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INFLUENCE OF AN EXTREME HIGH WATER EVENT ON SURVIVAL, REPRODUCTION, AND DISTRIBUTION OF SNAIL KITES IN FLORIDA, USA

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Abstract: Hydrology frequently has been reported as the environmental variable having the greatest influence on Florida snail kite (*Rostrhamus sociabilis*) populations. Although drought has received the most attention, high-water conditions also have been reported to affect kites. Years of high water generally have been reported to be favorable for nesting, although prolonged high water may be detrimental to sustaining suitable habitat. During 1994 and 1995, southern Florida experienced an extreme high water event. This event enabled us to compare survival, nesting success, number of young per successful nest, and spatial distribution of nesting before, during, and after the event. We found no evidence of an effect (either negative or positive) on survival of adult kites. In contrast, juvenile kites experienced the highest survival during the event, although our data suggest greater annual variability than can be explained by the event alone. We found no evidence of an effect of the high water event on nest success or number of young per successful nest. Nest success was highest during the event in the southern portion of the range but was quite similar to other years, both before and after the event. Our data do indicate a substantial shift in the spatial distribution of nesting birds. During the event, nesting activity shifted to higher elevations (i.e., shallower water) in the major nesting areas of the Everglades region. Nesting also occurred in Big Cypress National Preserve during the event, which is typically too dry to support nesting kites. Thus, our data indicate a potential short-term benefit of increased juvenile survival and an expansion of nesting habitat. However, the deterioration of habitat quality from prolonged high water precludes any recommendation for such conditions to be maintained for extended periods.

Key Words: flood, hydrology, nest success, reproduction, *Rostrhamus sociabilis*, snail kite, spatial distribution, survival

INTRODUCTION

The snail kite (*Rostrhamus sociabilis* Ridgway), listed as endangered in the United States, is highly dependent on wetlands (Howell 1932, Sykes 1983a, b). This is not surprising given that its almost exclusive food source of apple snails (*Pomacea paludosa* Say) is an aquatic species (Howell 1932). The snail kite also nests in trees, shrubs, or dense graminoid patches over water, where it is better able to avoid terrestrial nest predators (Sykes 1987). Hydrology frequently has been reported as being the environmental variable having the greatest influence on kite populations (reviewed by Sykes et al. 1995). Suggested hydrologic effects on kite populations include decreased survival (Beissinger 1986, Takekawa and Beissinger 1989) and/or reproduction (Snyder et al. 1989) during periods of drought and indirect effects on apple snail populations (Kushlan 1975) and habitat quality (Bennetts et al. 1994, 1998a, Kitchens et al. 2002).

Although drought has received the primary focus of potential hydrologic effects (e.g., Beissinger and Takakawa 1983, Takekawa and Beissinger 1989, Sykes et al. 1995), it also has been suggested that excessive water depths and/or prolonged inundation may be unsuitable for kites (Sykes 1983a, Bennetts et al. 1994). Water depths >1–2 m may (1) lack sufficient oxygen for apple snails (Hanning 1978), (2) pose an energetic barrier for apple snails by limiting food or access to emergent vegetation used to reach the water surface for respiration (Darby 1998), or (3) negatively influence nesting or foraging habitat structure (Bennetts et al. 1999, Kitchens et al. 2002). Prolonged inundation (e.g., >9 years) or hydrologic regimes (e.g., where wetlands are inundated on average >95% of the time or >5-year average between drying events) may likewise degrade habitat structure by reducing or eliminating woody and emergent vegetation used for nesting and foraging, respectively (Bennetts et al. 1994, 1999, Kitchens et al. 2002).

Florida experienced an extreme high water event (HWE) beginning in the autumn of 1994, which extended into 1995 (South Florida Water Management District 1997, Armentano 1998). This event enabled us to compare survival, nesting success, and spatial distribution before, during, and after the HWE. In this paper, we specifically focus on short-term (acute) effects of the HWE, with the full recognition that long-term (chronic) effects also occur. Snail kites may respond to long-term effects (e.g., the hydrologic regime) quite differently, and such effects have been discussed in detail elsewhere (e.g., Bennetts and Kitchens 1997a, Bennetts et al. 1998a, Kitchens et al. 2002).
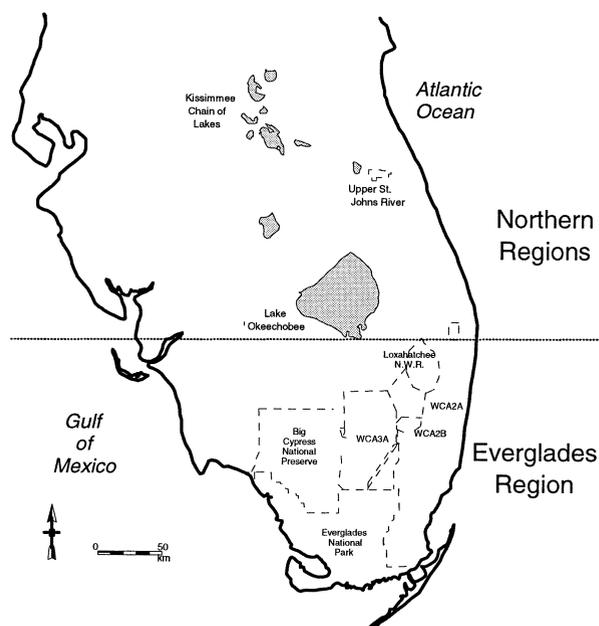

Figure 1. Central and southern Florida, including primary wetlands used by nesting snail kites from 1992 through 1997. For some analyses, comparisons were made between regions where high water levels were extreme (e.g., the Everglades) and where levels were high but much less extreme (e.g., northern regions).

METHODS

Within the United States, snail kites occur only in Florida (Sykes 1984), and all evidence suggests that individuals constitute a single population that shifts in distribution throughout the state, rather than separate subpopulations within the state (Bennetts and Kitchens 1997a, 1997b). Consequently, the spatial extent of this study covered the entire range of snail kites in the United States, which is comprised of wetlands throughout central and southern Florida (Figure 1). Descriptions of these wetlands have been provided in detail elsewhere (Bennetts and Kitchens 1997a, 1997b, Kitchens et al. 2002).

We evaluated the relative magnitude of the HWE using stage data from gauging stations maintained by the South Florida Water Management District, St. Johns River Water Management District, U.S. Army Corps. of Engineers, U.S. Geological Survey, and City of West Palm Beach. Specific gauges used are reported by Bennetts and Kitchens (1997a). We calculated the mean monthly stage ($\pm$ sd) for a 30-year period prior to the HWE. We then compared mean monthly stage values during the HWE to those of the 30-year average for that month. The number of standard deviations above or below the long-term average for a given month during the HWE was used as an indication of relative magnitude of the HWE.
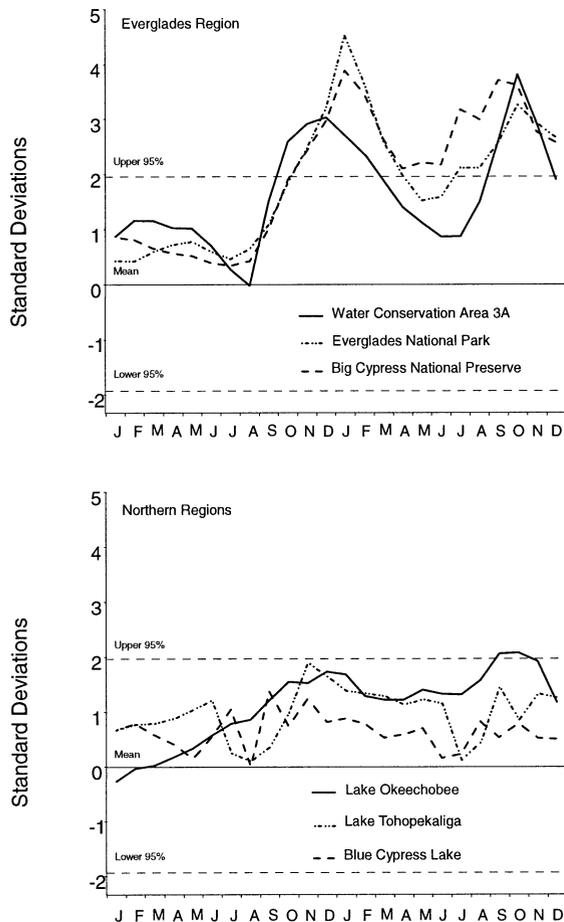
Figure 2. Number of standard deviations for water levels during 1994 and 1995 for each month above or below the 30-year mean for that month in representative wetlands used by snail kites in the Everglades and northern regions. Upper and lower limits of a 95% confidence interval are shown for reference.

The HWE began with Tropical Storm Gordon in October, 1994. The effects were most pronounced in the Everglades region, where water levels exceeded 4 standard deviations above the 30-year average in some wetlands (Figure 2). At Lake Okeechobee, in the central part of the kite's range, water levels were extreme (>2 standard deviations above the 30-year average) but not nearly so much as in the Everglades. Similarly, water levels in the other regions north of the Everglades were high but within a 95% confidence interval of the 30-year average. Consequently, for some subsequent analyses, we compared the Everglades region, where water levels were extreme, to other regions to the north, where water levels were high but much less extreme.

The most extreme water levels relative to the long-term average occurred during the 1994–1995 winter, with some residual effects in the 1995–1996 winter. Since our estimates of survival were from one breed-

ing season to the next, this event potentially would have affected our 1994 ($\approx$April 1994–April 1995) and 1995 ($\approx$April 1995–April 1996) study years. In contrast to survival, the HWE was considered potentially to have affected the 1995, but not the 1994 breeding seasons, because Tropical Storm Gordon occurred after the 1994 breeding season was completed. However, because water levels remained high during the winter of 1995–1996, there could have been some potential residual effects during the 1996 breeding season.

Annual survival of snail kites was estimated using capture-resighting data (Bennetts et al. (1999). We conducted capture-resighting sampling occasions during each breeding season from 1992 to 2000. Our capture and resighting sampling corresponded with the peak fledging time of snail kites (March–June). Thus, our estimates generally can be interpreted as survival from one breeding season to the next, regardless of whether a given animal was breeding. We estimated annual survival using a generalized Cormack-Jolly-Seber framework (Lebreton et al. 1992) originally developed by Cormack (1964), Jolly (1965), and Seber (1965). All survival analyses were conducted using the program MARK (White and Burnham 1999). Model selection was based on Akaike's Information Criteria (AIC), which was adjusted for overdispersion and small sample sizes (i.e., QAIC$_c$) (Akaike 1973 Hurvich and Tsai 1989, Burnham and Anderson 1998).

During any modeling endeavor, there is always uncertainty associated with the model selection process (Burnham and Anderson 1998). To account for this uncertainty, we used model averaging to derive estimates of survival and unconditional standard errors (Buckland et al. 1997). This approach weights several plausible models according to AIC values; the most plausible models receive the highest weight, while the least plausible models receive little or no weight.

During each year, we located nests using quasi-systematic searches of each area (Dreitz et al. 2001). We defined a nesting attempt and success in accordance with the recommendations of Steenhof (1987) and considered a nesting attempt to begin with the laying of the first egg. Success was defined as at least one young reaching 80% of age of first flight (Steenhof and Kochert 1982). We compared reproductive parameters (e.g., nest success and the number of young per successful nest) among regions and years using a generalized linear modeling framework. We estimated success as the proportion of nests successful and compared success among years and regions using logistic regression. The number of young per successful nest was considered as a multinomial random variable and was analyzed using loglinear models.

For each nest, we recorded the coordinates using a global positioning system (GPS), and the nest was

Table 1. Candidate models shown in order from the lowest $QAIC_c$ (best model) to highest. Model structure indicates whether estimates of survival (ϕ) and/or resighting probability (p) were dependent on time (t) or age class (a). An alternative time-dependent model to using a separate parameter for each year was using 2 parameters for whether or not it was during the high water event (HWE1 and HWE2 for models considering the event to have occurred during only 1995 or during both 1994 and 1995, respectively). An age class in parentheses (e.g., juv) indicates that the effect was modeled for that age class only. Also shown are the $QAIC_c$ values, the difference in $QAIC_c$ from the best model, the $QAIC_c$ weight used from model averaging, and the number of parameters.

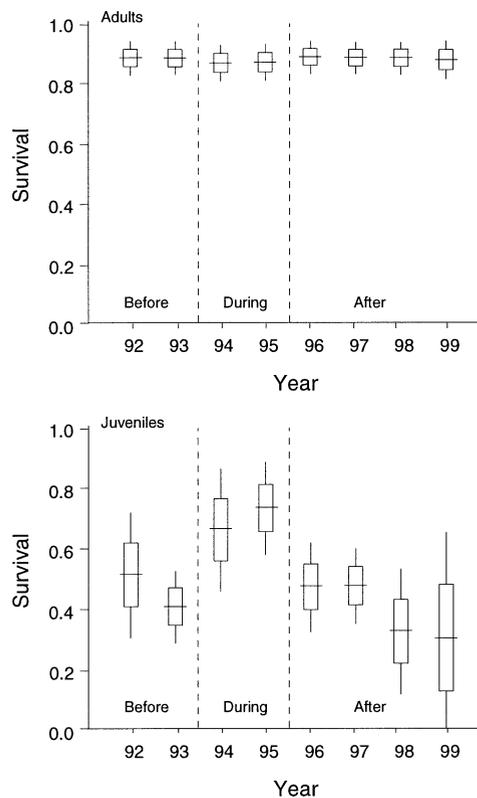| Model No.	Model Structure	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ Weight	No. Parameters
1	$\phi_{a,t(juv)}, p_t$	2217.02	0.00	0.561	17
2	$\phi_{a,HWE2(juv)}, p_t$	2218.98	1.96	0.211	11
3	$\phi_{a,HWE2}, p_t$	2219.50	2.48	0.163	12
4	$\phi_{a,HWE1(juv)}, p_t$	2222.41	5.39	0.038	11
5	$\phi_{a,HWE1}, p_t$	2224.35	7.33	0.014	12
6	$\phi_{a,t}, p_t$	2224.47	7.45	0.014	23
7	$\phi_{a,t}, p$	2258.19	41.17	0.000	17
8	$\phi_{a,t(juv)}, p$	2264.06	47.04	0.000	10
9	$\phi_{a,}, p$	2277.29	60.27	0.000	3
10	ϕ_{t}, p_t	2284.65	67.63	0.000	15
11	$\phi_{a,}, p_t$	2291.74	74.72	0.000	10
12	$\phi_{,} p_t$	2297.41	80.39	0.000	9
13	$\phi_{,t}, p$	2322.44	105.42	0.000	9
14	$\phi_{,,} p$	2346.22	129.20	0.000	2

Figure 3. Estimates of adult and juvenile survival before, during, and after the high water event. Estimates were derived as an average of the candidate models weighted by their by $QAIC_c$ value. Also shown are the unconditional standard errors (rectangles), and 95% confidence intervals (vertical line).

marked with an inconspicuous marker. The spatial distribution of nests in areas having extreme water levels was compared among years using multi-response permutation procedure (MRPP)(Berry et al. 1983, Mielke 1984), which can be used to test whether two or more sets of spatial locations (i.e., with X and Y coordinates) come from the same distribution (White and Garrott 1990).

RESULTS

Effects of the HWE on Survival

Based on $QAIC_c$, the most parsimonious model contained separate estimates of adult and juvenile survival, juvenile survival for each year, and resighting probability for each year (Table 1). Our estimates indicated that adult survival was higher and less variable than juvenile survival, providing some evidence that the HWE affected juvenile but not adult survival (Figure 3). The selected model indicated that juvenile survival was highest during 1994 and 1995, when the HWE occurred. Our estimates for these two years were also outside the confidence intervals of most other years. The model with the second lowest $QAIC_c$ score, and

not very different from the selected model, had two parameters for juvenile survival (during the HWE and not during the HWE) rather than a separate parameter for each year.

Effects of the HWE on Reproduction

We monitored the fate of 892 nests between 1992 and 1997. Our analysis indicated that nest success differed among years ($\chi^2 = 23.93$, df = 5, P < 0.001) and regions ($\chi^2 = 18.88$, df = 1, P < 0.001), and there was an interaction effect between years and regions ($\chi^2 = 12.65$, df = 5, P = 0.027). However, there was no evidence that nest success was related to the HWE. Nest success during the 1995 breeding season (i.e., the HWE) was 52% and was similar to success in 1992 (54%) and 1994 (52%), which preceded the HWE (Table 2). If this information was partitioned by region, success was greatest during the HWE in the Everglades region but, again, was very similar to other years in that region.

We determined the number of young produced from a sample of 331 successful nests. The number of

Table 2. Proportion of successful nests in the Everglades region, northern regions, and the total sample of nests during each year. Sample sizes given in parentheses. Year of high water event shown in bold.

Year	Everglades Region	Other Regions	Total
1992	0.53 (36)	0.54 (59)	0.54 (95)
1993	0.49 (97)	0.35 (43)	0.45 (140)
1994	0.55 (66)	0.49 (39)	0.52 (105)
1995	**0.56 (135)**	**0.42 (48)**	**0.52 (183)**
1996	0.52 (77)	0.28 (47)	0.43 (124)
1997	0.47 (192)	01.3 (53)	0.40 (245)

young per successful nest differed among years ($\chi^2 =$ 18.5, df = 5, P = 0.003) but not among regions ($\chi^2 =$ 0.2, df = 1, P = 0.626). There was no indication that differences among years were related to the HWE. The mean number of young per successful nest during the HWE (i.e., 1995) was 1.91 (± 0.17 se), which was intermediate among years. The number of young per successful nest was highest during 1992 and 1997 (2.09 $\pm$ 0.51 and 2.04 $\pm$ 0.29, respectively) and lowest during 1996 and 1993 (1.72 $\pm$ 0.17 and 1.73 $\pm$ 0.48, respectively).

Effects of the HWE on Spatial Distribution of Nests

Because water levels were most extreme in the Everglades and most of the nesting activity in the Everglades during this study occurred in Water Conservation Areas (WCAs) 3A and 2B, we compared the spatial distribution of nests in these areas before, during, and after the HWE. The spatial distribution of nests within WCA-3A overlapped considerably among years. The most dramatic exception occurred during 1995 (i.e., the HWE), when most areas in WCA-3A had water depths > 1 m and many areas had depths > 1.5 m. The distribution of nesting kites shifted dramatically to the north during the HWE and differed significantly from years before and after the HWE (MRPP test statistic $= -167.23$, P < 0.001) (Figure 4). This spatial shift was to an area (mostly within the Miccosukee Indian Reservation) of higher elevation and lower water depths than had been observed during other years. Shifts in distribution of nesting kites also occurred in WCA-2B. Although the distribution during the HWE differed from other years (MRPP test statistic = 2.24, P = 0.004), the extent of overlap with other years was more pronounced than in WCA-3A. In addition to shifts in distribution within wetlands, we also found 17 nests in the Stairstep Unit of Big Cypress National Preserve, where hydroperiods are generally much shorter than those that occur in WCA-3A or WCA-2B. Although birds have used this area regularly
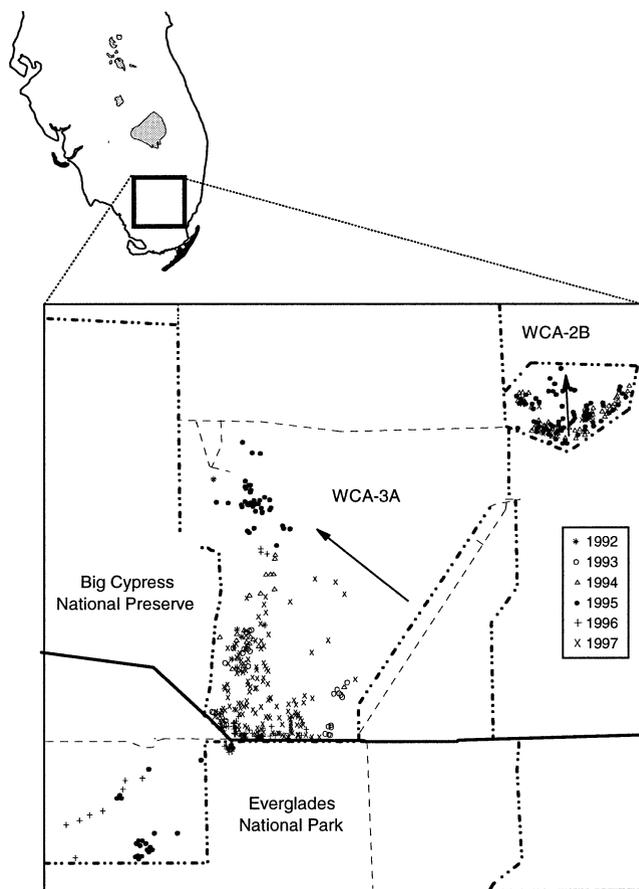

Figure 4. Distribution of snail kite nests in the southern Everglades from 1992 through 1997.

during the non-nesting season for foraging, we had no indication of nesting activity prior to 1995, despite regular surveillance. This area typically dries out during the latter part of the breeding season, but the area used by kites (primarily in Lostman's, Dixon, and East Sloughs) remained inundated during the entire 1995 breeding season. During 1996 and 1997, when more typical spring dry downs occurred, the number of nests located decreased to seven and one, respectively.

DISCUSSION

Effects of the HWE on Survival

We found no evidence that adult survival was influenced by the HWE, although our data did indicate that juvenile survival differed among years and was highest during the HWE. However, a model with a separate parameter for each year performed better than a model with two parameters for high-water years (1994 and 1995) and one for other years. This latter result suggests that there was more annual variation in juvenile survival than can be explained by the HWE alone.

During typical high-water years (i.e., within the

95% confidence interval), high water probably ensures that wetlands used for nesting do not dry during the nesting season. However, during extreme HWE events such as this one, it is unlikely that higher juvenile survival is a result of increased water depth in previously used wetlands. Our data show that nesting activity was actually shifting toward relatively shallower depths in both WCA-3A and WCA-2B and did not indicate that juveniles used deeper areas after fledging. Rather, higher survival was more likely due to habitat expansion caused by an increase in the flooded surface area of potential habitats during the HWE. Marginal habitats that typically tend to dry seasonally can remain inundated through the dry season. Most juveniles disperse from their natal wetlands during the first 90 days post fledging (Bennetts and Kitchens 2000), and they are most vulnerable during this period (Bennetts and Kitchens 1999). Thus, an increased surface area of inundated wetlands would reduce the chances of dispersing juveniles encountering unsuitable habitats during this critical period.

Effects of the HWE on Reproduction

We found no difference in nesting success and/or number of young per successful nest that could be attributed to the HWE. Most of the annual and regional differences seem attributable to generally higher success in the Everglades region and greater variability in the northern regions. This is not surprising since kites tend to nest in herbaceous vegetation in the northern regions and are more vulnerable to failure resulting from nest collapse (Snyder et al. 1989).

There are certainly reproductive parameters other than those we estimated (e.g., proportion of the breeding population attempting to breed and the number of attempts per year) that could have been affected by the HWE. Bennetts et al. (1998b) estimated that 100% of the adults attempted to breed during the HWE, but this has been previously assumed to occur during typical non-drought years (e.g., Nichols et al. 1980, Snyder et al. 1989, Beissinger 1995). Bennetts et al. (1998b) also estimated that adults made 1.4 nesting attempts per individual during the HWE. This estimate was below previous estimates of 2.7 (Snyder et al. (1989), later adjusted to 2.2 (Beissinger 1995). However, Bennetts et al. (1998b) estimated this parameter directly from radio-tagged birds, whereas Snyder et al. (1989) and Beissinger (1995) derived their estimates indirectly from winter population surveys and nest counts. At least some differences among these estimates likely reflect differences in estimation procedures (Bennetts et al. 1998b) and, thus, may be unrelated to the HWE. We also caution that the number of nests in our sample should not be interpreted as an estimate of the number

of kites breeding in that region. It is highly confounded by our search effort, which varied substantially among years due to observer differences, research priorities, and avoidance of overlap during concurrent nesting studies by other investigators.

Effects of the HWE on Spatial Distribution of Nesting

The shifts in nesting distribution to higher elevation during the HWE in both WCA-3A and WCA-2B were likely in response to foraging habitat quality. Although potential nest sites were still accessible during the HWE, water levels were well above previously reported ranges used by kites (e.g., Bennetts et al. 1988, Sykes et al. 1995) and may have been too deep for effective foraging because graminoid species in the foraging habitat (e.g., spike rush and maidencane) were largely submerged. Apple snails typically climb these plant species for surface respiration, at which time they are vulnerable to kites (Bennetts et al. 1994).

In conclusion, higher survival of juveniles, if attributable to the HWE, is certainly a positive short-term effect. Over longer time scales, however, stabilization of high-water regimes would result in a slow but steady conversion of wetlands to a more homogeneous aquatic state, degrading the wetland habitat value for snail kites (Bennetts et al. 1994, 1998a, Kitchens et al. 2002). The habitat degradation associated with excessively high or prolonged water levels may more than offset any positive short-term benefits. Thus, although our data indicate a potential positive influence of the HWE, we strongly encourage that long-term effects not be overlooked. Hydrologic variability, including periodic extremes (both high and low) is an intrinsic feature of this environment that is necessary for sustaining wetland communities that comprise high quality habitat for snail kites (Kitchens et al. 2002). The nomadic tendency of snail kites is well-suited to coping with this variability (Bennetts and Kitchens 1997b, Bennetts et al. 1998a, Bennetts and Kitchens 2000). Thus, maintaining consistently high water levels as a management strategy for increased juvenile survival of snail kites would very likely be counterproductive over longer time scales.

ACKNOWLEDGMENTS

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