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TEMPORAL VARIATION IN LOCAL WETLAND HYDROLOGY INFLUENCES POSTDISPERSAL SURVIVAL OF JUVENILE WOOD STORKS (*MYCTERIA AMERICANA*)

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ABSTRACT.—Since the 1960s, anthropogenic shifts in the timing and distribution of surface-water flows in the Everglades have pushed back the onset of reproduction in Wood Storks (*Mycteria americana*). Late nesting increases the probability that juveniles leave the colony during the summer rainy season, when water levels are high and prey animals unavailable. We used satellite telemetry to track first-year survival of 85 Wood Storks from southern Florida over 4 years. We further evaluated survival in relation to hydrologic and physiologic variables, including water depths, surface-water recession rates, May rainfall, use of wetland habitats, sex, total feather mercury, white-blood-cell counts, and heterophil:lymphocyte ratios for a subset of 71 birds, using a known-fates model in Program MARK. Juveniles that dispersed from the colony during favorable conditions (surface water depths <25 cm) had a first-year survival rate of 0.37 ± 0.06 (SE), compared with 0.15 ± 0.04 for those that dispersed into unfavorable conditions (depths >25 cm). General hydrologic conditions (favorable vs. unfavorable), wetland habitat use, and white-blood-cell counts were the best predictors of monthly survival, and the strongest effects were associated with the first month postdispersal. Our study is the first to show a relationship between temporally fluctuating hydrologic variables and survival of juvenile Wood Storks, highlighting the need to consider the timing of hydrologic manipulations when managing wetlands for birds. We conclude that human-induced changes in the temporal patterns of hydrology may have important consequences for the phenology and, ultimately, the demography of wetland birds. Received 26 October 2011, accepted 16 May 2012.

Key words: dispersal, Everglades, *Mycteria americana*, phenology, survival, wading birds, wetlands, Wood Storks.

La Variación Temporal en la Hidrología de los Humedales Locales Afecta la Supervivencia Post-dispersión de los Individuos Jóvenes de *Mycteria americana*

RESUMEN.—Desde la década de 1960, los cambios antropogénicos en la temporalidad y la distribución de flujos de agua superficial en los Everglades han retrasado el inicio de la reproducción en *Mycteria americana*. El anidamiento tardío incrementa la probabilidad de que los individuos jóvenes abandonen la colonia durante la temporada de lluvias en verano, cuando los niveles de agua son altos y los animales que sirven como presas no están disponibles. Usamos telemetría satelital para rastrear la supervivencia en el primer año de 85 individuos de *M. americana* del sur de Florida durante 4 años. Además evaluamos la supervivencia en relación con variables hidrológicas y fisiológicas, incluyendo profundidad del agua, tasas de retroceso del agua superficial, precipitación de mayo, uso de los hábitats en humedales, sexo, cantidad total de mercurio en las plumas, conteo de glóbulos blancos en la sangre, y el cociente heterófilos:linfocitos para un subconjunto de 71 aves. Para analizar estos datos empleamos un modelo de destinos conocidos en el programa MARK. Los individuos jóvenes que se dispersaron de la colonia cuando las condiciones eran favorables (profundidad del agua superficial <25 cm) tuvieron una supervivencia durante el primer año de 0.37 ± 0.06 , comparada con 0.15 ± 0.04 para aquellos que se dispersaron bajo condiciones desfavorables (profundidad >25 cm). Las condiciones hidrológicas generales (favorables vs. desfavorables), el uso del hábitat en humedales y los conteos de glóbulos blancos en la sangre fueron los mejores predictores de la supervivencia mensual, y los efectos más fuertes estuvieron asociados con el primer mes posterior a la dispersión. Nuestro estudio es el primero en mostrar una relación entre las variables hidrológicas temporalmente fluctuantes y la supervivencia de los jóvenes de *M. americana*. Esto resalta la necesidad de considerar la temporalidad de las manipulaciones hidrológicas cuando se administran los humedales para las aves. Concluimos que los cambios inducidos por el ser humano en los patrones temporales de hidrología podrían tener consecuencias importantes para la fenología y, finalmente, la demografía de las aves de humedales.

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THE WIDESPREAD LOSS of wetlands globally has increased the importance of managed wetlands for waterbirds and other aquatic animals. The quality of such artificial or restored wetlands as habitat depends on the effective management of a complex suite of environmental variables, including water depths, water-level fluctuations, food availability, and the timing of water-level manipulations (Parsons 2002, Ma et al. 2010). Foraging strategies of many waterbirds are highly constrained by hydroperiod and water depths, which control the abundance and availability of prey animals (Gawlik 2002). Thus, changes in hydrologic conditions over very short periods (i.e., days to weeks) that cause rapid changes in food availability are often linked to strong movement behavior and reproductive success (Frederick and Collopy 1989; Haig et al. 1998; Bancroft et al. 2002; Roshier et al. 2002, 2008).

In the Everglades of southern Florida, the distribution, abundance, productivity, and timing of nesting of several wading bird species (Ciconiiformes) have been linked to hydrologic parameters that influence food availability (Bancroft et al. 1988, Frederick and Collopy 1989, Ogden 1994, Frederick and Ogden 2001, Frederick et al. 2009). Nestling health and nest success have also been linked to hydrologic conditions and food availability for several ciconiiform species (Frederick and Collopy 1989; Herring et al. 2010, 2011). Rapid increases in water levels during the nesting season can cause the abrupt abandonment of entire colonies and mass mortality of abandoned young (Frederick and Collopy 1989, Frederick et al. 2009). In the case of the Wood Stork (*Mycteria americana*), colonies frequently fail after water-level reversals (Frederick et al. 2009). Little is known, however, about the influence of hydrology on survival once juvenile birds have left the nest.

Wood Stork colonies in southern Florida declined dramatically following the anthropogenic alteration of the Everglades (Ogden 1994), leading to the declaration of the Wood Stork as federally endangered in 1984 (U.S. Fish and Wildlife Service [USFWS] 1997, Coulter et al. 1999). Although Wood Stork numbers have increased across much of their range in the southeastern United States, nest numbers and productivity in the Everglades are extremely variable and remain low when compared with historical numbers (Brooks and Dean 2008). The decline in Everglades nesting by Wood Storks has been attributed to changes in hydrology that have decreased the quantity and quality of wetland habitats.

Wood Storks are tactile foragers, and to forage efficiently they require higher prey densities than other Everglades wading birds (Gawlik 2002). In its natural state, the Everglades produced a prolonged period of receding waters during November–May that concentrated prey in depressions and pools over the course of the dry season, followed by a rapid rise in water levels at the onset of the summer rainy season in late May–June (Fennema et al. 1994). The drainage and conversion of the Everglades for agriculture and urban development halved the area of wetlands, and those that remain have been compartmentalized by canals, levees, and roads, leading to widespread changes in hydroperiod and water depths (Light and Dineen 1994). At this time, movement of water through the system is intensively managed to meet multiple, often competing objectives related to water delivery, flood control, wildlife habitat, and ecosystem restoration (National Research Council 2011).

The loss of short-hydroperiod wetlands has decreased the amount of suitable foraging habitat for Wood Storks in the early dry season, leading to a much shorter period of food availability (Fleming et al. 1994). As a result, the timing of nesting has been delayed and Wood Storks typically do not initiate breeding until February (formerly November; Ogden 1994). Because the nesting cycle of the Wood Stork takes ~4 months (Kahl 1964, Coulter et al. 1999), individuals that initiate breeding in February rarely complete the nesting cycle before the start of the summer rainy season. Thus, the success of Wood Stork colonies now depends, in large part, on whether the start of the rainy season is delayed. If young do not disperse before the start of the rainy season, they are often left by their parents to starve (Frederick et al. 2009). Young birds that disperse are likely to encounter unfavorable foraging conditions (Ogden 1994).

Our objective was to assess whether temporally dynamic hydrologic conditions in Everglades wetlands influenced survival of dispersing juvenile Wood Storks in southern Florida. “Dispersal” typically refers to a three-stage process in which movement is initiated, occurs, and then ends when a destination is reached (Bennetts et al. 2001). Here, however, we use the term “dispersal” to refer to the initiation of movement away from the natal area and the term “postdispersal” to refer to events that occur after that movement has begun. We elected to use “postdispersal” rather than “postfledging” because juvenile Wood Storks generally spend several weeks returning to the nest after becoming capable of flight and we wanted to distinguish between these two periods. Dispersal was considered to have occurred when the bird left the colony permanently.

We used satellite telemetry data to estimate first-year survival of 85 juvenile Wood Storks that dispersed from two colonies in southern Florida over 4 years. During 2 years (2003 and 2005), birds dispersed during periods in which water levels in the Everglades were high and rising. During the other 2 years (2002 and 2004), water levels were low and, on average, within the optimal range (between –25 and 25 cm; Herring and Gawlik 2011) for foraging by Wood Storks (Fig. 1). We predicted that juveniles that dispersed during periods with higher water levels would have lower survival than those that dispersed in more optimal conditions. We also expected Wood Storks to move more quickly out of the Everglades region and to make greater use of non-wetland habitats during the wetter years than during more favorable ones, with negative consequences for survival. Because we had evidence that postdispersal survival was influenced, at least in part, by nestling health (Hylton et al. 2006), we also examined the influence of nestling physiology in relation to hydrologic variables on postdispersal survival of juvenile Wood Storks.

METHODS

Study area.—In 2002 and 2003, nestling Wood Storks were caught in the Tamiami West colony (25°45′31N, 80°32′4W), located on the northern boundary of Everglades National Park, Miami-Dade County, in the southeastern freshwater Everglades. In 2004 and 2005, transmitters were deployed in the Palm Beach Solid Waste Authority Rookery (26°46′06N, 80°08′45W), Palm Beach County, which is located near the northernmost reaches of the Everglades (Fig. 2). Analysis of hydrologic variables was confined to the

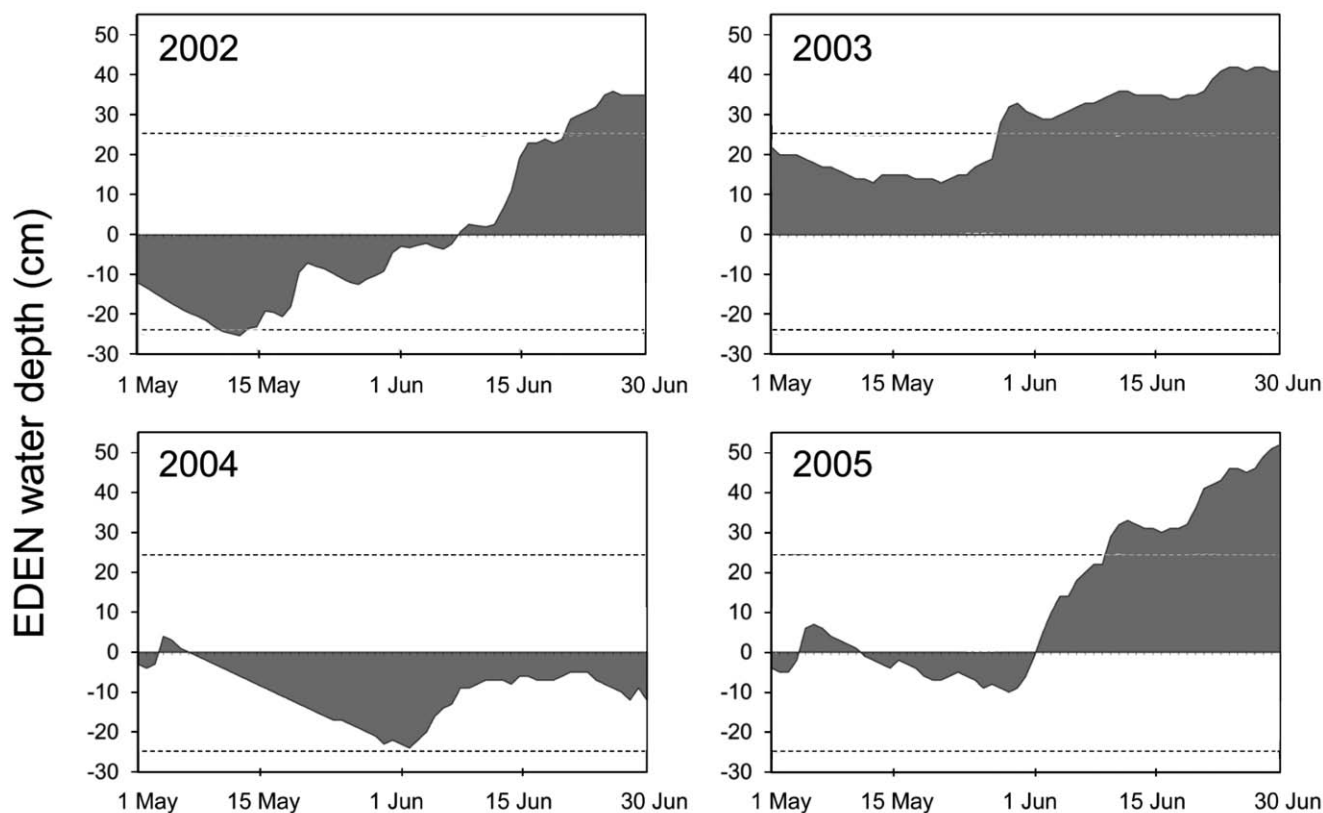


FIG. 1. Hydrographs for the Everglades Depth Estimation Network (EDEN) water surface in May and June, 2002–2005, with the shaded region showing average daily water depths (cm). Dashed gray lines indicate the upper and lower 95% confidence intervals of preferred water depths for foraging Wood Storks as reported by Herring and Gawlik (2011).

Everglades region, whereas habitat use was analyzed across the southeastern United States.

Telemetry.—As part of a larger study of Wood Stork demography and movements (see Hylton 2004, Borkhataria 2009), satellite transmitters were used to track 85 juvenile Wood Storks from southern Florida natal colonies in 2002–2005 (27 birds in 2002, 17 in 2003, 23 in 2004, and 18 in 2005). Nestlings were caught by hand at 4 to 6 weeks of age, before they were capable of flight. To minimize variability in survival caused by hatch order, the largest sibling in any nest was selected; we acknowledge that this may have introduced some bias into our study.

Transmitters were attached using a 0.75-cm-wide Teflon-ribbon backpack-style harness (Hylton 2004). In 2002 and 2003, all birds were outfitted with 35-g solar-powered Argos–PTT satellite tags (Microwave Telemetry, Columbia, Maryland; 10 h on:24 h off duty cycle; accuracy 100–1,000 m) with attached 10-g VHF transmitters (Advanced Telemetry Systems, Isanti, Minnesota, and American Wildlife Enterprises, Monticello, Florida). In 2004, seven birds were outfitted with the same equipment as in 2002 and 2003, but the majority of birds (16) were outfitted with 45-g solar-powered GPS–PTT satellite transmitters (Microwave Telemetry; hourly locations, 16 h on:8 h off duty cycle; accuracy 18 m) with attached 10-g VHF transmitters (Advanced Telemetry Systems). In 2005, only GPS–PTT transmitters with attached 10-g VHF transmitters were deployed.

Although the transmitters were ~10 g heavier in 2004 and 2005 than in the previous 2 years, in all years transmitters were <3% of the expected body weight of flight-capable Wood Storks (2.05–2.64 kg; Coulter et al. 1999) and within established weight guidelines for auxiliary markers (Fair et al. 2010). Differences in transmitter weight among years were therefore not expected to influence survival.

The transmitters had an expected battery life of 3 years, and devices that stopped moving or stopped transmitting during the first year were assumed to represent dead birds. When possible, death was confirmed by locating carcasses using the final locations transmitted and VHF telemetry. In some cases stationary transmitters were still transmitting locations when they were found, but in many cases they stopped transmitting because light transmission to the solar panel was blocked. In all cases, however, there was evidence of mortality at the retrieval location (carcasses, feathers, or bones) and transmitters resumed functioning once they were re-exposed to sunlight, giving us no reason to suspect that transmitters became unattached or stopped functioning within the first year. Mortality was confirmed by transmitter retrieval for 3 birds in 2002 (20% of suspected mortalities), 5 in 2003 (31%), 10 in 2004 (63%), and 11 in 2005 (73%). Downed transmitters were more easily found in 2004 and 2005 because of the accuracy of the GPS positions associated with the improved transmitter model.

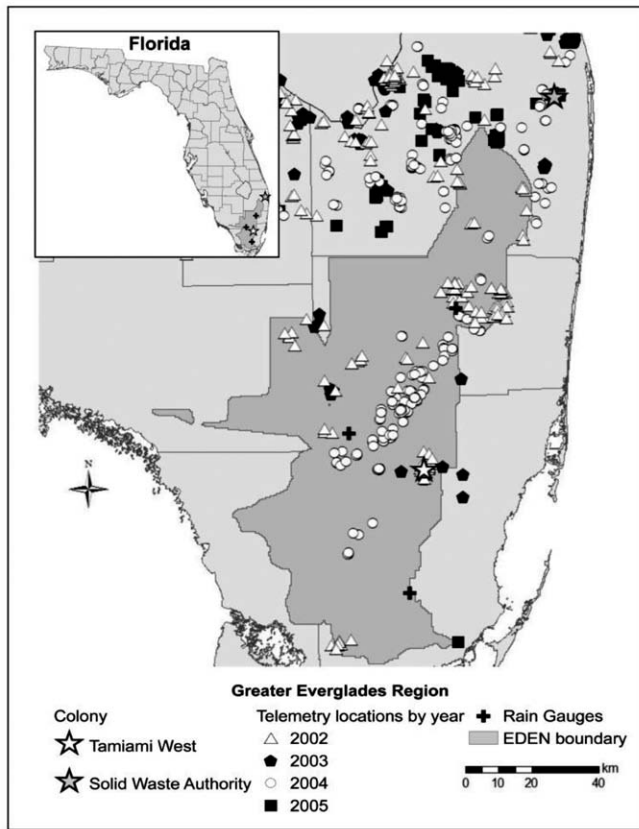


FIG. 2. Map of Wood Stork satellite telemetry locations in the Greater Everglades region as delineated by the Everglades Depth Estimation Network (EDEN) boundary. Satellite transmitters were attached to juvenile Wood Storks at the Tamiami West colony in 2002 and 2003 and at the Solid Waste Authority colony in 2004 and 2005. Location symbols in white correspond to years with favorable hydrologic conditions (surface water depths between -25 and 25 cm) and those in black to unfavorable conditions (surface water depths >25 cm). Rain gauges from north to south were South Florida Water Management District gauges 3A-36, 3AS3W3, and S332.

Nestling health.—Birds were given a brief physical exam before transmitters were attached, with 2–4 scapular feathers collected for mercury analysis (methods described in Frederick et al. 2004) and ≤ 2 mL of blood taken from the brachial vein for white-blood-cell (WBC) analysis and DNA sexing (methods described in Hylton et al. 2006). Mercury exposure presented a potential health risk because mercury exposure in Everglades wading birds and its adverse effects on growth rates and reproductive success have been well documented (Frederick et al. 1999, 2002, 2004; Sepúlveda et al. 1999; Heath and Frederick 2005). We also included WBC counts and the ratio of two WBC types (heterophils:lymphocytes) in the analysis because Hylton et al. (2006) reported a relationship between these parameters and juvenile survival for a subset of birds in the present study (2002 and 2003) and because elevated WBC levels may indicate a heightened immune response to contaminants, parasites, viruses, and other pathogens (Newman et al. 2007).

Everglades water depths and rainfall.—Water depths across the Everglades were estimated using the Everglades Depth Estimation Network (EDEN; water surface data obtained in July 2008), which integrates water-level measurements, ground-elevation models, and water-surface models to provide daily, spatially explicit depth estimates over a 400×400 m grid for the freshwater portion of the Everglades (Palaseanu and Pearlstine 2008, Liu et al. 2009). Because of the size and varied topography of the cells, depths could be negative when averaged across an entire grid cell. This did not indicate, however, that the entire cell was dry, because water would likely remain in depressions that might be very attractive to wading birds. Herring and Gawlik (2011), using water depths from the EDEN water surface, showed that foraging Wood Storks preferred depths between -25 and 25 cm.

We quantified water depths and recession rates for the week before and the week after dispersal for each bird. The week before dispersal was included because juvenile Wood Storks would have been capable of flight during this time but were still returning to the natal colony. Water levels during this 2-week period are likely to have influenced decisions on when and where to disperse. Mean daily water depths were calculated for each cell of the EDEN water surface (Fig. 2; hereafter “Everglades region”) over this dispersal period for each individual bird using the raster calculator in ARCGIS, version 9.3 (ESRI, Redlands, California), then averaged across the entire landscape to obtain a single value for that bird. Years were classified as favorable or unfavorable using mean EDEN depths during the dispersal period. The 2 years in which mean dispersal depths were within the preferred -25 to 25 cm range were considered favorable (2002 and 2004) and mean dispersal depths >25 cm unfavorable (2003 and 2005).

Because the response of Wood Storks to water depth has been shown to follow a quadratic curve, with the probability of use increasing with depth up to a threshold and then declining (Bancroft et al. 2002, Herring and Gawlik 2011), depths were transformed using the quadratic form $\text{depth} + \text{depth}^2$ and the transformed variable was used for survival analyses. Mean daily water-recession rates for each bird were calculated as the difference between water depths in each cell of the EDEN water surface at the start and end of the bird’s dispersal period divided by the length of the dispersal period (14 days) and averaged across the EDEN water surface. Positive values indicated rising water levels, and negative values indicated receding water levels.

Daily rainfall values in May were used to characterize early wet-season rainfall. Average daily rainfall in May for each year of the study was calculated using rainfall data collected by the South Florida Water Management District at three weather-monitoring sites, spanning the northern, central, and southern freshwater Everglades (3A-36, 3AS3W3, and S332, respectively; see Fig. 2). Because the data were not normally distributed, water depths, recession rates, and rainfall were compared among years using a nonparametric Kruskal-Wallis test. We then used a nonparametric post hoc multiple-comparison test (Dunn’s test) to evaluate differences among years (Elliott and Hynan 2011).

Habitat use and movements.—Habitat use was analyzed during the first 2 weeks after dispersal, focusing on this period for two reasons. First, the period immediately after the end of parental dependency is a critical time for juvenile birds (Anders et al. 1997, Naef-Denzer et al. 2001, Wiens et al. 2006). Second, inferences

from this period benefited from the highest number of birds with active transmitters (i.e., 68 of 85 individuals).

Habitat types were based on a combination of the classifications from the National Wetland Inventory (NWI; USFWS 2008) and the U.S. Geological Survey's 2001 National Land Cover Dataset (NLCD; Homer et al. 2004). The final habitat raster contained eight categories: forested wetland (NWI freshwater forested-shrub wetlands, NLCD forested wetlands), emergent wetland (NWI freshwater emergent wetlands, NLCD emergent wetlands), "other freshwater" (NWI ponds, lakes, riverine; NLCD open water), marine (NWI marine and estuarine deepwater and wetlands), developed (NLCD open space, low-, medium-, and high-intensity developed; barren), agriculture (NLCD cultivated crops, hay-pasture), upland forest (NLCD deciduous, evergreen, mixed), and other terrestrial (NLCD shrub-scrub, herbaceous).

Because the PTT transmitters collected information more slowly (1.81 ± 0.44 locations day^{-1}) than GPS-enabled transmitters, we randomly chose 2 locations day^{-1} bird $^{-1}$ from the GPS data set to represent habitat use and used all locations from the PTT data sets. Although Wood Storks are capable of moving long distances between days, we did not assume that points collected for a single individual were temporally or spatially independent. Although autocorrelation of locations may bias the statistical analysis of animal location data (Swihart and Slade 1985), eliminating autocorrelation by removing locations from a data set has been shown to reduce statistical power and to mask biologically relevant information (De Solla et al. 1999, Cushman et al. 2005). Because we evaluated only general patterns of use over a short period (14 days), we believe that the use of multiple locations per day was justified. We assumed that all birds acted independently of the others.

For each bird, locations were buffered by 1 km, a distance equal to the expected accuracy of the lowest-quality PTT locations. Buffers were combined to prevent overlap, and the area within the combined buffer was considered "used." The total area of each habitat type within the buffer was quantified and divided by the total area of the buffer zone to calculate proportional use of each habitat type. Although this measure of habitat use did not permit the classification of feeding sites within the buffer area (third-order habitat selection, sensu Johnson 1980), we used it to broadly categorize the overall matrix of habitats within the landscape used by each bird. Because "availability" may have been influenced by water depth and other factors that were not measured, we did not attempt to define "available" habitats. Therefore, no assumptions were made regarding habitat preferences, and the analysis was confined to broad-scale use alone.

We compared proportional habitat use in all years for birds that survived the 2-week postdispersal period and performed pairwise comparisons between years using multiresponse random-permutation procedure, a nonparametric method for comparing differences between groups on the basis of distances between groups in multidimensional space (McCune et al. 2002). Sorensen distances were used as the distance measure, and we report the test statistic (T), its associated P value, and the chance-corrected within-group agreement (A) as a measure of effect size.

We then combined the three wetland categories (forested wetlands, emergent wetlands, other freshwater, and marine) to calculate the total area within each buffer composed of wetland

habitats and combined the agricultural, developed, upland forest, and "other terrestrial" categories to calculate the total area of non-wetland habitat types. We considered buffers in which the majority of habitat was wetland to reflect predominant use of a wetland matrix. If <50% of the buffer was composed of wetlands, we considered the bird to be using a predominantly non-wetland matrix of habitats, acknowledging that isolated hydrologic features within the 1-km buffer, such as small wetlands, ponds, or ditches, likely influenced the use of these areas.

Birds were grouped according to the general hydrologic conditions they experienced upon dispersal (favorable vs. unfavorable), and predominant habitat use was compared between groups using a likelihood ratio test. We also report the percentage of locations recorded within the Everglades region each year.

Survival.—Although apparent survival rates have been published previously for the birds used in the present study (Hylton et al. 2006, Borkhataria et al. 2008), those analyses neither assessed how hydrologic factors accounted for variability in survival nor used a mark-resight framework. Here, we used Program MARK, version 5.1 (White and Burnham 1999), to evaluate support in the data for the influence of temporally varying hydrologic variables as well as a bird's sex and health (see below). A candidate set of models was constructed to address our hypotheses. This analysis was based on a subset of 71 birds for which we had a full complement of hydrologic variables and for which we knew sex and health. A known-fates model with individual covariates was used to estimate monthly postdispersal juvenile survival as well as the overall likelihood of birds surviving their first year. A separate analysis using all 85 birds was used for a general assessment of survival, contrasting the influence of overarching hydrologic conditions during the study (favorable vs. unfavorable years). To illustrate differences in the timing of mortality among years, we also present cumulative survival plots showing the proportion of birds surviving over time for the first year after dispersal.

Encounter histories were constructed using telemetry locations to determine whether a bird was still alive at the beginning of each month and at the end of the 12-month period. All birds whose transmitters stopped signaling during the first year were presumed dead, and no birds were censored. The known-fates modeling framework assumed that (1) postdispersal survival was independent (i.e., one bird's fate was not related to another's), (2) transmitters did not affect survival, (3) time of death was known exactly, (4) censoring was random and independent of survival, and (5) the study had a well-defined time origin. We believe that model assumptions were largely met.

We first modeled monthly survival to identify the model structure that best characterized variation in survival over time and among years. We constructed three basic models: (1) constant survival over the 12-month period, (2) survival influenced by year captured, and (3) survival variable over time for a specific time interval. We also considered a "general hydrologic conditions" model in which years were grouped as favorable vs. unfavorable conditions (2002 and 2004 vs. 2003 and 2005, respectively). Because we expected mortality to be highest early in the postdispersal period, we tested a suite of models in which survival varied in monthly increments. Thus, we considered models that distinguished survival during the first month but were constant thereafter, time-specific survival for the first and second months but

constant thereafter, and so on through the first 6 months. We did not consider further time increments to avoid overparameterizing models, given our relatively small data set.

The model structure with the lowest Akaike's information criterion (AIC) value was used to create the candidate set to address the questions posed in this work (Franklin et al. 2004, Anthony et al. 2006). We then assessed the influence of a suite of hydrologic and health variables on model fit. Hydrologic variables were as follows: Everglades water depths during the dispersal period, average daily recession rates during the dispersal period, average daily May rainfall during the year in which birds dispersed, and whether wetlands formed the majority of the bird's used habitat (coded as 1, vs. 0 for use of predominantly terrestrial landscapes). Physiologic variables were sex, total feather mercury, WBC count, and heterophil:lymphocyte ratio. Covariates were modeled as single, additive covariate models to evaluate the relative influence of each on survival. We also included models featuring multiple additive covariates, but we restricted these to covariates with strong support. We considered an effect strongly supported if the 95% confidence intervals (CIs) of the covariate β coefficient did not overlap zero. The rationale was to determine whether there was a combined influence of hydrologic variables, habitat use, and nestling health as hypothesized. We note that water depths, rainfall, and recession rates were not included in the "general hydrologic conditions" model because their influence on survival are captured under the favorable (2002 and 2004) versus unfavorable (2003 and 2005) conditions. All covariates were standardized before running analyses.

We used AIC corrected for small sample size (AIC_c) to select the most parsimonious model (Burnham and Anderson 2002). The model with the minimum AIC_c value was the model with the most support in the data. The difference in AIC_c values (ΔAIC_c) between the best-supported model and any other model was used to calculate model weights (w_i), which indicate the relative likelihood of the model, given the data (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ were considered to have highest support, and we report only models with $\Delta AIC_c \leq 10$ (Burnham and Anderson 2002). The relationship between the probability of survival and covariates was established using a logistic model (logit link) in MARK. Parameter estimates \pm SE are reported.

RESULTS

Nestling health.—Of the 84 birds for which we had data on sex, 32 were female and 52 were male. Total feather mercury concentrations ranged from 3.4 to 27.0 mg kg⁻¹ dry weight in 2002, 0.77 to 4.3 in 2003, 1.6 to 3.3 in 2004, and 0.54 to 3.7 in 2005. The WBC

counts ranged from 7,237 to 50,650 in 2002, 11,420 to 46,545 in 2003, 12,114 to 54,240 in 2004, and 4,114 to 32,457 in 2005. The heterophil: lymphocyte ratio ranged from 0.33 to 2.32 in 2002, 0.53 to 2.86 in 2003, 0.44 to 2.31 in 2004, and 0.58 to 3.81 in 2005. All three health parameters differed significantly among years (Table 1).

Everglades water depths and rainfall.—Mean water depths and recession rates for the dispersal period and daily rainfall values for May are presented in Table 2. Mean EDEN water depths were considerably higher in 2003 and 2005 than in 2002 and 2004 ($\chi^2 = 58.31$, $df = 3$, $P < 0.001$). Mean daily recession rates were variable but negative in all years, indicating rising water levels ($\chi^2 = 16.41$, $df = 3$, $P < 0.001$). May rainfall also differed among years ($\chi^2 = 16.55$, $df = 3$, $P = 0.001$). Changes in water levels and May rainfall were lowest in 2004, a year in which the onset of the rainy season was delayed.

Habitat use.—Wetland-dominated landscapes were used by 33 birds, whereas 55 birds made use of more terrestrial habitats. When birds were grouped according to the hydrologic conditions that characterized the year in which they dispersed, mean proportional use of combined wetland habitats (forested, emergent, and marine) was 0.53 ± 0.036 during favorable years and 0.39 ± 0.036 when birds dispersed into poor hydrologic conditions ($\chi^2 = 4.64$, $P = 0.031$). Proportional habitat use differed among years ($T = -3.299$, $A = 0.0392$, $P = 0.006$) for the 68 birds that survived the first 2 weeks after dispersal (Table 3). Use of the Everglades region by all juveniles was higher in 2002 and 2004 than in the 2 wetter years, with 26.3% and 22.9% of locations, respectively, occurring within the region. In 2003 and 2005, only 2.7% and 0.4% of locations occurred within the region (Fig. 2).

Survival.—Of the 85 birds followed in the present study, 23 were still transmitting locations 366 days postdispersal (27.1%). Dispersal dates ranged from 28 May to 26 July, with median dispersal dates earliest in 2003 (1 June) and latest in 2004 (11 July). Median dispersal dates were 13 June in 2002 and 25 June in 2005. Mortality occurred soon after dispersal for many birds in 2003 and 2005 but was spread more evenly throughout the year in 2002 and 2004 (Fig. 3).

For models constrained by hydrologic and physiologic covariates ($n = 71$), monthly survival was best described by a general hydrology model in which survival of birds that dispersed into favorable versus unfavorable conditions differed for the first month after dispersal, but was similar for months 2–5 and constant for months 6–12. This model also featured the influence of wetland habitat use and WBC count on the first month postdispersal ($w_i = 0.85$; Table 4). None of the individual hydrologic or physiologic variables exerted as much influence on survival ($w_i < 0.001$)

TABLE 1. Means (\pm SE) of three health-condition indicators obtained from nestling Wood Storks that dispersed from southern Florida in 2002–2005. Indicators were total feather mercury (THG), white-blood-cell (WBC) counts, and the heterophyll to lymphocyte ratio (H:L). Differences among years were tested with a Kruskal-Wallis test.

| | 2002 | 2003 | 2004 | 2005 | Kruskal-Wallis test | | |
|------------------------------------|--------------------|--------------------|--------------------|--------------------|---------------------|----|---------|
| | ($n = 17$) | ($n = 16$) | ($n = 23$) | ($n = 15$) | χ^2 | df | P |
| THG (mg kg ⁻¹ , dry wt) | 8.65 \pm 1.41 | 2.27 \pm 0.25 | 2.30 \pm 0.11 | 1.70 \pm 0.21 | 55.51 | 3 | <0.0001 |
| WBC (total count) | 23,981 \pm 2,237 | 22,808 \pm 2,589 | 26,354 \pm 2,402 | 13,632 \pm 2,043 | 15.37 | 3 | 0.0015 |
| H:L | 1.12 \pm 0.16 | 1.32 \pm 0.18 | 1.23 \pm 0.11 | 1.9 \pm 0.23 | 9.32 | 3 | 0.0253 |

TABLE 2. Means (\pm SE) and comparisons among years of Everglades water depths (from the Everglades Depth Estimation Network [EDEN]), recession rates, and rainfall during May. Group membership is based on the nonparametric Dunn's test ($\alpha = 0.05$). Depths and recession rates were estimated for the week before and the week after dispersal for 85 juvenile Wood Storks from southern Florida. Asterisk indicates that values were within the species' preferred foraging range, -25 to 25 cm.

| Year | <i>n</i> | EDEN water depth (cm) | Group |
|------|----------|--|-------|
| 2002 | 27 | 7.18 \pm 2.43* | A |
| 2003 | 17 | 29.29 \pm 0.9 | B |
| 2004 | 23 | -2.46 \pm 1.31* | A |
| 2005 | 18 | 36.43 \pm 3.39 | B |
| | <i>n</i> | Recession rate (cm day ⁻¹) | Group |
| 2002 | 27 | -1.53 \pm 0.12 | A, B |
| 2003 | 17 | -1.06 \pm 0.07 | B |
| 2004 | 23 | -0.69 \pm 0.12 | B |
| 2005 | 18 | -1.28 \pm 0.20 | B |
| | <i>n</i> | May rainfall (cm day ⁻¹) | Group |
| 2002 | 27 | 0.47 \pm 0.13 | A, B |
| 2003 | 17 | 0.71 \pm 0.2 | A |
| 2004 | 23 | 0.13 \pm 0.06 | B |
| 2005 | 18 | 0.42 \pm 0.13 | A, B |

as the general-hydrologic-conditions model (Table 4). Of the physiologic covariates, only WBC count exerted a strong influence on survival when combined with general hydrologic conditions. First-month survival was higher for birds that dispersed into favorable hydrologic conditions than for those that dispersed into poor conditions (95% CIs of β estimates did not overlap zero; Table 5). The influence of wetland habitat use was positive and strongly supported ($\beta = 0.945 \pm 0.400$, 95% CIs: 0.240–1.650), whereas the influence of WBC count was negative and strongly supported ($\beta = -0.924 \pm 0.378$, 95% CIs: -1.664 to -0.184). The estimated survival probability at the end of 12 months was 0.430 ± 0.073 (95% CI: 0.295–0.576) for birds that dispersed into favorable conditions, as compared with 0.255 ± 0.786 (95% CI: 0.132–0.435) when they did not, after accounting for the effects of habitat use and WBC counts ($n = 71$).

The general assessment of first-year survival in relation to hydrology yielded estimates of 0.369 ± 0.061 (95% CI: 0.258–0.495) when hydrologic conditions were favorable and 0.151 ± 0.042 (95% CI: 0.085–0.253) when unfavorable ($n = 85$). A model unconstrained by hydrology yielded a first-year survival estimate of 0.279 ± 0.049 (95% CI: 0.194–0.384, $n = 85$).

DISCUSSION

Our results provide evidence that survival of juvenile Wood Storks was closely related to the hydrologic conditions encountered early during dispersal from their natal colonies. General

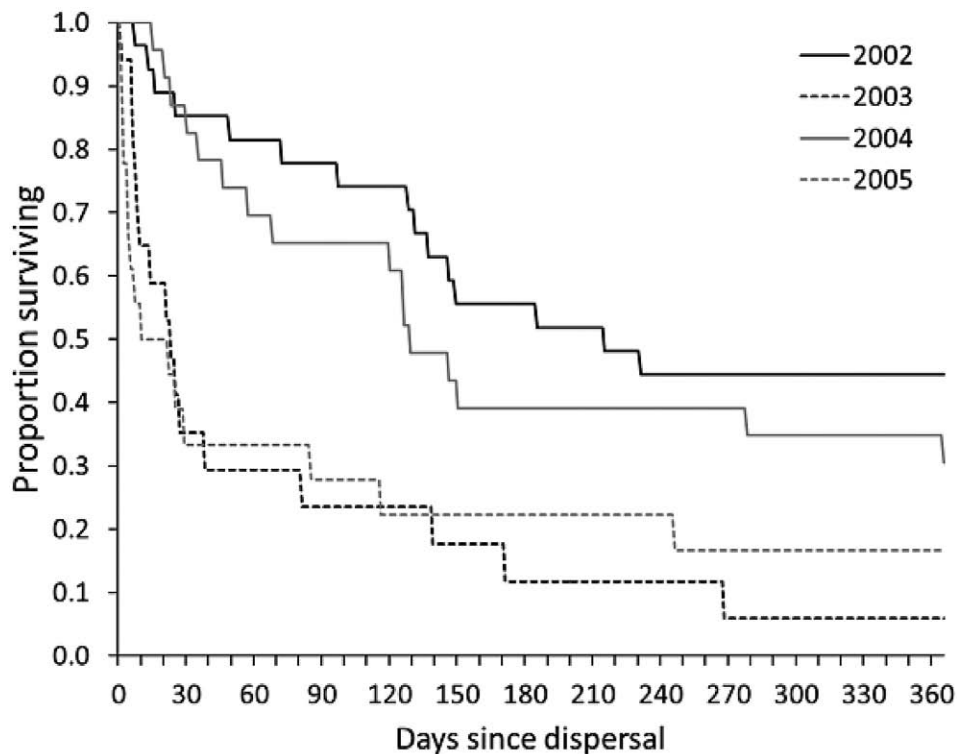


FIG. 3. Cumulative survival plot showing the proportion of birds that survived over time during the first year after dispersal for 85 juvenile Wood Storks from southern Florida in 2002–2005. Solid lines indicate that birds dispersed during favorable hydrologic conditions, and dashed lines indicate that birds dispersed during unfavorable conditions.

TABLE 3. Mean \pm SE proportional habitat use during the first 2 weeks after dispersal for juvenile Wood Storks in southern Florida, 2002–2005. Proportions are based on the area of each habitat type within 1 km non-overlapping buffers around telemetry locations in relation to the total area of the buffers. Only birds that survived the entire 2-week period were used in this analysis.

| Year | <i>n</i> | Mean proportional habitat use | | | | | | | |
|------|----------|-------------------------------|-----------------|-----------------|-------------------|-------------------|--------------------|-------------------|-----------------|
| | | Agriculture | Developed | Marine | Emergent wetlands | Forested wetlands | Terrestrial forest | Other terrestrial | Other water |
| 2002 | 25 | 0.22 \pm 0.04 | 0.07 \pm 0.01 | 0.04 \pm 0.02 | 0.29 \pm 0.04 | 0.23 \pm 0.03 | 0.07 \pm 0.02 | 0.04 \pm 0.01 | 0.04 \pm 0.01 |
| 2003 | 11 | 0.26 \pm 0.06 | 0.11 \pm 0.03 | 0.10 \pm 0.05 | 0.15 \pm 0.03 | 0.20 \pm 0.03 | 0.07 \pm 0.02 | 0.05 \pm 0.01 | 0.06 \pm 0.01 |
| 2004 | 23 | 0.26 \pm 0.05 | 0.07 \pm 0.01 | 0.05 \pm 0.02 | 0.28 \pm 0.06 | 0.18 \pm 0.02 | 0.08 \pm 0.02 | 0.04 \pm 0.01 | 0.04 \pm 0.01 |
| 2005 | 9 | 0.57 \pm 0.08 | 0.08 \pm 0.03 | 0.01 \pm 0.01 | 0.12 \pm 0.02 | 0.18 \pm 0.03 | 0.01 \pm 0.01 | 0.02 \pm 0.01 | 0.01 \pm 0.01 |

hydrology (favorable vs. unfavorable), broad-scale use of wetland habitats, and nestling health had strong effects on survival during the first month after dispersal, indicating rapid mortality in response to environmental conditions encountered soon after leaving the nest and providing further evidence that the transition to independence is a critical period for juvenile birds (cf. Anders et al. 1997, Naef-Denzer et al. 2001, Wiens et al. 2006). Differences in survival during this period alone resulted in much higher first-year survival rates for birds that dispersed into favorable conditions than for those that dispersed into unfavorable conditions (0.37 vs. 0.15).

Because their foraging and flight skills are still developing, juvenile birds may be particularly vulnerable to predation, starvation, and exposure during this period (Anders et al. 1997, Naef-Denzer et al. 2001, Wiens et al. 2006). We suggest that the primary mechanism that molds dispersal of juvenile Wood Storks is nutrition-mediated, in light of the strong linkages between availability of food, hydrology, and breeding success in this species and other wading birds in the Everglades (Bancroft et al. 1988, Frederick et al. 1992, Herring et al. 2010) and elsewhere (Cézilly et al. 1995, Gaines et al. 2000, Jovani and Tella 2004, Bryan and Robinet 2008), and given the strong relationship between hydrologic conditions and juvenile survival. Foraging skills in waterbirds may be developed over time (Recher and Recher 1969, Morrison et al. 1978), and juveniles often forage less efficiently than adults (Recher and Recher 1969, Bildstein 1983, Draulans 1987, Cézilly and

Boy 1988). Furthermore, juvenile Wood Storks have been shown to forage less efficiently than older birds and to have higher failed capture-attempt rates (Walsh 1990).

In 2003 and 2005, high water levels, the early onset of the summer rainy season, or both created unfavorable foraging conditions that resulted in birds moving away from the Everglades region and into more terrestrial agricultural and developed landscapes. Dry conditions associated with prolonged droughts have also been shown to affect habitat selection by Wood Storks (Gaines et al. 2000) and could influence juvenile movements and survival as well.

The positive association between the use of wetland-dominated landscapes and survival indicates that young birds that used more terrestrial landscapes soon after dispersal were more vulnerable to mortality. In 2005, many of the birds that died shortly after dispersing were recovered from agricultural habitats in south-central Florida, where flooded rice and fallow fields are known to attract large numbers of waders and other waterbirds (Townsend et al. 2006) despite relatively low aquatic prey densities (Sizemore 2009). However, because habitat use was quantified for only the first 2 weeks of dispersal, relationships between use of wetlands and survival later in life should not be inferred and should be investigated further in future studies.

As Hylton et al. (2006) found, nestling WBC counts also influenced postdispersal survival. Mercury levels, which were generally lower than those reported for juvenile Wood Storks from

TABLE 4. Model selection table for postfledging monthly survival estimates of 71 juvenile Wood Storks that dispersed from natal colonies in southern Florida in 2002–2005. Survival was modeled as time-dependent up to the first 6 months after dispersal, and constant for the remainder. Effects of general hydrology were modeled by grouping birds according to hydrologic conditions encountered during dispersal (favorable in 2002 and 2004, unfavorable in 2003 and 2005) but also included time-dependent terms. Individual covariates included water depth, recession rate, May rainfall, use of wetland habitats, sex, total feather mercury, white-blood-cell (WBC) counts, and the heterophil:lymphocyte ratio. The influence of hydrology and individual covariates on variability in survival was applied to first-month survival only. Only models with $\Delta AIC_c < 10$ are shown.

| Model | <i>K</i> | AIC_c | ΔAIC_c | w_i |
|---|----------|---------|----------------|-------|
| General hydrology + wetland habitat use + WBC | 9 | 238.136 | 0 | 0.856 |
| General hydrology + wetland habitat use | 8 | 243.368 | 5.232 | 0.063 |
| General hydrology + WBC | 8 | 244.112 | 5.976 | 0.043 |
| General hydrology | 7 | 246.321 | 8.185 | 0.014 |
| General hydrology + sex | 8 | 246.981 | 8.844 | 0.010 |
| General hydrology + heterophil:lymphocyte ratio | 8 | 247.753 | 9.616 | 0.007 |

TABLE 5. Monthly survival estimates for juvenile Wood Storks during the first year after dispersal from natal colonies in southern Florida. Survival was influenced by general hydrology (favorable vs. unfavorable), wetland habitat use, and white blood cells (WBC) during the first month post-dispersal ($n = 71$ birds). Estimates for the general hydrology model ($n = 85$ birds and no covariates) are also reported.

| Month post-dispersal | Survival estimate | | | |
|----------------------|---|-------------|------------------------|-------------|
| | General hydrology + wetland habitat use + WBC | | General hydrology only | |
| | Mean \pm SE | 95% CI | Mean \pm SE | 95% CI |
| 1 ^a | 0.954 \pm 0.033 | 0.823–0.990 | 0.898 \pm 0.050 | 0.522–0.788 |
| 1 ^b | 0.566 \pm 0.146 | 0.289–0.808 | 0.494 \pm 0.136 | 0.252–0.739 |
| 2 | 0.932 \pm 0.038 | 0.809–0.978 | 0.907 \pm 0.039 | 0.796–0.961 |
| 3 | 0.902 \pm 0.046 | 0.767–0.963 | 0.918 \pm 0.039 | 0.802–0.969 |
| 4 | 0.946 \pm 0.037 | 0.808–0.986 | 0.933 \pm 0.037 | 0.812–0.978 |
| 5 | 0.743 \pm 0.074 | 0.575–0.860 | 0.762 \pm 0.066 | 0.611–0.867 |
| 6+ | 0.962 \pm 0.015 | 0.918–0.983 | 0.958 \pm 0.015 | 0.918–0.980 |

^aFavorable hydrology at dispersal (2002 and 2004).

^bUnfavorable hydrology at dispersal (2003 and 2005).

inland Georgia colonies (Gariboldi et al. 2001) or for Great Egrets (*Ardea alba*) from Everglades colonies (Frederick et al. 2002), unrelated to survival. Failing to account for nestling health ignores the interdependence between two sequential demographic life stages and may overlook the additive effects of multiple stressors (Hoffman et al. 2009). Physiologic responses to poor environmental conditions during the nestling period could exacerbate the consequences of poor environmental conditions encountered during dispersal. It is possible that this interplay contributed to the differences in first-year survival between Wood Storks fledged in 2003 and 2005 and those fledged in 2002 and 2004.

Although we believe that the assumptions of the mark–resight analysis were met and that the survival estimates are valid, we acknowledge that there were several potential sources of bias. First, the effect of hatch order on Wood Stork survival is unknown, but if hatch order influenced subsequent survival, our selection of the largest sibling may have yielded biased results. We refrained from making inferences about hatch-order survival, focusing on treatment effects based on samples treated alike. Second, the possibility of transmitter failure cannot be ruled out in some cases, and it is possible that some birds may have been incorrectly classified as dead. Finally, we cannot completely rule out the possibility that transmitters affected survival. In the latter two cases, true survival would have been higher and estimates reported here viewed as conservative.

Historically, juveniles were less likely to encounter unfavorable hydrologic conditions associated with the onset of the rainy season because Wood Storks fledged and dispersed 2 to 3 months earlier. The alteration of Everglades wetlands during the late 20th century has resulted in Wood Storks initiating nesting up to 3 months later than was typical in the 1930s through 1960s (Ogden 1994). Shifts in breeding phenology and associated decreases in productivity have been attributed to decreased food availability early in the breeding season because of the compartmentalization of the Everglades and the loss of short-hydroperiod coastal wetlands (Ogden 1994, Davis et al. 2005, Frederick et al. 2009). Although there is recognition that the timing of water deliveries is an important aspect of restoration and that earlier nesting by Wood Storks is desirable, at this time the movement of water

through the Everglades is limited by poor water quality and a lack of storage capacity north of the Everglades (National Research Council 2011). As a result, young often fledge into high and rising water levels with low prey availability (Ogden 1994). Thus, perceived increases in productivity, as evidenced by young birds fledging successfully from their nests, may be deceptive if early wet-season water levels are high and hydrologic conditions are unfavorable for dispersing young.

The postfledging and dispersal period is a very sensitive life-history stage for long-lived birds (Stahl and Oli 2006, Sandvik et al. 2008), and juvenile survival is an important demographic parameter in long-lived species. Although population growth rates are generally most sensitive to adult survival, high variability in juvenile survival rates can have a larger effect on variation in population growth rates of long-lived species than adult survival (Sæther and Bakke 2000). For Wood Storks, the population growth rate is most sensitive to adult survival, juvenile survival, and fecundity, in that order (Borkhataria et al. 2008), and we suspect that the effect of hydrology on juvenile survival may be strong enough to affect the trajectory of populations (see Borkhataria 2009). In some years, up to half of the southeastern U.S. population of Wood Storks breeds in southern Florida (Brooks and Dean 2008), and it is possible that the region is acting as a population sink, particularly in years with unfavorable postfledging and dispersal conditions.

Human-induced changes in the temporal patterns of hydrology may have important consequences for the phenology and demography of wetland birds, as evidenced by the alteration of Wood Stork nesting patterns and the effects of late nesting on juvenile survival. Similar dynamics have been found in the Snail Kite (*Rostrhamus sociabilis*; Dreitz et al. 2004) and the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*; Baiser et al. 2008), both of which are sensitive to temporal variability in Everglades water depths. These examples from one of the world's largest managed wetlands illustrate the importance of considering the effects of the timing of hydrologic manipulations in addition to their direct effects when managing wetlands for wildlife. Furthermore, as wetland systems change in response to anticipated changes in

climate, additional species in the Everglades and elsewhere may experience a temporal mismatch between foraging requirements and conditions.

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