stieglitz and Thompson, 1967; Beissinger, 1988). This approach emerged largely from assumptions that reduced counts during a systematic annual survey implied population reduction in response to water levels in the surveyed areas (e.g., Sykes, 1979, 1983a; Beissinger, 1988, 1995) and the conclusion of Snyder et al. (1989) and Beissinger (1986) that nest success was
lower during years of low water. It was more recently suggested by a population viability analysis (Beissinger 1995) that the Florida population of snail kites would not be viable unless the interval between successive “droughts” exceeded 4.3 years. However, this model used the annual survey as a primary basis for verification and as a source of data for its most sensitive parameter, survival during drought years. The annual survey has been critically analyzed and its value in estimating annual changes in population size has been discredited (Bennetts et al., 1999). Regardless, the general perception has emerged that the occurrence of drought or drying implies a demographic catastrophe for kites and their forage base. The underlying foundation for this view is another perception that apple snails undergo massive mortality in response to drying (e.g., Beissinger, 1988). Recent work by Darby et al. (1997) has also discounted this generalization. This work indicates that the effect of drying on apple snails depends largely on its timing and duration and in many cases may not even affect survival of apple snails.

As a result, protection has centered on critical habitat/wetland units almost entirely within the Everglades and Lake Okeechobee watersheds (WCA-3A and the littoral system of Lake Okeechobee) as drought refugia (Federal Register 42 [155]: 40685-40688; 50 CAR Ch. 1; 10-1-94 ed.). Bennetts and Kitchens (1997b) presented the following argument critiquing this approach: (1) this spatial configuration of protected habitat ignores the vulnerability to simultaneous low water conditions in these proximal areas during droughts, and (2) continuous inundation in these units, while beneficial over the short term, will erode habitat quality over the long term. We agree that regionally widespread drydowns may affect the snail kite population and that the frequency should not be anthropogenically increased. However, the problem is that inferences regarding the return frequency of widespread regional droughts have frequently been interpreted to mean that the occurrence of local drying events should also be decreased, by whatever artificial means available. Local and widespread regional drying events, however, are not the same. Their ecological implications are vastly different. The critical issue that has been largely ignored by these

FIGURE 6.6  A conceptual illustration of how compartmentalization of wetlands with levees increases depth by decreasing the potential for lateral movement of water.
recommendations (however, see Sykes, 1983a) is that the lack of periodic drying can detrimentally affect the kites' nesting and foraging habitat (Bennetts et al., 1994; Bennett and Kitchens, 1997a). Bennett and Kitchens (1997b) use the shifts in distribution of nesting birds in WCA-3A over a 30-year period to demonstrate this point. Birds originally nested in the longest hydroperiod portion of the marsh following initial impoundment in the 1960s. However, nest distributions steadily shifted up the elevational gradient through time toward shallower and consequently shorter hydroperiod areas. In this system, while the traditional nesting area is still subject to some inter-annual variability, the area is subject to increased hydroperiods and ponding depths as a result of impoundment (Zaffke, 1983; David, 1996). This has resulted in major shifts in both foraging and nesting habitat composition and quality. The nature of these habitat conversions, and a concern regarding recovery times, is detailed below.

**Habitat Responses to Increased Hydroperiods or Decreased Return Intervals Between Drydowns**

A discussion of the tolerances of the plant species that comprise the principal foraging and nesting habitats of the kite must span several temporal and spatial scales. Lists of wetland species found in these habitats are presented in Loveless (1959) for the Everglades and Pesnell and Brown (1977) and Ager and Kerce (1970) for lakes. Our discussion is limited to the dominant or indicator species. Tables 6.1 and 6.2 summarize numerous studies examining relationships between species occurrence and hydrology in the South Florida hydroscape. Four conclusions are immediately obvious: (1) there is considerable variability among studies as to the preferences or tolerances regarding hydroperiod for any given species, which probably reflects differences in soils, site histories, and disturbance regimes; (2) the relative hydroperiod distinction for these community types tends to remain relatively constant within sites; (3) virtually none of the species can tolerate continuous inundation; and (4) practically all studies document detrimental habitat conversions over time resulting from the excessive depths and hydroperiods following impoundment intended to reduce hydrological variability. This last observation warrants further discussion.

**Foraging Habitat Alterations**

The predominant conversion noted in these studies is the transformation of wet prairie communities to slough communities in areas subjected to excessive depths or hydroperiods (e.g., WCA 1, 2, and 3) (U.S.D.I., 1972; McPherson, 1973; Dineen, 1974; Worth, 1983; Zaffke, 1983; Wood and Tanner, 1990; David, 1996), or to sawgrass communities in the Everglades Park and other sites subjected to reduced hydroperiods (Kolipinski and Higer, 1969; Alexander and Crook, 1974; Davis et al., 1994), or flow velocities (hypothesized by Davis et al., 1994) as a result of impoundment. Extended hydroperiod affects were discernible at some sites in transition from one type to another. For example, Wood and Tanner (1990) attributed a significant reduction in species in wet prairie communities in sites in WCA-3A to extended hydroperiods when comparing the results of their studies to that of Zaffke (1983) for the same sites. Similar conversions in the littoral system of Lake Okeechobee have also been noted (Ager and Kerce, 1970; Milleson, 1987). The net result of conversion of wet prairie to sloughs is the loss of prime snail kite foraging habitat. Although snail kites will readily forage in slough communities (Sykes, 1983a; Bennetts et al., 1994; Sykes et al., 1995), data from more than 5000 locations of radio-tagged birds (Bennetts and Kitchens, unpubl. data) indicate that wet prairie communities are used to a far greater extent than sloughs for foraging.

**Nesting Habitat Alterations**

Another notable conversion is the general loss of tree islands. These declines are generally attributable to extended hydroperiods or increased depths in the Conservation Areas (McPherson, 1973; Dineen, 1974; Alexander and Crook, 1974; Worth, 1983). Milleson (1987) noted a reduction in
<table>
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<tr>
<th>Investigators; Location</th>
<th>Sloughs</th>
<th>Wet Prairies</th>
<th>Sawgrass</th>
<th>Tree Islands</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nymphaea/Nuphar</td>
<td>Eleocharis</td>
<td>Rhynchospora</td>
<td>Panicum</td>
</tr>
<tr>
<td>David, 1996; WCA-3</td>
<td>96%</td>
<td>75%</td>
<td>91%</td>
<td>61%</td>
</tr>
<tr>
<td>Zaffke, 1983; WCA-3</td>
<td>95–99%</td>
<td>50–94%</td>
<td>50–82%</td>
<td>N/A</td>
</tr>
<tr>
<td>Lowe, 1986; Upper St. Johns Marsh</td>
<td>N/A</td>
<td>75–90%</td>
<td>94%</td>
<td>80–87%</td>
</tr>
<tr>
<td>Goodrick, 1984; WCA-2 and WCA-3</td>
<td>88%</td>
<td>74%</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>McPherson, 1973; WCA-3</td>
<td>87–98%</td>
<td>78–85%</td>
<td>76–93%</td>
<td>69–75%</td>
</tr>
</tbody>
</table>

*Note: Hydroperiods are expressed as percentages of time inundated. Data are reported either for habitats or for indicator species for habitat.*

* Range of mean values for different stations.

* Range of mean value for range.

* N/A = data not reported.
<table>
<thead>
<tr>
<th>Investigator(s); Location</th>
<th>Conversion</th>
<th>Cause</th>
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<tr>
<td>McPherson, 1973; WCA-3</td>
<td>Tree island recession</td>
<td>Flooding due to impoundment</td>
</tr>
<tr>
<td>Alexander and Crook, 1984; South Florida</td>
<td>Tree island losses</td>
<td>Fire and flooding</td>
</tr>
<tr>
<td>Dineen, 1974; WCA-2</td>
<td>Losses of wet prairie species</td>
<td>Impoundment</td>
</tr>
<tr>
<td>Davis, et al., 1994; South Florida</td>
<td>Loss of tree islands</td>
<td>Flooding to permanent pool</td>
</tr>
<tr>
<td>Wood and Tanner, 1990; WCA-3, ENP, NESS</td>
<td>Wet prairies in converting to slough communities</td>
<td>Impoundment, extended hydropoid</td>
</tr>
<tr>
<td>Kolpinski and Higer, 1969; ENP</td>
<td>Decrease in wet prairie</td>
<td>Decreased hydropoid due to impounding upstream</td>
</tr>
<tr>
<td>Dineen, 1972; WCA-2</td>
<td>Increase in sawgrass</td>
<td>Area continuously flooded for 10 yr</td>
</tr>
<tr>
<td>Schortemeyer, 1980</td>
<td>Wet prairie species reduced</td>
<td></td>
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<tr>
<td>Ager and Kerse, 1970; Lake Okeechobee</td>
<td>Tree islands water damaged</td>
<td></td>
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<tr>
<td>Milleson, 1987; Lake Okeechobee</td>
<td>Reduced wet prairie species</td>
<td>Extended hydropoid and depths due to impoundment</td>
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<td></td>
<td>Reduced extent of Salix</td>
<td>Elevated water stages in lake</td>
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<td></td>
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<td>Elevated water stages</td>
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</table>

Willow heads in Lake Okeechobee’s littoral zone following prolonged elevated stages, between 1973 and 1981. This trend continued through 1989, according to Richardson and Harris (1995). Given the extended time frames required for recovery of these tree species and the vulnerability of seedlings to fire or flooding (Gunderson et al., 1988; Gunderson, 1994), these losses are significant. The losses have occurred fairly rapidly, in 6 to 7 years (Ager and Kerse, 1970; U.S.D.I., 1972), but recovery to comparable age structure and stature may require decades. Thus, losses appear to occur within time periods of flooding that correspond roughly to the lower limit of drydowns suggested by Beissinger. The conflicting nature of these time frames is not trivial. Gunderson (1994) suggests this mimics the temporal domain of decades for natural phenomena (El Niño) that occur on similar time scales that are capable of causing considerable detrimental impacts to these tree communities. The prospect for rapid recovery is thus further compounded by the impacts of natural flood/drought frequencies operating in the South Florida hydroscape. Losses of historical colonial roosts and nesting sites resulting from the impoundment and stabilization of hydrologic regimes no doubt have occurred in the past and can only be expected to be exacerbated by continuing these same regimes. 

**Up Against the Wall**

While kites continue to nest in numbers in WCA-3, the trend has been for nesting to shift toward higher elevations and shorter hydropoid periods (Bennetts et al., 1988). In fact, many of the adults that nest in the southern portion of the Water Conservation Area actively forage the marshes of nearby Everglades National Park, where the hydropoid periods are considerably shorter and the hydrology considerably more variable (R.E. Bennett, pers. observ.). As noted earlier, Zaffke (1983), Wood and Tanner (1990), and David (1996) have documented the conversion of wet prairies to aquatic sloughs in that area, with concurrent losses of interspersed herbaceous and woody species. The
immense size of the area (237,000 ha) and the inability to completely stabilize its hydrologic regime are mitigating factors; however, in time the area could continue to convert to less desirable habitat. Given that nesting is already occurring in the highest elevations within WCA-3A (south of Alligator Alley), there may be nowhere else for shifts to occur within this unit if the current trend continues. That is, kites are up against the "hydrologic wall."

The tendency for loss under extended flooding, of emergent species and entire communities or zones comprising coenoclines has also been observed in other wetland ecosystems (Van der Valk and Welling, 1988; Van der Valk, 1991). Van der Valk and Welling (1988) documented drastic reductions in percent cover and distribution and abundances of species within the coenocline of experimental units with increased water depths in as little as three years. This phenomenon is particularly acute in impounded systems where depth and hydroperiod become controlling variables as the water mass is constrained to vertical rather than lateral expansions/retractions in response to volumetric changes (Figure 6.6). In the natural state, microtopographic relief played at least as influential a role as landscape gradient in maintaining the dynamic, interspersed mosaic of the Everglades hydroscape (Gunderson, 1994). In an impounded system, water depths exceed the tolerances, and the variability attributable to local topography can no longer provide conditions favorable for emergent species comprising kite habitat (Figure 6.7). From all evidence (Zaffke, 1983; Wood and Tanner, 1990; David, 1996), the shifting mosaic associated with inter- and intra-annual hydroperiod and depth variability in WCA-3 is virtually "drowned out," with succession tending progressively toward a more aquatic phase. Thus, vegetation change has become unidirectional, rather than a dynamic switch between slough and wet prairie phases in response to environmental variability. This unidirectional trend is increasingly degrading this important habitat resource.

**Hydrology and Habitat Quality**

Both kites and wetlands respond to changes in hydrological regimes. In situ plant communities respond through successional processes at time scales spanning months to several decades. Kites are capable of two types of responses: (1) behavioral responses typically on the order of daily time scales (e.g., simply dispersing to a more suitable location in response to unfavorable hydrologic conditions at a particular locale), or (2) population responses over a period of months or years (e.g., changes in survival or reproduction) (Bennetts and Kitchens, 1997b). The following is a conceptual model (Bennetts and Kitchens, 1998) that integrates critical aspects of wetland and kite responses to hydrology.

**Depth**

The empirical relationship between snail kites' use of a given habitat and water depth has been well recognized and has been illustrated by the distribution of nests or foraging birds with respect to water depth (e.g., Stiegitz and Thompson, 1967; Sykes, 1987; Bennetts et al., 1988). We have observed that kites typically abandon foraging areas after water depths reach a critical depth of < 10 cm.

**Drydown Intervals**

Drying events result in periodic reductions in the availability, although not necessarily abundance of snails as kite food. Consequently, the response of kites is simple. They either move or die. Bennetts and Kitchens (1997a) observed that the numbers of kites using a particular area were reduced by about 50% in the year following a drydown. Incremental recovery to pre-drydown numbers occurred within three years. Recovery of snails and the return of kites probably depend considerably on the timing and severity (i.e., magnitude and duration) of a given drying event (Darby et al., 1997).
Long-Term Hydroperiods

Although the occurrence of drying may temporarily decrease local prey availability, the absence of drying results in changes in plant communities as detailed above. Recovery of herbaceous species subjected to "over-flooding" conditions can occur in as little as one year (Worth, 1983). However, recovery of suitable stature and structure of woody species for optimal nesting habitat has been documented to require more than 9 years in the littoral system of Lake Okeechobee (Milleson, 1987).

We hypothesize that overall habitat quality is a function of the combined suitability of each of these hydrologic variables or scales. Each regulates a different aspect of the environment important to kites. In combination, these factors regulate: (1) the behavior of apple snails, and consequently their availability to kites; (2) apple snail population dynamics; and (3) plant community change. Habitat quality therefore requires alignment of suitable conditions for each of these factors. This alignment (Figure 6.8) can be viewed as a dynamic "window" of hydrologic conditions at a given point in time and space in which snail kites occur (Bennetts and Kitchens, 1997a).

PARADIGMS: EXISTING AND PROPOSED

Past perception regarding management of snail kites is counter to the wetland dynamics under which this system and snail kites have evolved and persisted. The "dynamic landscape hypothesis" (Bennetts and Kitchens, 1998), better reflects the natural dynamics of the South Florida hydroscope. Table 6.3 outlines this proposed paradigm and contrasts it with misperceptions of the existing paradigm. The existing paradigm is a hypothesis based on the notion that droughts are catastrophic to kite populations and must be mitigated through the creation and maintenance of selected permanently inundated, drought-free refugia. This hypothesis/paradigm is flawed in that it neglects important aspects of both temporal and spatial scale on the persistence of kites in South Florida.
Evidence is now clear that this strategy eventually erodes the quality of both the primary and refugia habitats rendering these areas ineffective in the long term. We propose a new hypothesis/paradigm based on the fact that temporal and spatial variability is, and always has been, an intrinsic feature of the environment of the South Florida hydroscape, under which snail kites have persisted.

There are at least two critical management implications of this dynamic landscape view for the snail kite (Bennetts and Kitchens, 1997a). The first is that attempts to create artificially stable habitat by reducing hydrologic variability will erode the quality of habitat over longer time scales. The second is that spatial extent and distribution of habitat across the region are critical. Providing adequate refugia from drought should be accomplished by maintaining high-quality habitat across a large enough area (e.g., in several watersheds) to encompass regional climatic variability, rather than by prolonging local inundation. A broadly distributed spatial extent enables areas to incur periodic drying (necessary for plant communities) on a stochastic basis through climatic variability, rather than trying to “counteract” natural rainfall patterns with artificial hydrology (Bennetts and Kitchens, 1997b). Any reduction in the spatial extent and region-wide distribution of snail kite habitat effectively reduces the range of the kites and increases the probability of droughts affecting the entire range (Bennetts and Kitchens, 1997a).

ADAPTIVE MANAGEMENT RECOMMENDATIONS

The management of the South Florida hydroscape is an excellent opportunity for the protection, management, and conservation of snail kites as an adaptive management exercise; however, adaptive management must be more than just iterative trials of different management scenarios. A key feature of a sound adaptive management program is that learning is incorporated as an explicit goal of the adaptive management process (Lee, 1993). Iterative trial of management strategies without an explicit learning goal is haphazard, not adaptive. According to Lee (1993), adaptive management embodies a simple concept: “Policies are experiments; learn from them.” Further, Lee (1993) contends that an effective adaptive management program must: (1) be explicit about what to expect from management policies that are implemented (models help in this regard), (2) have monitoring schemes in place that are capable of evaluating system responses to management actions, and (3) allow participants to transform the resulting comparisons into learning, make corrections in their actions, and change actions and plans accordingly.
<table>
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<th>Proposed Paradigm</th>
<th>Existing Paradigm</th>
<th>Key Management Considerations</th>
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<td>Variability in snail kite distribution at a local level is to be expected. Snail kites are nomadic and shift frequently throughout a habitat network.</td>
<td>Although the nomadic tendencies of snail kites has been previously recognized, periodic reductions in local bird numbers is frequently interpreted as a local reduction in habitat quality.</td>
<td>When local reductions occur during nesting, it may even be considered as a &quot;take&quot; as defined under the endangered species act when actions can be taken to prevent the response from occurring (e.g., holding water in impoundments). While we agree that an anthropogenic management action that results in reductions of kites locally should constitute a &quot;take&quot;; natural drying that can be &quot;prevented&quot; from occurring should not.</td>
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<td>Responses of snail kites to &quot;local&quot; drying events is largely behavioral (i.e., they move), whereas a &quot;numerical&quot; response occurs primarily in cases of &quot;droughts&quot; with a spatial extent covering all or most of the kite’s range in Florida.</td>
<td>Numerical responses of kites occur in response to &quot;droughts&quot; regardless of their spatial extent.</td>
<td>Under the old paradigm the spatial extent of &quot;droughts&quot; has never been specified. Consequently, there has been no distinction between periodic &quot;local&quot; drying, which is necessary to maintain the habitat and widespread regional droughts, which occur rarely (e.g., once every 10–15 years) and whose demographic effects can be minimized by a broad spatial extent of quality habitat. Under the new paradigm, spatial extent of habitat is deemed critical to viability of snail kites in Florida.</td>
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<td>Local drying events, at natural frequencies, are considered as an essential component of a functioning ecosystem.</td>
<td>Drying events are considered as demographic catastrophes in which survival and reproduction of kites plummet.</td>
<td>The old paradigm views drying events as requiring stabilization. We agree with previous authors (e.g., Sykes, 1979; Beissinger, 1988; Bennett et al., 1988, Beissinger, 1995; Sykes et al., 1995) that suitable snail kite habitat is mandated for relatively long periods (e.g., 1–5 yr average return interval of drying events, with considerable variability). However, excessive stabilization results in a slow but steady conversion of wetlands to a more homogeneous aquatic state, degrading their habitat value for snail kites over long time scales.</td>
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<td>Hydrologic variability, both temporal and spatial, is and always has been an intrinsic feature of the environment of snail kites in southern and central Florida.</td>
<td>Variability in hydrology is potentially detrimental to snail kites and water levels should be kept stable and high.</td>
<td>It is the hydrologic variability that likely enables the coexistence of species (e.g., snail kites and wood storks) with seemingly different hydrologic requirements. The habitats for each can be maintained, although they do not necessarily occur at the same sites at the same time.</td>
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<td>The fitness of individual birds is enhanced by an asynchronous and variable environment. Birds may be less sensitive to localized disturbance events because of their ability to escape such events (Wiens, 1989). Asynchrony of disturbance would help to ensure that some refugia are available during most disturbance events.</td>
<td>The fitness individual birds is threatened by a variable environment.</td>
<td>The behavioral responses of snail kites to drying events appear well adapted to cope with natural climatic variability. Snail kites exhibit behavior quite adapted to hydrologic variability. When environmental conditions of the wetland site they currently occupy deteriorate, the birds respond by moving to more favorable sites.</td>
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<td>Periodic disturbance events such as fire, hurricanes, and local and regional droughts are integral parts of southern Florida’s landscape patterns (Davis et al., 1994). Attempting to increase stability in a dynamic ecosystem is not only difficult but undesirable ecologically.</td>
<td>Periodic disturbance, especially droughts, should be minimized so as to create a &quot;stable&quot; environment.</td>
<td>In virtually every ecosystem where disturbance processes have been markedly reduced, there has been a subsequent realization of their ecological importance (Pickett and White, 1985).</td>
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We have begun the process for the first component required for an effective adaptive management program by explicitly outlining the key contrasting features of the existing and proposed paradigms. This outline can, and should, be viewed as a series of alternative hypotheses to be tested in an adaptive management program. General predictions can easily be derived from the outline we have provided. For example, we would predict that the response of snail kites to “local” drying events is primarily behavioral, consisting of a redistribution of kites to alternative habitats. Only in cases of “widespread regional droughts” occurring throughout all or most of the watersheds occupied by kites would we predict a numerical response at the population level. The existing paradigm does not identify spatial extent as an important component of “drought” response by snail kites. References are often to drying of individual wetlands (e.g., WCA-3A) (Takekawa and Beissinger, 1989). Thus, under this hypothesis, a numerical response would be predicted, regardless of the spatial extent of a given drying event. Predictive models can take this a step further and generate specific predictions about the response of the system to various management actions. However, these models must incorporate the best ecological knowledge concerning the ecosystem in order to make reliable predictions about how the ecosystem and its components will respond to a proposed management action. A predictive model for the snail kites, using an individual-based, spatially explicit approach, has been developed as part of the Across Trophic Level Simulation System (DeAngelis, 1997) being developed for evaluating hydrologic alternatives within the South Florida Ecosystem Restoration Initiative (Science Subgroup, 1993). The current version of the model is being tested against historic survey data on the snail kite (Mooij et al., in press). On the basis of such models and the management goals that have been set, a particular set of management options is chosen.

By explicitly stating our hypotheses and predictions, we also can begin the second primary component, monitoring. All too often, monitoring is viewed as something required by legal or political mandates, rather than as an opportunity to understand the ecological responses of the system being managed. Several key components are required for an effective monitoring program — it must be (1) capable of distinguishing among the predictions of explicitly stated hypotheses; (2) based on the best available science and established sufficiently prior to the management implementation so that changes caused by particular management options are properly measured and sorted out from the noise of natural environmental variability; and (3) be designed flexibly enough to incorporate appropriate temporal and spatial scales required to accomplish the above.

For example, the response of snail kites to drying events has been much debated. We suggest (predict) that a behavioral response is far more common than a numerical response. Thus, any monitoring program intended to evaluate this hypothesis must be able to distinguish between behavioral and numerical responses. Local and/or short-term evaluations that monitor only a portion of the population at one location have a high probability of producing spurious conclusions. Behavioral (i.e., movement) and demographic (i.e., numerical) responses in these evaluations are easily confounded. The capture-mark-resighting technique presently in place for the snail kite resolves this distinction when carried out for at least 2 to 3 years beyond the event of interest. This approach explicitly estimates decreased resighting of birds temporarily inhabiting drought refugia, from decreased survival. This program also has now been in place for several years prior to the initiation of upcoming restoration policies.

We have suggested that habitat quality erodes under a stabilized high-water regime. We hypothesize herein, based on strong evidence to date, that prolonged flooding of a site, without occasional drydowns, leads to vegetation changes reducing suitability as a nesting area. Thus, we would predict that the distribution of snail kites within a given wetland under prolonged or continuous inundation will shift toward sites with higher elevations and shorter hydroperiods. Under the existing paradigm, no upper limit of drying frequencies is suggested, and it is often implied the longer the inundation, the better (Beissinger, 1995). We would predict under this hypothesis that habitat quality and distribution of the birds should remain relatively stable. This hypothesis can be tested if the nesting distribution at individual sites is monitored regularly, provided that spatial information is recorded.
(e.g., using a GPS). Simply monitoring total population size for the whole region will not give specific information relevant to site quality. The total population may be doing relatively well, even while nesting habitats are stressed by long hydroperiods to the point that they will inevitably decline in the future. Spatial and temporal heterogeneity are key attributes of the system that must be explicitly included in the monitoring, modeling, and management decision-making. However, for this hypothesis we emphasize from the outset that the time scales over which a response is expected are quite long. Monitoring must be of sufficient duration and/or repeated for several years at periodic intervals of longer time scales to enable evaluation of shifts at the time scale of decades. Year to year variation is to be expected, and the appropriate measure or gauge is general trends over the long term rather than a direct annual association between water levels and distribution.

Beissinger (1995) recently predicted that kite populations would not become stable until the frequency between successive droughts (no spatial extent identified) exceeds 4.3 years. We suggest that this hypothesis, as stated, has to some extent already been tested. Most wetland habitats used by snail kites in Florida have had drying return frequencies less than 4.3 years over the past three decades (Bennetts et al., 1988; Bennett and Kitchens, 1997a). During this time, the population has been steadily increasing (Sykes, 1979, 1983b; Bennett et al., 1994, 1999), rather than decreasing as predicted by the Beissinger hypothesis. However, we fully recognize that proponents of the existing paradigm will not have had an opportunity to express agreement with the predictions as we have expressed them. Perhaps Beissinger (1995) intended his hypothesis to imply widespread regional droughts, rather than local drying, although no spatial extent was defined. In this respect, we would encourage all proponents of alternative viewpoints to state their hypotheses explicitly along with their corresponding predictions, for only if such hypotheses and predictions are made explicit (e.g., the spatial extent of droughts, if that is deemed important) can we reliably evaluate their predictions and thereby protect this endangered species.

CONCLUSION

The endangered snail kite is the only species occurring throughout the South Florida freshwater hydrocape and whose entire U.S. population is restricted to the these wetlands. Habitat quality for this species is dependent on hydrology and wetland plant communities that support their principal food source, the apple snail. Consequently, there is direct linkage between changes in hydrology to changes in habitat quality for the kite. Previous management recommendations have focused on "freezing" or stabilizing specific hydrologic conditions in large-scale impounded wetland units to provide critical habitat for the maintenance of this species. This is counter to the natural dynamics under which these wetland systems evolved, resulting in a fragmented system of fixed components rather than a spatially continuous mosaic. Intra- and inter-wetland heterogeneity is thus reduced by constraining water to vertical rather than lateral expansions/retractions, in response to increases or decreases in water volume. Both kites and wetlands respond to changes in resulting hydrological regimes. Kites are capable of behavioral responses in time scales on the order of days or population responses on the order of months to years. On the other hand, the in situ plant communities respond through successional processes at time scales spanning months to several decades. Consequently, the reversal of these successional changes in vegetation, unfavorable to the kites, that have resulted from continuous flooding may require time frames that exceed the life span of individual kites. Thus, a focus is needed that addresses both snail kite population dynamics and plant community dynamics at spatial and temporal scales that are pertinent to both. In this chapter, we described habitat quality for snail kites in the context of fulfilling their foraging and reproductive requirements. We further discussed the linkages between the population dynamics of this species and the ecosystem processes that regulate habitat quality. We suggested that the adaptive behavioral responses of kites, while essential to their persistence, are less effective without a parallel adaptive management strategy for these wetlands as a whole. This strategy is translated
into a proposed paradigm based on maintaining the spatial extent and natural hydrologic variability of the South Florida hydroscape.

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